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REVIEW AND MORPHOLOGY OF *AMPHITOMELLA* BITTNER, 1890 (BRACHIOPODA, CARNIAN) FROM SAN CASSIANO FORMATION (CORTINA D'AMPEZZO, ITALY)

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Key-words: Functional Morphology, Systematic Paleontology, Brachiopoda, Athyridida, Carnian, Eastern Dolomites (Italy).

Riassunto. Con l'analisi del taxon *Amphitomella hemisphaeroidica* (Klipstein, 1844), unico rappresentante del genere di Bittner (1890), si continua lo studio del materiale (collezione R. Zardini) proveniente dalla parte superiore della Formazione di San Cassiano affiorante nella conca ampezzana.

Caratteristici di questo taxon sono i setti mediani, presenti su ambedue le valve e sviluppati in altezza sino a venire in contatto fra loro, suddividendo così la cavità del mantello. Morfologia, ultrastruttura ed ontogenesi vengono per la prima volta descritte in dettaglio. Internamente al margine anterolaterale sono presenti creste e solchi che permettono un incastro perfetto tra le due valve, riducendo al minimo l'apertura della conchiglia. I cardinalia sono massicci, con lamina cardinale e cavità cardinale ben sviluppate, atte ad accettare robusti muscoli diduttori. Il brachidio presenta un giogo complesso, dotato di sella jugale da cui origina la biforcazione delle lamelle secondarie; tale ricostruzione si discosta sensibilmente da quella proposta da Bittner (1890), sulla quale viene in parte basata la classificazione tassonomica sino ad oggi proposta.

I caratteri morfologici esaminati concordano con un modo di vita adagiato su di un fondale mobile; i bordi periferici impediscono l'ingresso di particelle estranee, mentre i setti mediani facilitano la circolazione dell'acqua entro la cavità del mantello.

Si discute, infine, l'inquadramento tassonomico del genere *Amphitomella*; esso viene considerato appartenente all'ordine Athyridida, superfamiglia Athyridacea, mentre resta ancora aperta l'attribuzione a livello di famiglia e sottofamiglia.

Abstract. Within the compass of Cassian brachiopod faunas from the Ampezzan Valley (Belluno), *Amphitomella hemisphaeroidica* (Klipstein, 1844), a taxon noted in the literature for the abnormal development of its median septum in both valves, is analysed. This structure has been examined in detail with regard to morphology, ontogenesis and ultrastructure.

Other significant diagnostic and morphofunctional characters are: brachidium, cardinalia, peripheral margin. For the first time, the presence of the saddle in the brachidium is reported, thereby changing Bittner's reconstruction (1890). The cardinalia comprise a cardinal lamina and a cardinal pit; they are massive and probably thus fitted for the attachment of very developed diductor muscles. The anterolateral margin presents snugly fitting internal ridges and grooves and an external gutter covered by mantle; these elements reduce the gape of the shell and affect the mode of absorption of nutrients. Median septa are thus necessary for enhancing water flow through the mantle cavity.

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All these characters accord with the external morphology, suggesting a mode of life on a soft, mobile bottom. *Amphitomella hemisphaeroidica* is attributed to superfamily Athyridacea M'Coy, 1844, but its attribution to family is still arguable.

Introduction.

In a survey of Triassic brachiopods from the area near Cortina d'Ampezzo, *Amphitomella hemisphaeroidica* (Klipstein, 1844), sole representative of *Amphitomella* Bittner, 1890 is examined.

Systematic classification has been argued because of its peculiar internal characters (Bittner, 1890; Dagys, 1974; Grunt, 1986). Since we have abundance of available specimens, we believe a detailed examination of those characters is expedient.

The material examined in this study is from the collection of R. Zardini, to which numbers of specimens are referred; it comes from the following localities, already described by Benigni & Ferliga (1989): Campo, Tamarin, Sass de Stria, Rumerlo,

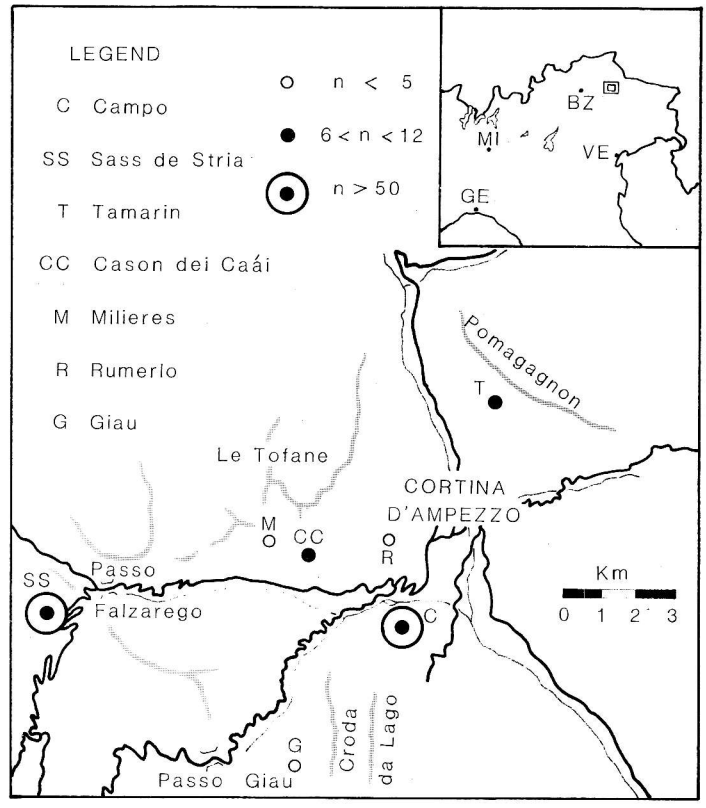

Fig. 1 - Sketch-map showing the location of fossiliferous sites where *Amphitomella hemisphaeroidica* (Klipstein) was collected.

Milieres, Cason de Caái, Giau (Fig. 1). The fossiliferous levels belong to the upper part of the San Cassiano Formation.

Both young as well as adult shells, mostly complete were observed (Tab. 1). The state of preservation was good; only in a few cases was there a depression in the lateral peripheral area of the shell.

The material is temporarily housed in Museo di Paleontologia, Dipartimento di Scienze della Terra, Milano.

AMPHITOMELLA HEMISPHAEROIDICA (Klipstein)	Campo	Tamarin	Milieres	Rumerlo	Cason de Caái	Sass de Stria	Giau	Total
Whole shells	73	12	4	2	7	56	1	155
Pedicle valves	7	0	0	0	0	2	0	9
Brachial valves	6	0	0	0	1	1	0	8

Tab. 1 - Frequency of specimens at different localities.

Paleontological description.

Phylum **Brachiopoda**

Class **Articulata**

Order **Athyridida** Boucot, Johnson & Staton, 1964

Superfamily *Athyridacea* M'Coy, 1844

Family incerta

Subfamily incerta

Genus *Amphitomella* Bittner, 1890

Type-species: *Terebratula hemisphaeroidica* Klipstein, 1844

Amphitomella hemisphaeroidica (Klipstein, 1844)

Pl. 1-6

1844 *Terebratula hemisphaeroidica* Klipstein, p. 222, pl. 15, fig. 10a, b.
1853 *Terebratula hemisphaeroidica* - Gray, p. 44 (*fide* Laube).
1864 *Spirigera hemisphaeroidica* - Laube, p. 406.
1865 *Spirigera hemisphaeroidica* - Laube, p. 17, pl. 13, fig. 1a-g.
1890 *Spirigera hemisphaeroidica* - Bittner, p. 82.
1890 *Spirigera (Amphitomella) hemisphaeroidica* - Bittner, p. 299, text-fig. 3.
1892 *Spirigera (Amphitomella) hemisphaeroidica* - Bittner, p. 13.
1920 *Amphitomella hemisphaeroidica* - Diener, p. 64.
1974 *Amphitomella hemisphaeroidica* - Dagys, p. 211.

Material. 172 specimens, 67 measured. Campo N. 5858/1-86; Tamarin N. 5859/1-12; Milieres N. 5860/1-4; Rumerlo N. 5861/1-2; Cason de Caái N. 5862/1-8; Sass de Stria N. 5863/1-59; Giau N. 5864.

Description.

External characters (Pl. 1). Biconvex shell, longer than wider in young specimens, length and width equal in adult stages, maximum width always occurring at the posterior commissure. Outline suboval to semicircular in the largest shells. Cardinal margin curved, short, developed umbonal ridges which define an extensive palintrope on the pedicle valve. Extended posterior commissure with a sinuous course, heavily inclined in shells with suboval outline, and a subhorizontal course in those with semicircular outline. Lateral commissure from weakly rectilinear (young shells) to markedly sinuous (adult shells). Anterior commissure rectimarginate in the majority of cases, in larger shells with a slight sulcus. Curved umbo with subcircular to suboval, mesothyridid, foramen. Median keel present on either valve, extending from the umbonal region to the anterior margin, the outline being sharper in the brachial valve. Pedicle valve convex as brachial valve in shells with suboval outline, more swollen and with maximum convexity in the anterior half in shells with semicircular outline. In the latter case, the brachial valve appears opercular.

