

LOWER EOCENE (MIDDLE ILERDIAN) BRACHIOPODS FROM THE CAMPO REGION, CENTRAL PYRENEES, NORTH-EASTERN SPAIN

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Bitner, M.A. 2000. Lower Eocene (Middle Ilerdian) brachiopods from the Campo region, Central Pyrenees, north-eastern Spain. [Braquiópodos del Eoceno inferior (Ilerdiense medio) de la región de Campo, Pirineos Centrales, noreste de España.] *Revista Española de Paleontología*, **15**(2), 117-128. ISSN 0213-6937.

ABSTRACT

Three brachiopod species, *Terebratulina tenuistriata* (Leymerie, 1846), *Argyrotheca vidali* (Mallada, 1878), and "*Terebratula*" n. sp., are recognized in the marls and calcareous silts of the Lower Eocene Puebla Formation of the Campo region in the Central Pyrenees, north-eastern Spain. The rich and well preserved material of *T. tenuistriata* and *A. vidali* allows to recognize the range of their morphological variability and to evaluate the status of earlier established species. The investigated assemblage is characterized by the small, pedunculate taxa adapted to life on a soft bottom anchoring directly in a soft substrate or attaching to very small, hard substrates.

Keywords: Brachiopoda, taxonomy, Lower Eocene, Ilerdian, Spain.

RESUMEN

Se han identificado tres especies de braquiópodos: *Terebratulina tenuistriata* (Leymerie, 1846), *Argyrotheca vidali* (Mallada, 1878), y "*Terebratula*" n. sp., en los limos carbonatados y margas del Eoceno inferior de la Formación Puebla en la región de Campo de la Zona Central Pirenaica (noreste de España). La abundancia y buena conservación del material de *T. tenuistriata* y *A. vidali* ha permitido reconocer el rango de su variabilidad morfológica y evaluar el estatus de las especies descritas previamente. El conjunto estudiado se caracteriza por ser taxones pedunculados pequeños, adaptados a vivir sobre substrato blando, anclándose en dicho substrato, o bien adheridos a partículas duras.

Palabras clave: Brachiopoda, taxonomía, Eoceno inferior, Ilerdiense, España.

INTRODUCTION

Brachiopods are relatively rare, usually both in species and in number, in the Eocene deposits of Europe, nevertheless they were the subject of study of many researchers (Nyst, 1843; Leymerie, 1846; Davidson, 1852, 1870, 1874; Morgan, 1883; Vincent, 1893, 1923; Oppenheim, 1896, 1901a, b, 1903; Cossmann, 1902; Sacco, 1902; Cossmann and Pissarro, 1903; Doncieux, 1905, 1926; Fabiani, 1913; Dainelli, 1915; Abrard, 1926; Gochev, 1933; Elliott, 1938, 1954, 1955; Meznerics, 1943; Zelinskaya, 1962, 1975; Barczyk, 1973; Makarenko, 1974; Woźny, 1977; Popiel-Barczyk and Barczyk, 1987; Calzada *et al.*, 1988; Calzada, 1994; Calzada and Urquiola, 1994; Popiel-Barczyk, 1996). In many cases, however, material described in the 19th or the beginning of the 20th centuries has never been

reinvestigated, and new species were often described on a very limited material, not taking into account intraspecific variation. Moreover, in many cases it is difficult to evaluate the status of those species based on description and illustrations which are not sufficient. Thus, the re-examination and redescription of the Eocene brachiopod material is strongly needed. The material collected in the Campo region and containing three brachiopod species permitted to resolve only some of those taxonomic problems.

It is worth mentioning that also in North America and the Caribbean region the Eocene brachiopods are relatively rare (Toulmin, 1940; Cooper, 1979, 1988; Donovan *et al.*, 1993; Sandy *et al.*, 1995), unlike in the Southern Hemisphere and Japan where they are an important element of fauna (Hatai, 1940; Lee, 1986; Bitner, 1996).

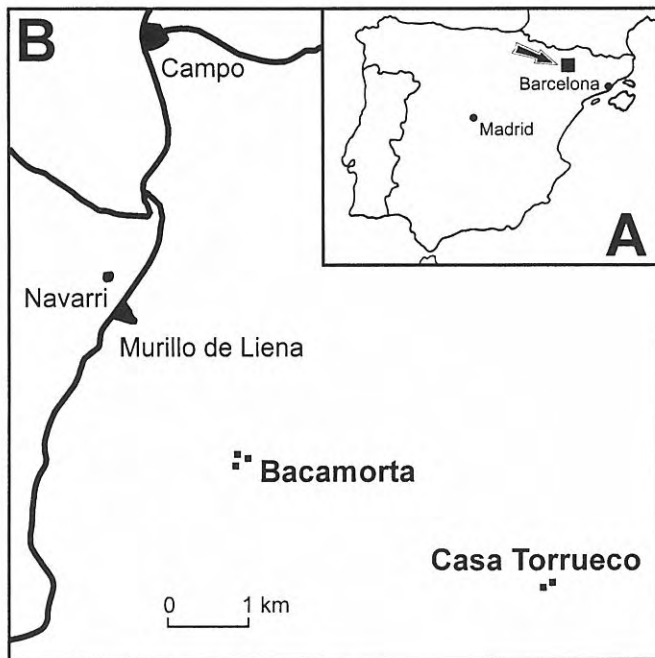


Figure 1. A. Location map; the study area in B is arrowed. B. Sketch location of studied sites.

LOCATION, MATERIAL AND METHODS

The brachiopod-bearing deposits in the Campo region, Central Pyrenees belong geologically to the Tremp-Graus basin, and are a part of the more than 700 m thick sequence of the Ilerdian and Cuisian parastratotype (Tosquella, 1988; Molina *et al.*, 1992; Serra-Kiel *et al.*, 1993). The Ilerdian is represented by thick and relatively continuous marine deposits. The Early and lowermost Middle Ilerdian consists of limestones alternating with marls in the upper part, while the rest of the Middle and Late Ilerdian is composed of more than 550 m thick silty marls (Molina *et al.*, 1992). Based on the rich microfossil record the age of the Ilerdian is defined as Upper Paleocene-Lower Eocene (Molina, 1996).

The investigated brachiopods come from the extremely fossiliferous silts and marls of the Middle Ilerdian Puebla Formation, equivalent to the La Pobra level of Tosquella (1988). In addition to brachiopods, the diverse marine fauna includes foraminifers, ostracods, sponges, bryozoans, bivalves, echinoids, crinoids, serpulids, and crabs.

