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GLOTTIDIA (BRACHIOPODA: LINGULIDAE) FROM THE EOCENE LA MESETA FORMATION, SEYMOUR ISLAND, ANTARCTICA

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Abstract: The specimens previously described as *Lingula antarctica* Buckman from late Eocene strata on Seymour Island, Antarctic Peninsula, should be assigned to the genus *Glottidia*. The morphological features and taxonomic characters of *G. antarctica* are described and illustrated and compared with those of other known species of *Glottidia*. A full description of *G. antarctica* is provided and the diagnosis of the genus is emended. Variations in the disposition of the septa and in the shape of the pedicle groove are viewed as evolutionary features among the *Glottidia*. *Glottidia antarctica* probably lived in shallow, nearshore warm-temperate waters of normal salinity, perhaps in the intertidal zone. The presence of *Glottidia* rather than *Lingula* in the Antarctic Peninsula is consistent with the known geographical distribution of fossil and living *Glottidia*, i.e. restricted to the coasts of the American continent and Europe where *Glottidia* has been recorded in strata of Tertiary age.

Key words: Eocene, Seymour Island, Antarctica, Brachiopoda, *Glottidia*.

SEVERAL collections of brachiopods found in the La Meseta Formation, a late early–late Eocene sandstone on Seymour Island, Antarctic Peninsula, include a single inarticulated brachiopod species, *Lingula antarctica* Buckman, 1910. It is fairly common at many localities in the uppermost units, Telm6 and Telm7 (for details, see Sadler 1988 and Stilwell and Zinsmeister 1992). This species was originally described by Buckman (1910), who based it on two incomplete specimens. Other specimens were later figured by Owen (1980), Wiedman *et al.* (1988) and Bitner (1996*a*, *b*, 1997), but the internal features were never described.

A new analysis of the material deposited in the Institute of Paleobiology (Warszawa) of the Polish Academy of Sciences reveals that the species referred to as *Lingula antarctica* in fact belongs to *Glottidia* (as Buckman originally suspected), which is, with *Lingula*, the only other extant lingulide genus. The excellent preservation of imprints of the soft parts in the valves, i.e. traces indicating the arrangement of muscles, and the shape of the main anterior mantle canals (vascula lateralia) and of the umbonal regions, provides evidence that this species shares the characteristics that define the extant species of *Glottidia* (see Emig 1983; Emig and Vargas 1990). Previously, the taxonomic characters established as valid for living lingulide taxa have been applied successfully to fossil linguloid taxa as old as Cambrian (see Biernat and Emig 1993; Márquez-Aliaga *et al.* 1999; Emig 2002, 2003*a*, *b*). However, fossil *Glottidia* are very poorly represented in the literature: a few fossils from strata of Tertiary age have been described by Chuang (1964*a*–*c*) from the USA and Europe, and more recently by Figueiras and Martinez (1995) from the Miocene Camacho Formation of Uruguay. '*Glottidia*' *rostrata* described by Thomson and Owen (1979) from the Lower Cretaceous of south-eastern Alexander Island (Antarctica) does not belong to *Glottidia*.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The specimens described here were collected from the La Meseta Formation exposed in the northern part of Seymour Island, Antarctic Peninsula. This sequence, about 720 m thick (Feldmann *et al.* 2003), consists of loosely consolidated sandstones, sandy siltstones, claystones, pebbly sandstones and shell beds with a rich marine fauna (Sadler 1988; Stilwell and Zinsmeister 1992). Based on faunal composition and sedimentary considerations these deposits are interpreted as having been deposited in warm-temperate conditions in a nearshore, tidally influenced, shallow-marine environment (Stilwell and Zinsmeister 1992). Sadler (1988) divided the La Meseta

Formation into seven lithofacies units (Telm1–Telm7). The age of the lower part the formation, based on dinoflagellate cysts, is considered to be late early Eocene (Cocozza and Clarke 1992), while $^{87}Sr/^{86}Sr$ data indicate an age of late late Eocene for the upper part, Telm 7 (Dingle and Lavelle 1998; Dutton *et al.* 2002; Feldmann *et al.* 2003).

All of the specimens of *Glottidia antarctica* described here come from the uppermost units Telm6 and Telm7, which are characterized as medium- to fine-grained sandstones with intervals of fine-grained sand and silty clay laminations (Sadler 1988; Stilwell and Zinsmeister 1992). The *Glottidia* are associated with other brachiopods, primarily *Bouchardia antarctica* Buckman, 1910, and with a rich marine fauna dominated by bivalves, gastropods, echinoids and crinoids (Stilwell and Zinsmeister 1992; Bitner 1996*a*).