Biometric characteristics (data only for Campo, locality with the greatest number of specimens measured. L = length; W = width; T = thickness):

	L	W	T	W/L	T/L	T/W	N. sp.
$\bar{x}$	5.45	5.29	2.87	0.97	0.53	0.54	28
s	0.92	0.96	0.52	0.07	0.06	0.06	28
sm	0.17	0.18	0.098	0.013	0.011	0.011	28

Internal characters (Pl. 2-5). Pedicle valve with fairly wide delthyrial chamber. Massive teeth, smooth, elongated, hardly protruding; median septum already visible posteriorly, rising considerably to form a platform anteriorly (Pl. 4), in small shells with rounded profile, in larger shell with subrectangular profile and a sulcus on top; joined near the anterior margin with a ridge present along the antero-lateral margins of the valve; the latter defines a flattened peripheral area corresponding to the winged-shape portion of the valve. Brachial valve with raised cardinal process, massive, triangular, with deep cardinal pit, drop-like, and raised, thick cardinal lamina which bends again the cardinal pit (Pl. 5). Dental sockets elongated, deep; inner socket rigdes fused with cardinal process. Thin crura springing from cardinal process at cardinal lamina. Spirally coiled brachidium, composed of about six convolutions, apices of cones pointing towards lateral margin. Jugum with saddle, stem prolonged postero-ventrally, almost reaching median septum, splitting into two jugal branches which follow the primary lamella for half a convolution. Median septum present for the entire length of the valve, not very raised posteriorly; it emerges rapidly at a point one-third from the umbo reaching height equal to the thickness of the valve. Near the anterior margin, septum branches off into two ridges, separated by a not very deep sulcus. The two ridges continue along the lateral and latero-posterior margins defining the internal edge of the valve.

Ultrastructure (Pl. 6). Primary layer at times replaced, but fibrous, compact. Contact with secondary layer is marked, with a linear course (Pl. 6, fig. 1). Secondary layer multistriate with lamellae of considerable size, visible under a light microscope, imbricated, having a suboval outline (Pl. 6, fig. 2).

Remarks. Our specimens correspond very well both to the types of Klipstein (1844) as well as those illustrated by Laube (1865). Little differences were observed in the outline, the course of cardinal margin, anterior commissure, median septum and internal peripheral margin of young and adult shells. Even Klipstein (1844) in erecting the species points up the different patterns of the frontal margin and outline in relation to size. He stresses that the sulcus on brachial valve is marked only in adult shells, and the great differences in dimension point up the trend from spheroid to round and parabolic shells.

Distribution. *Amphitomella hemisphaeroidica* (Klipstein) is reported from Carnian of Dolomites.

Significant internal characters of genus Amphitomella.

Median septum.

Morphology. The outstanding feature of the genus *Amphitomella* is a well developed median septum in both the valves. Bittner (1890, 1892) describes them first, noting their imposing antero-median development, and stresses that their snug fit likens them to a single structure. Dagys (1974) mentions taxonomically significant well-developed median septa. Grunt (1986) draws attention only to the median septum in the pedicle valve, defined as raised and massive, while hardly mentioning the presence of a median septum in the brachial valve.

Analysis of the Ampezzan specimens shows that the two median septa arise posteriorly and extend for the entire length of the valve. Initially, for the first third of the length of the valve, their course is vestigial, then there is a small elevation with a rounded triangular section. At the widest point of the valve, they rise fairly sharply, the outline becoming thick and blade-like, reaching a height equal to the thickness of the valve. They join at the commissural plane and follow this course for the remaining two-thirds of the shell (Pl. 2, 3).

The septum of the pedicle valve can be discerned in the cardinal area (Pl. 2), with a sharp outline; it soon broadens anteriorly, becoming triangular in shape (Pl. 4, fig. 1).

The septum of the brachial valve is shorter than that of the pedicle valve, being displayed only after the cardinal lamina (Fig. 2). At the highest point there is a groove into which the septum of the pedicle valve fits snugly. Anteriorly, this groove widens and deepens, cutting into the anterior margin (Pl. 4, fig. 2).

In young growth stages, the median septum is not equally developed in the two valves. In the pedicle valve, posteriorly, it is not displayed at all (Fig. 3); anteriorly it does not broaden as in adult shells, but retains its blade-like appearance (Fig. 3). In the brachial valve, the groove on top of the septum doesn't reach the external margin.

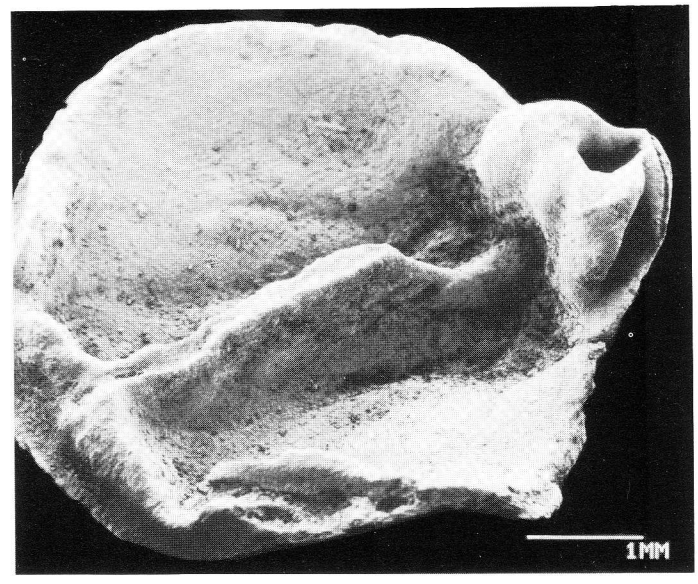

Fig. 2 - *Amphitomella hemisphaeroidica* (Klipstein). Brachial valve, interior. Note morphology of median septum and relation to other features. Campo, N. 5858/74.

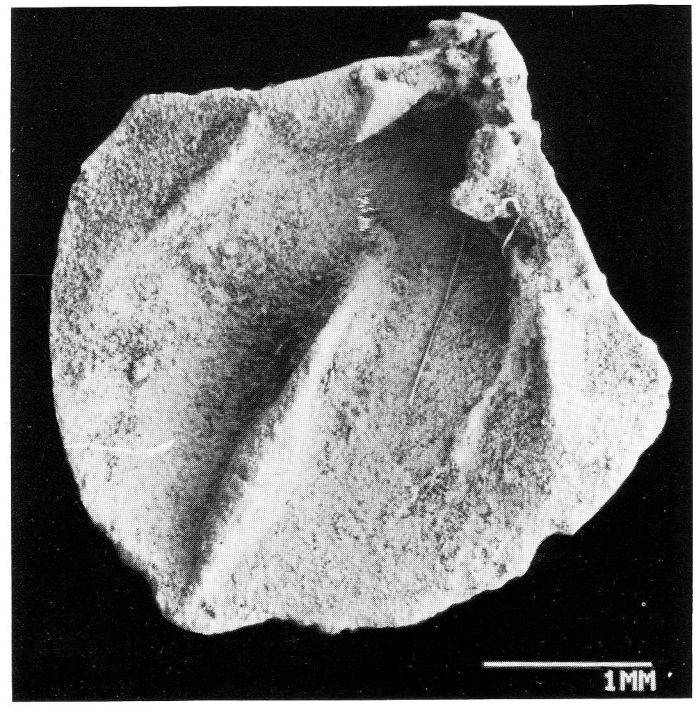

Fig. 3 - *Amphitomella hemisphaeroidica* (Klipstein). Pedicle valve, young specimen, interior. Note morphology of median septum and subperipheral ridge not yet fully developed. Campo, N. 5858/75.

The median septa of *Amphitomella* are robust and massive structures, their presence also affecting the external morphology of the shell: in coincidence with them, a keel is clearly discerned, extending for the entire length of the valves (Pl. 1).

Ultrastructure and ontogenesis. The ultrastructure of the median septa of *Amphitomella* has not been analyzed before; SEM examination of transverse sections yields significant information about the ontogenetic development of this unique morphologic character.