The brachiopods described in this paper come from two localities, Bacamorta and Casa Torruenco, in the Campo region, Central Pyrenees, north-eastern Spain (Fig. 1). They were collected directly in the field from the weathering surface enriched in fossils; seven bulk samples (five from Bacamorta and two from Casa Torruenco) weighting about 4-5 kg were also taken and then washed at the laboratory (mesh 0.5 mm). The brachiopods are in 95 percent articulated, however, they are sometimes slightly damaged or crushed. Many of them, especially smaller specimens, were covered by epitaxial calcite cement and/or by sediment, thus being very difficult to clean. The total number of collected

specimens is 1606 (1325 from Bacamorta and 281 from Casa Torruenco). There are also many fragments of various size.

The investigated material is housed in the Institute of Paleobiology of the Polish Academy of Sciences (Warsaw) under the collection number ZPAL Bp.XLIII.

SYSTEMATIC DESCRIPTION

ORDER TEREBRATULIDA Waagen, 1883

SUBORDER TEREBRATULIDINA Waagen, 1883

Superfamily CANCELLOTHYROIDEA Thomson, 1926

Family Cancellothyrididae Thomson, 1926

Genus *Terebratulina* d'Orbigny, 1847

Type species: *Anomia retusa* Linnaeus, 1758.

Terebratulina tenuistriata (Leymerie, 1846)

Figs. 2, 3, 4 A-F, 5 A-G

- 1829 *Terebratulina striatula* J. de C. Sowerby, 69-70 (*partim*), pl. 536, fig. 5 (*non* figs. 3-4).
- 1846 *Terebratulina tenuistriata* Leymerie, 363, pl. 15, fig. 11.
- 1846 *Terebratulina Defranci* Brongniart; Leymerie, 367, pl. 15, fig. 12.
- 1846 *Terebratulina tenuistriata* Leym.; d'Archiac, 214, pl. 7, fig. 14.
- 1847 *Terebratulina tenuistriata* Leym.; d'Archiac, 412, pl. 13, fig. 12.
- 1852 *Terebratulina striatula*, Sow., Sp.; Davidson, 14-15, pl. 1, figs. 16, 16a, 16b.
- 1870 *Terebratulina striatula* (Sow. ?); Davidson, 400-401, pl. 19, figs. 21, 21a.
- 1874 *Terebratulina Putoni* Baudon; Davidson, 155-156, pl. 7, fig. 15.
- 1874 *Terebratulina Woodi* Nyst; Davidson, 157, pl. 8, fig. 10.
- 1893 *Terebratulina Woodi*, Nyst; Vincent, 45-47, pl. 3, figs. 8-11.
- 1893 *Terebratulina Putoni*, Baudon; Vincent, 48.
- 1893 *Terebratulina Delheidi*, nov. sp.; Vincent, 48-50, pl. 3, figs. 5-7.
- 1901a *Terebratulina striatula* Sowerby; Oppenheim, 258, pl. 15, fig. 15.
- 1905 *Terebratulina tenuistriata* Leymerie; Doncieux, 90-92, pl. 4, figs. 7-10.
- 1913 *Terebratulina striatula* Sowerby; Fabiani, 32-33, pl. 4, figs. 3-5.
- 1915 *Terebratulina striatula* Sowerby; Dainelli, 408.
- 1926 *Terebratulina tenuistriata* Leymerie; Doncieux, 12-15, pl. 1, figs. 41-43; pl. 2, figs. 1-19.
- 1926 *Terebratulina tenuistriata* Leymerie; Abrard, 270.
- 1933 *Terebratulina tenuistriata* Leym.; Gochev, 29.
- 1938 *Terebratulina wardenensis* sp. nov.; Elliott, 128-131, fig. 23: 1-20.
- 1943 *Terebratulina striatula* Sowerby; Meznerics, 34-35, pl. 2, fig. 7.
- 1954 *Terebratulina wardenensis* Elliott; Elliott, 723.

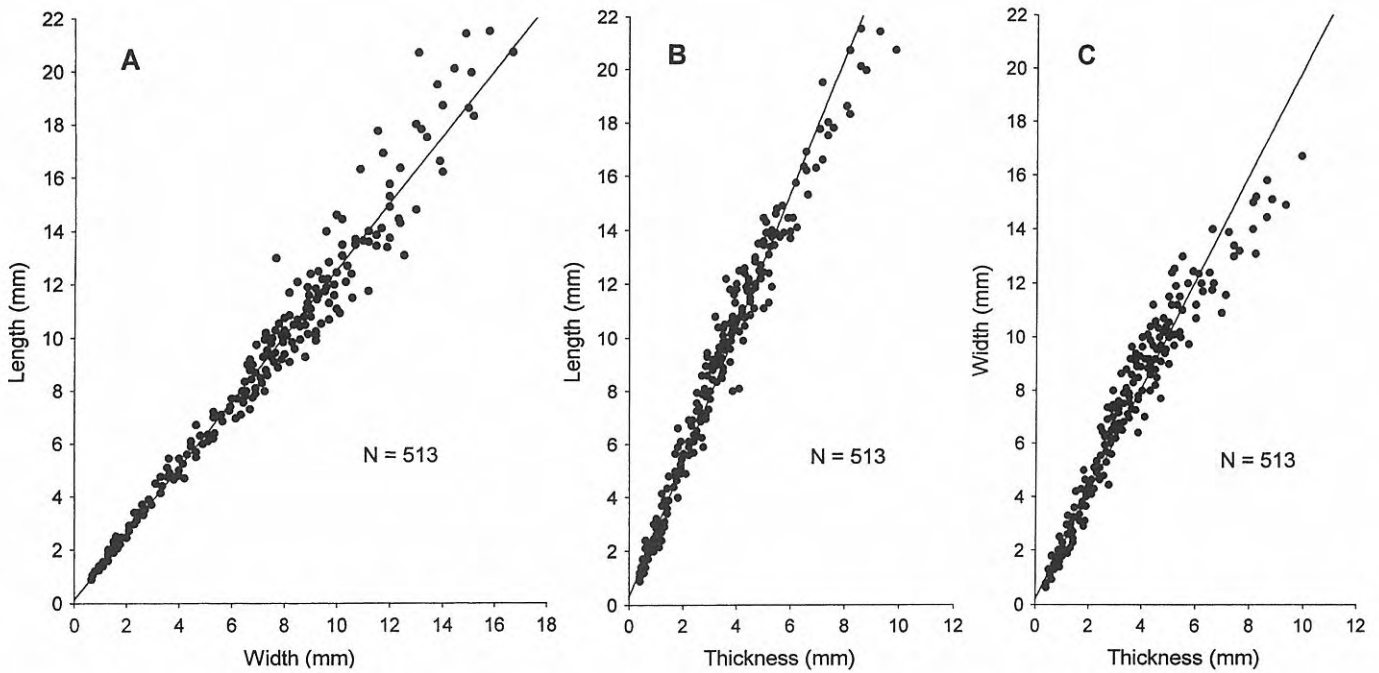


Figure 2. Intraspecific variability of *Terebratulina tenuistriata* (Leymerie, 1846) from the Campo region. Scatter diagrams plotting length/width (A), length/thickness (B), width/thickness (C). N - number of specimens.

