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ANISACTINELLA BITTNER, 1890 (BRACHIOPODA, TRIASSIC): MORPHOLOGICAL STRUCTURES AND THEIR FUNCTIONAL MEANING

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Riassunto. È stato riesaminato alla luce delle moderne indagini (SEM, peels) il genere *Anisactinella* Bittner, 1890, analizzando in particolare *Anisactinella quadriplecta* (Münster, 1841) e *Anisactinella maurensis* Taddei Ruggiero, 1968.

Il materiale, costituito da forme giovanili ed adulte, proviene da aree diverse. *Anisactinella quadriplecta* è stata raccolta nella parte superiore della Formazione di San Cassiano (Carnico) affiorante nella conca ampezzana (Belluno), *Anisactinella maurensis* nei livelli marnosi associati a calcari neri della Formazione di Monte Facito (Anisico? - Ladinico inf.), affioranti a Pietra Maura (Bacino del Lagonegro, Basilicata).

Lo stato di conservazione per entrambe le specie si può definire buono ed ha permesso di condurre indagini complete sia sulla morfologia esterna ed interna della regione posteriore, sia sul brachidio. I risultati hanno evidenziato che nell'interarea brachiale il processo cardinale emerge all'esterno della conchiglia, dando luogo ad una nuova struttura morfologica, denominata "apofisi esterna del processo cardinale". Tale processo è sempre stato osservato all'interno delle valve, celato in modo più o meno accentuato dalle strutture deltidiali (sensu Rudwick, 1970) della valva peduncolare.

Molto significativa è risultata la relazione tra superficie interna delle valve, che replica in negativo l'ornamentazione esterna, e la disposizione degli spiralia. Questi ultimi infatti si addossano contro la superficie interna delle valve incastrandosi nell'intervallo tra costa e costa interne, deformando così l'andamento dei coni. In particolare, le basi dei coni nella valva brachiale si incuneano nella prima costa laterale, lasciando libero lo spazio corrispondente alla costa mediana e divergendo dorsalmente.

Le analisi morfofunzionali hanno dimostrato un legame tra questi due caratteri morfologici, in quanto l'apofisi esterna del processo cardinale svolge una azione di ostacolo all'apertura delle valve; dall'altra parte la disposizione degli spiralia, così infossati nei solchi intercostali interni, risulta una soluzione adattativa effettivamente vantaggiosa solo se si ha una minima apertura delle valve.

Inoltre nell'ambito della revisione della fauna a Brachiopodi della Formazione di San Cassiano dell'area di Cortina d'Ampezzo è stata riesaminata criticamente *Anisactinella quadriplecta* con le sue numerose "varietà".

Summary. SEM and peel observations were carried out on two taxa of the genus *Anisactinella* Bittner, 1890, namely *Anisactinella quadriplecta* (Münster, 1841) and *Anisactinella maurensis* Taddei Ruggiero, 1968.

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The presence of a peculiar morphologic structure, herein named external apophysis of the cardinal process, has been observed for the first time.

The function of this structure may be the hindrance of the opening of the shell. In fact, the morphology of both the valves and the brachidium, as well as their relationships are efficient only if the valves open slightly. This may account for the presence of the external structure.

Anisactinella quadriplecta recovered from the San Cassiano Formation, Cortina d'Ampezzo area (Belluno) is revised. Its high variability has been put to evidence on the basis of a crytical analysis.

Introduction.

The analysis of *Anisactinella quadriplecta* (Münster, 1841) and *Anisactinella maurensis* Taddei Ruggiero, 1968 led to the description of new morphological characters of the genus *Anisactinella* Bittner, 1890, and to the understanding of their functional meaning. Furthermore, the re-examination of *Anisactinella quadriplecta* offers a new contribution to the revision of the brachiopod fauna of the upper San Cassiano Formation (Carnico), Cortina d'Ampezzo area (Belluno) which was started by Benigni and Ferliga (1989, 1990) with the examination of the genera *Thecospira* Zugmayer, 1880 and *Diplospirella* Bittner, 1890.

Anisactinella quadriplecta is the only representative of the genus in the San Cassiano Formation. The taxon, which shows a remarkable variability, is widespread throughout the area, since it is present at 11 out of 14 localities (Fig. 1) that yielded brachiopod assemblage reported in the literature (Benigni & Ferliga, 1990); however, it is not abundant (Table 1).

The specimens, collected by R. Zardini, are both juvenile and adult, the former well preserved, the latter often fractured and deformed; therefore the analysis of the internal characters is difficult to be carried out. Some disarticulated valves, both pedicle and brachial are also present.

Anisactinella maurensis is represented by topotypes collected and kindly donated by M. Gaetani from marls associated with black limestones of the Monte Facito Formation (Ciarapica et al., 1990 a) outcropping at Pietra Maura (Lagonegro Basin, Southern Italy: IGM 199 II NO). The age of this unit is considered to be Anisian?-Early Ladinian on the basis of microfacies (Ciarapica et al., 1990 a, b) and conodonts (Mietto et al., 1990). The specimens are complete, and direct observation of internal morphology was prevented by the absence of disarticulated valves. The state of preservation of the shell material is good, without evident fractures or deformation; specimens with recrystallized nucleus are frequent, however, this does not totally obliterate the brachidium.

Juvenile as well as adult specimens belonging to both taxa were observed with SEM, and peels of serial transverse sections were viewed by means of conventional optical microscopy, in order to make a better comparison between internal and external structures.

The material is temporarily entrusted to the Museo di Paleontologia, Dipartimento di Scienze della Terra, Milano.