There is no difference in the ultrastructure of the septum of the brachial and pedicle valves. The two septa are composed of secondary fibres, comparable in size with those of the rest of the valve. In the umbonal region the first ontogenetic stages of both septa are preserved embedded in the fibres of the secondary layer. In particular (Fig. 4a-d):

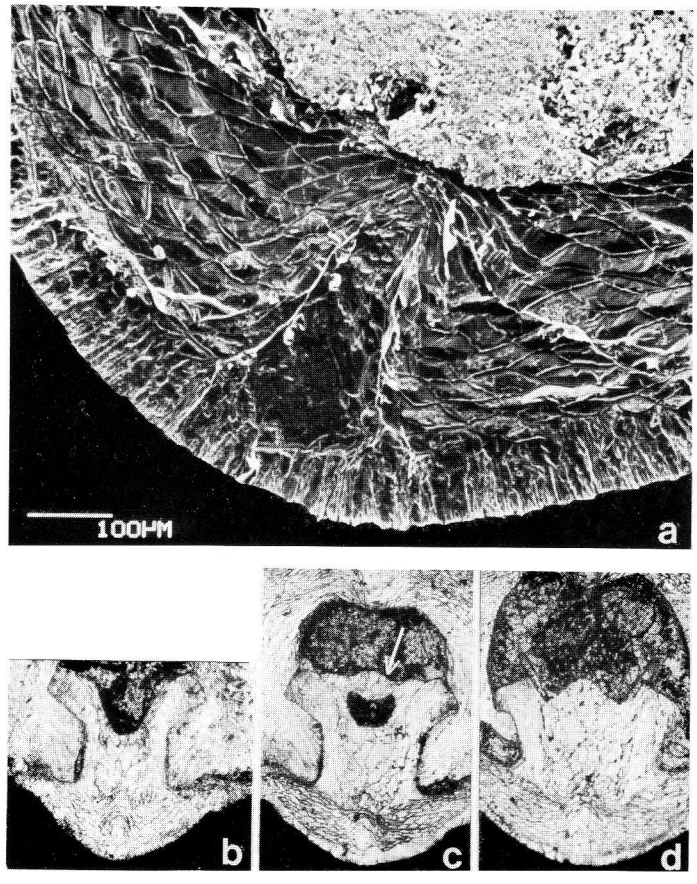

Fig. 4 - *Amphitomella hemisphaeroidica* (Klipstein). a) Pedicle valve. Umbonal area: median septum in young growth stage buried under the fibres of secondary layer (primary layer below). b-d) Brachial valve: ontogenetic development of median septum buried in secondary layer: b) at 1.10 mm from umbo, at cardinal pit; c) at 1.20 mm from umbo, at first appearance of cardinal lamina. Note retroflexed rim (arrow); d) at 1.50 mm from umbo, at cardinal lamina. Campo, N. 5858/53.

a) the septa arise from the primary layer;
b) they are composed of few secondary fibres;
c) they do not emerge as a positive structure on the valve surface;
d) there is no resorption of the septum in the cardinal area.

Near the jugum, the median septa show their definitive ultrastructure (Fig. 5). An elongated axis arises at the base of the secondary layer, made of subrectangular, broadened fibres, orthodoxically stacked to the top of the septum; these are flanked on both sides by four or five layers of diamond-shaped fibres, flattened parallel to the septum. This axis deflects the fibres of the surrounding secondary layer, which lean against its side, partially covering it (Fig. 6).

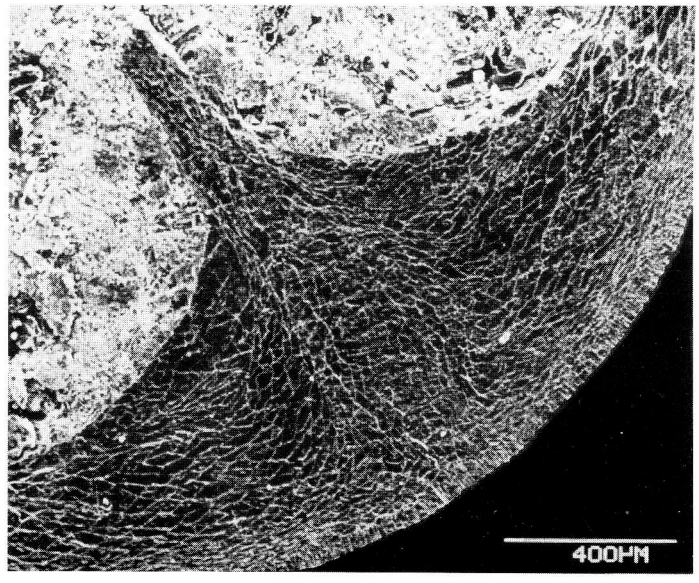

Fig. 5 - *Amphitomella hemisphaeroidica* (Klipstein). Pedicle valve. Development of median septum at jugum. Campo, N. 5858/40.

Peripheral margin.

Near the anterolateral margin, the internal surface of both the valves of *Amphitomella* shows a broaden surface, named here peripheral margin, delimited by characteristic thickenings.

The pedicle valve reveals a flattened, expanded peripheral surface, starting from the teeth and extending to the anterior margin; it is bounded internally by a thin, raised ridge joined anteriorly to the median septum; externally, a thin groove runs parallel to it (Pl. 4, fig. 1). In young specimens, this area is still incomplete; it occurs only at the widest point of the valve, forming two wing-like expansions; the inner ridge occurs only there, as a pair of elevations, thick, elongated, with rounded outline, slightly divergent (Fig. 3).

The peripheral margin of the brachial valve is bounded internally by a very thick ridge, with sharp outline, joined posteriorly to the socket ridges, and anteriorly, at right angles, to the median septum; here it is interrupted by the groove of the median septum (Pl. 4, fig. 2). In young specimens the morphology of the peripheral margin of the brachial and pedicle valves is similar.

When the valves are closed, the subperipheral ridge of the brachial valve fits snugly into the groove of the pedicle valve (Fig. 7); externally, the outermost shell

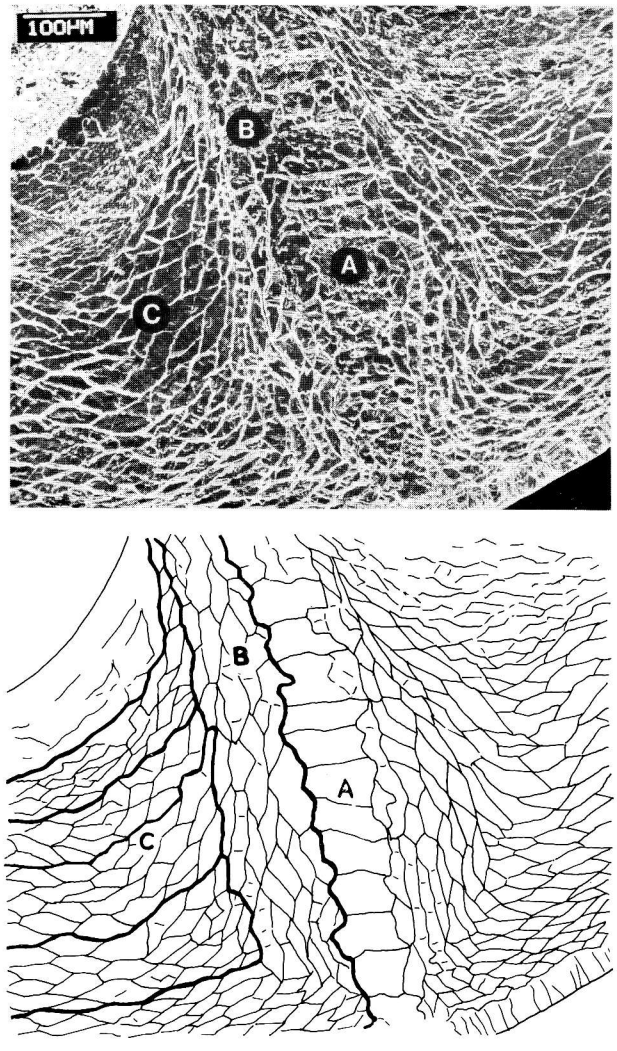

Fig. 6 - *Amphitomella hemisphaeroidica* (Klipstein). Pedicle valve. a) Detail of Fig. 5. b) View of trend of secondary fibres at septum. A = axis of median septum; B = layer of diamond-shaped fibres parallel to axis of median septum; C = layers of fibres orthodoxically stacked which gradually bury the septum.

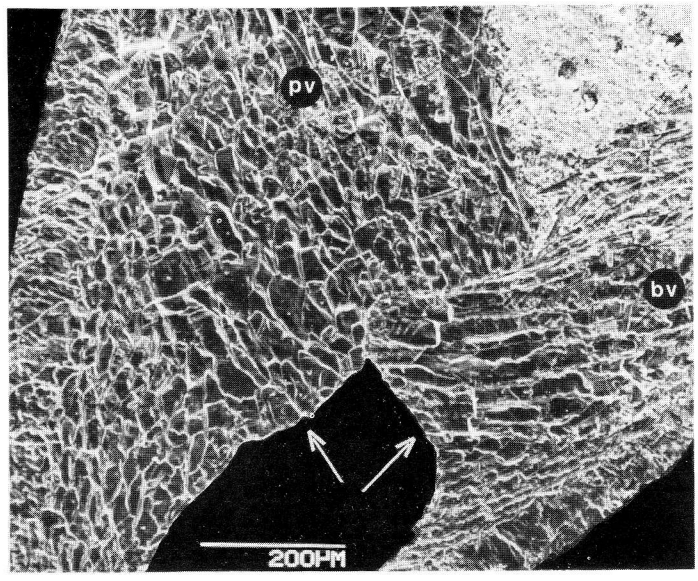

Fig. 7 - *Amphitomella hemisphaeroidica* (Klipstein). Transverse section before jugum, peripheral area. Note snug fit of subperipheral ridge of brachial valve (bv) and external groove of pedicle valve (pv); absence of primary layer at peripheral gutter (arrows). Campo, N. 5858/40.

