

Riv. It. Paleont. Strat.	v. 96	n. 1	pp. 39-76	tav. 7-14	Maggio 1990
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**DIPLOSPIRELLA BITTNER, 1890 (BRACHIOPODA): MORPHOLOGY AND  
REVIEW OF THE CARNIAN SPECIES FROM THE  
SAN CASSIANO FORMATION (CORTINA D'AMPEZZO, ITALY)**

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*Key-words:* Morphology, Systematic Paleontology, Brachiopoda, Athyridida, Carnian, Upper San Cassiano Formation, Eastern Dolomites, Italy.

*Riassunto.* Con il presente lavoro si continua la revisione dei taxa appartenenti al phylum Brachiopoda presenti nella parte superiore della Formazione di San Cassiano affiorante nella conca ampezzana (Belluno); sono descritte in dettaglio anche tutte le località in cui il phylum è stato segnalato.

Dal punto di vista tassonomico si riesamina il solo genere *Diplospirella* Bittner, 1890 perchè è il taxon più abbondante (4334 esemplari) e più diffuso (11 località) nell'area considerata. Sono evidenziati sia al SEM che attraverso peels nuovi aspetti morfologici dei caratteri interni della valva brachiale. Per la prima volta infatti sono analizzati e descritti i cardinalia, molto complessi, costituiti da due piastre cardinali massicce e da una struttura verticale di collegamento, per la quale si propone il termine di "Cardinal lamina". Tale struttura delimita a sua volta una fossetta, anch'essa mai segnalata, per la quale si suggerisce la denominazione "Cardinal pit".

Le sezioni seriali trasversali, effettuate a distanza di 0,05 mm una dall'altra, hanno messo in luce, per la prima volta, la presenza di un giogo molto complesso, l'assenza di un collegamento scheletrico tra spiralia e crura, la presenza di spine lungo tutto il margine delle lamelle sia primaria che secondaria.

Il genere *Diplospirella* è rappresentato, nella conca ampezzana, da tre specie: *Diplospirella wissmanni* (Münster), *Diplospirella sufflata* (Münster), *Diplospirella aureolata* (Cornalia). Quest'ultima è poco segnalata, perchè la sua aureola periferica è stata spesso interpretata come il risultato di un processo diagenetico e non come un carattere morfologico del taxon.

Infine si precisa che il genere in esame viene attribuito all'ordine *Athyridida*, accettando così la proposta di Dagens (1974).

*Summary.* All the localities with Upper San Cassiano Formation Brachiopod faunas present in the Ampezzan valley are described. The genus *Diplospirella* Bittner, 1890, namely, the species *Diplospirella wissmanni* (Münster), *Diplospirella sufflata* (Münster), and *Diplospirella aureolata* (Cornalia) are re-examined. Analysis under SEM and of several transverse sections has revealed new morphologic elements: Cardinal lamina and Cardinal pit in the cardinalia; a complex jugum; the absence of a skeletal connection between spiralia and crura. The proposal advanced by Dagens (1974) attributing the genus *Diplospirella* to the order *Athyridida* is accepted.

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Financial support from MPI 40% "Paleontologia del Triassico" (M. Gaetani).

### Introduction.

The strata of the San Cassiano Formation are known to have a rich and diversified fauna which includes corals, sponges, molluscs, echinoids, bryozoa and brachiopods. These faunas were studied in their entirety by Münster (1834) (fide Fürsich & Wendt, 1977), Wissmann & Münster (1841), Klipstein (1844), Cornalia (1848), Laube (1865), Loretz (1875). Further, Laube (1864) briefly reviewed the collections of Münster (in Wissmann & Münster, 1841); Bittner (1890, 1892) examined brachiopod faunas from several localities in the Alpine Trias and in particular, taxa from San Cassiano beds.

Since then, exhaustive investigations have been carried out on the fossiliferous levels of the San Cassiano Formation and all the above groups, except brachiopods, revised.

The purpose of this study is to continue the examination begun with the family *Thecospiridae* Bittner, 1893 (Benigni & Ferliga, 1989) of the brachiopod fauna of the San Cassiano beds in the area around Cortina d'Ampezzo (Belluno), revising the species belonging to the genus *Diplospirella* Bittner, 1890.

The material used in this study is from the collection of R. Zardini, to whom this article is dedicated in memory of his unceasing and valuable field work, which has permitted the assembly of specimens unique in number and scientific interest.

The method used for collection and preparation of the specimens examined has already been described by Benigni & Ferliga (1989).

This material is temporarily housed in the Dipartimento di Scienze della Terra - Museo di Paleontologia, Milano.

### Fossiliferous localities.

The brachiopods examined come from a number of different localities in the Cortina d'Ampezzo valley, and four outcrops in neighbouring areas, where they were recovered in marly limestone (Fig.1). The symbols used by Zardini (1978) to identify each locality have been maintained. The areas within the Cortina d'Ampezzo valley are always connected to limited sliding (Panizza, Zardini & Spampiani, 1986; Benigni & Ferliga, 1989).

All the localities indicated by Zardini (pers. comm.) as having brachiopod faunas are described in detail on the strength of his data. Some localities (Alpe di Specie, Misurina, Giau, Sass de Stria, Rumerlo, Ciou del Conte, Campo, Costalaresc) were revisited by the present Authors.

The localities identified to the west of Cortina d'Ampezzo (Fig. 2, *b*) were:

- Campo (C), 1200 m asl. From the outlying hamlet Campo di Sotto one takes the road leading to Lago Pianoze. Approximately 100 m from the bridge over Rio Costeana, one leaves the road to enter the wood, and after about 200 m reaches the outcrop, recognizable by the recent landslide.

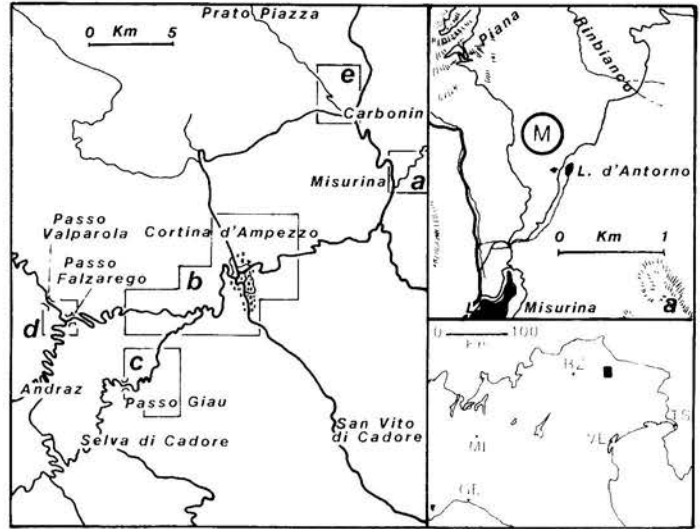


Fig. 1 - Sketch map of the Cortina d'Ampezzo region showing the location of fossil localities (a-e). Framed areas are magnificated in Fig. 1, a and 2.  
a) Geographical location of Misurina locality.

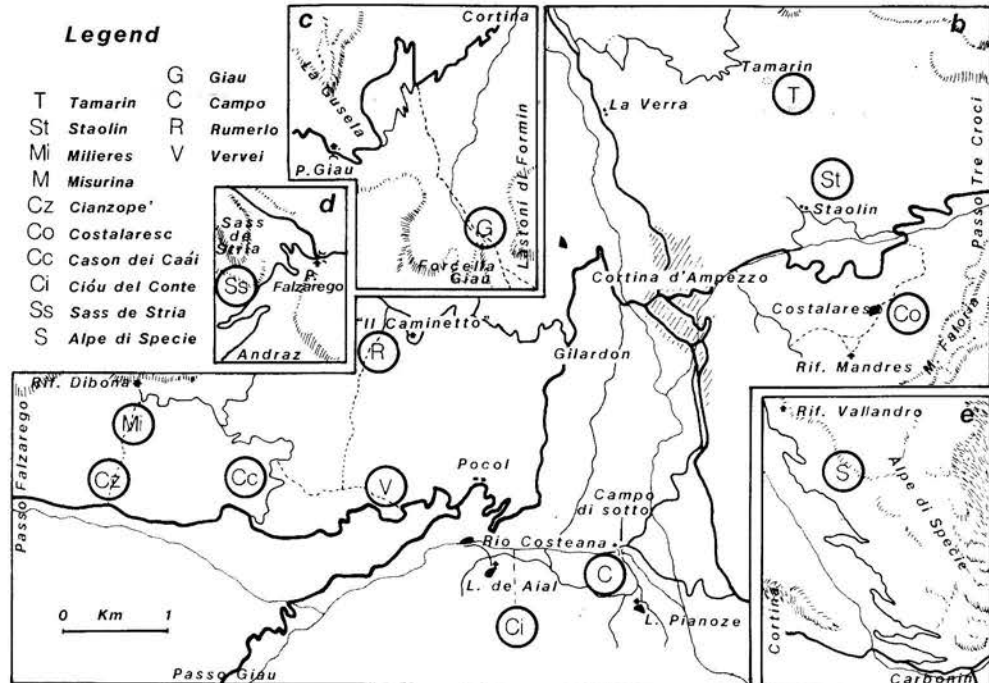


Fig. 2 - (b-e) Magnificated geographical location of fossiliferous sites of the Cortina d'Ampezzo region.

- Ciou del Conte (CI), 1350 m asl. This is reached by the path leading from Lago Pianoze to Lago de Aial. Shortly before reaching the Lago de Aial refuge, alt. approx. 1350 m, one leaves the path on the right to penetrate the wood for a few dozen meters, until reaching a limited expanse of ground devoid of grass mantle, which yielded a part of the specimens examined in this study.

- Rumerlo (R), 1600 m asl. One leaves the Cortina - Falzarego state road shortly after passing the hamlet known as Gilardon, and takes the road leading to the Pietofana refuge as far as the hut "Il Caminetto". The fossiliferous levels surface in the meadowland just above the hut, where there is no grass mantle.

- Vervei (V), 1700 m asl. One takes the Cortina - Falzarego state road, about 2.5 km from Pocol; on the right, there are several scarps extending over approx. 150 m where our material was found.

- Milieres (MI), 1800-1900 m asl. Not far below the Dibona refuge, in the woods, there are areas devoid of a grass mantle, where our material was collected.

- Cason dei Caài (CC), 1800 m asl. Leaving the Cortina - Falzarego state road, one takes the road leading to the Dibona refuge. After the first few bends, one reaches the ruins of buildings formerly used for stabling horses (Caài). At this point appear the outcrops considered in this study.