SYSTEMATIC PALAEONTOLOGY

All specimens described in this paper are housed in the Institute of Paleobiology, Warszawa, Poland, and distinguished by the prefix ZPAL. The systematic analysis below follows the classification proposed by Holmer and Popov (2000).

Order LINGULIDA Waagen, 1885
Superfamily LINGULOIDEA Menke, 1828
Family LINGULIDAE Menke, 1828

Genus GLOTTIDIA Dall, 1870

Type species. Lingula albida Hinds, 1844, from Magdalena Baja, Mexico.

Emended diagnosis. Shell strongly elongate in outline, lateral margins subparallel to parallel, anterior margin slightly rounded to nearly straight. Mantle canal system with papillae; main canals (vascula lateralia) in both dorsal and ventral valves terminating at the same level. Ventral valve with a pedicle groove, the edges of which are triangular or subparallel, and with lateral vestigial propareas; two divergent septa, serving as sites for the attachment of the internal oblique muscles and as support for the perimial line of the body wall; pedicle nerve curving around an unpaired posterior adductor muscle; ventral lophophoral cavity extending anteriorly to occupy 33–43 per cent of the length of the valve. Dorsal valve with a median septum extending from the posterior adductor muscle anteriorly to the composite 'lateral + internal oblique' muscles; posterior margin rounded, with a median beak; anterior oblique muscles closely spaced, sometimes bisected by a median septum; dorsal lophophoral cavity extending anteriorly to occupy 19–33 per cent of the valve length.

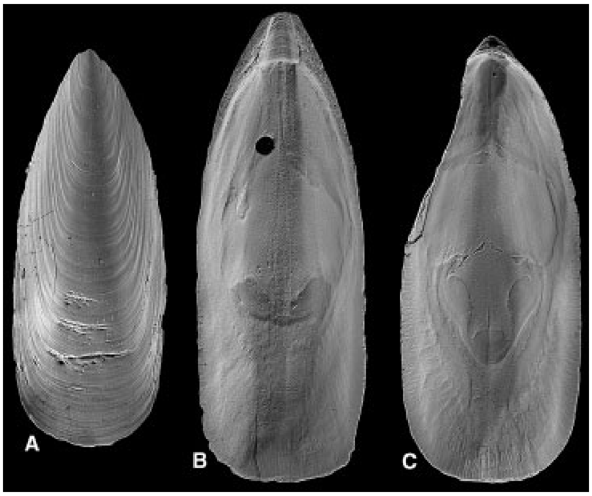
Remarks. The diagnosis of genus *Glottidia* proposed by Emig (2003*a*) is emended above. The diagnoses of both the genus and *G. antarctica* are consistent in content and breadth with the diagnoses of the extant lingulide taxa (Emig 1983). The known geological range of *Glottidia* is Eocene–Recent.

Glottidia antarctica (Buckman, 1910)
Text-figures 1–4

1910 *Lingula antarctica* Buckman, p. 9, pl. 1, fig. 7.
1964*b* *Glottidia glauca* Chuang, p. 157, fig. 1.
1980 *Lingula antarctica* Buckman; Owen, p. 126, fig. 10.
1988 *Lingula antarctica* Buckman; Wiedman *et al.*, fig. 2.18–20.
1996*a* *Lingula antarctica* Buckman; Bitner, p. 70, pl. 18, figs 1–2.
1996*b* *Lingula antarctica* Buckman; Bitner, p. 22, pl. 2, fig. 1.
1997 *Lingula antarctica* Buckman; Bitner, fig. 2a.

Material. 23 complete specimens, nine ventral valves, 13 dorsal valves, and many broken fragments (ZPAL Bp.XXXVII).

Diagnosis. Ventral valve: umbonal region slightly acute-angled with a rather rounded beak and a subparallel pedicle groove that is not continuous with the inner valve side; anterior and median internal oblique muscles similarly elongate; posterior internal oblique muscle rounded; posterior adductor muscles centred over the septa; two oblique septa, widened and curved, the left septum slightly longer than that on the right and generally more arcuate; both



TEXT-FIG. 1. *Glottidia antarctica*. A, external view of ventral valve, ZPAL Bp.XXXVII/4. B, internal view of a ventral valve which shows a drill hole from a naticid gastropod, ZPAL Bp.XXXVII/1. C, internal view of a dorsal valve, ZPAL Bp.XXXVII/5. All ×2. Compare with Text-figure 3A, D.