- 1973 *Terebratulina delheidi* Vincent; Barczyk, 492-496, text-figs. 1-4, pl. 1, figs. 1-9.
- 1987 *Terebratulina rudis* Koenen; Popiel-Barczyk and Barczyk, 94-96, text-figs. 2-3, pl. 1, figs. 1-3.
- 1987 *Terebratulina* aff. *rudis* Koenen; Popiel-Barczyk and Barczyk, 96, pl. 1, figs. 4-5.
- 1987 *Terebratulina* sp.; Popiel-Barczyk and Barczyk, 96-97, pl. 1, fig. 6.
- 1992 *Terebratulina striatula* Sowerby; Altichieri, 217.

Dimensions (in mm; see also Fig. 2):

	L	W	T
ZPAL Bp.XLIII/1	21.5	15.8	8.6
ZPAL Bp.XLIII/2	20.7	13.1	8.2
ZPAL Bp.XLIII/3	21.4	14.9	9.3
ZPAL Bp.XLIII/5	19.1	15.0	8.8
ZPAL Bp.XLIII/10	14.9	11.2	5.1
ZPAL Bp.XLIII/11	16.6	13.9	7.2
ZPAL Bp.XLIII/15	10.7	9.8	5.7

Material: 728 complete specimens, three ventral valves and 21 dorsal valves from Bacamorta, and 80 complete specimens, four ventral valves and five dorsal valves from Casa Torrueco. Some specimens are slightly damaged.

Diagnosis

Medium-sized *Terebratulina* ornamented by numerous fine ribs; anterior commissure incipiently to broadly uniplicate; ring-like brachidium with long crura.

Remarks

The species *Terebratulina tenuistriata* (Leymerie) is the commonest one in the investigated material (more than 800 specimens). It was already noted from the

Paleogene deposits of southern France and northern Spain, being known from the Thanetian (Upper Paleocene) to the Bartonian (Middle Eocene).

The specimens under study are consistent with those described and illustrated by Leymerie (1846) and Doncieux (1905, 1926) from the Montagne Noire, however they differ from them in being slightly smaller. A great variability in shell outline and convexity, already reported by Doncieux (1905, 1926), is also visible in the studied material. The outline, independently of the size, can vary from ovaly elongate to nearly circular (see Fig. 4 B-E). The shell is always biconvex but in various degree. The anterior commissure rectimarginate in young specimens becomes slightly uniplicate in adults. The shell surface is covered with numerous, very fine ribs, and the changes in ornamentation can be observed during ontogenesis. The individuals of 1-2 mm long have only 10-12 ribs (Fig. 5 A-C) which increase rapidly in number with a brachiopod age. In younger specimens, usually till 8 mm long, ribs are clearly granular, becoming completely smooth and very fine in larger specimens. The foramen is large, oval to circular, mesothyrid to permesothyrid, restricted anteriorly by two small, triangular, disjunct deltidial plates. The cardinalia with prominent inner socket ridges and cardinal process developed as a transverse subcircular area, and brachidium forming a ring-like loop (Fig. 3) represent typical characteristics of the genus *Terebratulina*.

The Eocene specimens of *Terebratulina* were also described under the name *T. striatula* (Sowerby), even recently this name was used by Altichieri (1992). However, the specific name *striatula* is not valid for the Tertiary species. Sowerby (1829) found the specimens from the London Clay (Eocene) very similar to the Upper



Figure 3. *Terebratulina tenuistriata* (Leymerie, 1846), ring-like brachidium seen from dorsal side, ZPAL Bp.XLIII/6, Bacamorta, sample 1, x 20.

Cretaceous species *Terebratula striatula* Mantell, 1822, and used this name of the Cretaceous species for his Eocene specimens. Davidson (1852), however, found both forms were distinct and restricted the name *striatula* only to the Tertiary specimens, wrongly believing that the forms from the Chalk were conspecific with the Swedish Cretaceous species *T. striata* (Wahlenberg, 1821), and thus the specific name *striatula*, as a younger one, can be used to the Tertiary forms. As shown by Elliott (1938) and later by Owen (1988), in his revision of the Cretaceous brachiopods, the name *Terebratulina striatula* (Mantell) should be correctly applied only to the Upper Chalk forms. Since the name for Tertiary forms was occupied, Elliott (1938) proposed a new specific name *wardenensis* to replace the name *striatula*. Examining the large material from Spain, as well as from France and England (collections in The Natural History Museum in London), and descriptions and illustrations of the Eocene specimens attributed to *T. striatula* (*sensu* Sowerby, 1829) and *T. tenuistriata* I found no difference between those two species. Also other authors (e.g. d'Archiac, 1846; Davidson, 1870; Oppenheim, 1901a; Fabiani,

1913) pointed out a great similarity of *T. striatula* (*sensu* Sowerby, 1829) and *T. tenuistriata*. Slight differences in ornamentation of both species fit well within the range of the intraspecific variability. Thus, *T. tenuistriata* and *T. striatula* (*sensu* Sowerby, 1829) should be considered as synonyms, thereby *T. tenuistriata* and *T. wardenensis* are also synonyms, and the name *tenuistriata* has priority over the name *wardenensis*.

The specimens from the Eocene of Belgium (Davidson, 1874; Vincent, 1893) described as *Terebratulina Putoni* Baudon, *T. Woodi* Nyst, and *T. Delheidi* Vincent have all the features consistent with those of *T. tenuistriata* and are included by me into the synonymy of the latter. Both Davidson (1874) and Vincent (1893) stressed a great similarity of those species to the English species *T. striatula* Sowerby, the species considered in this paper as synonymous with *T. tenuistriata*.

Terebratulina delheidi Vincent from the Eocene of the Tatra Mts. (Barczyk, 1973) are smaller than the specimens of *T. tenuistriata* from Spain, however, outline and style of ribbing point to their being conspecific. It is interesting to mention that Barczyk (1973) included *T. striatula* into the synonymy of *T. delheidi*.

Also Sacco (1902) described several forms from the Eocene of Italy as the varieties of *Terebratulina caputserpentis* (Linnaeus, 1767), however, many of them may be situated within the intraspecific variability of *T. tenuistriata*.

Zelinskaya (1975), with material from the Eocene of the Ukraine, recognized and created many species of *Terebratulina*, based sometimes only on one specimen. The particular *Terebratulina* species created by her differ often between each other only slightly in size, outline, and differently defined sinus on a ventral valve. Some of those species seem to be very similar to the studied material. Nevertheless in many cases it is difficult to estimate the validity of the species because of insufficient description and poor quality of illustrations.