- Cianzopè (CZ), approx. 1750 m asl. Still on the right of the Cortina - Falzarego state road, at that altitude, there are small extensions of outcrop devoid of grass mantle.

To the east of Cortina d'Ampezzo the following localities were identified (Fig. 2, *b*):

- Tamarin (T), 1550-1660 m asl. Shortly after La Verra, one leaves the Cortina - Dobbiaco state road, following a mule track into the wood in a NNE direction. The locality is marked by a landslide.

- Staolin (ST), 1450-1600 m asl. This is a very wide area in slow, continuous movement, just above the outlying hamlet of Staolin.

- Costalaresc (CO), 1450-1600 m asl. Above Lago Costalaresc, along the west slope of the Faloria mountain, there is a recent (1951) landslip from which our material was taken.

Of the other four localities, Giau surrounds the Cortina d'Ampezzo valley, whereas Sass de Stria, and in particular Misurina and Alpe di Specie are adjacent to the Cortina d'Ampezzo area.

- Giau (G) (Fig. 2, *c*), 2990 m asl. Following the road from Pocol to Passo Giau, at an altitude of 2000 m asl., one takes the footpath for Forcella Giau. After a short distance, on the left of the path, one sees a wide area of detritus, in which an abundance of fossil remains are to be found, including part of the material examined in this study. This detritic material comes from limestone and yellowish biocalcarenite beds situated at the base of the Lastoni di Formin.

- Sass de Stria (Ss) (Fig. 2, *d*), 2200-2250 m asl. The specimens examined were collected along the state road leading from Passo Falzarego to Livinallongo, approx. 1 km from the Pass, on the right of the road, on the slope, where there has been a small landslide.

- Alpe di Specie (S) (Fig. 2, e), 1900-2000 m asl. A very well known locality, reached by leaving the Cortina - Dobbiaco state road a few hundred meters before Carbonin, and following a mule track leading to the Prato Piazza refuge. After the first few bends in the path, once out of the wood, one reaches the Alpe di Specie meadows, where the outcrops are situated.

- Misurina (M) (Fig. 1, a), 1850-1900 m asl. According to Zardini (pers. com.) this name was intended to cover a somewhat wide area extending from Lago Misurina as far as Monte Piana. The surfaces, never very extensive, and marked by slight landslides, yield a wealth of fossils.

As mentioned earlier, we have taken this opportunity of describing all the Ampezzan localities where the faunas include brachiopods; among them the genus *Diplospirella* is to be found at: Campo, Rumerlo, Vervei, Milieres, Cason dei Caài, Tamarin, Staolin, Giau, Sass de Stria, Alpe di Specie, Misurina.

#### General remarks on *Diplospirella* Bittner from the Ampezzan area.

The subfamily *Diplospirellinae* is represented in the Ampezzan area by the genera *Diplospirella* and *Anisactinella*. This survey considers only species belonging to the genus *Diplospirella*, because of the large number of specimens found, and the fact that this genus is so widespread in the relevant area.

Over 4300 specimens were examined from 11 of the principal localities with brachiopod faunas indicated by Zardini. Thus, the genus is also the most frequent among the taxa belonging to the phylum *Brachiopoda* described in the Ampezzan valley.

Of the three species identified, *Diplospirella sufflata* (Münster) presents the largest number of specimens (2360, i.e. 54.46%), and is predominant at Alpe di Specie, Giau, Misurina. Followed by *Diplospirella aureolata* (Cornalia), with a total of 1338 specimens (30.87%), predominant at Campo and Sass de Stria, whereas *Diplospirella wissmanni* (Münster) is always subordinate in number to the former two (636 specimens) (Table 1).

SPECIES	Locality											TOTAL
	Alpe di Specie (S)	Giau (G)	Misurina (M)	Sass de Stria (Ss)	Campo (C)	Rumerlo (R)	Vervei (V)	Milieres (MI)	Cason dei Caài (CC)	Tamarin (T)	Staolin (ST)	
<i>D. wissmanni</i>	479	22	34	9	47	4	-	12	6	22	1	636
<i>D. sufflata</i>	1574	504	69	28	73	-	1	39	25	47	-	2360
<i>D. aureolata</i>	938	45	25	47	186	1	1	39	23	32	1	1338
TOTAL	2991	571	128	84	306	5	2	90	54	101	2	4334

Tab. 1 - Frequency of taxa from different localities (complete specimens).

Both young as well as adult forms were observed for all three taxa.

The mode of preservation of the specimens examined was, on the whole, good. The shell is always present, though decorticated, thus deprived of the primary layer. In the secondary layer the ultrastructure is always clearly legible, even under a light micro-

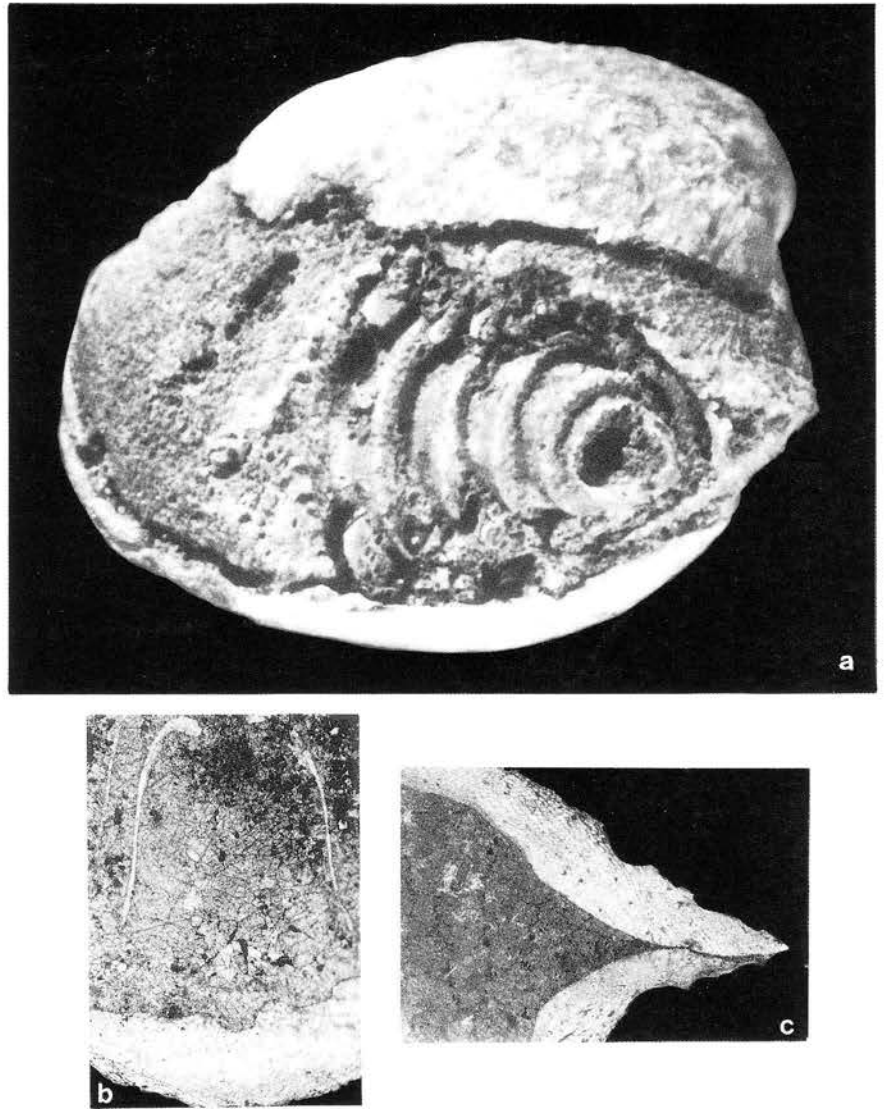


Fig. 3 - *Diplospirella sufflata* (Münster). *a*) Partially decorticated specimen. Brachidium still visible as an internal model. *b*) Recrystallized specimen. Still visible: internal shell structure, primary lamella of the brachidium, part of the infilling undergoing recrystallization (above, right). *c*) *Diplospirella aureolata* (Cornalia), specimen infilled with coarse sediment, brachidium not preserved. Alpe di Specie N. 5827/40 (*a*), N. 5827/52 (*b*), N. 5836/20 (*c*).

scope (decorticated surface and peels). The inner surface of the valve and the cardinalia are always complete.

Greater difficulty is encountered when it comes to the brachidium, which is a highly fragile structure, and feebly connected to the cardinalia, thus liable to mechanical damage postmortem from infilling with coarse sediment (Fig. 3, c). Further, it has been observed that the brachidium is easily obliterated during diagenesis. In some cases, the spiral course of the brachidium is still visible as an internal mould, though the double lamella characteristic of this genus is no longer visible (Fig. 3, a). In the majority of cases, recrystallization of the nucleus is virtually complete, leaving only ghosts of the original structure visible (Fig. 3, b). Thus, we were able to observe the spiralia or part of them only in a few specimens. The data were insufficient to permit reconstruction of the brachial apparatus, with the exception of *Diplospirella wissmanni* (Münster).

#### Genus *Diplospirella* Bittner: morphological notes.

Analysis of the Ampezzan species has shown that they are forms with permesothyrigid foramen, reduced deltidial plates, anterior commissure from rectimarginate to weakly uniplicate. No sulcus on the brachial valve was ever observed, as affirmed for the diagnosis of this genus in Boucot et al. (1965, "Treatise" p.H 664).

The cardinalia, first illustrated by Bittner (1892) but never described, are complex. They are A-shaped (Fig. 4), and consist of:

- two massive cardinal plates, subrectangular in outline, divergent from the umbo. In cross-section they appear to be formed by secondary J-shaped subparallel lamellae;
- a vertical structure, extending to the inner surface of the brachial valve, which connects the two cardinal plates. This element bounds a triangular cavity lying between the two divergent plates, isolating it from the umbonal chamber (Fig. 5, a, e).

The name "Cardinal lamina" is proposed for this structure.

This new term is introduced to designate a structure observed here for the very first time. The term "cardinal" indicates the position it occupies; the term "lamina" has been chosen to emphasize its sheetlike appearance and its transversal position between cardinal plates, perpendicular to the inner surface of the brachial valve.

Further, the socket bounded by the cardinal lamina also needs defining, and here we propose the term "Cardinal pit" (p. in Fig. 4,5). "Pit" is preferred to "cavity" as it bears more relation to the size of the socket examined.