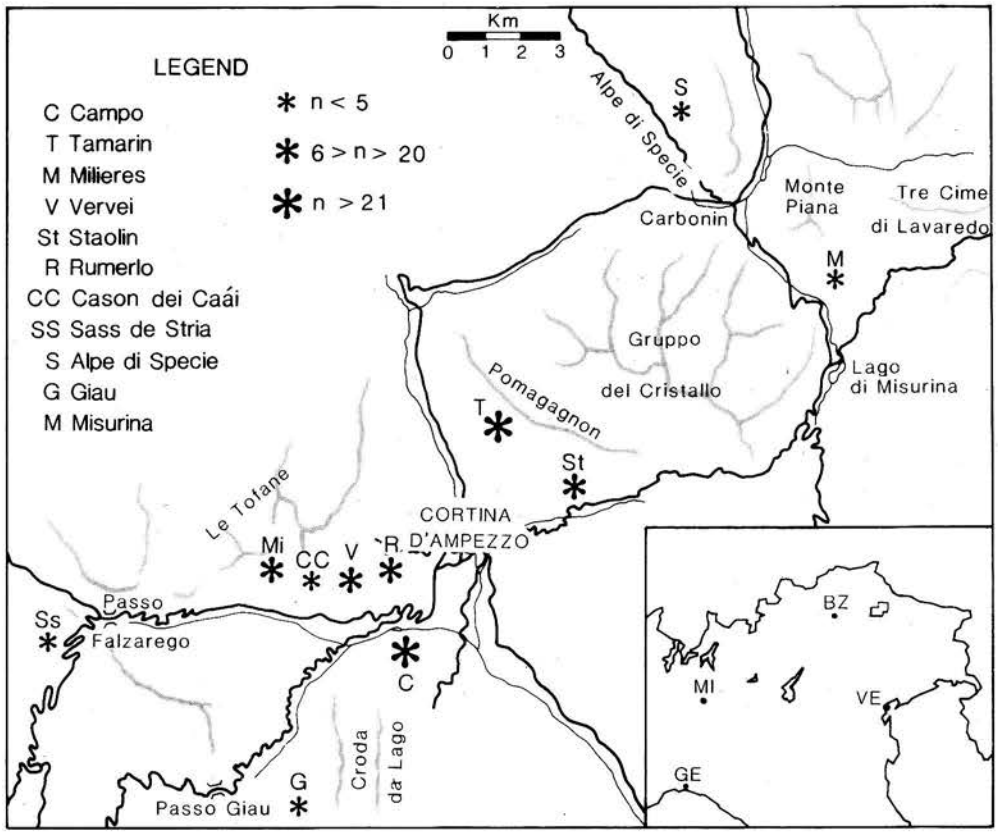


Fig. 1 - Location of the fossil localities in the San Cassiano Formation of the Cortina d'Ampezzo area (Belluno). n: number of specimens.

Anisactinella quadriplecta (Münster)	*Campo (C)*	*Tamarin (T)*	*Milieres (M)*	*Vervei (V)*	*Staolin (ST)*	*Rumerlo (R)*	*Cason dei Caài (CC)*	*Sass de Stria (Ss)*	*Specie (S)*	*Giau (G)*	*Misurina (M)*	*TOTAL*
Whole shells	38	22	11	6	3	2	1	5	3	1	1	93
Disarticulated valves	11	19	4	3	-	-	-	-	-	-	-	37

Table 1 - Frequency of the taxon *Anisactinella quadriplecta* (Münster) in the localities of the Cortina d'Ampezzo area.

Notes about morphological terms: plates or not?

In the descriptions of the morphology of the posterior area, parts such as pseudodeltidium, deltidium, deltidial plates are generally considered as plates (Moore, 1965, pp. H139-H155). In the present study the terms structure or element, instead of plate, are used referring to the delthyrial covers in agreement with Rudwick's remarks (1970, p. 59). In fact, the term plate indicates one element which is independent from the rest of the valve and with its own way of growth, while the delthyrial covers are parts of the valve surface and develop concomitant to it. Examples of plates are the stegidium (Cowen, 1968) and the cooperculum (Hoover, 1983).

Analogous considerations can be drawn about the internal structures of the valves. Terms such as dental plates and cardinal plates actually indicate elements with are a part of the valve and not isolated structures.

In order to avoid further confusion we suggest that newly discovered structures should be named taking into account that distinction. Terms such as lamina, lamella, apophysis may replace plate.

Posterior area.

External morphology. This part of the shell has been already described for *Anisactinella quadriplecta* by Münster (in Wissmann & Münster, 1841), Laube (1865) and Bittner (1890). However, the authors focussed their attention only on the pedicle region.

Taddei Ruggiero (1968), describing the new species *Anisactinella maurensis* wrote: "La linea cardinale è pressochè rettilinea; l'apice è piccolo e diritto; il foramen è rotondo; l'area è piccola, triangolare, ben delimitata" (1).

Also in the diagnosis of the genus *Anisactinella* given by Boucot et al. (1965) in Treatise, p. H664, the external morphology of this region is not considered but for a brief mention to "Cardinal plate well developed". Therefore, the external and internal characters of the posterior area are herein dealt with in detail.

The genus *Anisactinella* includes shells with a narrow interarea and with a few millimeters-long cardinal margin, which in *Anisactinella maurensis* is longer than in *Anisactinella quadriplecta*. The ventral interarea is more developed than the dorsal one. The supra-apical, ovoidal foramen is present (Fig. 2).

The element which covers partially the delthyrium is peculiar. In fact, it is a unique irregularly triangular structure showing, in the median position of the posterior margin, an arcuate outline in *Anisactinella quadriplecta* (Fig. 3), while it is almost straight in *Anisactinella maurensis* (Fig. 4). This structure has not relationships with the

(1) "The hinge line is almost rectilinear; the apex is small and straight, the foramen is round; the area is small, triangular and well defined".