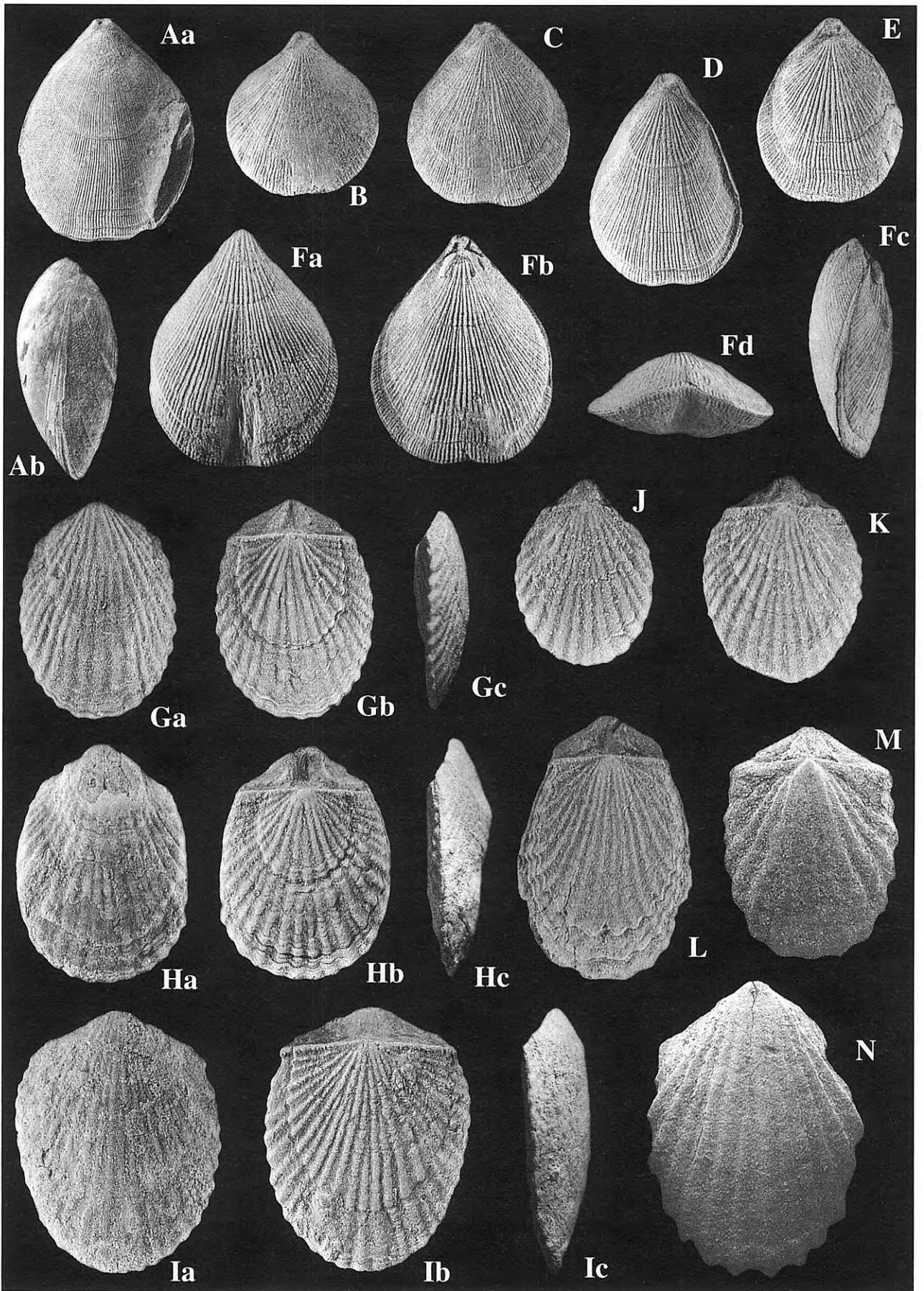
Further investigations of Eocene representatives of *Terebratulina* are badly needed to clarify taxonomic status of those numerous species.

Occurrence

It is known from the Upper Paleocene and Eocene of Europe (from Spain to Bulgaria).

SUBORDER TEREBRATELLIDINA Muir-Wood, 1955
Superfamily MEGATHYRIDOIDEA Dall, 1870

Figure 4. A-F. *Terebratulina tenuistriata* (Leymerie, 1846), Bacamorta; A. Complete specimen, ZPAL Bp.XLIII/5, sample 1, x 2, a, dorsal view; b, lateral view; B-E. Dorsal views of complete specimens, ZPAL Bp.XLIII/15-18, sample 2, x 3; F. Complete specimen, ZPAL Bp.XLIII/10, sample 4, x 3, a, ventral view; b, dorsal view; c, lateral view; d anterior view. G-N. *Argyrothecca vidali* (Mallada, 1878); G. Complete specimen, ZPAL Bp.XLIII/34, sample 2, x 4, a, ventral view; b, dorsal view; c, lateral view; H-I. Complete specimens, ZPAL Bp.XLIII/43-44, Bacamorta, sample 3, x 4, a, ventral views; b, dorsal views; c, lateral views; J-M. Dorsal views of complete specimens; J-L. ZPAL Bp.XLIII/31-33, Bacamorta, sample 2, x 4; M. ZPAL Bp.XLIII/55, Casa Torruenco, sample 2, SEM x 8; N. Ventral view of complete specimen, ZPAL Bp.XLIII/56, Casa Torruenco, sample 2, SEM x 10.



Remarks

Megathyrid brachiopods were earlier assigned to the superfamily Terebratelloidea, however, detail studies of the loop ontogeny of the megathyrid brachiopods and terebratelloids show significant differences, thus indicating the necessity to separate megathyrids into a different superfamily (MacKinnon and Smirnova, 1995). Also immunological data confirm that they are phylogenetically different (Endo *et al.*, 1994).

Family **Megathyrididae** Dall, 1870
Genus *Argyrotheca* Dall, 1900

Type species: *Terebratula cuneata* Risso, 1826.

Argyrotheca vidali (Mallada, 1878)
Figs. 4 G-N, 5 H-P, 6

- 1870 *Terebratulina* ? *Michelottina* (Dav.); Davidson, 401, pl. 19, figs. 22, 22a, b, c.
1878 *Terebratula vidali* Mallada, 398, pl. 12, figs. 1-5.
1901a *Terebratulina Michelottina* Davidson; Oppenheim, 257, pl. 15, fig. 16.
1913 *Terebratulina michelottina* Davidson; Fabiani, 36-37, pl. 4, figs. 15, 15a.
1926 *Cistella lemoinei* nov. sp.; Abrard, 271, fig.
1954 *Cistellarcula wrigleyi*, sp. nov.; Elliott, 726-727, pl. 15, figs. 8-12.
1992 *Terebratulina michelottina* Davidson; Altichieri, 217.
1994 *Argyrotheca lemoinei* (Abrard); Calzada and Urquiola, 21-22, figs. 3, 5:2a-c.
1994 *Argyrotheca vidali* (Mallada); Calzada and Urquiola, 22-24, figs. 4-5:3a-c.