This kind of cardinalia cannot be classed with those found in other forms belonging to the superfamily *Athyridacea*, because of the vertical development of its elements and:

- a) the presence of the cardinal lamina;
- b) the pit isolated from the inner surface of the valve (Fig. 4; 5, c);
- c) the massive appearance of the cardinalia as a whole, without posterior perforations (Fig. 5, a-d).

Among the species ascribed to the genus *Diplospirella*, the following differences were observed (Pl. 7, fig. 1,2):

a) the cardinal plates are less thick in *Diplospirella sufflata* (Münster) than in either *Diplospirella wissmanni* (Münster) or *Diplospirella aureolata* (Cornalia);

b) the considerable extension of inner socket ridges from the cardinal plates in *Diplospirella sufflata* (Münster). The dental sockets are thus very scooped, spoon-shaped, bounding the teeth anteriorly (Fig. 6, a-b).

It was Bittner (1890, p.297) who first defined the appearance of the brachidium as diplospiral: "Der Kürze wegen soll künftig diese Art des Baues der Spiralkegel, die, wie gleich bemerkt sei, bei den triadischen Spiren-tragenden Brachiopoden eine sehr grosse Verbreitung besitzt, als "diplospire" Anordnung der Spiralkegel bezeichnet werden". Again, Bittner (1890) described it as being composed of two lamellae, the primary larger and the secondary smaller, both with denticulated edges.

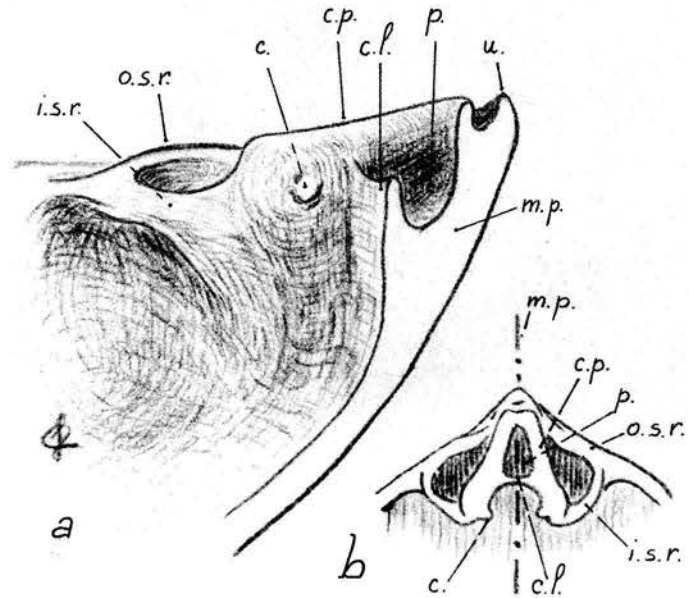


Fig. 4 - Diagram of cardinalia of *Diplospirella*. a) Perspective view (section in plane of symmetry). b) Plane view. u. = Umbo; c.p. = cardinal plate; i.s.r. = inner socket ridge; o.s.r. = outer socket ridge; c. = crus; c.l. = cardinal lamina; m.p. = median plane; p. = cardinal pit.



The brachidium (Pl. 14, fig. 2) has a highly complex central structure (jugum sensu Williams & Rowell, 1965 "Treatise") which has only sketchily been described in the literature. The jugum of *Diplospirella* is similar in pattern to the one advanced for *Athyris* in "Treatise" (1965; p.H 103, fig. 108) and to which we refer for terms.

Analysis of the serial transverse sections of *Diplospirella wissmanni* (Münster) at a distance of 0.05 mm one from the other (Pl. 8, 9; Fig. 7) has revealed that:

- the jugal stem is well developed, projected posteriorly, and bifurcates giving rise to accessory lamellae;

- the saddle is thickened, has a ventral apophysis and two latero-ventral apophyses. The latter are projected anteriorly and are more developed than the central structure. The apophyses are provided with long, thin spines (Fig. 8);

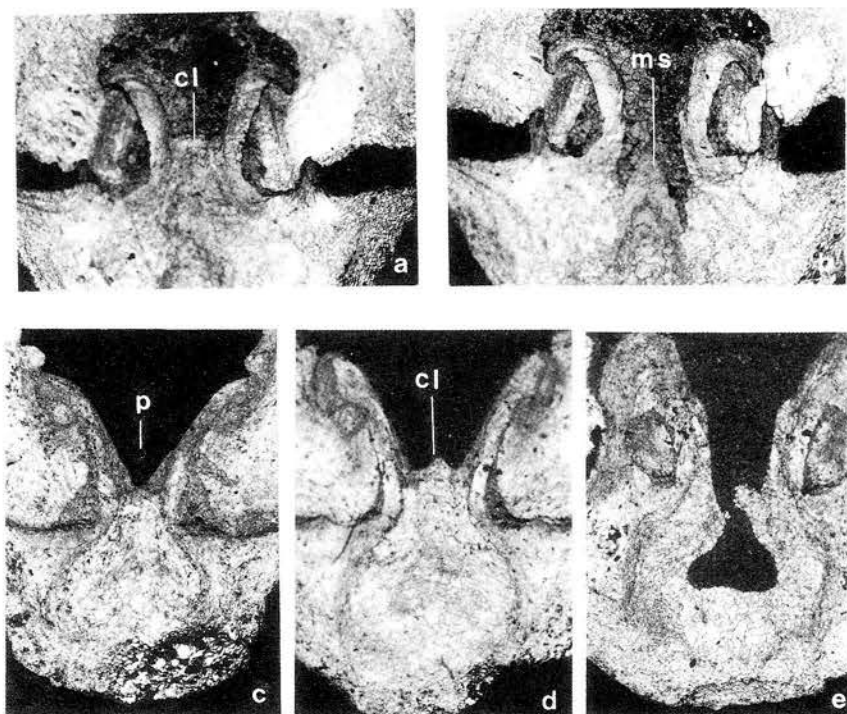


Fig. 5 - Transverse sections of cardinalia. *a*) *Diplospirella sufflata* (Münster), detail of cardinal lamina (cl) (1.3 mm); *b*) same specimen (1.4 mm); note median septum (ms); *c*) *Diplospirella wissmanni* (Münster), detail of cardinal pit (p) (2.80 mm); *d*) same specimen, cardinal lamina (cl) (3.10 mm); *e*) same specimen, beginning of umbonal chamber (3.30 mm). In both species the umbonal chamber does not continue beyond the cardinal lamina but is bounded by the lamina; thus, the massive umbo. Alpe di Specie N. 5827/36 (*a, b*), Misurina N. 5819/20 (*c-e*).

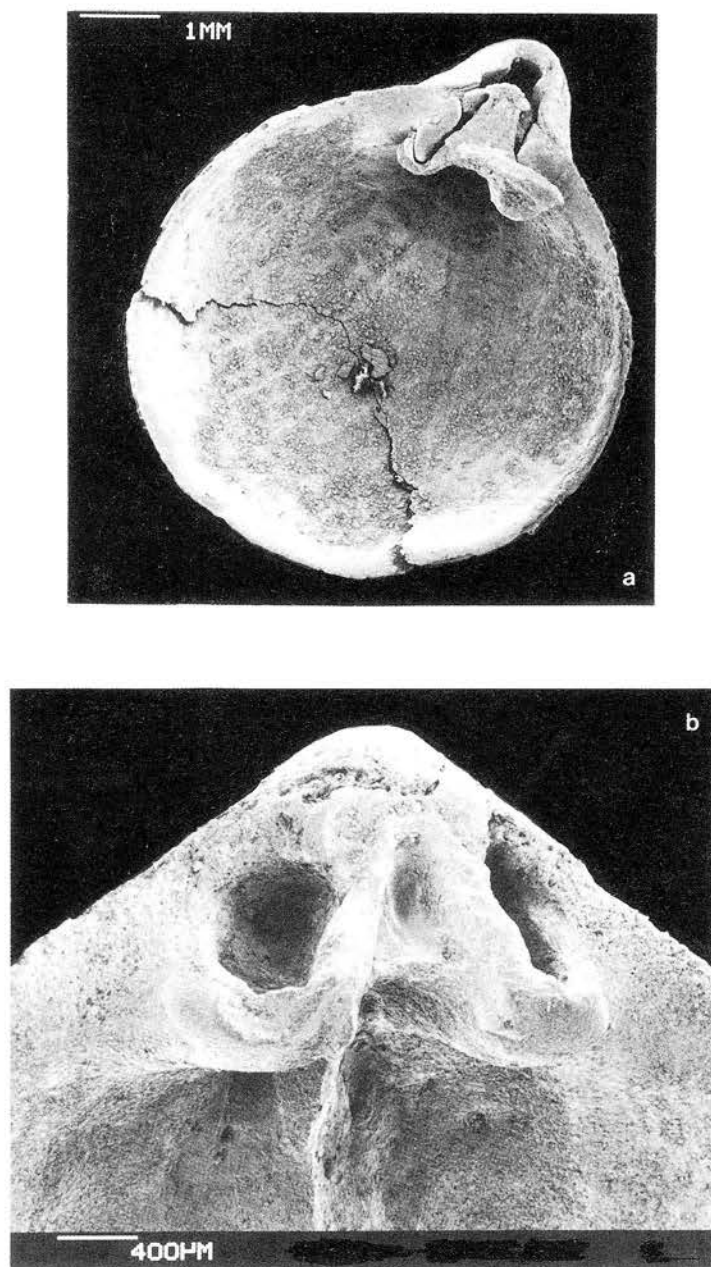


Fig. 6 - *Diplospirella sifflata* (Münster). *a*) Internal surface of pedicle valve and fragment of cardinalia attached to it. *b*) Brachial valve, detailed view of cardinalia with markedly scooped, spoon-like dental sockets. Alpe di Specie N. 5827/31 (*a*), N. 5827/32 (*b*).

- the lateral branch of the jugum is folded back and forks off dorsally before connection with the primary lamella (Fig. 9, *d*). It is provided with thin lateral spines (Fig. 9, *a, b*);
- the primary lamella, at the point of attachment to the lateral branch of the jugum appears thickened and broadened (Fig. 9, *c*).

Both primary and accessory lamellae have long, thin spines (Fig. 10, *a*). Numerous observations of well preserved specimens have enabled us to establish that the spines are distributed along the entire length of the lamella (Fig. 10, *a, b*).