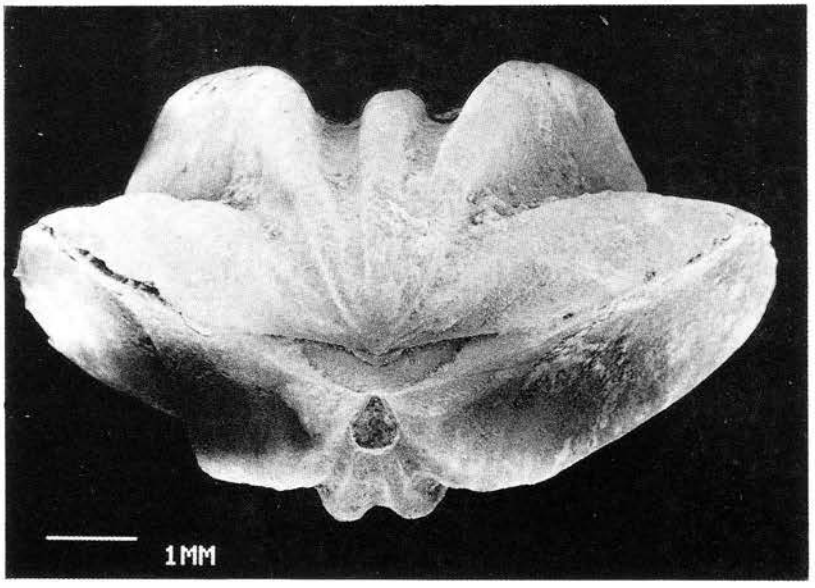


Fig. 2 - *Anisactinella quadriplecta* (Münster). View of the posterior area. The supra-apical foramen, the inter-area, the small cardinal margin and the external apophysis of the cardinal process can be seen. Milieres N. 5849/4.

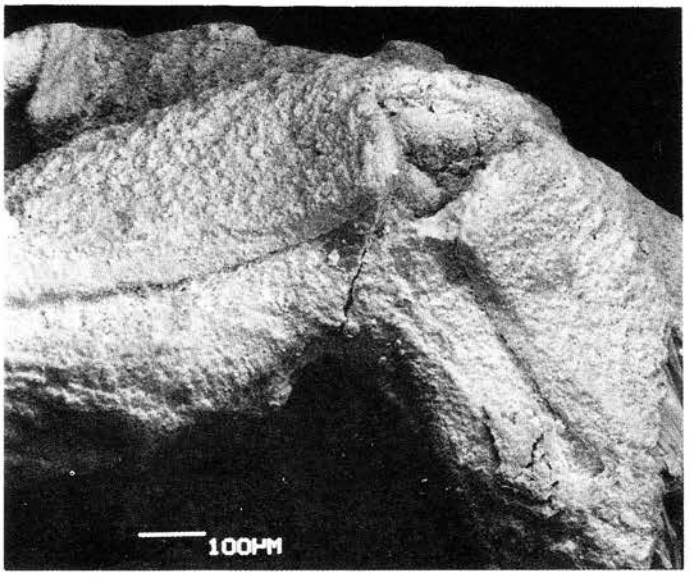


Fig. 3 - *Anisactinella quadriplecta* (Münster). Pedicle valve. Detail of the "atypical pseudodeltidium". Note the curved shape of the dorsal margin. Tamarin N. 5848/27.

foramen (Fig. 4), and therefore cannot be considered a deltidium nor shows the typical morphology of a pseudodeltidium, which is perfectly triangular. However, it has same function and position of the latter because it covers partially the delthyrium. Accordingly, we do not introduce a new name and prefer to consider it an atypical pseudodeltidium (Fig. 3, 4). This choice has been made to avoid further proliferation of morphological terms which are too many and often synonymous of one another. It is of note that Bittner (1890) in his description of *Anisactinella quadriplecta* reported on a large delthyrial aperture closed by a pseudodeltidium.

The posterior region of the brachial valve is extremely narrow and it is possible to determine the whole characteristics of its morphology only by means of SEM observations. This may account for the scantiness of informatiom up to now.

The interarea is very narrow, like a linear border (Fig. 5, a).

The most characteristic element of the brachial posterior region is the cardinal process which unusually protrudes outside the shell, being not covered by the atypical pseudodeltidium.

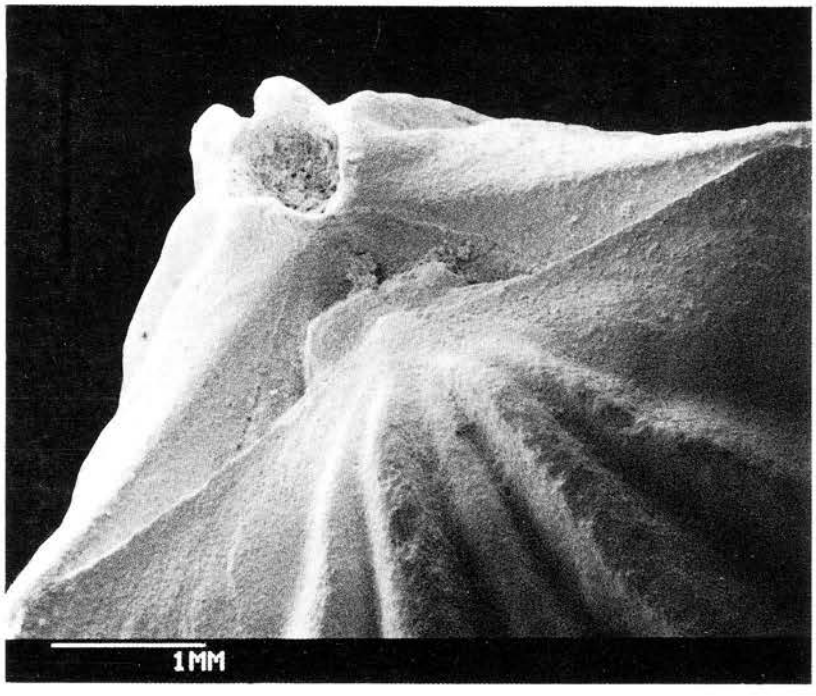


Fig. 4 - *Anisactinella maurensis* Taddei Ruggiero. Dorsal view of posterior region: foramen separated from the atypical pseudodeltidium. External apophysis of the cardinal process with subrectangular shape. Pietra Maura N. 6644.