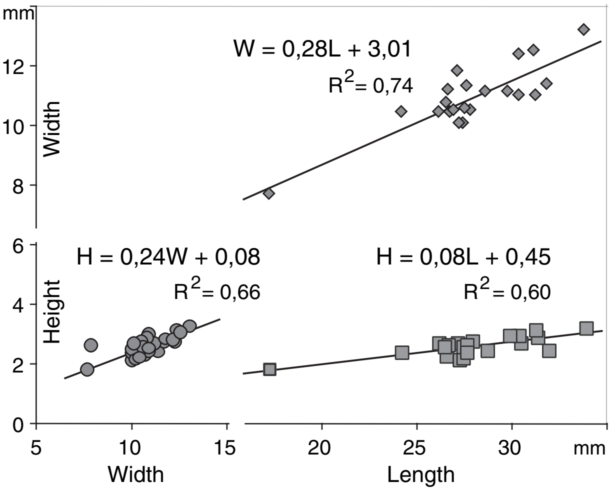
septa originating posteriorly at the level of the pedicle groove edges. Dorsal valve: narrow dorso-central ridge at the level of the anterior oblique muscles; umbonal region slightly acute with a rather rounded beak. Anterior mantle canals oblique, curved forward concavely. Text-figure 3 is part of this diagnosis, mainly for the muscle arrangement and the disposition of the mantle canals and septa.

Description

This description of the specimens studied includes all the characters with taxonomic significance as well as features with no taxonomic value.

Shell shape and size. The shell is biconvex, elongate in outline, with the lateral sides parallel. It is ornamented with concentric oblong growth lines; the anterior edge ranges in the degree of curvature from slightly rounded to nearly straight (Text-figs 1, 3). The valve measurements of *Glottidia antarctica* are given on Table 1 and their regression curves on Text-figure 2.

Dorso-central ridge. A fairly narrow dorso-central ridge (Text-figs 1C, 3D–E) at the level of the anterior oblique muscles is present and appears to be a taxonomic character that distinguishes *G. antarctica* from the other *Glottidia* species (see Comparison below).



TEXT-FIG. 2. *Glottidia antarctica*. Regression curves of the measurements given in Table 1.

Umbonal regions. These regions are slightly acute with a rather rounded beak (Text-figs 1, 3–4). On the dorsal valve the beak profile is oblique and slightly concave (Text-figs 1C, 4C–D). On the ventral valve, the edges of the pedicle groove are subparallel. This groove is discrete from the inner side of the valve (Text-figs 1B, 4A–B).

Septa. The septa in both valves were dissolved almost completely as a result of taphonomic processes; however, their trace can be detected without difficulty on the inner side of each valve (Text-figs 1C, 3C–F; Table 1). Both septa of the ventral valve are obliquely curved, the left septum being generally more arcuate than the right septum. This latter is invariably slightly longer than the left one (Text-figs 1A, 3A–C). Posteriorly, the septa extend separately forward from the lateral edges of the pedicle groove (Text-figs 3A–C, 4A–B).

Muscle arrangement. The emplacement of muscles has not been reported previously for this species (Text-figs 1B–C, 3A–B, D–E). As a whole, the anterior oblique muscles have a rather rounded shape and a ridge separates them vertically on the inner side of the dorsal valve (see dorso-central ridge above).

On the ventral body side, both anterior and median internal oblique muscles are elongated and the posterior internal oblique muscle is rounded (Text-fig. 3A–C). The posterior adductor muscle is centred over the septa (Text-figs 3A–B, 4A). The composite ‘lateral + internal oblique’ muscles are shifted posteriorly (Text-figs 1C, 3D–E).