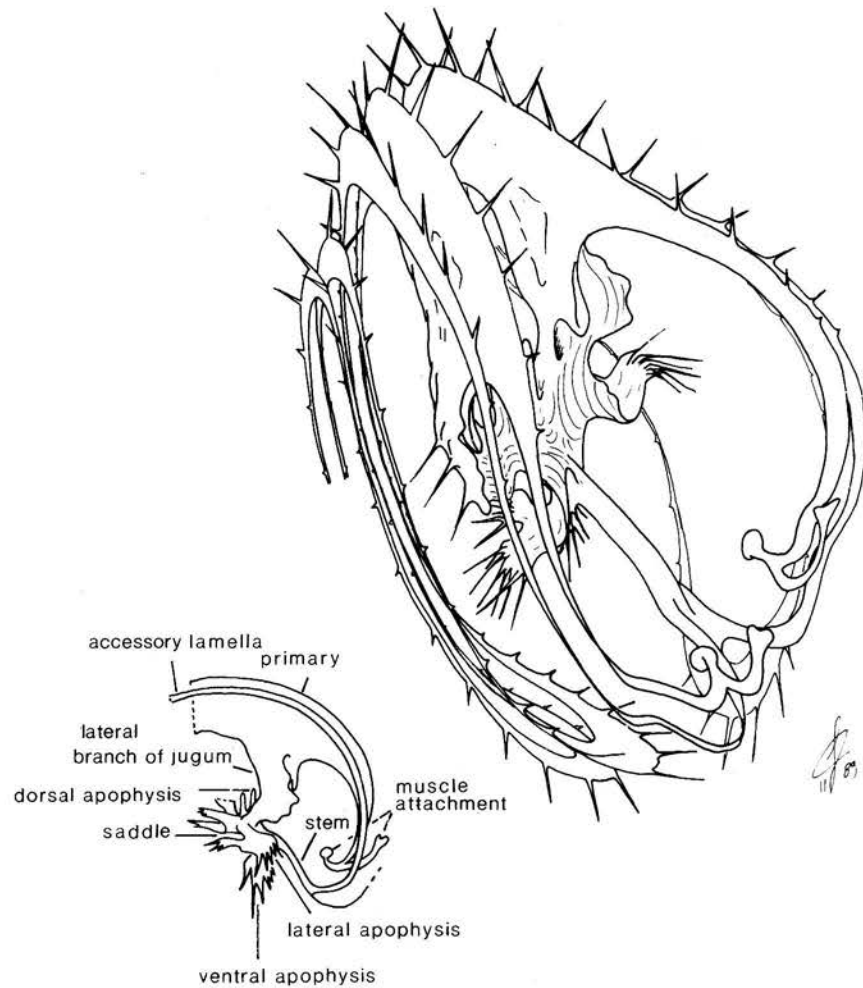


Fig. 7 - Reconstruction of brachidium of *Diplospirella wissmanni* (Münster), based on peels. To simplify, only the first convolution of the spirillum is shown.

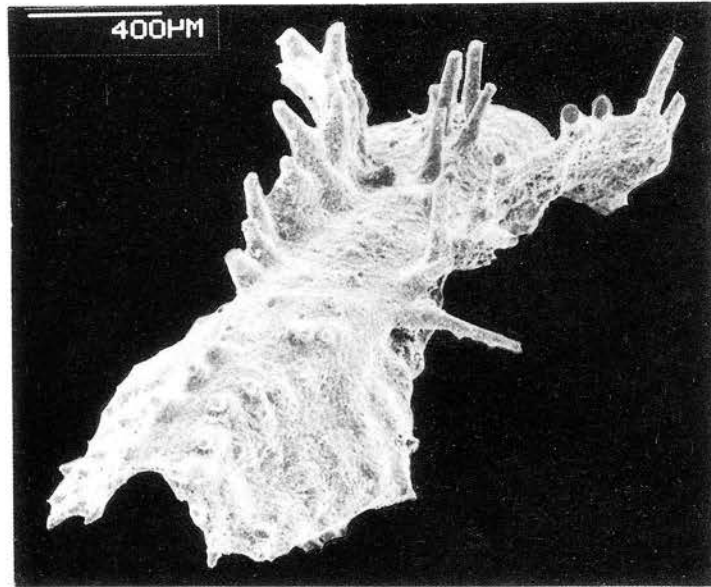


Fig. 8 - *Diplospirella sufflata* (Münster). The saddle, with well developed spines. Alpe di Specie N. 5827/29.

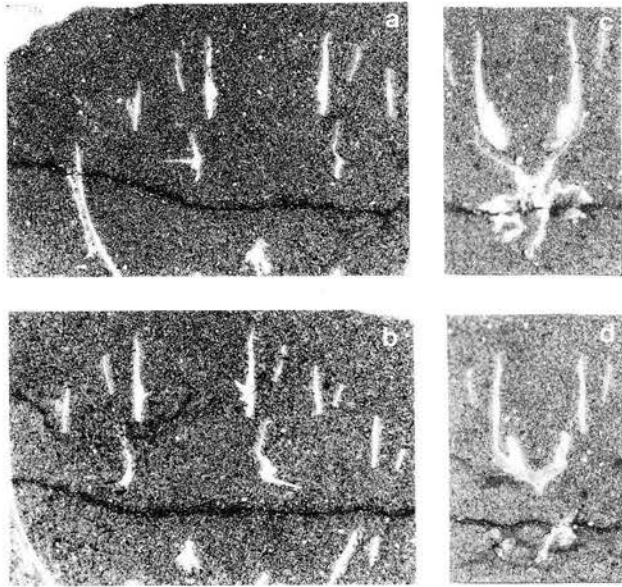


Fig. 9 - *Diplospirella wissmanni* (Münster). Detail of spines on lateral branch of jugum: a) 5.65 mm from umbo; b) 5.70 mm from umbo; c) thickening of primary lamella at point of connection with lateral branch of jugum (6.05 mm); d) dorsal bifurcation of lateral branch of jugum (6.22 mm). Misurina N. 5819/20.

The spiralia are not joined to the crura. The latter are like massive, rounded projections on the cardinal plates, distally placed. In the peels, the crura are clearly seen to be complete, thus not the result of a break in a more extensive structure (Fig. 11, *a, b*). Their squat appearance suggests they may be a base for the attachment of organic tissue (muscle and/or body wall) connected to the brachidium. Similar forms with brachidium discontinuous with crura have already been recorded among *Athyridida* in Paleozoic, by Copper (1986).

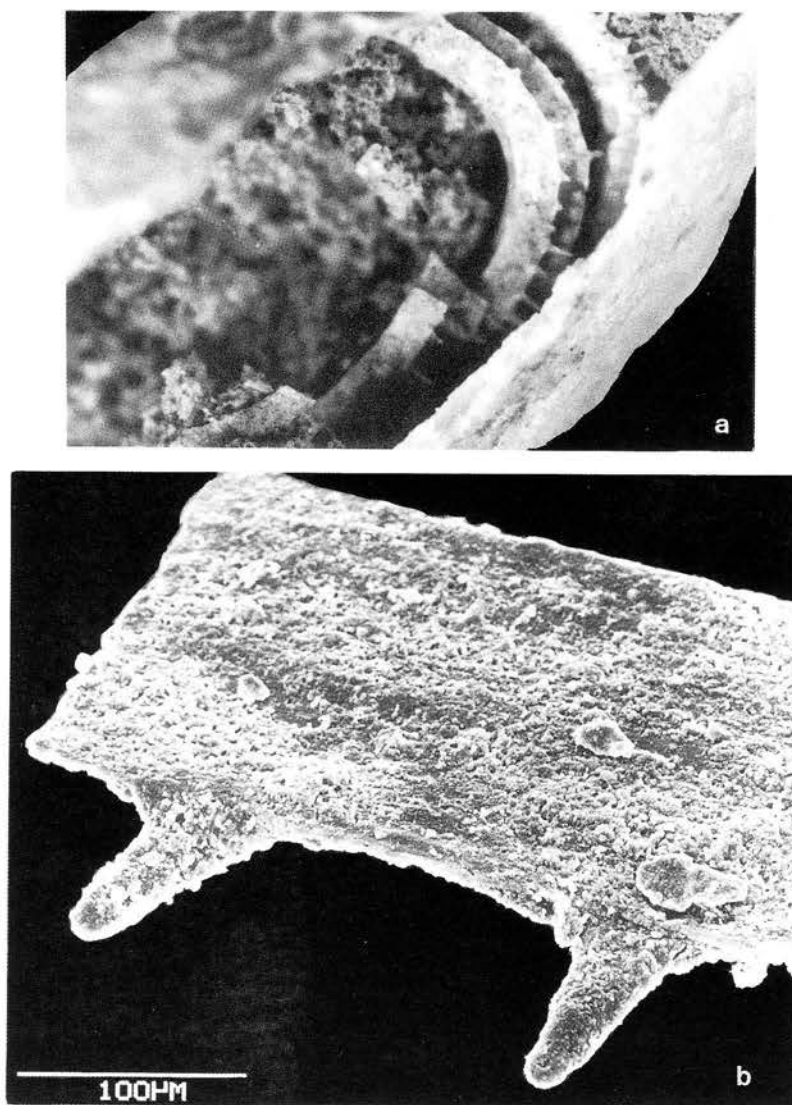


Fig. 10 - *Diplospirella sufflata* (Münster). *a*) disposition of spines on primary and secondary lamella; *b*) detail of spines on primary lamella. Alpe di Specie N. 5827/42 (*a*), N. 5827/28 (*b*).

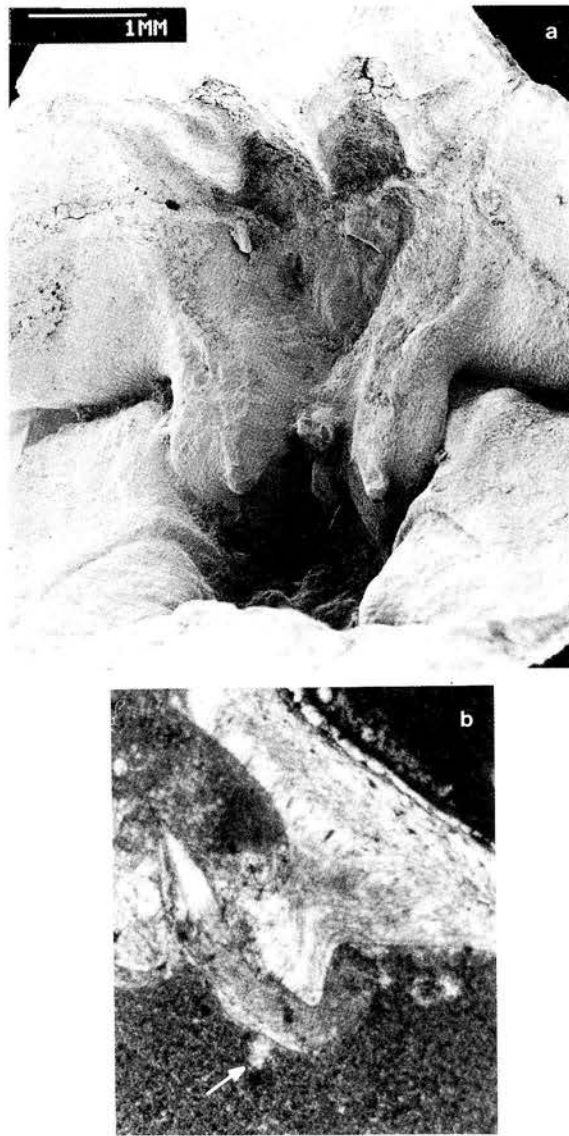


Fig. 11 - *Diplospirella sufflata* (Münster). *a*) Internal view of brachial valve (above) joined to pedicle valve (below). Visible on brachial valve: crura, muscle field, cardinal lamina. *b*) Detail of the articulation at the crus. (Section parallel to the plane of symmetry; arrow indicates crus). Alpe di Specie N. 5827/49 (*a*), N. 5827/38 (*b*).