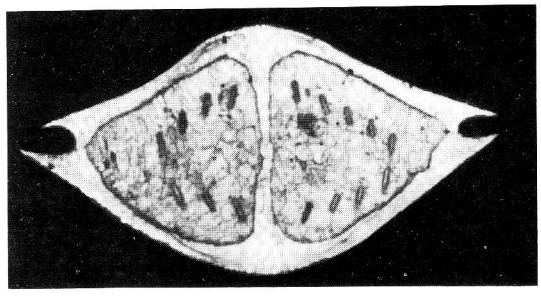

Fig. 8 - *Amphitomella hemisphaeroidica* (Klipstein). Transverse section at distance of 3.95 mm from umbo. Note peripheral gutter corresponding with space between valve margin and subperipherical ridge. Further, note how contact between median septa creates two separate chambers. Campo, N. 5858/61.

margins of the two valves do not join, leaving a gap between them, defined here as the "peripheral gutter" (Fig. 8); its internal surface consists of secondary fibres through the outermost shell edge (Fig. 7); thus the mantle extended externally to the subperipheral ridges as far as the valve margins, completely covering the peripheral gutter.

Cardinalia.

The cardinalia of *Amphitomella* Bittner, 1890 are massive, very protruding, triangular in outline, similar to those of *Diplospirella* Bittner, 1890; both of them are characterized by the presence of cardinal lamina and cardinal pit (sensu Benigni &

Ferliga, 1989), obstructing the development of an apical cavity, in contrast to the majority of Athyridida. The features observed are (Pl. 5, fig. 1, 2):

a) two massive cardinal plates (cp), anteriorly divergent, distally thickening, fusing with the inner socket ridges;

b) inner socket ridges (isr) which circumscribe deep, egg-shaped dental sockets (s);

c) thin crural bases (cb), partially fused with cardinal plates, clearly visible only distally;

d) well-developed cardinal lamina (cl), in a forward position between the cardinal plates. The anterior surface has a central bulge connected dorsally to the median septum, flanked by two hollows; the ventral margin appears trilobed, and is bent backwards, pointing to the cardinal pit (Fig. 4c, d). The cardinal lamina is composed of modified secondary fibres, with an irregular outline;

e) cardinal pit (p) with drop-like outline, deep, and wedged under the rim of the cardinal lamina.

The cardinalia of *Amphitomella* are robust structures, thus the presence of a well developed muscle apparatus may be inferred.

Brachidium.

Amphitomella has an athyroid spiral brachidium, sketchily described only by Bittner (1890). Boucot et al. (1965, p. 665, fig. 8), and Grunt (1986) refer solely to Bittner's reconstruction (1890, p. 299, fig. 3). According to it, the lateral branches of the jugum are fused ventrally where the accessory lamellae branch off; this is defined as "jugum as in *Athyris*, but lacking saddle" (Boucot et al., 1965).

A more accurate reconstruction is now advanced, on the basis of transverse sections. The jugum (Fig. 9) is sited centrally, posteriorly, and occupies the space between

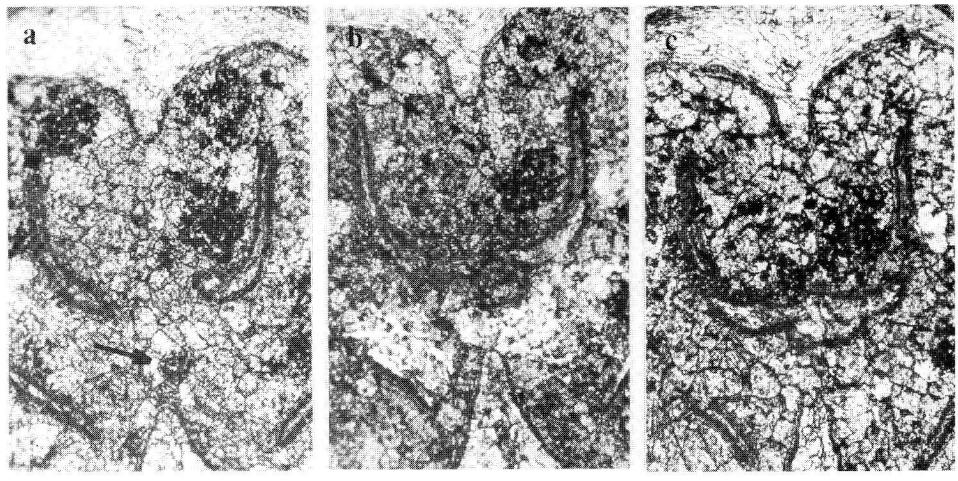

Fig. 9 - *Amphitomella hemisphaeroidica* (Klipstein). Transverse section at jugum. a) 2.70 mm from umbo: lateral branches break away from primary lamella; also note stem (arrow); b) 2.80 mm from umbo: lateral branches fuse together; stem is not yet joined; c) 2.85 mm from umbo: note jugal saddle. Campo, N. 5858/61.

the two median septa, before they join. The lateral branches (Fig. 9a) extend ventrally from the first coil of the primary lamellae, bending and fusing medially into a platform (Fig. 9b). From here, anteriorly to the lateral branches themselves, the stem (Fig. 9c) extends postero-ventrally, until it almost comes to rest on the ventral median septum; there it forks off, giving rise to two accessory lamellae extending for half of the first coil of the spiralium.

The thickened central structure to which the lateral branches are fused and from which the jugal stem arises is a separate piece and accords with the definition of saddle given by Williams & Rowell (1965b). Thus, in contrast to the view held by previous Authors, *Amphitomella* presents a jugum complete with saddle (Fig. 10). In general, the spiralium has six convolutions; fragments of primary lamellae show traces of very closely knit spines.

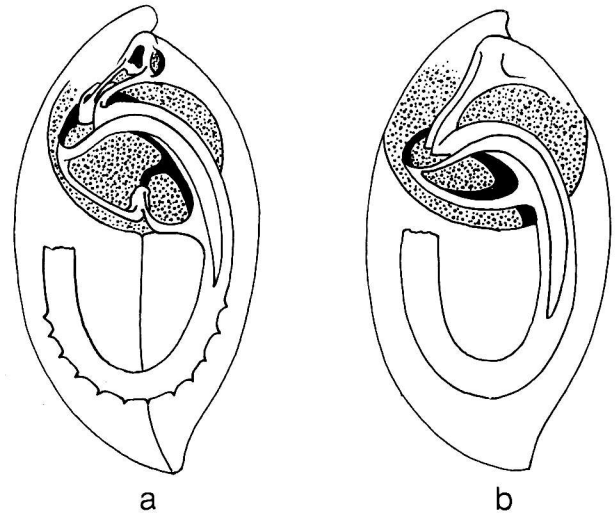

Fig. 10 - Reconstruction of brachidium of *Amphitomella hemisphaeroidica* (Klipstein). a) On the basis of serial sections reported in the present article; b) according to Bittner (1890). The different relationship of primary and secondary lamella are clearly seen, expecially the presence of stem and saddle in the reconstruction advanced by the present Authors.

The median septum in Articulata.

Previous Authors have insisted on the anomalousness of the septa of *Amphitomella*, and attempted to attribute a functional as well as a phylogenetic significance to them. In fact, septa standing so high above the valve floor as to divide the mantle cavity into two compartments are rare among Articulate brachiopods. In all orders, the median septum is a structure frequently found in the brachial valve, variably pronounced and extended, and having different functions.

a) Median septum as a feature of the muscle field.

In many taxa the muscle scars are separated by an elevated structure known as "median septum"; it usually arises from a differentiation in the fibres of the secondary layer in the muscle field (Williams, 1968; Mackinnon & Williams, 1974). In taxa with developed muscle platforms the term median septum, instead, refers to a vertical structure which acts as support to the platform (eg. *Camerophoria*).

b) Median septum as support to the brachidium or lophophore.

The median septum may develop posteriorly and there support the brachidium, which then extends freely anteriorly (eg. *Megerlia*); or else it may extend into the antero-median part of the shell, providing support for the anterior part of the brachidium itself (eg. *Megathiris*); in the latter case, brachidium and median septum may even be fused (eg. *Magas*, *Pamirotheca*). In some taxa a proper brachidium is absent; a "brachidial apparatus" arises from the median septum and extends posteriorly (eg. *Thecospirella*, *Hungaritheca*). Finally, in some Orthida the median septum, which develops only anteriorly in the valve, is inferred as support for the lophophore (eg. *Tropidoleptus*, in Williams & Rowell, 1965a, fig. 112/1).

c) Median septa - special cases.

In several Articulate orders, single taxa present in the brachial valve a median longitudinal structure with a vertical, bladelike course. It is always very raised, well beyond the commissural plane of the shell, and always reaches the anterior rim of the valve. In *Phragmorthys* this kind of median septum develops in the umbonal region, rising gradually and breaking off anteriorly "in a curve conforming to the anteromeridian longitudinal profile of the pedicle valve" (Williams & Rowell, 1965a, fig. 131); fig. 131 c shows, however, that it never comes into contact with the pedicle valve. *Dimerella* has a very high dorsal median septum standing as high as the internal surface of the pedicle valve (Ager, 1965, fig. 481, 3c).