Dimensions (in mm; see also Fig. 6):

	L	W	T
ZPAL Bp.XLIII/33	10.5	7.0	2.7
ZPAL Bp.XLIII/34	8.7	6.4	2.3
ZPAL Bp.XLIII/35	11.8	6.7	3.3
ZPAL Bp.XLIII/39	12.0	8.6	3.4
ZPAL Bp.XLIII/42	12.3	8.9	3.6
ZPAL Bp.XLIII/43	10.4	7.5	2.9
ZPAL Bp.XLIII/44	11.6	9.0	3.0

Material: 425 complete specimens, 10 ventral valves and 11 dorsal valves from Bacamorta, and 166 complete specimens, nine ventral valves and five dorsal valves from Casa Torruenco.

Emended diagnosis

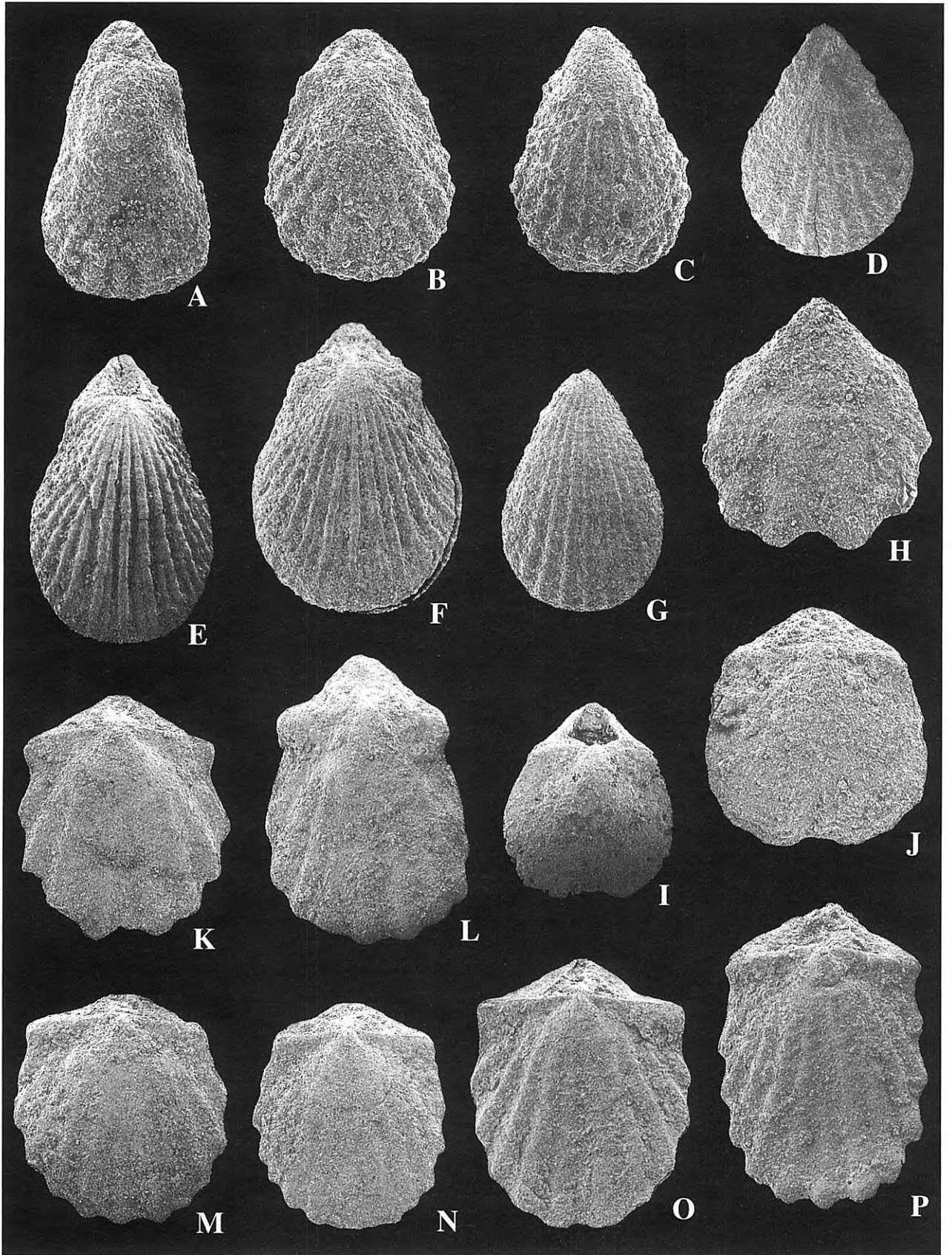
Argyrotheca variable in outline from subrectangular to elongate oval, always longer than wide, and ornamented by coarse ribs varying from 18 to 30 in number.

Remarks

The Eocene *Argyrotheca* species from Spain were recently revised and described by Calzada and Urquiola (1994) on the basis of the material from the Vic Basin, Catalonia. They recognized three species: *Argyrotheca batalleri* (Abrard, 1926), *A. lemoinei* (Abrard, 1926) and *A. vidali* (Mallada, 1878). Although they pointed out to a great similarity of the two last species, they preferred to leave them as different taxa. Those two species were separated, however, from each other only on the basis of the characters such as shell outline, small differences in size, and slightly differently defined ribs which usually can vary considerably in one species. Examining the rich material (more than 600 specimens) from the Campo region and the collection from the Museu Geològic del Seminari described by Calzada and Urquiola (1994) I reached the conclusion that all those features fit very well within the intraspecific variability range. I have found that all the intermediate forms can be observed, thus, *A. lemoinei* and *A. vidali* are considered by me as conspecific, with the specific name *vidali* having the priority.