The absence of a skeletal connection between spiralia and crura explains the complex morphology of the jugum, which becomes the point of equilibrium of a brachidium that would otherwise be too complex and "heavy" to remain stable.

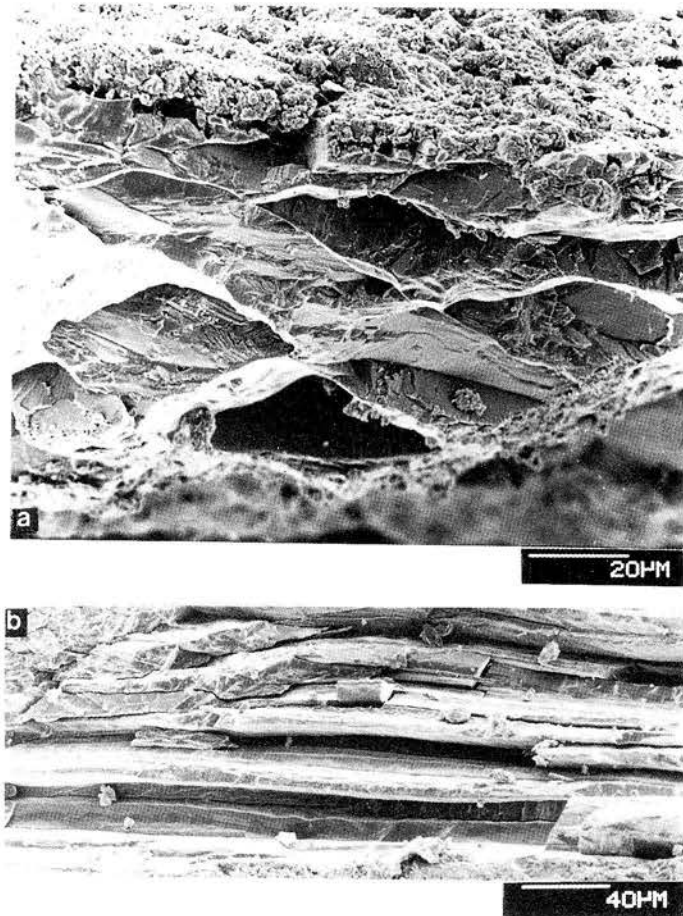


Fig. 12 - *Diplospirella sufflata* (Münster). *a*) Brachial valve. Transverse section, anterior region (primary below). Shape and outline of fibers of secondary layer. *b*) Pedicle valve. Longitudinal section, anterior region (primary below). Disposition of fibers of secondary layer. Alpe di Specie N. 5827/25 (*a*), N. 5827/26 (*b*).

The jugum thus develops a structure that is:

- expanded laterally (apophysis) so as to better balance the "weight" of the double spires;
- projected ventrally so as to compensate the initial dorsal thickening of the primary lamella.

SEM and peel analysis of the ultrastructure of the shell has revealed the presence of a well developed secondary layer (Fig. 12 *a, b*) consisting of very wide lamellae, as wide as 60  $\mu\text{m}$ . MacKinnon (1974) had already drawn attention to the size of the lamellae, which can be observed even under a light microscope.

Thus, the radial fibers with a marked median convergence observed by Bittner (1890), and which he regards as diagnostic of genus, are lamellae from the secondary layer, which that Author probably observed on decorticated shells.

## Paleontological descriptions

Taxonomic classification of the species determined is based on the proposal of Dagys (1974); we accept his grounds for promoting the suborder *Athyrididina* Boucot, Johnson & Staton, 1964 to order *Athyridida*. Consequently the order *Spiriferida* Waagen, 1883 is divided into three orders: *Atrypida*, *Athyridida*, *Spiriferida*.

Anyway, even if this view has not yet been officially accepted, other Authors besides Dagys (1974), such as Copper (1986) and Siblík (1988) have recently felt the need to make a distinction among the orders: *Atrypida*, *Athyridida* and *Spiriferida*.

### Phylum Brachiopoda

#### Class Articulata

Order Athyridida Boucot, Johnson & Staton, 1964

Suborder Athyrididina Boucot, Johnson & Staton, 1964

Superfamily *Athyridacea* M'Coy, 1844

Family *Spirigerellidae* Grunt, 1965

Subfamily *Diplospirellinae* Schuchert, 1894

Genus *Diplospirella* Bittner, 1890

Type-species *Terebratula wissmanni* Münster, 1841 (in Wissmann & Münster, 1841)

#### *Diplospirella wissmanni* (Münster, 1841)

Pl. 7, fig. 2; Pl. 8, 9; Pl. 13, fig. 1, 2; Pl. 14, fig. 1, 2; Text-fig. 5, 7, 9, 13, 14, 16

- 1841 *Terebratula wissmanni* Münster, in Wissmann & Münster, p. 64, pl. 6, fig. 18 a-c.  
 1864 *Spirigera wissmanni* - Laube, p. 406.  
 1865 *Spirigera wissmannii* - Laube, p. 15, pl. 12, fig. 5 (a, b) (*non* c-i).  
 1890 *Spirigera wissmanni* - Bittner, p. 79, pl. 2, fig. 6, 7, 9 (*non* 8); p. 148, pl. 29, fig. 22; p. 299, text-fig. 4; p. 112, 137, 157, 164.  
 1892 *Spirigera (Diplospirella) wissmanni* - Bittner, p. 27, pl. 2, fig. 23 (*non* 6, 7); p. 19.  
 1892 *Spirigera* cfr. *wissmanni* Bittner, p. 33.  
 1900 *Spirigera (Diplospirella) wissmanni* - Bittner, p. 33, pl. 3, fig. 7, 8.  
 1902 *Spirigera (Diplospirella) wissmanni* - Bittner, p. 512.  
 1903 *Spirigera* aff. *wissmanni* Kittl, p. 729.  
 1903 *Spirigera wissmanni* - Broili, p. 160, pl. 18, fig. 5.  
 1910 *Spirigera (Diplospirella) wissmanni* - Scalia, p. 19, pl. 2, fig. 8 a-c.  
 1913 *Spirigera* aff. *wissmanni* Toulou, p. 96, pl. 5, fig. 24.  
 1930 *Diplospirella wissmanni* - Gugenberger, p. 76.  
 1974 *Diplospirella wissmanni* - Dagys, p. 162, pl. 45, fig. 4.  
 1974 *Diplospirella wissmanni* - MacKinnon, pl. 13, fig. 5, 6; pl. 14, fig. 1-4; pl. 15, fig. 1; pl. 30, fig. 4.

**Material.** 636 specimens, 178 measured. N. 5817/1-479; N. 5818/1-22; N. 5819/1-34; N. 5820/1-9; N. 5821/1-47; N. 5822/1-4; N. 5823/1-12; N. 5824/1-6; N. 5825/1-22; N. 5826.



## Description.

**External characters.** Small biconvex shell, very rounded subpentagonal to semi-circular in outline, tending to be equal in width and length, maximum width nearest to posterior region. Extensive curved posterior commissure, lateral commissure with rectilinear to slightly sinuous course, anterior commissure rectimarginate or weakly unipli-cated, but no fold on brachial valve nor sulcus on pedicle valve were ever observed. Lateral and anterior commissures with bladeli-like outline. Pedicle valve convex with permesothyriddid foramen. Developed palintrope, umbonal ridges feebly marked. Brachial valve convex, as pedicle valve. In the wider specimens, at times the valves tend to flatten towards the lateral edge of the shell, giving rise to two alate expansions (Pl. 14, fig. 1). Smooth shell.

## Biometric characteristics (1):

	Alpe di Specie					
	L	W	T	W/T	T/L	T/W
N. sp.	114	126	135	105	126	114
$\bar{x}$	6.43	6.42	3.81.	0.99	0.59	0.59
s	1.35	1.38	0.90	0.08	0.06	0.06
sm	0.12	0.12	0.08	0.008	0.006	0.006

**Internal characters.** Pedicle valve with subtriangular delthyrial cavity, well developed teeth, elongated, smooth, triangular in section. Extensive bilobed muscle field. Median septum extending for 2/3rds the length of the valve, barely hinted at in the umbonal region, more developed in height anteriorly, becoming triangular in shape (Fig. 13, a, b).

Brachial valve with well developed cardinalia and very thick cardinal plates, hollowed dental sockets, bounded by a more pronounced inner than outer socket ridge. Muscle field initially wholly separated by a not very high, sharp median septum extending to half the length of the valve (Fig. 14). Distally, it is flanked by short ridges which separate it further. Spirally coiled brachidium with double lamella consisting of 7 convolutions.

**Ultrastructure.** Primary layer fibrous, composed of coarse calcite fibers. Contact with secondary layer is linear. Secondary layer lamellar in appearance, with long, multi-riate, orthodoxically packed lamellae, subparallel and compact.

**Remarks.** Laube (1865) attributed to *Diplospirella wissmanni* (Münster) "*Terebratula*" *bucki* Klipstein, 1844 and "*Terebratula*" *subcurvata* Münster, 1841, because, although the two taxa present differences from the species under review in the frontal re-

(1) Data only for localities with more than 100 specimens collected.