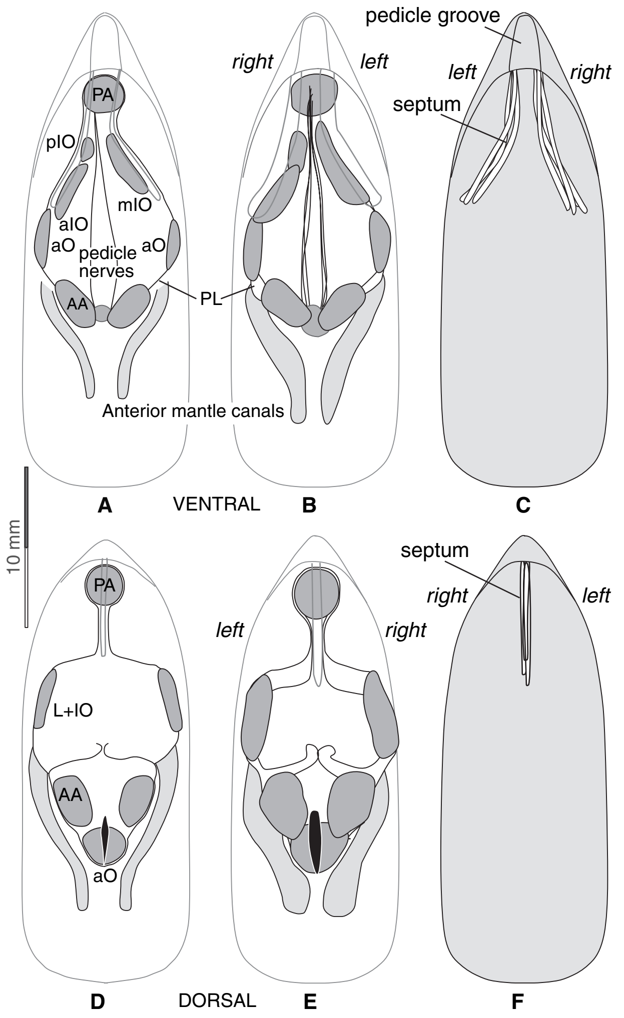
Mantle canal disposition. The two main anterior canals are oblique, curved forward concavely (Text-figs 1B–C, 3A–B, D–F) on both body sides. The anterior mantle papillae, a taxonomic marker characterizing the genus, can be seen as weak impressions on some valves. The extension of the mantle canal tips is expressed as a percentage of valve length (Table 2; Text-figs 1B–C, 3A–B, D–E).

Lophophoral cavity. The length of the lophophoral cavity, which is the part of the mantle cavity occupied by the lophophore, is the distance between the distal limit of the anterior adductor muscle scars (ventral valve) and the anterior oblique muscle scars (dorsal valve) to the anterior edge of the valve (Text-figs 1A–B, 3A–B, D–E): the measurements are given on Table 2.

Nerve imprints. The two tiny V-shaped grooves in the median part of the body are impressions of the pedicle nerves (see Biernat and Emig 1993), a common feature in many linguloid species (Text-figs 1B, 3A–B).

TABLE 1. The range in size and the mean dimensions and ratios of the valves of *Glottidia antarctica*, in mm.

	Length (L)	Width (W)	Height (H)	W/L	H/L	H/W		Septum/L (per cent)
Dorsal valve	17·3–33·9	7·6–13·1	1·8–3·2	0·37–0·44	0·08–0·10	0·21–0·27		26·4–32·8
n = 14	28·3	11·0	2·6	0·39	0·09	0·24	*n* = 9	28·3
Ventral valve	24·3–31·9	10·0–11·3	2·3–2·7	0·35–0·43	0·08–0·10	0·21–0·27		39·6–40·1
n = 8	27·4	10·6	2·4	0·39	0·09	0·23	*n* = 3	39·8



TEXT-FIG. 3. *Glottidia antarctica*. A, arrangement of the body muscles and disposition of the two main anterior canals of the mantle of a specimen, and B, their variability in the specimens studied, on the ventral side of the body. C, variability of the two septa in the ventral valve (see also Table 1). D, arrangement of the body muscles and disposition of the two main anterior canals of the mantle of a specimen, and E, their variability in the specimens studied, on the dorsal side of the body. F, variability of the median septum in the dorsal valve (see also Table 1). Abbreviations pertaining to muscles. AA, anterior adductor; aIO, anterior internal oblique; aO, anterior oblique; L+IO, composite 'lateral and internal oblique'; mIO, median internal oblique; PA, posterior adductor; pIO, posterior internal oblique; PL, perimial body line.

Remarks. Buckman (1910, p. 9) noted that *Lingula antarctica* is 'very much like *Glottidia palmeri*, but it does not show any indication of the internal median ridge characteristic of the dorsal valve of that genus'. However, his figure 7b shows clearly the median septum of the dorsal valve and the muscle arrangement characteristic of *Glottidia*. Furthermore, Buckman (1910, p. 9) commented that the species 'is somewhat like *Lingula dumortieri*', which is now considered as *Glottidia dumortieri* by Chuang (1964*c*). Owen (1980) and Wiedman *et al*. (1988) figured only the external aspects of two valves.