This micromorphic species is generally elongate and varies from subrectangular with a straight hinge line, nearly so long as the maximum width, to oval with a shorter hinge margin and the greatest width at the mid-length, and drop-like in outline with very short hinge line and the greatest width in the anterior half (see Fig. 4 G-L). The shell is strongly punctate and covered with numerous rounded ribs. Individuals of 1 mm or less long, however, are smooth having only shallow sulcus on both valves (Fig. 5 I-J). In slightly larger specimens 4-6 rounded, very low ribs, with shallow grooves, appear on the anterior margin (Fig. 5 H). The ribs increase by intercalation and 18-30 ribs can be observed in adults. The shell is unequally biconvex, with the ventral valve much deeper, the dorsal one is nearly flat. The beak with sharp beak ridges and well developed area is truncated by a large, triangular, hypothryrid pedicle opening restricted by two small deltidial plates; the pedicle collar well developed and supported by a low median septum. The dorsal median septum extends

Figure 5. **A-G** *Terebratulina tenuistriata* (Leymerie, 1846), young specimens; A-B. Dorsal views of complete specimens, ZPAL Bp.XLIII/19-20, Bacamorta, sample 5, SEM x 40; C. Ventral view of complete specimen, ZPAL Bp.XLIII/21, Bacamorta, sample 5, SEM x 30; D-F. Dorsal views of complete specimens, Bacamorta, SEM x 15, D, F - ZPAL Bp.XLIII/22-23, sample 5, E. - ZPAL Bp.XLIII/30, sample 7; G. Ventral view of complete specimen, ZPAL Bp.XLIII/24, Bacamorta, sample 5, SEM x 15. **H-P** *Argyrotheca vidali* (Mallada, 1878), young specimens; H. Ventral view of complete specimen, ZPAL Bp.XLIII/51, Bacamorta, sample 7, SEM x 40; I-J. Dorsal views of complete specimens, Bacamorta, SEM x 40, I - ZPAL Bp.XLIII/50, sample 6, J - ZPAL Bp.XLIII/45, sample 5; K-N. Dorsal views of complete specimens, ZPAL Bp.XLIII/46-49, Bacamorta, sample 5; K - SEM x 25; L-M - SEM x 20; N - SEM x 15; O-P. Dorsal views of complete specimens, ZPAL Bp.XLIII/59-60, Casa Torruenco, sample 2, SEM x 15.



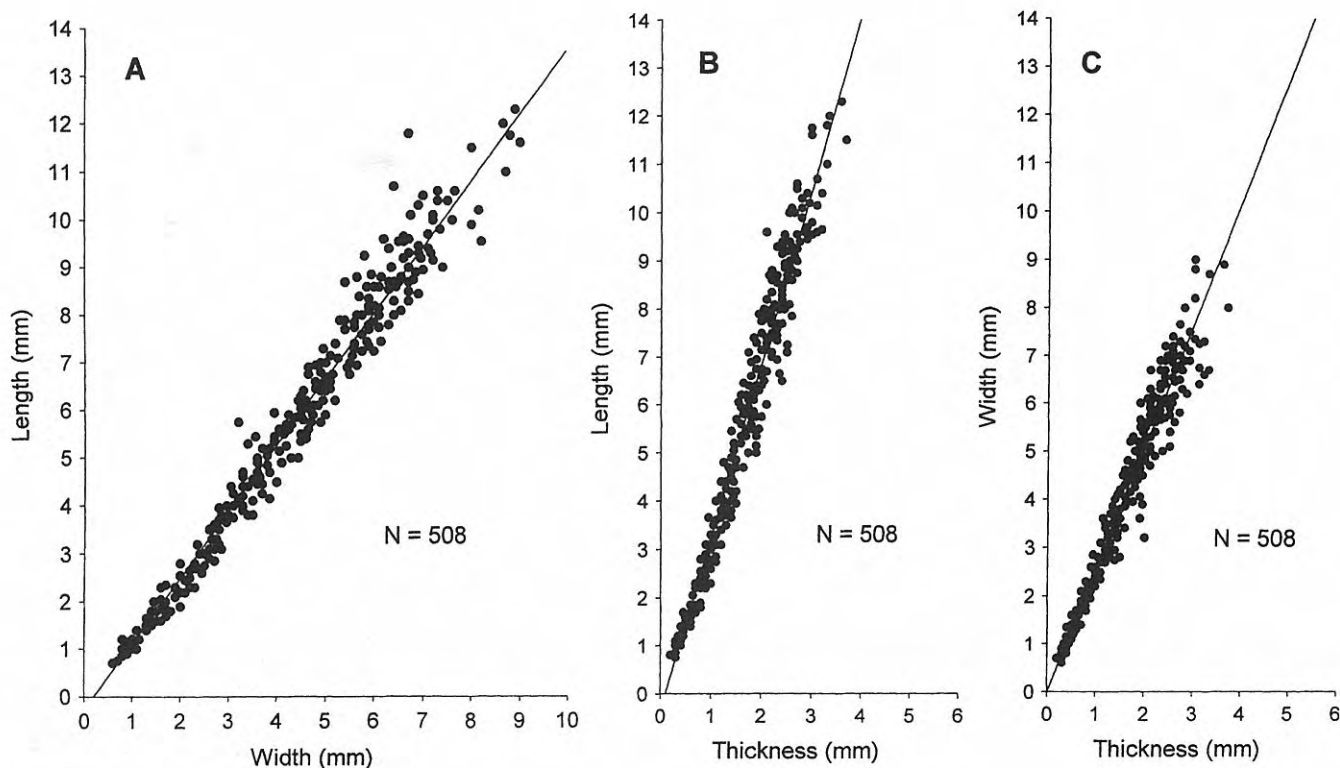


Figure 6. Intraspecific variability of *Argyrotheca vidali* (Mallada, 1878) from the Campo region. Scatter diagrams plotting length/width (A), length/thickness (B), width/thickness (C). N - number of specimens.

for two-thirds the length of the valve. It is highest posteriorly and bears 8-10 serrations facing ventrally. The brachial loop is not preserved in the studied material.

The species *A. vidali* can be easily distinguished from another Spanish Eocene species occurring in the Vic Basin, *A. batalleri* (Abrard) by its shell outline and ornamentation. *A. batalleri* is subsquare in outline and covered with sharper ribs with grooves between them wider than ribs themselves.

The specimens described by Davidson (1870) under the name *Terebratulina* ? *Michelottina* exhibit typical characteristics of the genus *Argyrotheca*, such as straight hinge line, nearly equal to the shell width, flat area with large and triangular hypothryid pedicle opening restricted by narrow deltidial plates. Moreover, in size, outline and ornamentation of rounded ribs *T. michelottina* agrees very well with *A. vidali*.

Elliott (1954) created a new genus and species, *Cistellarcula wrigleyi*, for the specimens from the Eocene strata of the French Pyrenees. Elliott's material, although represented only by few specimens rather poorly preserved, is entirely consistent with *A. vidali*. I agree with the opinion of Calzada and Urquiola (1994) that the characters used by Elliott (1954) to create a new genus are not sufficient to distinguish those two genera, i.e. *Argyrotheca* and *Cistellarcula*.

Occurrence

Lower and Middle Eocene of southern Europe (France, Spain and Italy).

Family uncertain

"*Terebratula*" n. sp.

Figs. 7-8

Dimensions (in mm; see also Fig. 8):

	L	W	T
ZPAL Bp.XLIII/103	1.4	1.1	
ZPAL Bp.XLIII/105	2.0	1.8	0.6
ZPAL Bp.XLIII/106	2.6	2.2	0.8
ZPAL Bp.XLIII/120	2.4	2.2	0.8
ZPAL Bp.XLIII/122	2.1	1.8	0.6
ZPAL Bp.XLIII/125	3.1	2.8	1.1
ZPAL Bp.XLIII/126	2.5	2.3	0.8

Material: 127 complete specimens from Bacamorta, and 12 complete specimens from Casa Torrucco. Few specimens are slightly crushed.