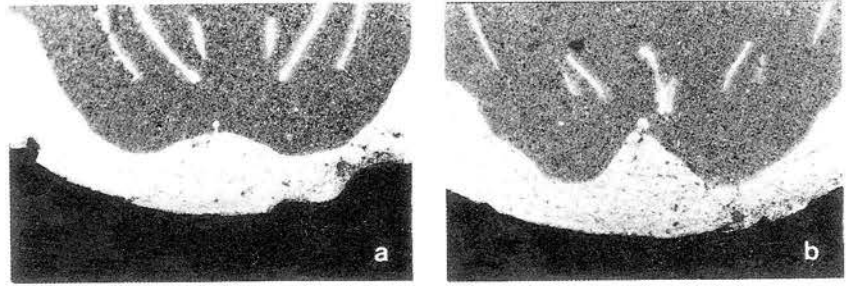


Fig. 13 - *Diplospirella wissmanni* (Münster). Pedicle valve. Detail of median septum: *a*) 4.30 mm from umbo; *b*) 5.45 mm from umbo. Initially seen as a thin ridge implanted in a low, broad platform (*a*); subsequently more massive, triangular in section (*b*). Misurina N. 5819/20.

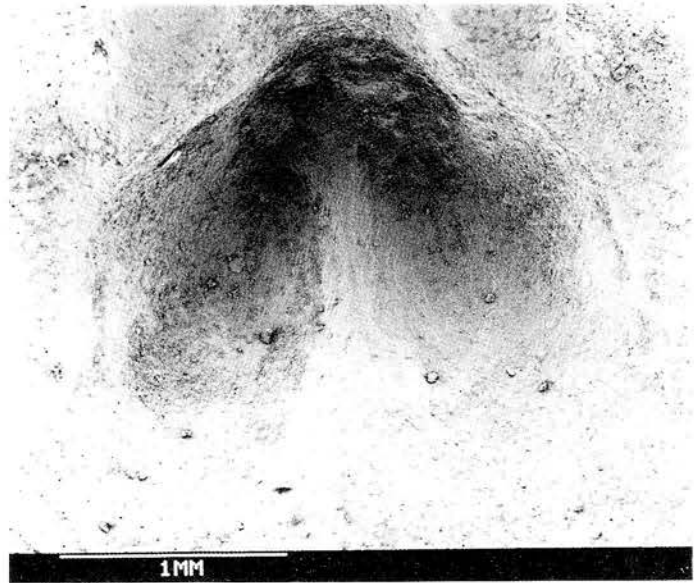


Fig. 14 - *Diplospirella wissmanni* (Münster). Internal surface of brachial valve. Detail of muscle field and median septum. Alpe di Specie N. 5817/15.

gion, they are strikingly similar posteriorly. In accord with Bittner (1890) we reject this suggestion, preferring to maintain the taxa separate.

The shells figured by Laube (1865) and referred to as *Diplospirella wissmanni* (Münster) are unlettered. In referring to them we introduce letters *a* through *i* starting from upper row, left to lower row, right. In our opinion the specimen of fig. 5a, b, in pl. 12, only is *Diplospirella wissmanni* (Münster).

We do not regard as synonyms of *Diplospirella wissmanni* (Münster) the specimens illustrated by:

- Bittner (1890), pl. 2, fig. 8, because of the outline and presence of folds on the brachial valve, extending from umbo;
- Bittner (1892), pl. 2, fig. 6, 7 because of the course of anterior commissure.

A review of the bibliography shows that although *Diplospirella wissmanni* (Münster) is very widespread, it has not been well defined. Even Münster (1841) states that this taxon was erected on specimens that were not very well preserved. This has created some confusion, thus the taxon referred to has been described as rectimarginate, unipli-cate, sulcate, with elongated outline, extended or reduced cardinal margin. Among the different illustrations of *Diplospirella wissmanni* (Münster), those which best show the morphological characters of the taxon are: Bittner (1890), pl. 2, fig. 7, 9 and pl. 29, fig. 22; Bittner (1892), pl. 2, fig. 23; Bittner (1900), pl. 3, fig. 7; Broili (1903), pl. 18, fig. 5.

**Distribution.** This species is recorded from Carnian of Northern and Southern Alps, Sicily, Jugoslavia, Bakony Mt. We reject the occurrence in Ladinian of Southern Alps indicated by Bittner, 1892.

**Occurrence.** Alpe di Specie, Giau, Misurina, Sass de Stria, Campo, Rumerlo, Milieres, Cason dei Caài, Tamarin, Staolin.

#### ***Diplospirella sufflata* (Münster, 1841)**

Pl. 7, fig. 1; Pl. 10, 12; Text-fig. 3, 5, 6, 8, 10, 11, 12, 15, 16

- Non 1816 *Terebratula sufflata* Schlotheim, pl. 7, fig. 10, 11 (fide Davidson).
- 1841 *Terebratula sufflata* Münster, in Wissmann & Münster, p. 63, pl. 6, fig. 15 a, b.
- 1864 *Terebratula subsufflata* - Laube, p. 406.
- Non 1865 *Terebratula indistincta* - Laube, p. 6, pl. 11, fig. 4-10.
- 1890 *Spirigera sufflata* - Bittner, p. 80, pl. 2, fig. 10.
- 1892 *Spirigera sufflata* - Bittner, p. 17, pl. 2, fig. 1, 2.
- 1900 *Spirigera (Diplospirella) sufflata* - Bittner, p. 33, pl. 5, fig. 18.
- 1903 *Spirigera sufflata* - Broili, p. 159, pl. 18, fig. 2.
- 1910 *Spirigera (Diplospirella) cfr. sufflata* Scalia, p. 20, pl. 2, fig. 9.
- 1930 *Diplospirella sufflata* - Gugenberger, p. 76.

**Material.** 2360 specimens, 409 measured. N. 5827/1-1574; N. 5828/1- 504; N. 5829/1-69; N. 5830/1-28; N. 5831/1-73; N. 5832; N. 5833/1- 39; N. 5834/1-25; N. 5835/1-47.

#### **Description.**

**External characters.** Biconvex shell, suboval in outline, length greater than width. Short, curved cardinal margin. Lateral commissure curved to rectilinear. Anterior commissure rectimarginate, in some cases unipli-cate, without sulcus or fold. Pedicle valve with recurved umbo, suboval permesothryridid foramen; extremely reduced palintrope. Brachial valve globose, like pedicle valve, attaining the greatest convexity in the median region. Smooth shell.

## Biometric characteristics (1):

	Alpe di Specie					
	L	W	T	W/L	T/L	T/W
N.sp.	213	288	303	213	213	288
$\bar{x}$	5.99	4.97	3.78	0.82	0.61	0.74
s	0.86	0.73	0.61	0.05	0.05	0.07
sm	0.05	0.05	0.03	0.003	0.003	0.004

	Giau					
	L	W	T	W/L	T/L	T/W
N.sp.	119	121	120	119	119	120
$\bar{x}$	7.80	6.63	4.72	0.84	0.60	0.71
s	1.15	1.09	0.89	0.09	0.06	0.08
sm	0.10	0.09	0.08	0.008	0.005	0.007

**Internal characters.** Pedicle valve with wide, subrectangular delthyrial cavity; long, not very thick, pointed teeth. In some cases a slight protuberance is noted in the vicinity of distal end of tooth (Fig. 15, *a, b*). Well developed muscle field with longitudinal sulci; median septum appears raised, triangular in section, pointed, expanding to half of the valve.

Brachial valve with deep, elongated dental sockets, delimited by the inner being more pronounced than the outer socket ridges. Median septum expanding from cardinal lamina, raised, almost rounded in outline, extending to up to a third of length of valve. Muscle field not clearly impressed, developed only in the apical region. Brachidium composed of two spirally coiled lamellae.

**Ultrastructure.** Primary layer not well preserved, partially observed only on one specimen, appears fibrous and reduced in thickness. Secondary lamellar layer compact. Long, overlapping calcite lamellae, slightly inclined in relation to outer and inner valve surface (Fig. 12, *a, b*).

**Remarks.** Münster (1841) regarded his form as a "short variety" of Schlotheim's "*Terebratula sufflata* (1816). In effect, it is a case of homeomorphy insofar as Schlotheim's taxon (1816) belongs to the order *Terebratula* as illustrated by Davidson (1857) in pl. 1, fig. 21, whereas Münster's taxon (1841) to the order *Athyridida*. In reexamining Münster's collection (1841) Laube (1864) keeps the two entities separate, designating Münster's taxon as *Terebratula subsufflata* d'Orbigny (1847). Subsequently,

(1) Data only for localities with more than 100 specimens collected.

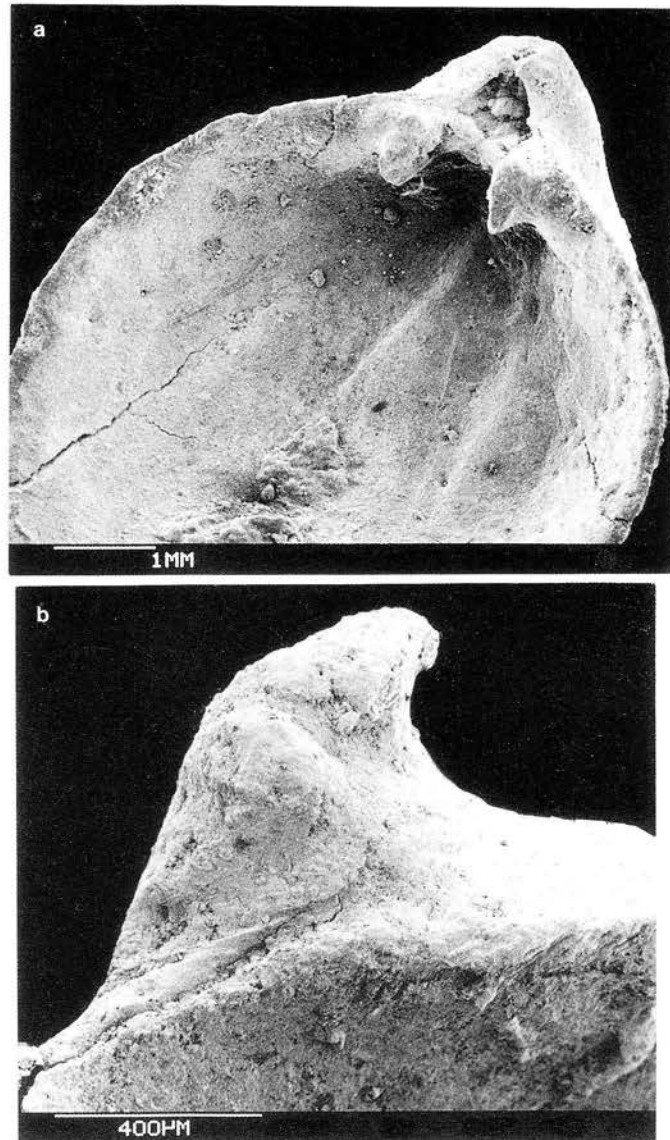


Fig. 15 - *Diplospirella sufflata* (Münster). *a*) Pedicle valve: internal surface and external view of umbonal region. *b*) Detail of tooth with distal protuberance. Alpe di Specie N. 5827/47.

several Authors, while attributing this taxon to Münster (1841), cite Schlotheim (1816) doubtfully in synonymy.