Transversal sections of the posterior region of specimens with hinged valves show the edge of the cardinal process in an external position with respect to the atypical pseudodeltidium (Fig. 6, b, e, f, g). Only in the proximity of the hinge line the cardinal process fits into the delthyrial cavity (Fig. 6, c, d). Therefore, the externally visible structure is not merely a surface which emerges in corrispondence with the atypical pseudodeltidium basal hollow. In the observed specimens, the cardinal process actually shows a marked external apophysis that leans against the atypical pseudodeltidium (Fig. 4 and 5, b).

For these morphological characteristics we propose to denominate the structure: "External apophysis of the cardinal process". The term "apophysis" is here introduced because it corresponds to an external projection of the cardinal process.

The external morphology of the examined cardinal process is peculiar, and has been observed up to now only in *Anisactinella,* being present in all growth stages (Fig. 6, a). In fact, the cardinal process is generally completely covered by the pedicle valve in those forms having a narrow interarea.

This structure is always more wide than long and shows different shapes according to species: in *Anisactinella quadriplecta* (Fig. 7) it is semicircular while in *Anisactinella maurensis* it is subrectangular (Fig. 4 and 5, b).

Furthermore, the external apophysis of the cardinal process is expanded in such a way not to fit exactly into the basal hollow of the atypical pseudodeltidium. The lateral angles protrude and lean on this latter (Fig. 5, b), resulting in an obstacle to the opening of the valves.

Internal morphology. In the posterior region of the pedicle valve the teeth represent the most significant structure. Massive and with triangular profile, the teeth are well developed and protrude directly from the floor of the valve (Fig. 8, a, b). The brachial valve in this same zone of the shell shows these significant structures (Fig. 9):

- well developed socket ridges, the more evident of which is the internal one;
- cardinal process;
- apical cavity.

The cardinal process, which has been in part already described, can be easily observed in the internal part of the brachial valve where it represents the most important element. It consists of a high, massive, plate-like, subtrapezoidal feature which protrudes towards the brachial valve (Fig. 10). It makes a bridge with respect to the apical cavity (Fig. 11, d).

The apex of the cardinal process, represents the external apophysis and does not fit within the delthyrial cavity. The muscles are attached to the surface facing the pedicle valve. The attachment of the muscles is favoured by the presence of two lateral

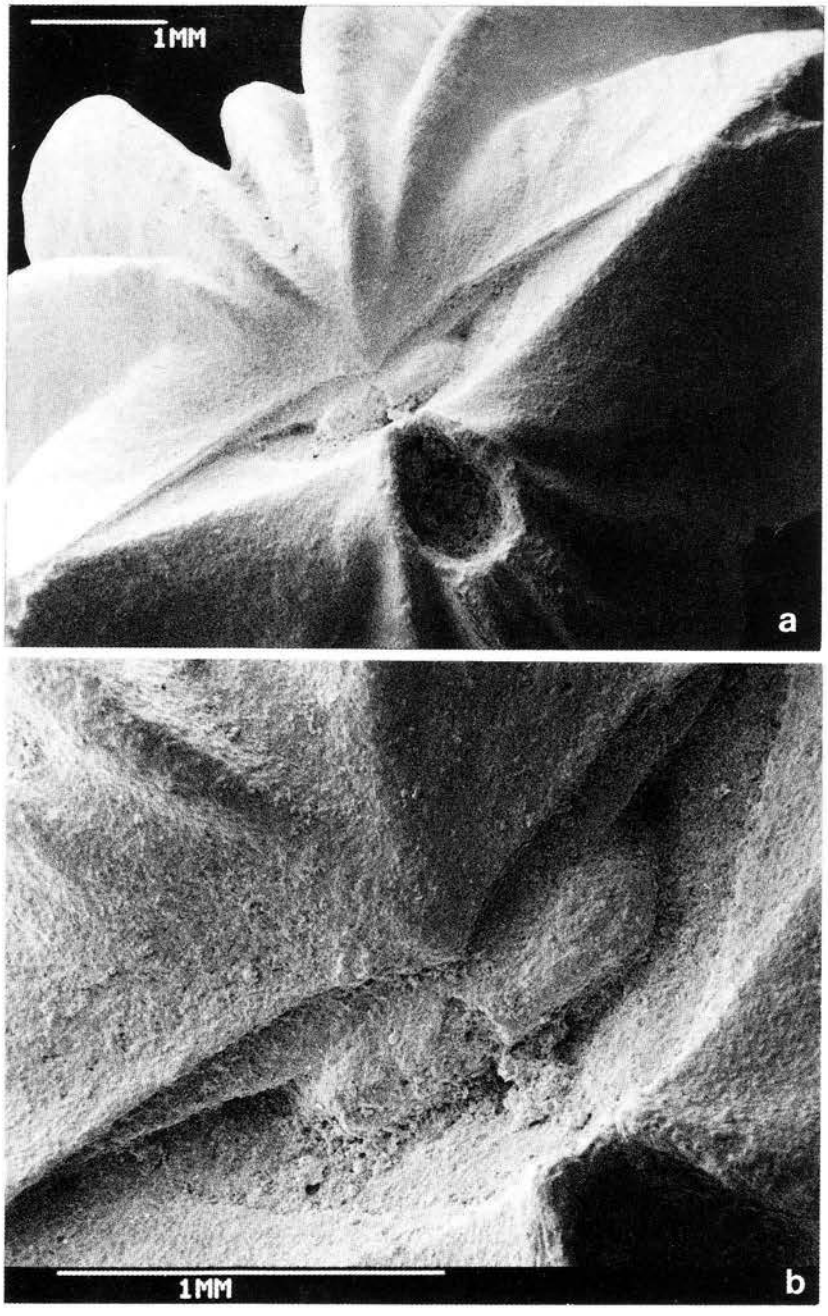


Fig. 5 - *Anisactinella maurensis* Taddei Ruggiero. Same specimen as in Fig. 4. Posterior view. a) Visible the narrow interarea of the brachial valve; b) detail of the same interarea with the external apophysis of the cardinal process leaning on the atypical pseudodeltidium. Pietra Maura N. 6644.