In these examples the median septum acts as a partition, dividing the mantle cavity into two posteriorly communicating compartments; according to Williams & Rowell (1965a) this separation in *Phragmorthys* is also correlated to the separation of the lophophore into a right and a left half. We believe the principal function of this type of median septum, characterized by an abnormal development, is exactly to divide the mantle cavity into two symmetrical compartments, and that this disposition, which crops up in different groups and is also found in recent shells has adaptive advantages.

In our view, the median septa of *Amphitomella* represent a special case in this third category; the taxon in fact is characterized by an "internal partition" comprising not only a single brachial septum, but two equally developed septa. This points to a highly specialized structure having other functions besides those reported above.

On the other hand, there are considerable differences between the mode of growth of septa in *Amphitomella* and in other taxa in which the septum supports the

brachidium, for example *Megerlia*. In *Amphitomella* during ontogenesis the septum ceases to be functional posteriorly when it is buried beneath the new secondary layer fibres; in *Megerlia* it springs posteriorly from the fibres of the secondary layer, thus the last to develop, in direct contact with the mantle. We are therefore dealing with structures similar as regards position, but profoundly different in their mode of growth. It is thus reasonable to infer that even their functions may differ.

In conclusion, we believe that "median septum" is a generic descriptive term, comprising structures with different functions and mode of growth, having in common only their median position within the valve.

Functional morphology.

The very well developed median septa of *Amphitomella* accord with the other morphological characteristics of this taxon. In particular:

1) *external morphology of the shell.* The extended wing-shaped cardinal margin, the pedicle valve more convex than the brachial valve, the marked median keel, and an extremely small foramen all point to a taxon which leans on or is perhaps slightly embedded in a sandy, low energy, soft bottom, anchored by means of a reduced pedicle to shells or other small elements; this is also in accord with the scarcity of disarticulated valves, the state of preservation of the primary layer of the majority of specimens, and the absence of shell abrasion due to very little movement, or none at all, post-mortem.

2) *Subperipheral ridges.* In this environment the organism must be protected from the accidental penetration of foreign particles through the commissure. When the valves are open, the postero-lateral overlapping of subperipheral ridges is enough to obstruct the gap between them, "sealing" the shell in this area and concentrating waterflow anteriorly.

3) *Peripheral gutter.* The area which absorbs the flow of currents, hence nutrients, is thus very reduced compared to shells in which absorption occurs virtually along the entire peripheral edge. The peripheral gutter, covered by the mantle, helps to channel the flow of water anteriorly, thereby allowing the organism to "pick up" particles along the entire shell perimeter (Fig. 11a).

4) *Disposition of conical spiralia.* The bases of the spiral cones remain parallel to the symmetrical plane of the shell, instead of diverging anteriorly, as in other taxa; hence, anteriorly, they correspond with the actual aperture of the shell. This way, inhalant currents can be easily separated from exhalant currents and chanelled into the space between shell wall and spiral cones. In this conjectural assumption, the interspace between shell and surface of the spiralia is the inhalant chamber, whereas the central area of the mantle cavity, divided by the median septa, acts as an exhalant chamber (Fig. 11b).

The median septa separate the two exhalant currents from each spiral cone, channelling each of them towards the small exit without mingling together; thus the

absence of turbulence helps the downflow of water, hampered by the shell's restricted aperture.

A single median septum on the brachial valve, as in *Dimerella*, in effect would be enough to divide the exhalant chamber, but in this case there would be at least three disadvantages:

a) Mingling of currents. When the valves open, the lophophore, the brachidium and the brachial median septum move together with the brachial valve away from the pedicle valve. With only one septum on the brachial valve, this movement would create all along the internal surface of the pedicle valve an area momentarily without barriers, allowing inhalant and exhalant currents to mingle. A septum on the pedicle valve as well, prevents this.

b) Weight of valve. A single septum extending through the entire shell thickness would weigh too heavily on the brachial valve, making it hard for the valve to open. But with two septa the load is halved.

c) Equilibrium. A single septum on the brachial valve would eventually shift the centre of gravity of the shell upwards, making it less stable; a thickening also on the brachial valve offsets this, lowering the centre of gravity and improving shell equilibrium.

The only problem with this internal disposition is still the weight of the brachial valve. The genus *Amphitomella* must therefore have been provided with strong diductor muscles, capable of ensuring shell opening. The massive cardinal process with deep cardinal pit and retroflexed cardinal lamina provides a structure robust enough to afford solid insertion of very well-developed diductor muscles, and thus accords with the other internal features examined.

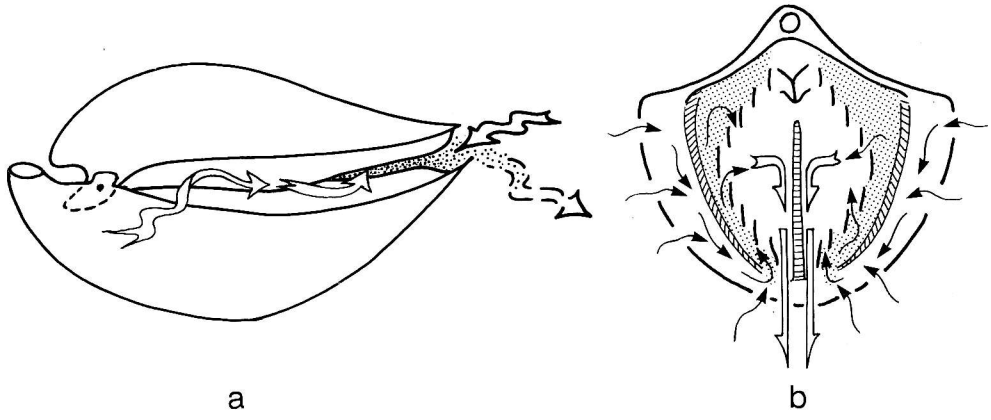

Fig. 11 - Sketch of the course of inhalant and exhalant currents in *Amphitomella hemisphaeroidica* (Klipstein). a) Lateral view: inhalant current, hampered by subperipheral ridge, chanelled along peripheral gutter to anterior area. b) Section parallel to commissural plane: black arrows = inhalant currents; white arrows = exhalant currents; dotted area = inhalant chambers; white area = exhalant chambers; barred area = overlapping of median septa and subperipheral ridges.

Taxonomic problems.

Taxonomic classification of *Amphitomella* is still arguable, although Grunt recently (1986, 1989) suggested to attribute this genus to the superfamily Nucleospiracea Davidson, 1881.

Bittner (1890) stressed that "its internal construction shows such a remarkable peculiarity as to warrant classification in a special group", identifying it within the "*Spirigera* group" as a subgenus. Boucot et al. (1964) place it in the family Athyrididae M'Coy, 1844, but leave open its subfamily attribution. Dagys (1974) believes "the unique development of the septa" to be taxonomically significant, and since this character is not found in any other Athyridida concludes that even the attribution of this taxon to the order Athyridida is uncertain. Grunt (1986), basing her evidence solely on data in the literature, "extremely conventionally" assigns the genus to the superfamily Nucleospiracea Davidson, 1881. In her diagnosis of the superfamily, based on specimens belonging to the paleozoic genus *Nucleospira*, she emphasizes the following:

a) the presence of a long, thin median septum in the brachial valve, and a corresponding median structure in the pedicle valve, described as a "fold composed of a primary layer enveloped by secondary layer fibres, and not projecting onto the valve floor". Although the ontogenesis of this structure is peculiar, it is considered as a buried, non-functional median septum;

b) the presence of a jugal stem, not split into jugal branches;

c) the absence of a jugal saddle.

The attribution of *Amphitomella* to the same family of *Nucleospira* is based on the presence of a median septum on the pedicle valve and on the absence of a jugal saddle (Grunt, 1986). According to this Author, the genus *Amphitomella* is a Triassic descendent of *Nucleospira*, which has developed a functional pedicle median septum in adult as well as in young growth stages. Attribution to Nucleospiracea is maintained by this Author in her successive work (Grunt, 1989).

Our data on San Cassiano specimens do not agree with the diagnosis of Nucleospiracea above proposed (Grunt, 1986); in particular:

a) the raised median structure of the pedicle valve of *Amphitomella* has an ultrastructure and an ontogenesis quite comparable with that of the septum of the brachial valve; it is thus a median septum and not a "fold in the shell" (Grunt, 1986);

b) the jugal stem splits into two jugal branches;

c) the jugal saddle is clearly present and well developed.

Consequently, we do not accept the attribution of the genus *Amphitomella* to the superfamily Nucleospiracea.

What we propose is a partial taxonomic classification, since the various Authors do not appear to concur in the choice of significant characters at different taxonomic levels. We attribute *Amphitomella* to the order Athyridida Boucot, Johnson & Staton, 1964, and reject the assumption of Dagys (1974), since we do not consider median septa significant at this taxonomic level.

We attribute the genus *Amphitomella* to the superfamily Athyridacea M'Coy, 1884, and accept the definition given by Dagys (1974): "Athyridida with entire cardinal plate".