Bittner (1890), while keeping the two taxa separate, points out that *Diplospirella sufflata* (Münster) could possibly be regarded as a variety of *Diplospirella wissmanni*

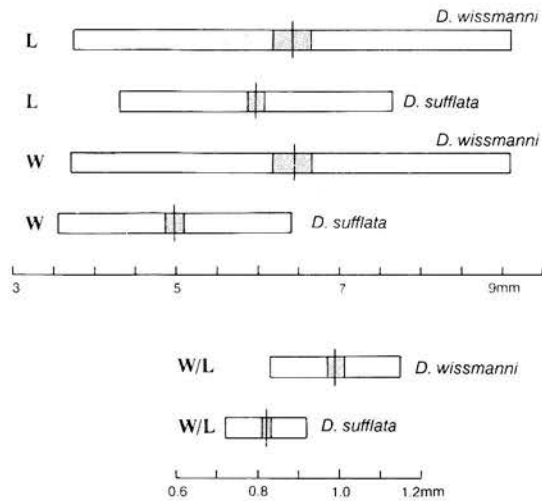


Fig. 16 - Diagram of average values, fiducial range and  $x+t$  5% sm range in *Diplospirella wissmanni* (Münster) and *Diplospirella sufflata* (Münster) in respect of absolute dimensions and their dimensional ratios. Alpe di Specie.

(Münster). On the contrary, we believe there are effective differences between the two species:

- the outline (subpentagonal, rounded in *Diplospirella wissmanni*, suboval, elongated in *Diplospirella sufflata*);
- the length of cardinal margin (extensive in *Diplospirella wissmanni*, short in *Diplospirella sufflata*);
- the contact between posterior and lateral commissure (suberect in *Diplospirella wissmanni*, rounded in *Diplospirella sufflata*);
- the median septum of pedicle valve (expanding more lengthwise in *Diplospirella wissmanni*, but attaining full development only in the median region, shorter, in *Diplospirella sufflata*, where it is clearly identifiable from its point of departure);
- the muscle field of pedicle valve (broader in *Diplospirella wissmanni* than in *Diplospirella sufflata*);
- the inner socket ridges (less developed in *Diplospirella wissmanni* than in *Diplospirella sufflata* where they reach the point of "enveloping" the teeth (Pl. 7).

The above differences are also borne out by a comparison of absolute measurements of the variables (L) length, (W) width, and relative ratios (Fig. 16), ascertained in the localities where the two taxa are more frequently found.

Finally, Laube (1865) regards *Diplospirella sufflata* (Münster) as belonging to *Terebratula indistincta* Beyrich, 1863. We do not share this view, insofar as Beyrich's taxon (1863) is not well defined. In erecting this species, Beyrich (1863) describes two specimens which he does not illustrate, but refers only to pl. 6, fig. 13d in Münster (1841) ("*Terebratula*" *vulgaris* "var". *minor* Münster, 1841). Bittner (1890), too, made a distinc-

tion between the two taxa; indeed, on the strength of the internal characters examined on the plesiotypes, he ascribes "*Terebratula*" *indistincta* Beyrich, 1863 to his new genus *Dioristella* Bittner, 1890. Beyrich's species was subsequently designated by Diener (1920) for the type species *Dioristella*. The problem of the true identity of *Terebratula indistincta* Beyrich is still an open question.

Distribution. This taxon is recorded from Carnian of Northern and Southern Alps and Bakony Mt.

Occurrence. Alpe di Specie, Giau, Misurina, Sass de Stria, Campo, Vervei, Milieres, Cason dei Caài, Tamarin.

### *Diplospirella aureolata* (Cornalia, 1848)

Pl. 11; Pl. 13, fig. 3-5; Text-fig. 3, 17, 18, 19

1848 *Terebratula aureolata* Cornalia, p. 42, pl. 3, fig. 6 a-d.

1865 *Spirigera Wissmannii* - Laube, p. 15, pl. 12, fig. 5 e, f (*non* a-d; g-i)

Material. 1338 specimens, 242 measured. N. 5836/1-938; N. 5837/1-45; N. 5838/1-25; N. 5839/1-47; N. 5840/1-186; N. 5841; N. 5842; N. 5843/1-39; N. 5844/1-23; N. 5845/1-32; N. 5846.

#### Description.

External characters. Biconvex shell with brachial valve generally more convex than pedicle valve, rectimarginate, in the majority of cases suboval to semicircular in outline. Posterior commissure with sinuous course, lateral and anterior commissure rounded and bladelike. Short, curved cardinal margin. Pedicle valve with suberect umbo, suboval permesothyridid foramen, faint umbonal ridges, reduced palintrope. In both valves, a central region is observed, markedly globose, and a peripheral region flattened like an aureole, from which it derives its species name. This aureole is widest in the anterior region, in some specimens attaining a width one third its total length. This character is already apparent in young shells and increases with shell growth. No ornament.

#### Biometric characteristics (1):

	Alpe di Specie					
	L	W	T	W/L	T/L	T/W
N.sp.	193	202	202	147	193	202
$\bar{x}$	6.45	6.06	2.82	0.94	0.44	0.46
s	1.03	1.31	0.60	0.08	0.06	0.06
sm	0.07	0.09	0.04	0.006	0.004	0.004

(1) Data only for localities with more than 100 specimens collected.

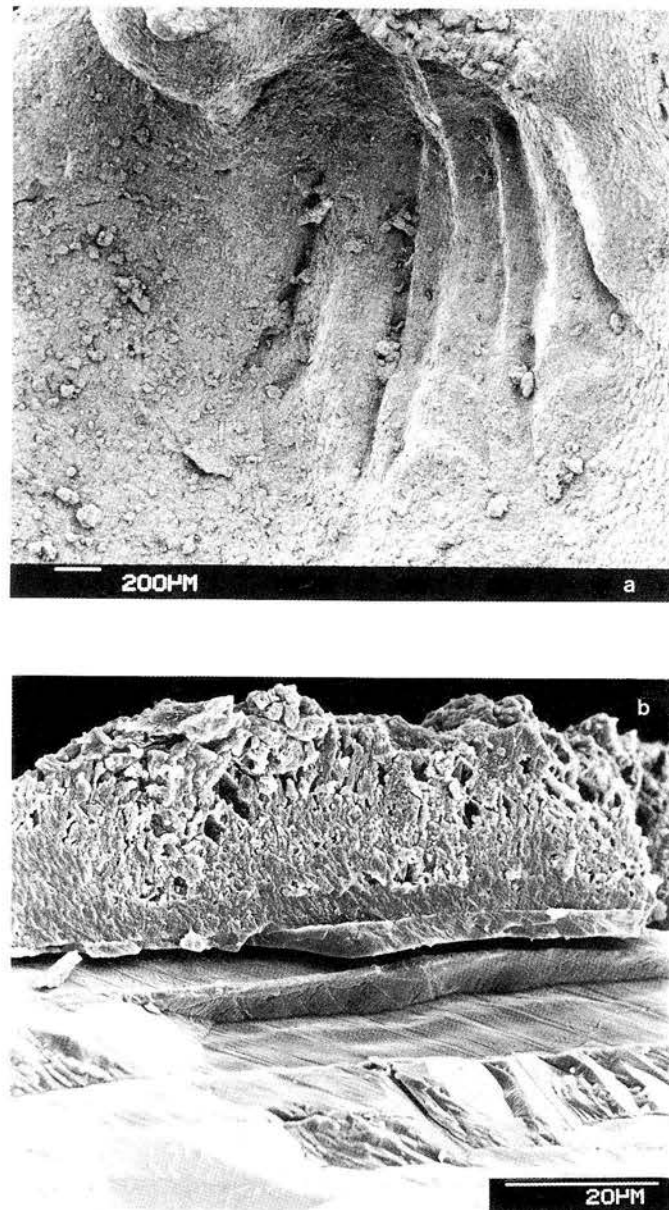


Fig. 17 - *Diplospirella aureolata* (Cornalia). *a*) View of interior of brachial valve. Detail of radial grooves corresponding to a muscle field. *b*) Pedicle valve. Transverse section, anterior region. Fibrous appearance of primary layer (above) and contact between primary and secondary layer. Alpe di Specie N. 5836/22 (*a*), N. 5836/19 (*b*).



Internal characters. Pedicle valve with subtriangular delthyrial cavity. Short, squat teeth, subtriangular in outline. Muscle field not clearly visible. Hint of median septum in apical region, developed in median region where it becomes triangular in section, not very raised.

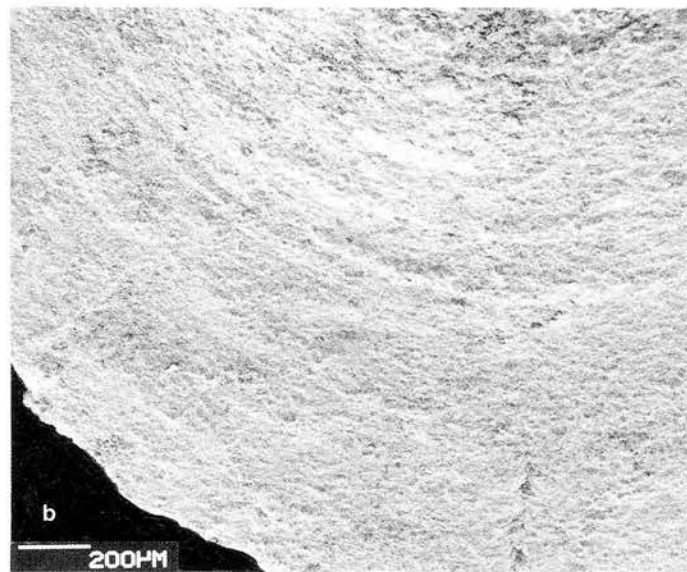
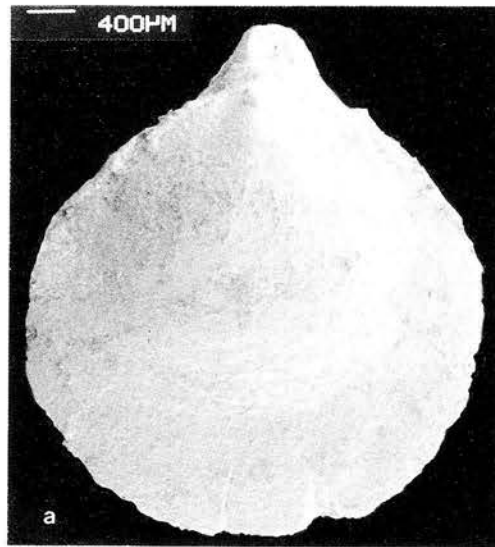


Fig. 18 - *Diplospirella aureolata* (Cornalia). *a*) Dorsal view. Marked difference between peripheral aureole and central region. *b*) Detail of an undisturbed course of fibers of secondary layer at point of intersection between aureole and central region of the shell. Alpe di Specie N. 5836/9.