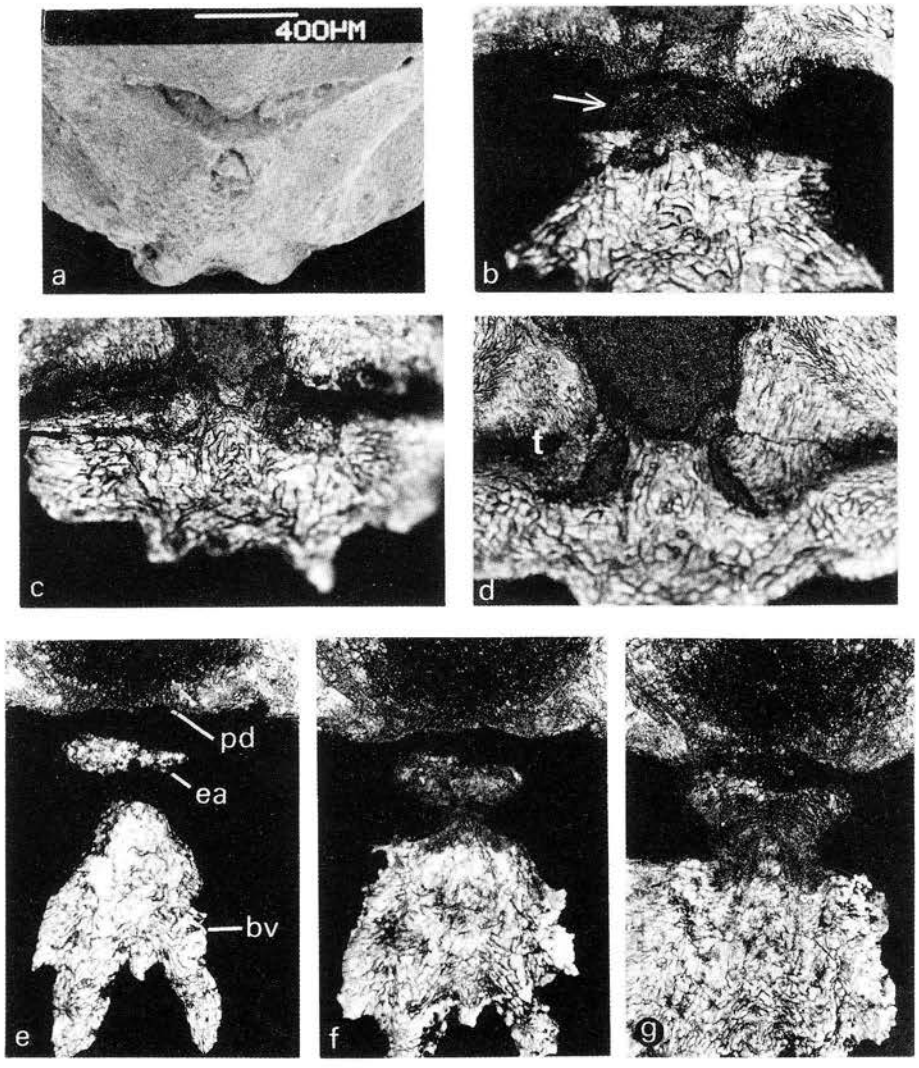


Fig. 6 - *Anisactinella quadriplecta* (Münster). a) Juvenile specimen. The external apophysis of the cardinal process is already well developed; b) 0.50 mm, the external apophysis of the cardinal process (arrow) leans against the atypical pseudodeltidium; c) 0.70 mm, detail before the hinge line. The cardinal process begins to fit into the delthyrial cavity; d) 0.90 mm, detail of the cardinal process and teeth (t).
Anisactinella maurensis Taddei Ruggiero; e) 1.15 mm, atypical pseudodeltidium (pd), external apophysis of the cardinal process (ea); umbonal area of the brachial valve (bv); f) 1.25 mm; g) 1.35 mm, the external apophysis of the cardinal process is joint to the brachial valve.
Tamarin N. 5848/5 (a); N. 5848/2 (b-d). Pietra Maura N. 6645 (e-g). (For transverse sections, distances are from pedicle umbo).

and divergent ridges that in their distal position are connected with the inner socket ridges. Accessory ridges occur at a median position in the distal part: one in *Anisactinella quadriplecta* (Fig. 10 and 11, b), three in *Anisactinella maurensis* (Fig. 11, d).