Taxonomic attribution to family and subfamily, in our view, should remain pending. The subdivisions of superfamily Athyridacea more recently put forward are in fact contradictory. Dagys (1974) promotes subfamily Spirigerellinae Grunt, 1965 to the rank of family, including both Paleozoic taxa (*Spirigerella, Araxathyris*) as well as all Triassic taxa with complex jugum without visceral foramen. In contrast, Grunt (1986) separates the Paleozoic taxa with visceral foramen *Spirigerella* and *Araxathyris* from the Triassic taxa, dividing the superfamily Athyridacea into two families: Spirigerellidae (Paleozoic taxa), and Diplospirellidae (Triassic taxa, e.g. *Diplospirella*, *Tetractinella*).

In our opinion, the genus *Amphitomella* should be classified as a taxon belonging to that group of Triassic taxa having a cardinal process without visceral foramen, a complex jugum and a brachidium that may develop in a single or double spiralium, as already conjectured by Bittner (1890: "genus *Spirigera*, subgenus *Amphitomella*"). In effect, there is argument for affinity with *Diplospirella* (cardinal process, jugum with saddle) as well as with *Tetractinella* (secondary lamellae as far as half of first volution of spiralium). We do not consider the median septum in the pedicle valve such a taxonomically significant character: a median septum clearly discernible on the pedicle valve is also present, for example, in *Diplospirella* (Benigni & Ferliga, 1990); in *Amphitomella* this character is developed to an excess only as an adaptive response to a special type of habitat.

We suggest that further study of the other Triassic taxa with complex jugum and brachidium with single or double spiralium is necessary at this stage, to explain whether the affinities found among certain genera in regard to cardinal process (absence or presence of cardinal lamina) are taxonomically more significant than those for a brachidium with single or double spiralium.

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PLATE 1

Fig. 1 - *Amphitomella hemisphaeroidica* (Klipstein). a-e) Ventral, dorsal, lateral, anterior, posterior view. Sass de Stria, N. 5863/34; x 6.8.
Fig. 2 - *Amphitomella hemisphaeroidica* (Klipstein). a-e) Ventral, dorsal, lateral, anterior, posterior view. Sass de Stria, N. 5863/42; x 6.8.
Fig. 3 - *Amphitomella hemisphaeroidica* (Klipstein) (Juvenile specimen). a, b) Ventral, dorsal view. Sass de Stria, N. 5863/10; x 7.2.
Fig. 4 - *Amphitomella hemisphaeroidica* (Klipstein) (Juvenile specimen). a, b) Ventral, dorsal view. Tamarin, N. 5859/5; x 7.2.

PLATE 2

Amphitomella hemisphaeroidica (Klipstein). Serial transverse sections (acetate peels).
Fig. 1 - Campo, N. 5858/61; x 10.
Fig. 2 - Same specimen; x 7.
Fig. 3 - Campo, N. 5858/53; x 7.8.
Fig. 4 - Same specimen; x 6.5.

PLATE 3

Amphitomella hemisphaeroidica (Klipstein). Serial transverse sections (acetate peels). Same specimen as Pl. 2, fig. 3 and 4; x 6.5.

PLATE 4

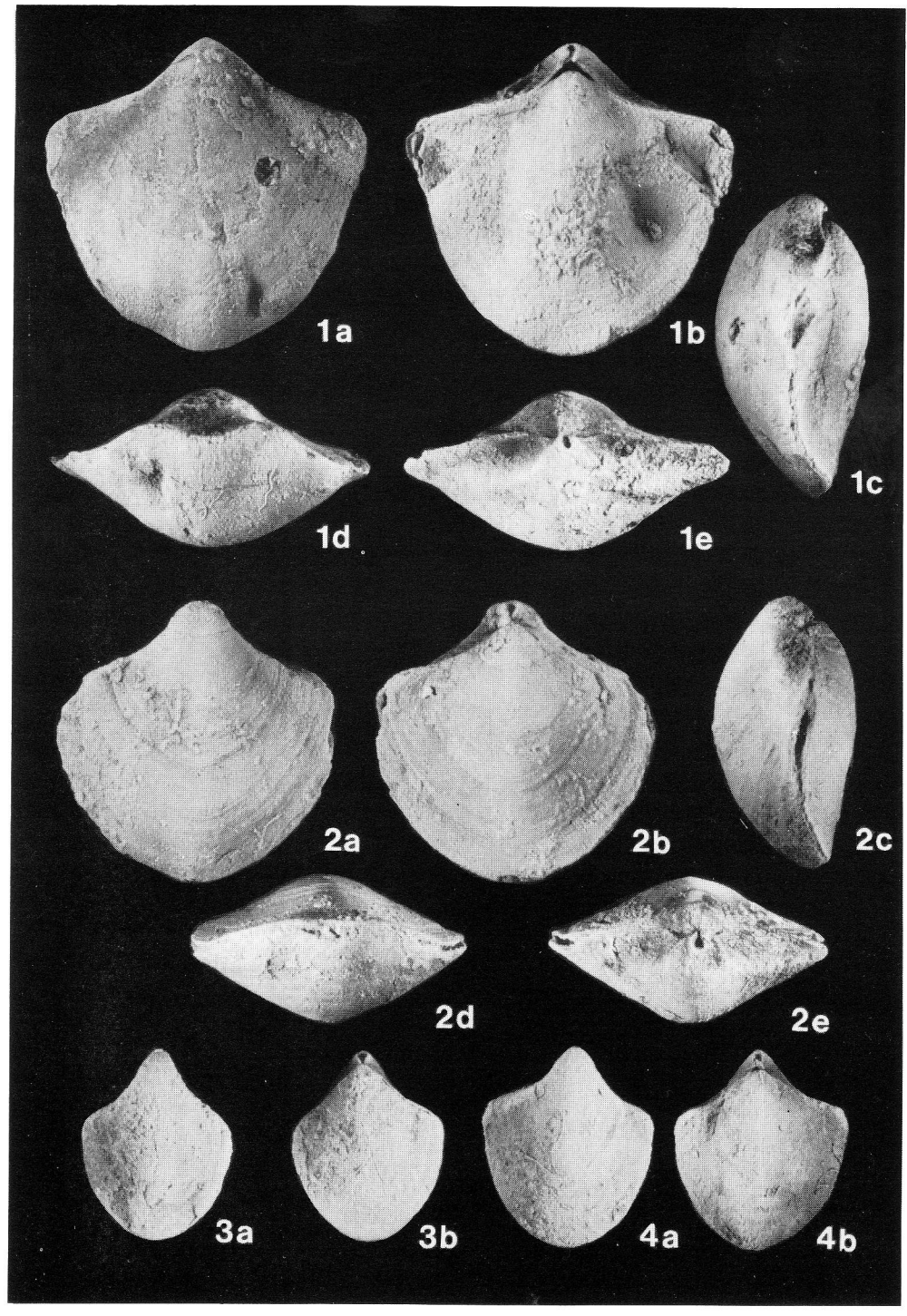
Amphitomella hemisphaeroidica (Klipstein).
Fig. 1 - Pedicle valve, internal view. The median septum widens anteriorly, becoming triangular in shape; note groove outside subperipheral ridge (arrows). Campo, N. 5858/78.
Fig. 2 - Brachial valve, internal view. Note wide anterior groove of median septum, cutting into subperipheral ridge. Campo, N. 5858/80.

PLATE 5

Amphitomella hemisphaeroidica (Klipstein). Brachial valve, detail of cardinal area. Same specimen as Pl. 4, fig. 2. Campo, N. 5858/80.
Fig. 1 - Ventral view.
Fig. 2 - Anterolateral view. cb = crural base; cl = cardinal lamina; cp = cardinal plates; isr = inner socket ridge; p = pit; s = dental socket.