Description

The shell is very small (max. length 3.1 mm), thin and translucent, weakly biconvex, with the dorsal valve slightly more convex. The shell outline varies from ovaly elongate in young specimens to subcircular in adults. The shell surface is completely smooth, no growth lines are visible. In two specimens there are fragments of surface with punctae visible. The ventral beak is straight, pointed. The pedicle opening is large, triangular, of hypothryid type, restricted by two narrow, disjunct deltidial plates. The hinge line is short and slightly curved. The anterior commissure is rectimarginate. Through the translucent shell no significant internal structure is visible.

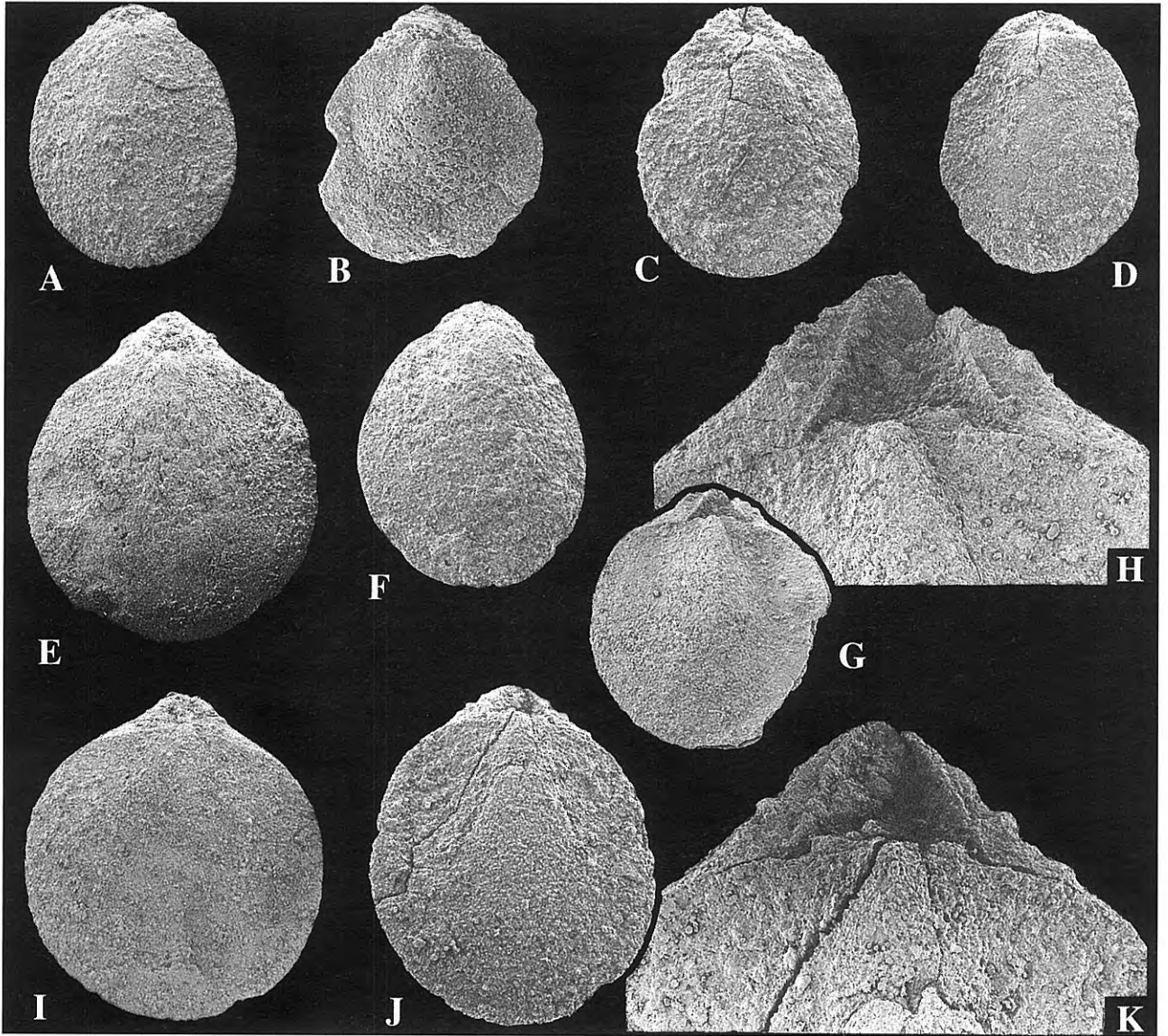


Figure 7. "*Terebratula*" n. sp., Bacamorta; **A-C.** Dorsal views of complete specimens, ZPAL Bp.XLIII/101-103, sample 7; A - SEM x 25, B-C - SEM x 30; **D-F.** Dorsal views of complete specimens, ZPAL Bp.XLIII/121-123, sample 9; D - SEM x 40, E-F - SEM x 25; **G-H.** Complete specimen, ZPAL Bp.XLIII/104, sample 7; G - dorsal view, SEM x 20; H - enlarged of G to show details of the posterior part of the shell, SEM x 65; **I.** Dorsal view of complete specimen, ZPAL Bp.XLIII/120, sample 9, SEM x 20; **J-K.** Complete specimen, ZPAL Bp.XLIII/105, sample 7; J - dorsal view, SEM x 25; K - enlarged of J to show details of the posterior part of the shell, SEM x 65.

Remarks

The state of preservation, unknown internal structures and the absence of any characteristic features make the determination of the systematic position of this micromorphic species very difficult. In some cases overgrowth by cement crystals may obliterate the shell microstructure, not allowing even to differentiate between terebratulids and rhynchonellids. Those smooth, small terebratulids, for instance, display a great similarity to the rhynchonellid genus *Cryptopora* Jeffreys, as already noted by Pajaud and Tambareau (1970). The punctuation, however, preserved in two specimens excludes such possibility. Also the absence of the dorsal median septum, which should be clearly visible through the translucent shell, makes the discussed specimens

different from *Cryptopora*. The same difficulties were also pointed by Pajaud in Pajaud and Tambareau (1970) and in Pajaud and Plaziat (1972) who studied similar material from the Upper Paleocene. He decided to attribute informally his new species to "*Terebratula*". In effect, I follow Pajaud's approach attributing also the studied specimens to "*Terebratula*", however not creating formally a new species.