Comparison with fossil species. Several fossil species have been referred to *Glottidia*. The W/L ratios of *Glottidia glauca* Chuang, 1964 from the Eocene of La Salle County (Texas, USA) vary from 0·43 to 0·47 according to Chuang (1964*b*). Because of the poor preservation of the specimens, the description of the species lacks detail, but the disposition of the ventral septa appears similar to that of *G. antarctica*: 'more widely divergent than in *G. inexpectans* and in *G. albida* and more curved than in the latter' (Chuang 1964*b*, p. 158). Based on this character, *G. glauca* must be considered a synonym of *G. antarctica*. A single specimen referred to *Glottidia albida* is reported from the Eocene of California by Hertlein and Grant (1944).

According to Chuang (1964*a*), *G. inexpectans* from the Yorktown Formation (Miocene) of Hampton (Virginia, USA) shows a closer relationship to *G. palmeri* than to *G. albida*. The size indicated by this author for valve length is 37·5 mm and for width, 14·2 mm (W/L ratio, 0·38). These measurements exceed those of *G. albida* for which the maximum length is about 31 mm and the width is 15 mm. Chuang's (1964*a*) figure 1 shows the pedicle groove and the large median impression of the posterior adductor muscle in the ventral valve to be similar to that of *G. antarctica*. However, Chuang stated that the scar of the posterior adductor muscle is shifted to the left on the inner side of the dorsal valve, but in the extant species this shift occurs mainly in the ventral valve (Emig 1983; Emig and Vargas 1990). A median ridge also exists between the imprints of the anterior oblique muscles. The ventral septa in *G. inexpectans* are rather similar to those of *G. audebarti*.

From the Miocene of Uruguay, *Glottidia bravardi* Figueiras and Martinez, 1995 was originally referred to as *Lingula bravardi*, but was considered a *nomen nudum* because it was never described or figured (Frenguelli 1930; Figueiras and Martinez 1995). A comparison with *Glottidia antarctica* is impossible because only fragments of several valves are available. The *Lingula* collected near Puerto San José (Chubut, Argentina) was referred by Frenguelli (1930) to *Lingula bravardi* from Uruguay.

Chuang (1964*c*) considered that the species described as *Lingula dumortieri* by Nyst (1843) from the Pliocene of Antwerp (Belgium) should be referred to *Glottidia*. '*Lingula*' *dumortieri* has septa and the scar of the posterior adductor muscle is asymmetric, shifted to the left on the inner side of the dorsal valve as in *G. inexpectans*, although this disposition occurs mainly in the ventral valve of extant species (see Emig 1983; Emig and Vargas

TABLE 2. Variation in the length of the lophophoral cavity (Lc) and the anterior mantle canals (Mct) in *Glottidia antarctica* expressed as percentages of the length of the whole valve and compared with those of the genus *Glottidia* (Biernat and Emig 1993). Lc is the distance between the distal limit of the muscle scars (i.e. anterior adductors on the ventral valve and anterior obliques on the dorsal valve) and the anterior margin of the valve. Mct is the distance in mm separating the tips of the canals from the anterior margin of the valve expressed as a percentage of the length of the valve.

		Lophophoral cavity (%)				Mantle canal tip (%)				Mct – Lc (%)	
		Ventral		Dorsal		Ventral		Dorsal		Ventral	Dorsal
	nV/nD	range	mean	range	mean	range	mean	range	mean	mean	mean
G. antarctica	3/8	33–35	34	24–26	25	13–16	15	15–16	15	18	10
Glottidia	35/35	33–43	38	19–33	26	9–15	13	12–15	14	25	12

1990). Buckman (1910) pointed out that in some respects *Lingula antarctica* is like *L. dumortieri*; both species are now referred to *Glottidia*.

Finally, the species described as '*Glottidia*' *rostrata* by Thomson and Owen (1979) from the Lower Cretaceous of Alexander Island (Antarctica) does not show the characters of *Glottidia*: the extension of the septa is about 80 per cent of the valve length for the median septum in the dorsal valve and about 85 per cent for the two divergent ones in the ventral valve. The shape of the valves is not linguliform. This species may well represent a new linguloid form.