PLATE 6

Amphitomella hemisphaeroidica (Klipstein).
Fig. 1 - Transversal section. Contact between primary layer (below) and secondary layer. Campo, N. 5858/78.
Fig. 2 - Secondary layer. Campo, N. 5858/81.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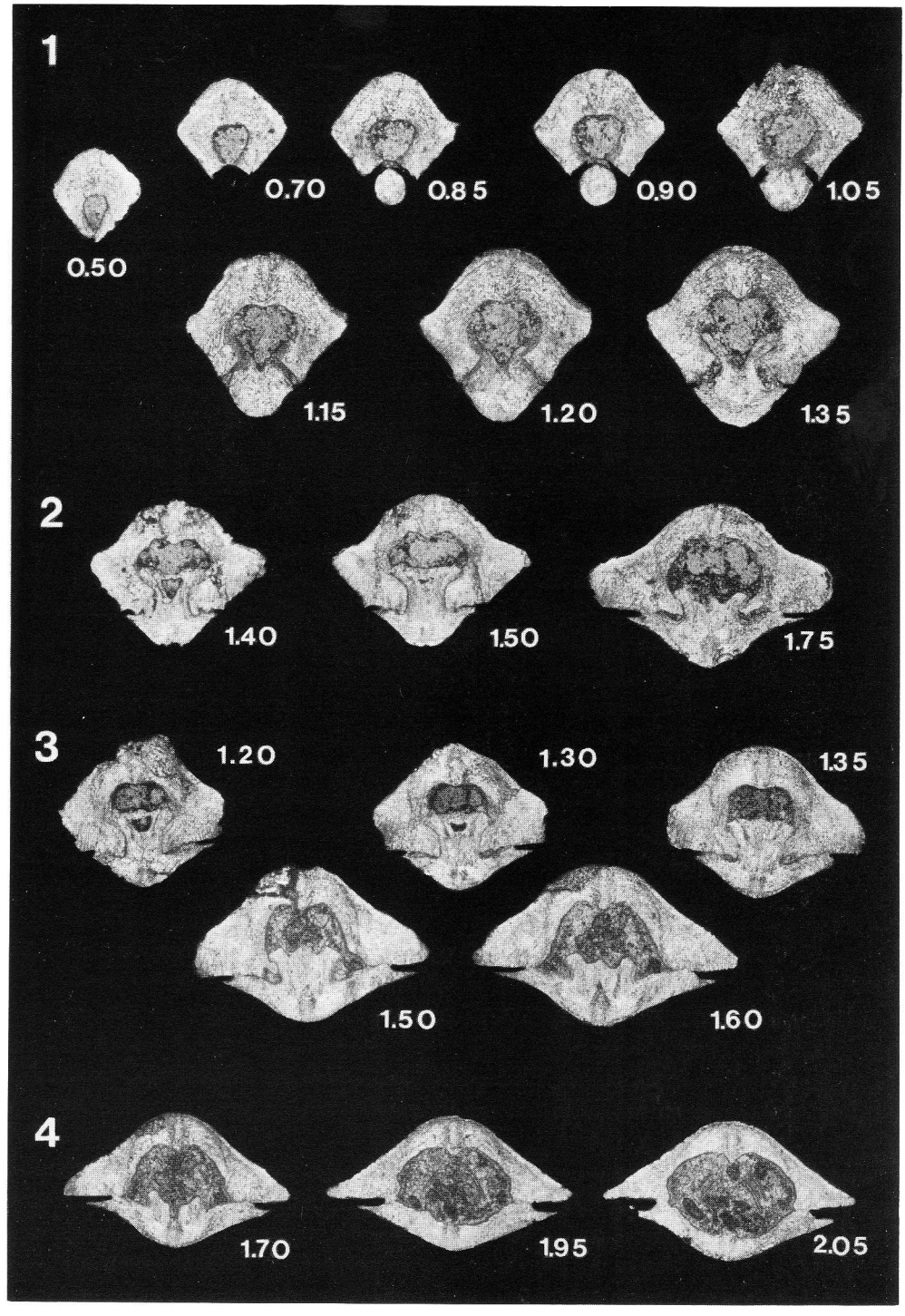
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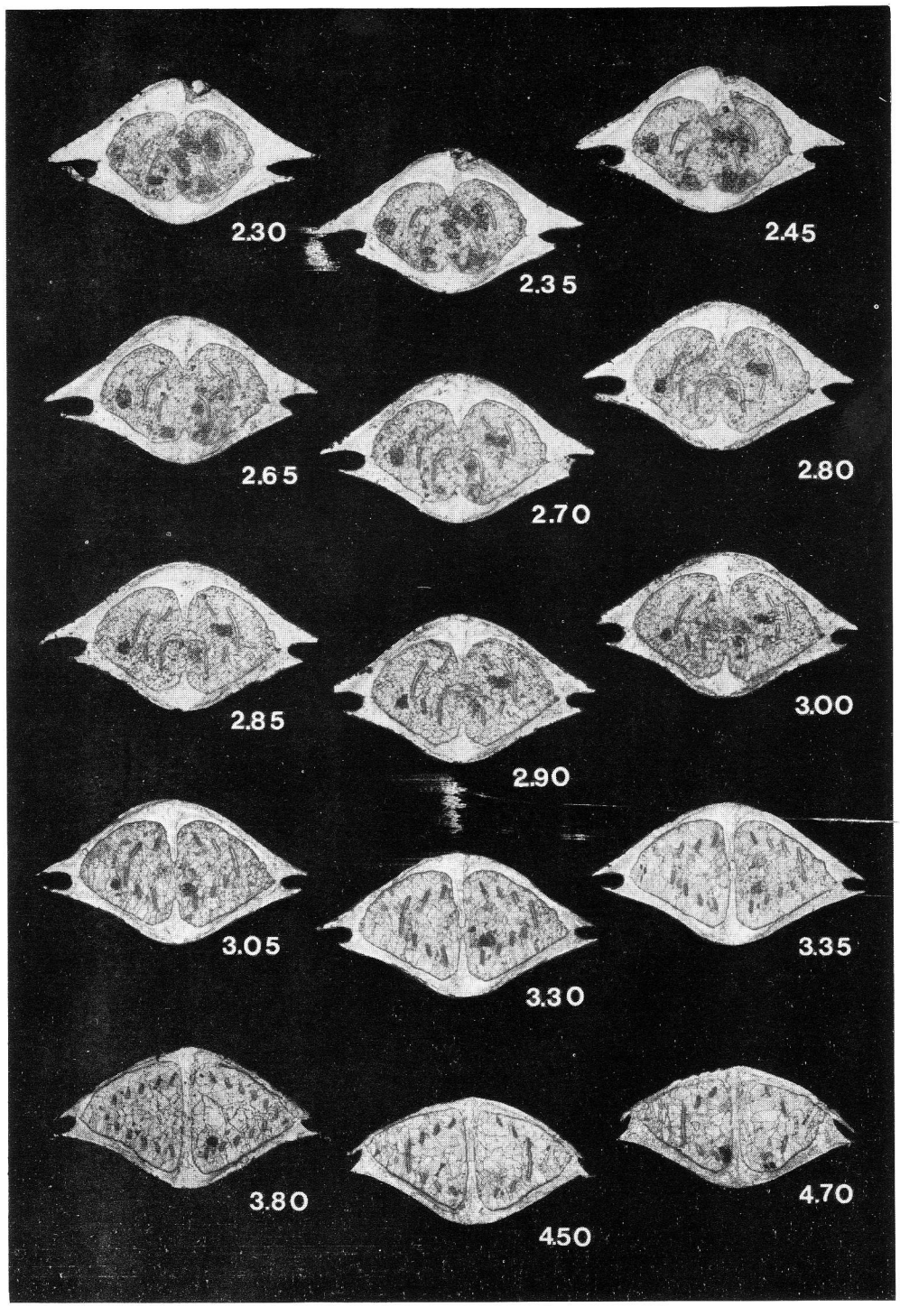