The specimens from the Campo region are very close to the Upper Paleocene species "*Terebratula lapichensis*" Pajaud (in Pajaud and Tambareau, 1970: 318-320). They differ from this species, however, in being slightly smaller and having rectimarginate anterior commissure. They also display an opposite than the specimens from the Petites Pyrénées tendency in the shell shape -

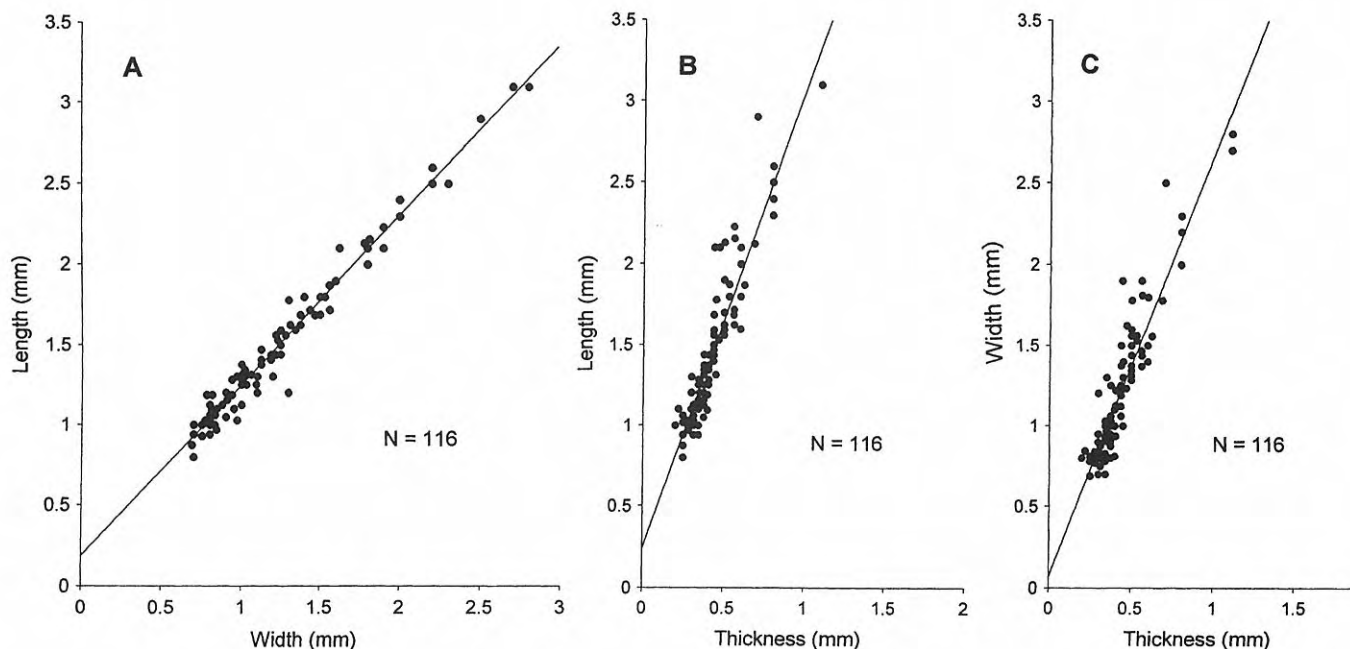


Figure 8. Intraspecific variability of "*Terebratula*" n. sp. from the Campo region. Scatter diagrams plotting length/width (A), length/thickness (B), width/thickness (C). N - number of specimens.

immature specimens are elongate becoming transverse when adults (compare Fig. 8A and fig. 4B in Pajaud and Tambareau, 1970).

The specimens under study show also some similarities to the species "*T. liusa*" from the Thanetian of the Basque region described by Pajaud in Pajaud and Plaziat (1972). They differ from them, however, in much larger size, in more transverse shell outline and in having rectimarginate anterior commissure.

Occurrence

Lower Eocene of north-eastern Spain.

ECOLOGICAL CONDITIONS OF THE BRACHIOPOD FAUNA

The investigated brachiopod assemblage from the Campo region, although rich in specimens (more than 1600), is of low diversity; only three brachiopod genera are represented. The brachiopod fauna is generally well preserved; 95 percent of the specimens are articulated, indicating lack or a short distance of *post-mortem* transport. Epizoans on the brachiopod shells are very rare. They include bryozoans, serpulids, oysters, and foraminifers. Also predatory activity is very low. Gastropod borings are observed on five specimens only. Few specimens show signs of nonlethal predatory attacks of some unknown predator.

The particular species display slightly different frequency patterns. *Terebratulina tenuistriata* (Leymerie) and *Argyrothecca vidali* (Mallada) are present in all collecting samples, while "*Terebratula*" n. sp. was found in five samples, in two others being absent.

The composition of fauna and type of sediment may

suggest similar interpretation of the ecological conditions as for the white chalk assemblage with dominance of small, pedunculate taxa inhabiting soft bottom (Surlyk, 1972). The species from the Campo region belong to two ecological categories among those distinguished by Surlyk (1972). *T. tenuistriata*, the largest species in the investigated material, belong to a group of medium-sized brachiopods that lived attached directly to the fine sediment by a rooted pedicle, well known mode of life of Recent *Terebratulina* species (Curry, 1981). The micromorphic pedunculate species, *A. vidali* and "*Terebratula*" n. sp. belong to another group of minute forms that were able to use very small, hard substrates, such as small bryozoans, mollusc shell fragments or serpulids recognized in the sediment.

ACKNOWLEDGEMENTS

I would like to express my gratitude to Drs Josep Serra-Kiel and Josep Tosquella (Barcelona University) for introducing me into the field. Dr. J. Tosquella also helped me in collecting brachiopods. Part of the work was done during my stay at the University of Barcelona thanks to invitation by Professor Salvador Reguant and Dr. Pere Busquets (Barcelona University). Special thanks are due to Professor Jordi Martinell (Barcelona) for accepting me in his lab. Drs Sebastián Calzada (Barcelona) and Barbara Studencka (Warszawa) kindly assisted by arranging facilities to study the material stored in the Museu Geològic del Seminari and Muzeum Ziemi, respectively. Through the kindness of Ms. Sarah Long (London) I had the opportunity to study the brachiopod collections housed in The Natural History Museum, London. I am particularly thankful to Dr. Ellis F. Owen (London) for reading the manuscript and

improving the English language. I am also indebted to Dr. Josep Serra-Kiel who read the manuscript and suggested some modifications. Ms. Sarah Long and Dr. Neda Motchurova-Dekova (Sofia) helped me with some papers difficult to find. Ms. Laia Alegret Badiola (Zaragoza) and Dr. J. Serra-Kiel helped me with the Spanish abstract. This paper benefited from the thoughtful reviews of Drs Fernando Álvarez (Oviedo) and Eustoquio Molina (Zaragoza). The photographs were taken by Ms. Grażyna Dziewińska (Warszawa) to whom I am very grateful. The SEM micrographs were taken in the SEM laboratory of the Institute of Paleobiology (Warszawa) using Philips XL-20 scanning microscope.

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