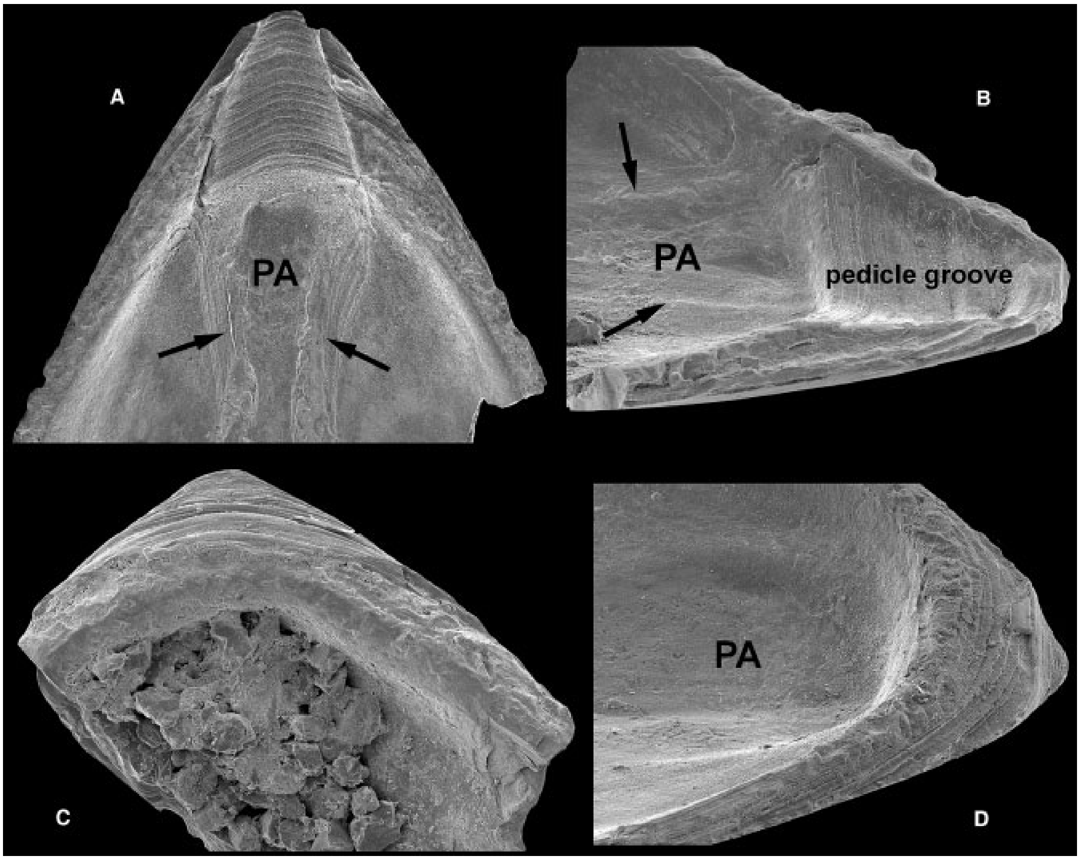
Comparison with Recent species. Glottidia antarctica is a well-defined species that shows many distinctive features. The general shape of the shell of *Glottidia antarctica* is similar to that of *G. audebarti* (see Emig 1983; Emig and Vargas 1990). The W/L ratios (Table 1) are similar to those of *G. albida* (W/L, 0·37–0·44; mean, 0·39; n, 35), *G. pyramidata* (W/L, 0·33–0·44; mean, 0·38; n, 43) and *G. audebarti* (W/L, 0·33–0·42; mean, 0·35; n, 35) (data from Emig 1983; Emig and Vargas 1990; Kowalewski *et al.* 1997). The H/L ratios (Table 1) vary little in the species of *Glottidia*, ranging from 0·09 to 0·11 (mean, 0·09; n, 35). However, the H/W ratios indicate that the valves of *G. antarctica* are more convex (Table 1) than those of the other *Glottidia* species (H/W, 0·15–0·24; mean, 0·20; n, 35). A difference of the same order in fossil and extant species was reported previously by Biernat and Emig (1993) between extant *Lingula* and the related Mesozoic *Lingularia*. Here the difference in H/W ratio is, respectively, 0·14–0·25 (mean, 0·20) and 0·20–0·44 (mean, 0·32).

These results indicate that biometrical variations of the *Glottidia* shell are very limited in both extant and fossil species. The attempt by Kowalewski *et al.* (1997) to discriminate the extant species of *Glottidia* on six shell characters was not entirely successful. Consequently, any taxonomic differentiation must include morpho-anatomical characters, thus ensuring the use of valid criteria as demonstrated by Biernat and Emig (1993) and Emig (2002, 2003*b*).

The pedicle groove has subparallel edges as in *G. inexpectans*; no data are available for other fossil species, but extant species have a triangular groove. Such a difference also exists between the Mesozoic *Lingularia* and the Recent *Lingula*. Thus, this character can be considered as a symplesiomorphy of the family Lingulidae inherited from a common ancestor. The discontinuity of the pedicle groove with the inner side of the ventral valve of *G. antarctica* (Text-figs 1B, 4A–B) occurs also in *G. audebarti* and *G. albida*.