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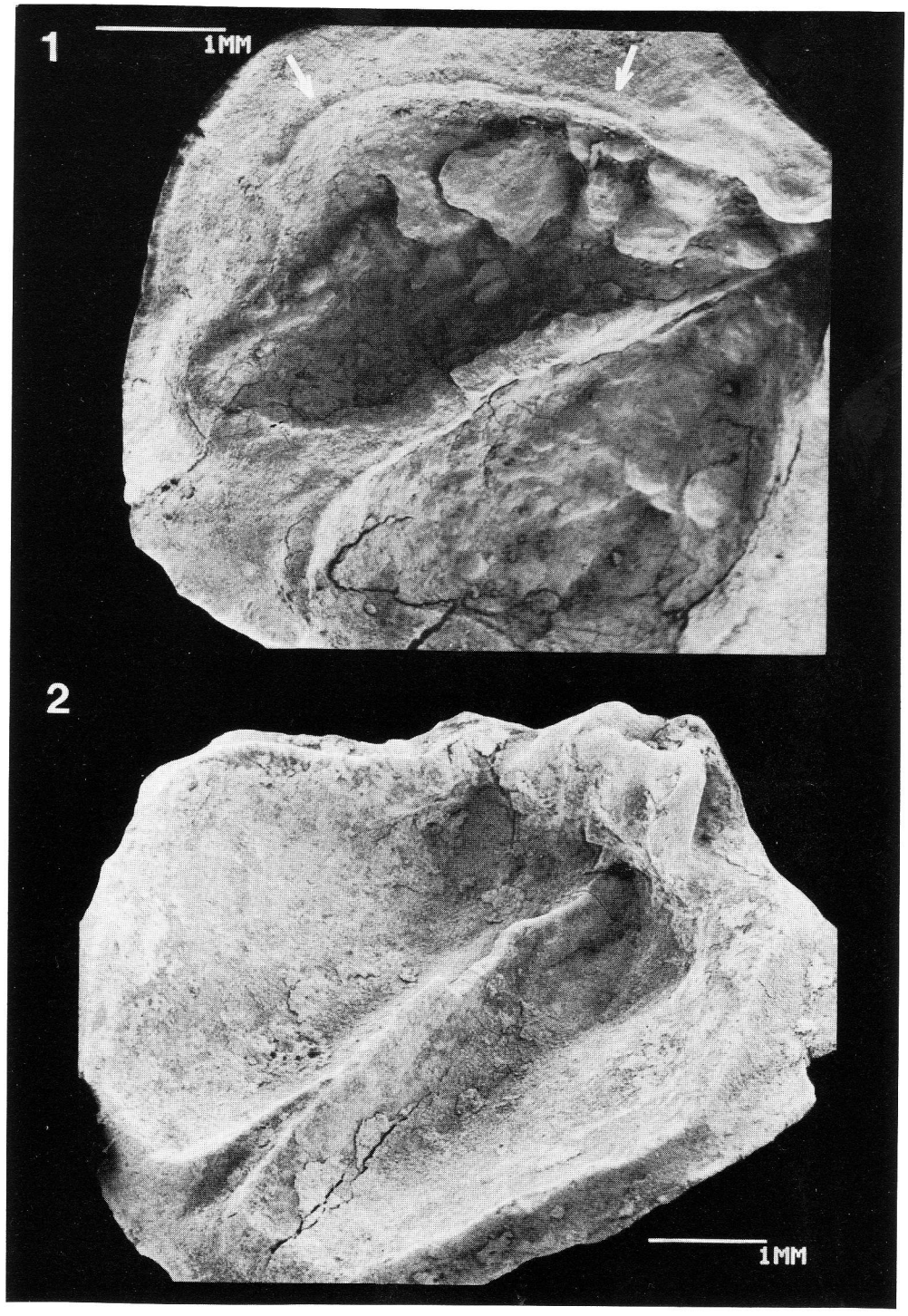
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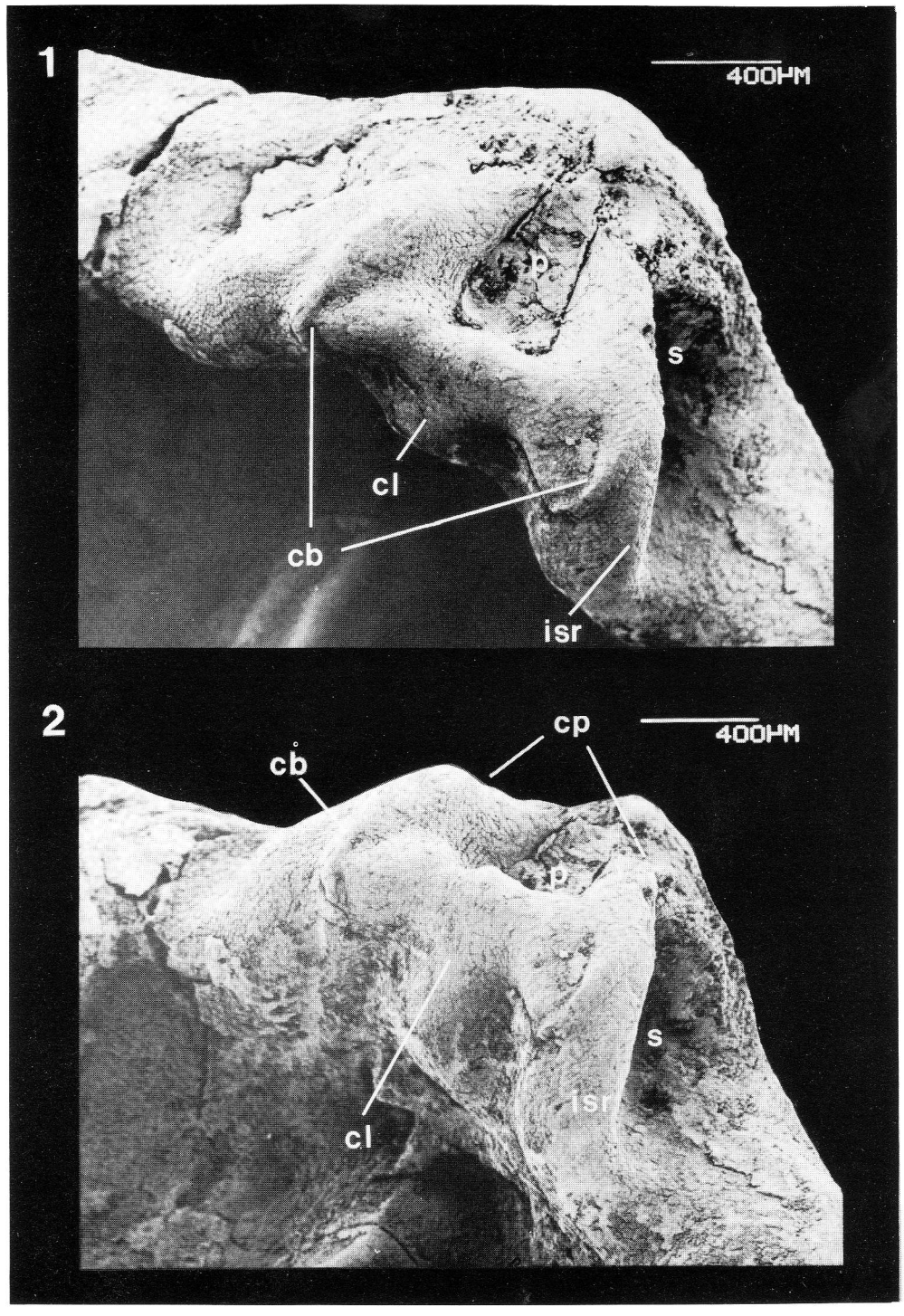
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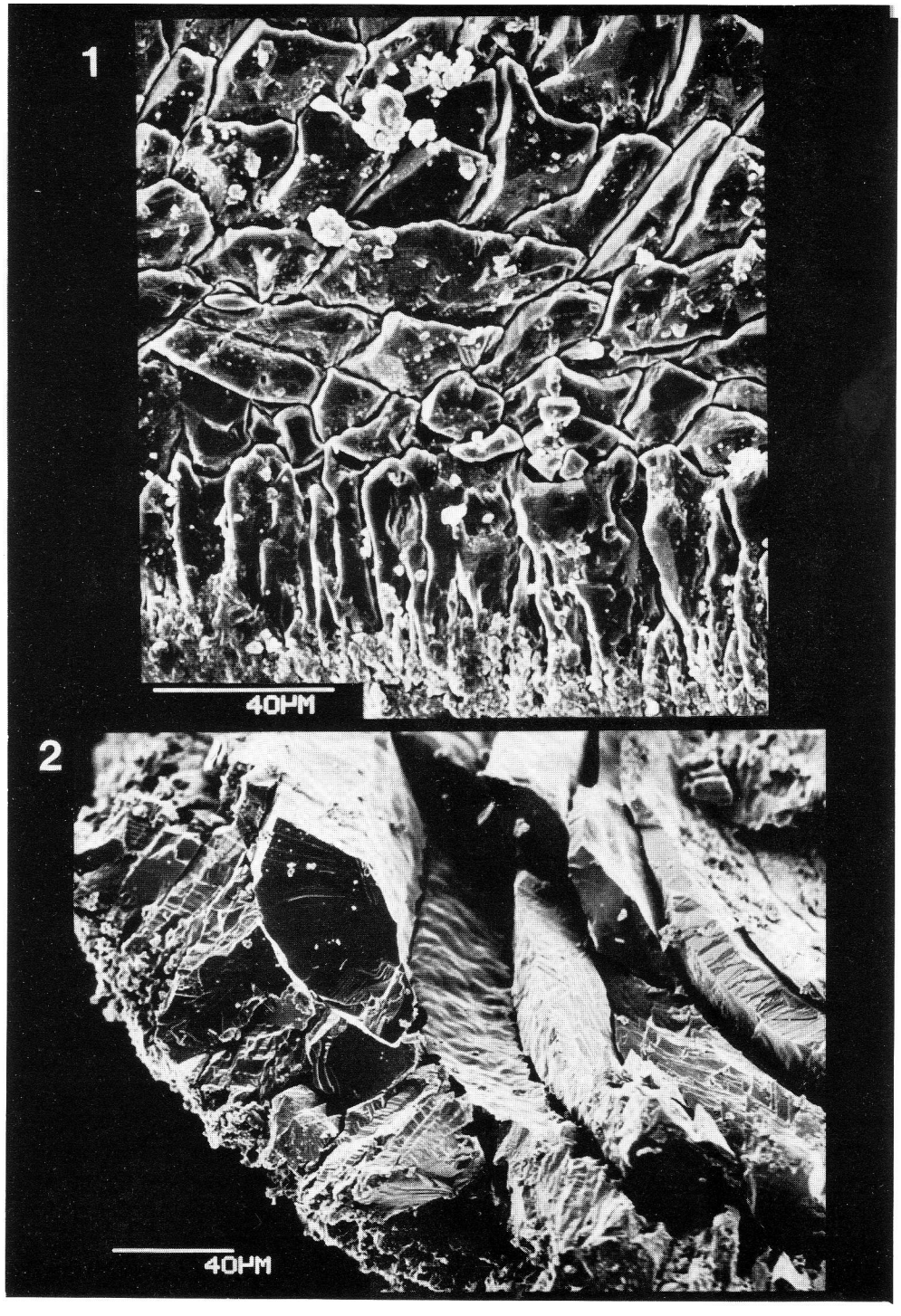
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