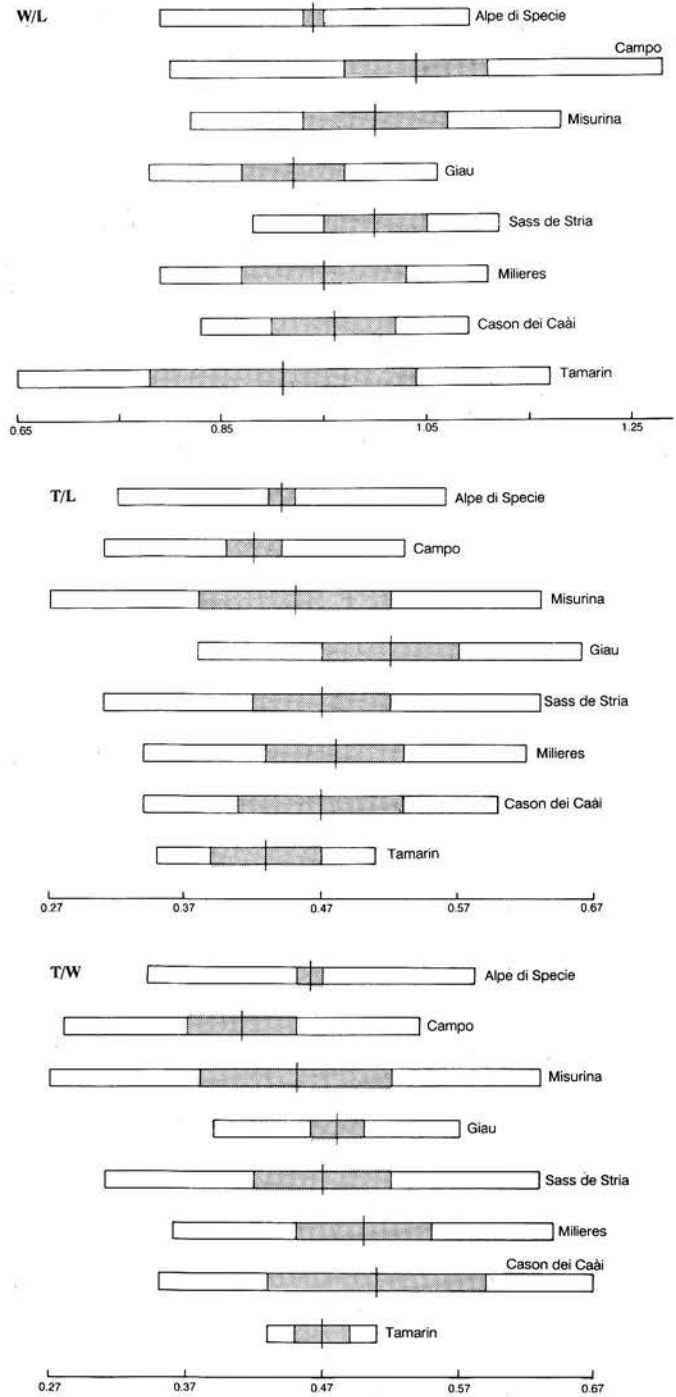


Fig. 19 - Diagram of dimensional ratios in *Diplospirella aureolata* (Cornalia), Alpe di Specie.

Brachial valve with deep dental sockets, bounded by a well developed inner ridge. Muscle field weakly impressed. No median septum. In some specimens, radial grooves are observed extending from cardinal lamina up to one third the length of the valve (Fig. 17, *a*).

**Ultrastructure.** Primary layer fibrous and compact. The fibers are arranged sub-parallelly, inclining  $60^\circ$  from inner surface of layer. Contact between primary and secondary layers is linear. Multistriate secondary layer, composed of overlapping lamellae, subrectangular in outline (Fig. 17, *b*).

**Remarks.** The aureole found in these shells is to be regarded as a distinct character of the species, because it is already present in young forms, expands with growth in shell size, and is observed in a large number of specimens from different localities.

Further, through SEM analysis and peels it has been possible to establish that the fibers of the secondary layer, where they pass from the bulging central to the external flattened region of the valve, do not show any signs of a break (Fig. 3, *c*, Fig. 18, *a,b*; Pl. 13, fig. 1). Thus, the assumption that the aureole may be caused by a diagenetic crushing effect is to be ruled out. We believe, in accord with Cornalia (1848), that this morphology is peculiar to the shell, and not acquired through an external event.

The flex point present in any radial profile is a weak spot, so the shell could be easily broken near the circular line which delimitates the aureole. Such fractures are clearly visible in most of the specimens examined. In our view, they are not the cause, but only a consequence of the aureolata morphology.

Since this is the first time that a number of specimens from different localities have been measured, comparison with the trend of their external biometric characteristics appears a significant exercise. Fig. 19 shows that the WL, TL and TW ratios fall within the fiducial range, index of a fair degree of homogeneousness of the biometric characteristics considered in the different localities.

It is our opinion that some of the forms illustrated by Laube (1865) as *Spirigera Wissmannii* in pl. 12, fig. 5 (5 e, 5 f) should be regarded as belonging to the same species as *Diplospirella aureolata* (Cornalia).

We do not concur with Bittner's (1890) unsupported opinion that the taxon in question is conspecific with *Diplospirella wissmanni* (Münster). The two taxa referred to above are, without any shadow of a doubt, to be regarded as two different forms, not only because of the aureole in *Diplospirella aureolata* (Cornalia) but also because the latter presents: an outline tending to suboval, a short cardinal margin, valves less convex, more developed deltidial plates, a median septum and muscle field decidedly less marked.

**Distribution.** *Diplospirella aureolata* (Cornalia) is recorded from Carnian of Southern Alps.

**Occurrence.** Alpe di Specie, Giau, Misurina, Sass de Stria, Campo, Rumerlo, Vervei, Milieres, Cason dei Caài, Tamarin, Staolin.

*Acknowledgements.*

The authors sincerely thank C. Rossi Ronchetti and M. Gaetani for critical review of the manuscript. Sincere thanks are also extended to A. Rizzi (C.N.R.) for SEM, G. Chiodi for photographs and S. Antico for graphics.

Drawings by C. Ferliga.

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## PLATE 7

- Fig. 1 - Cardinalia: *Diplospirella sufflata* (Münster).
- Fig. 2 - Cardinalia: *Diplospirella wissmanni* (Münster).

## PLATE 8

*Diplospirella wissmanni* (Münster).

Serial transverse sections from 1.10 mm to 5.10 mm from umbo (acetate peels). Misurina N. 5819/20. Length 10.40 mm, width 8.75 mm, thickness 6.35 mm; x 4.

## PLATE 9

*Diplospirella wissmanni* (Münster).

Same specimen as in Pl. 8.

Serial transverse sections from 5.25 mm to 6.35 mm from the umbo (acetate peels).

## PLATE 10

*Diplospirella sufflata* (Münster). Serial transverse sections (acetate peels).

Fig. 1 - Alpe di Specie N. 5827/36. Length 7.00 mm, width 5.90 mm, thickness 5.00 mm; x 6.

Fig. 2 - Alpe di Specie N. 5827/62. Length 6.50 mm, width 6.00 mm, thickness 4.50 mm; x 5.

## PLATE 11

*Diplospirella aureolata* (Cornalia). Serial transverse sections (acetate peels).

Fig. 1 - Alpe di Specie N. 5836/7. Length 7.50 mm, width 8.10 mm, thickness 3.60 mm; x 4.5.

Fig. 2 - Misurina N. 5836/10. Length 6.95 mm, width 6.45 mm, thickness 3.25 mm; x 5.

Fig. 3 - Detail of the jugum (3.40 mm from the umbo). Same specimen as in fig. 1; x 40.

## PLATE 12

Fig. 1 - *Diplospirella sufflata* (Münster). a-e) Ventral, dorsal, lateral, anterior, posterior views. Misurina 5829/25; x 4.

Fig. 2 - *Diplospirella sufflata* (Münster). a-e) Ventral, dorsal, lateral, anterior, posterior views. Giau 5828/12; x 5.

Fig. 3 - *Diplospirella sufflata* (Münster). a-e) Ventral, dorsal, lateral, anterior, posterior views. Giau 5828/3; x 5.

## PLATE 13

Fig. 1 - *Diplospirella wissmanni* (Münster). a-e) Ventral, dorsal, lateral, anterior, posterior views. Milieres 5823/9; x 4.

Fig. 2 - *Diplospirella wissmanni* (Münster). a-e) Ventral, dorsal, lateral, anterior, posterior views. Partially decorticated specimen showing, in dorsal and anterior views, the fibers of secondary layer which converge towards median plane. Alpe di Specie 5817/85; x 4.

Fig. 3 - *Diplospirella aureolata* (Cornalia). a-e) Ventral, dorsal, lateral, anterior, posterior views. Alpe di Specie 5836/40; x 5.

Fig. 4 - *Diplospirella aureolata* (Cornalia). a-e) Ventral, dorsal, lateral, anterior, posterior views. Juvenile stage: the aureola is clearly developed. Milieres 5843/20; x 5.

Fig. 5 - *Diplospirella aureolata* (Cornalia). a, b) Ventral, anterior views. Specimen with typical circular outline. Milieres 5843/16; x 5.

## PLATE 14

Fig. 1 - *Diplospirella wissmanni* (Münster). Dorsal view showing alate expansions. Milieres 5822/9.

Fig. 2 - *Diplospirella wissmanni* (Münster). Internal view of pedicle valve. Visible part of brachidium. Alpe di Specie 5817/26; x 12.75.