The dorso-central ridge distinguishes *G. antarctica* (Text-figs 1C, 3D–E) because this ridge does not exist in the other species of *Glottidia* according to Biernat and Emig (1993), with the exception of an occasional weak ridge in *G. audebarti*. This feature can be considered a remnant of a lingulide ancestry because the same feature occurs in *Lingularia* and *Lingula*; consequently it is a symplesiomorphy shared by all the Lingulidae as defined by Emig (2003*a*).

The ventral septa in *G. antarctica* are wider and curve more than in other species of *Glottidia*; so this character can be considered diagnostic. They extend also separately forward from the lateral edges of the pedicle groove (Text-figs 3A–C, 4A–B), contrary to those of the other species where the septa join below the triangular pedicle groove (Emig 1983). Both ventral septa in *G. antarctica* extend forwards slightly more (Table 1) than in *G. audebarti* where it ranges from 34 to 42 per cent (mean, 37; n, 32) of the valve length (Emig and Vargas 1990; Kowalewski *et al.* 1997). As in *G. palmeri* and *G. audebarti*, the right septum is invariably slightly longer than the left one (Text-figs 1A, 3A–C). The unique median septum of the dorsal valve (Text-figs 1C, 3D–F; Table 1) extends forwards a distance similar to that in *G. audebarti* where the septum ranges in length to occupy 25–35 per cent of the valve (mean, 29; n, 32) and as in *G. pyramidata* where



TEXT-FIG. 4. Scanning electron micrographs of *Glottidia antarctica*. Internal umbonal region of ventral valves with the pedicle groove and the scar of the posterior adductor muscle (PA). A, frontal view with posterior part of the septa, indicated by arrows, ZPAL Bp.XXXVII/7; ×10. B, lateral view; internal umbonal region of dorsal valves, ZPAL Bp.XXXVII/8; ×15. C, frontal view, ZPAL Bp.XXXVII/9; ×20. D, lateral view with the scar of the posterior adductor muscle, ZPAL Bp.XXXVII/10; ×20.

the septum occupies 22–37 per cent (mean, 29; n, 43) (Emig and Vargas 1990; Kowalewski *et al.* 1997).

The general muscle arrangement is similar to that observed in all *Glottidia*, especially the site of insertion of the perimial line on the septa. As in *G. pyramidata* and *G. audebarti*, the posterior adductor muscle is centred over the septa (Text-figs 3A–B, 4A) and is not shifted to the right (over the left septum) as in *G. albida* and *G. palmeri* (see Emig 1983). As in all *Glottidia*, in the dorsal body side, the composite 'lateral + internal oblique' muscles are shifted posteriorly (Text-figs 1C, 3D–E), when compared to the same muscles in *Lingula* where they are centred on the rounded part of the perimial line.

The shape of the anterior mantle canals in *G. antarctica* (Text-figs 1B–C, 3A–B, D–E) is similar to those of most species of *Lingula* and *Lingularia* (Emig 1983; Biernat and Emig 1993), although the disposition of these canals varies from one species to another. In the extant *Glottidia* these canals are subrectilinear to slightly convex; this arrangement in *G. antarctica* also seems to be plesiomorphic among the *Glottidia*.

Because the extension of the lophophoral cavity in *G. antarctica* is similar to that in the extant species of *Glottidia* (Table 2), the validity of this feature as a phylogenetic characteristic of *Glottidia* is substantiated, confirming its significance, as discussed by Biernat and Emig (1993): the reduction of the lophophoral cavity, directly related to the volume of this cavity in the lingulide shells, is an important evolutionary tendency from the Palaeozoic linguloid, i.e. *Pseudolingula* and *Langella*, until the Recent *Glottidia*. The shortening of the length of the mantle canals among the lingulides is related to a reduction in size of the lophophoral cavity (as shown in Mct and Mct-lc, Table 2) when compared with the same measurements in *Lingula* and *Lingularia*, distinguishing *Glottidia* beyond question (Biernat and Emig 1993; Emig 2003*a*).

Finally, as demonstrated by this study on fossil *Glottidia antarctica*, a morphologically simple shell necessitates the use of detailed anatomical characters to determine both its phylogeny and its relationships. Consequently, neither a palaeontological nor a neontological approach is, in itself, a satisfactory solution to taxonomic problems because each is based on characters that are not time-dependent. A valid approach to the phylogeny of the linguloids must use impressions depicting the arrangement of soft body parts in fossils and compare them with those of the living representatives.