Dagys (1974) described the presence of a groove on the lateral surface of the cardinal process of *Anisactinella quadriplecta* into which a denticulum-like structure of

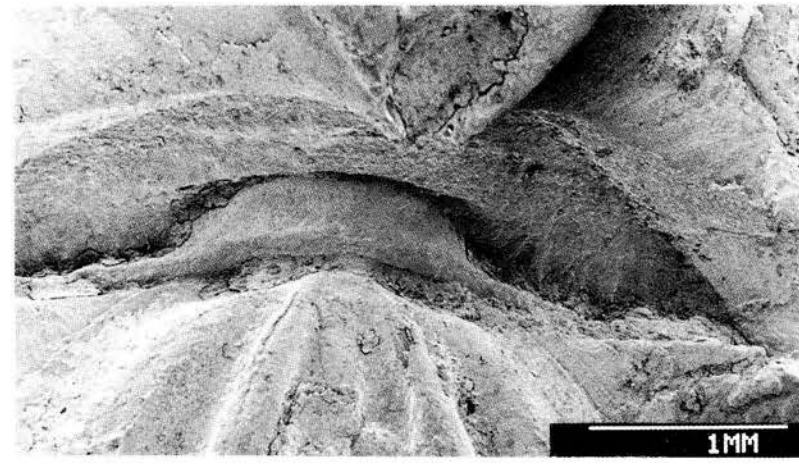


Fig. 7 - *Anisactinella quadriplecta* (Münster). External apophysis of the cardinal process. Note the arcuate outline. Campo N. 5847/20.

the pedicle valve fits. This structure protrudes from the internal surface of the valve immediately below the tooth and is clearly visible in Dagys' fig. 12. However, it has never been observed by us perhaps because of the scarcity of specimens. Again, the structure seems to hinder the opening of the valves. In *Anisactinella maurensis* the lateral surface of the cardinal process is smooth and regular, devoid of grooves. The examined structure may therefore be a specific character of *Anisactinella quadriplecta.*

This kind of cardinal process greatly differs from the others described in literature in having a) a part external to the shell and b) the consequent position of attachment of the muscles.

The apical cavity deeply wedges itself below the cardinal process. Therefore, the "cardinal lamina" is not present as in the genus *Diplospirella*, a taxon which belongs to the same subfamily *Diplospirellinae* to which also the genus *Anisactinella* belongs. The cardinalia of the two genera are very different because in the genus *Diplospirella* the cardinal process is replaced by cardinal plates, cardinal lamina and cardinal pit that obliterate the apical cavity.

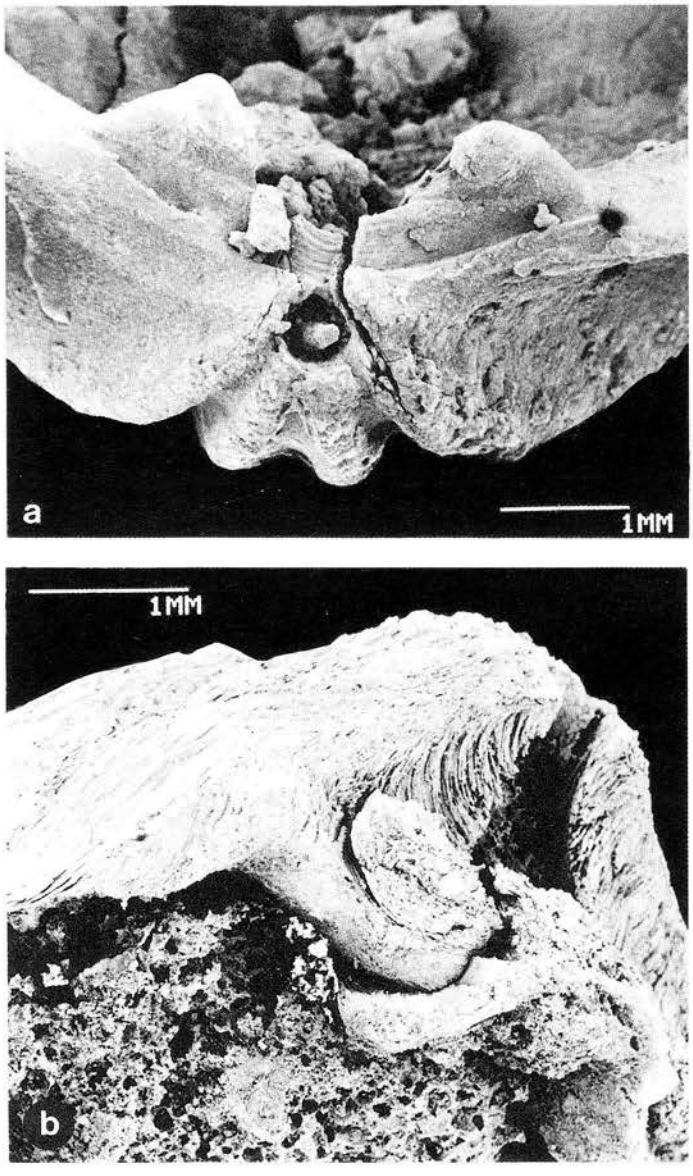


Fig. 8 - *Anisactinella quadriplecta* (Münster). a) Pedicle valve. Posterior view of the teeth. b) Tooth fitting into the dental socket. Tamarin N. 5448/39 (a). Campo N. 5847/48 (b).

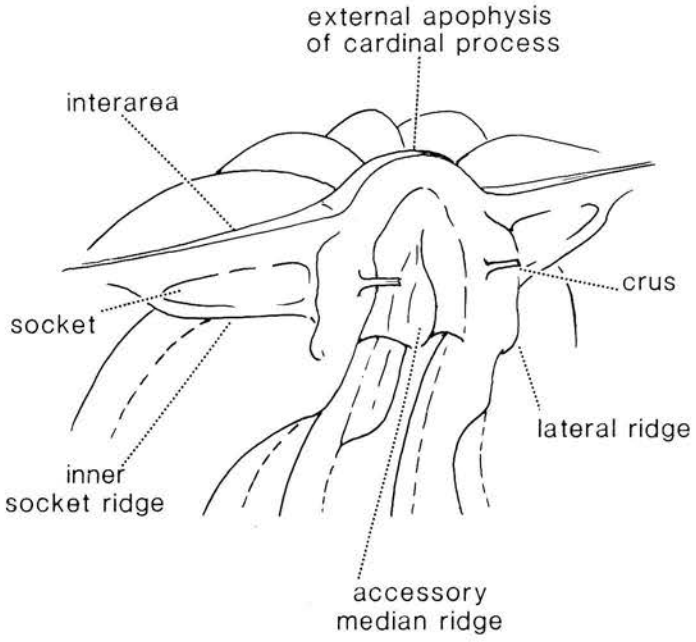


Fig. 9 - Schematic representation of the posterior area of *Anisactinella quadriplecta* Münster. (Brachial valve).