PALAEOENVIRONMENTAL AND BIOGEOGRAPHICAL IMPLICATIONS

The uppermost units (Telm6 and Telm7) where *Glottidia antarctica* shells were deposited in a low-energy, shallow-marine environment include several shelly concentrations (i.e. turritellid gastropod, venerid bivalve and irregular echinoid levels) with intervals of *in situ* assemblages (Wiedman *et al.* 1988; Stilwell and Zinsmeister 1992; Bitner 1996*a*). Sea surface temperature estimates based on ^{18}O values ranged from 14·5 to 15·5°C in the early and middle Eocene to 10·5°C in the late Eocene (Dutton *et al.* 2002). Such conditions are consistent with those in which most of the species of *Glottidia* live today: a shallow near-shore environment often near an estuarine or deltaic area, perhaps in the intertidal zone, in temperate to subtropical water of normal salinity, as for *Glottidia audebarti* in the Gulf of Nicoya (Costa Rica) and the Gulf of California (Mexico) for example (Emig 1983; Emig and Vargas 1990). The geographical range of *Glottidia*, like that of *Lingula*, extends to temperate waters in the Northern Hemisphere but appears to be restricted to the tropics in the Southern Hemisphere (see Emig 1997). *Glottidia* has not been reported in the southern portion of South America either offshore in existing seas or in Tertiary and Quaternary deposits. The southernmost occurrences of extant species of *Glottidia* are on the Peruvian and Brazilian coasts (Emig 1997) while fossil records report *G. bravardi* in the Miocene of Uruguay (Figueiras and Martinez 1995) and of Argentina (Frenguelli 1930).

The presence of shells of *G. antarctica* with both valves close to each other suggests that fossilization began with a rapid lowering of water levels in the burrow, leading to death with no escape possible in a confined situation not subject to reworking subsequently (Emig 1986). This interpretation is consistent with a low-energy, intertidal environment, at least until death occurred and fossilization began, an occurrence that presumably was caused by a drastic event. The global cooling on Seymour Island, when the temperature decreased from 15·5 to 10·5°C in the late Eocene to early Oligocene, related to the opening of the Tasman Sea and Drake Passage seaways (Dingle and Lavelle 2000; Dutton *et al.* 2002), affected the littoral marine benthic communities with the disappearance of crabs, sharks and most teleosts (Aronson and Blake 2001), as well as of populations of *Glottidia antarctica*. In lingulides a temperature decrease below the annual minimum can induce a lethal mantle retraction (Emig 1986, 1997). According to Kowalewski (1996), shells of *in situ* dead *G. palmeri* may be preserved in burrows 10–20 cm below the sediment surface. These shells, ranging from 20 to 36 mm in length, may remain for at least one year in the sediment with some changes in the physical properties of the shell. Consequently, judging from the perfect condition of most valves of *G. antarctica*, almost all of them retaining internal morphological imprints, this excellent preservation required a rapid and undisturbed burial.

Ecological requirements, i.e. temperature and salinity ranges, can differ from one lingulide population to another and thus cannot be extrapolated to all the populations of a species and even less to the genus. Attempts to make such extrapolations lead to biases in (palaeo)ecological interpretations (Emig 1997).

Three valves of *G. antarctica* were drilled by a naticid gastropod (Text-fig. 1B): the drill holes are conical in shape with a diameter ranging from 1·8 to 2·0 mm (Bitner 1996*b*). Another valve drilled by a gastropod was figured by Wiedman *et al.* (1988, fig. 2.19). Kowalewski and Flessa (1994) reported a single drill hole in a valve fragment of the extant *G. palmeri* from about 1000 valves collected; the predator may well have been a naticid or muricid gastropod.

The presence of *Glottidia* and not *Lingula* in the Antarctic Peninsula is consistent with the present geographical distribution of both genera. The occurrence of *Glottidia* is restricted to the American continent and *Lingula* occurs almost everywhere else, except Europe. However, the Tertiary records of *Glottidia* in western Europe (Chuang 1964*c*) broaden the distribution of this genus to both sides of the Atlantic Ocean, extending its range on both continents north of the equator at least to Pliocene times. The Donau glaciation at the end of the Late Pliocene may explain the disappearance of the genus from European waters.

Glottidia is known from the Eocene onwards, as confirmed herein, while *Lingula* perhaps evolved as early as the Late Cretaceous (Emig 1997, 2003*a*). Contrary to the suggestion of Wiedman *et al.* (1988), the Tertiary *Lingula waikatoensis* (see also Lee and Campbell 1987) is not related to *Glottidia antarctica*.

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