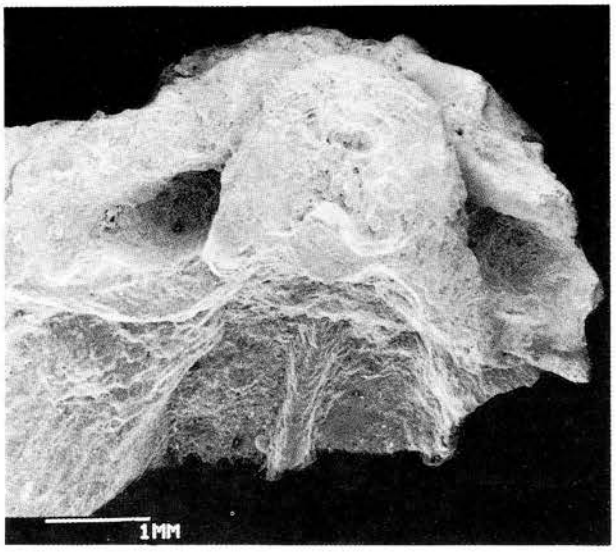


Fig. 10 - *Anisactinella quadriplecta* (Münster). Internal view of brachial valve. The cardinal process is partially corroded. It is possible to observe the median ridge and the lateral ridges in continuity with inner socket ridges. Vervei 5850/8.

Brachidium.

It is necessary to describe some aspects of the brachidium before discussing the morphological function of the previously described structures.

The brachidium of *Anisactinella* is of *"Athyris"* - type in that it consists of cone-shaped spiralia with laterally pointing apexes. Each cone is composed by double spineless lamellae.

The crura are well developed. In *Anisactinella quadriplecta,* the crura are long, thin, projecting ventrally and joined to the lateral ridges of the cardinal process at the dental sockets (Fig. 11, a, b and 12). In *Anisactinella maurensis* the crura are short and stocky, in distal position and continuous with the inner socket ridge (Fig. 11, e).

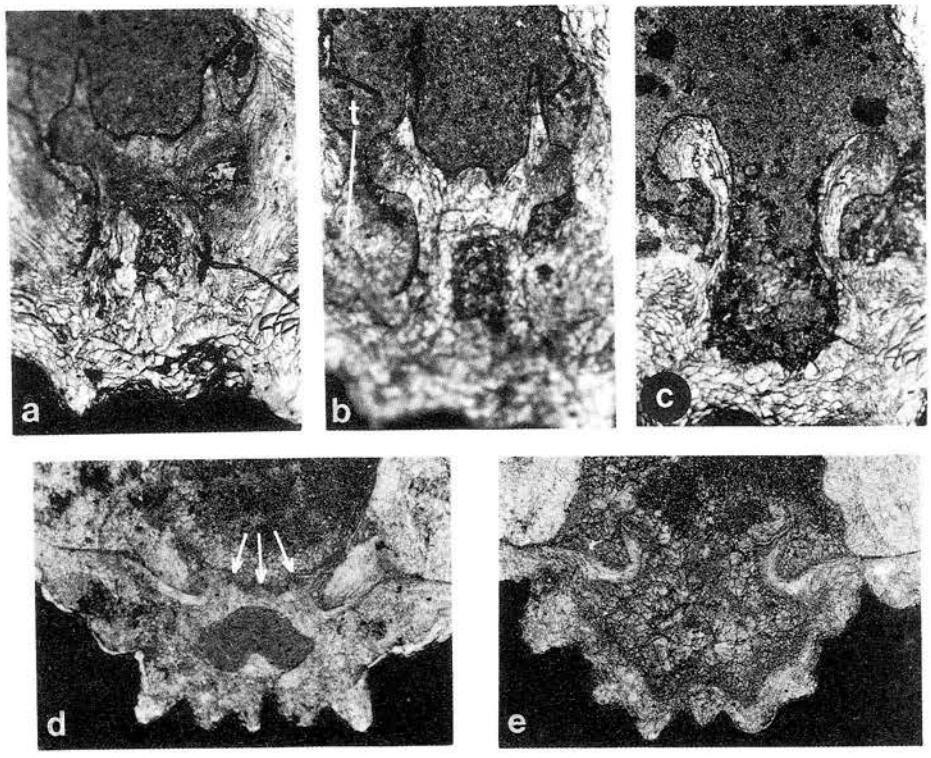


Fig. 11 - Transverse sections, distances are from pedicle umbo. *Anisactinella quadriplecta* (Münster); a) 1.00 mm, visible thin, sharp crura which start from the lateral ridges of the cardinal process; b) 1.05 mm, note the median ridge of the cardinal process, the crura and the umbonal cavity. Teeth are still present (t); c) 1.20 mm, lateral ridges of the cardinal process extending beyond the inner socket ridges.
Anisactinella maurensis Taddei Ruggiero; d) 1.80 mm, note the ridges on the cardinal process (arrows), umbonal cavity, median septum; e) 2.00 mm, detail of the crura. Tamarin 5848/2 (a-c). Pietra Maura N. 6645 (d-e).

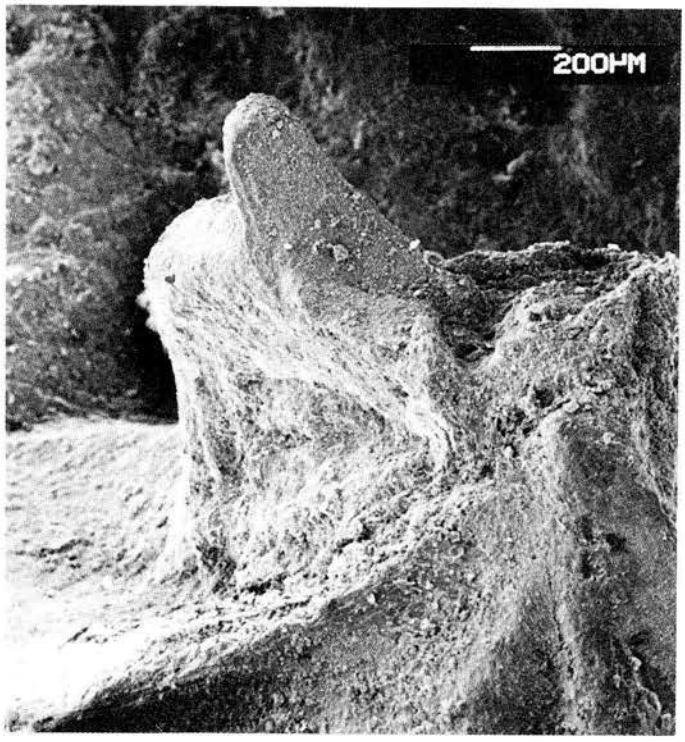


Fig. 12 - *Anisactinella quadriplecta* (Münster). Brachial valve, posterior view. Lateral ridges of the cardinal process which support the crus. (To the left: broken inner socket ridge). Campo N. 5847/39.

The jugum is in posterior and dorsal position, leaning against the internal surface of the brachial valve. It shows two lateral apophyses extending towards this latter. It does not show apophyses protruding towards the pedicle valve (Fig. 13).

In the taxon *Anisactinella maurensis* the primary lamellae at the level of the jugum thicken ventrally and curl up towards the plane of simmetry until they coalesce in a massive jugum. From the jugum two thick lateral apophyses, subparallel to the primary lamellae, extend to about half the length of the lamellae (Fig. 13, c). In *Anisactinella quadriplecta* the primary lamellae are thin and converge towards the middle, without welding, because they fit into a massive, wide and subrectangular structure. The lateral apophyses are thinner and shorter compared to the ones of *Anisactinella maurensis* (Fig. 13, a, b).

The spiralia are joined to the crura and consist of about 8 convolutions. They lean against the internal surface of the valves. Because this surface reflects the external ornamentation, the cones of the spiralia are deformed. The bases of cones diverge dorsally because the first convolution fits into the lateral costa (Fig. 14; Pl. 31, fig. 2).

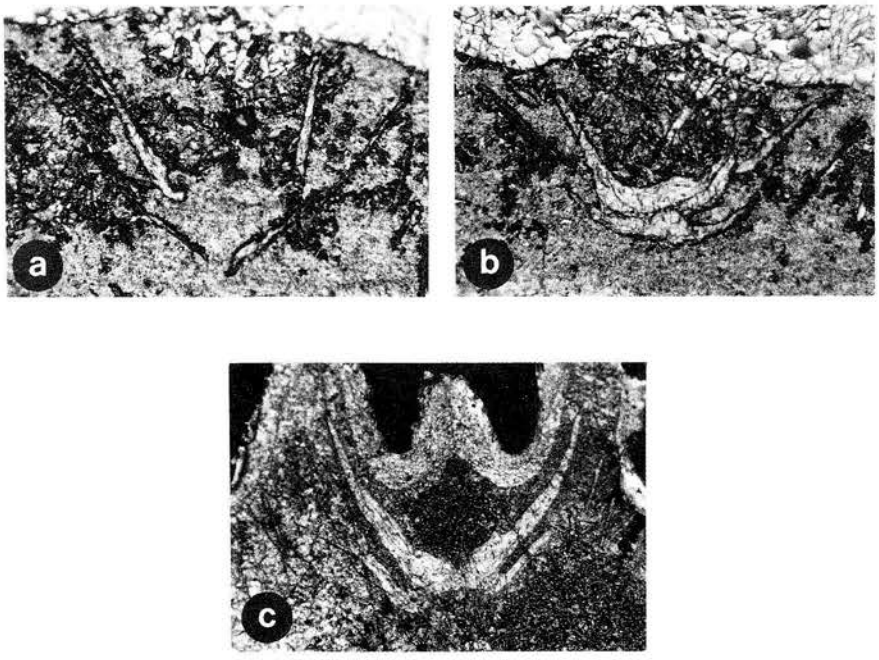


Fig. 13 - Transverse sections, distances are from pedicle umbo. Brachial valve at the top. *Anisactinella quadriplecta* (Münster); a) 2.10 mm, detail of primary and secondary lamellae immediately before the jugum; b) 2.15 mm, detail of the jugum.
Anisactinella maurensis Taddei Ruggiero; c) 3.00 mm, detail of the jugum. Tamarin N. 5848/2 (a, b). Pietra Maura N. 6646 (c).

As a consequence, the space corresponding to the median costa is free. This morphological character is more accentuated in *Anisactinella maurensis* than in *Anisactinella quadriplecta.*

It was not possible to observe juvenile specimens of *Anisactinella quadriplecta* because few shells are in a good state of preservation. However, in a perfectly preserved specimen of *Anisactinella maurensis* the brachidium shows at least three visible convolutions (Pl. 31, fig. 3).

Comparison with the brachidium of Diplospirella Bittner, 1890.

With respect to the genus *Diplospirella* Bittner (cf. Benigni & Ferliga, 1990), belonging to the same subfamily *Diplospirellinae,* the brachidium of *Anisactinella* Bittner shows a more simple jugum which is devoid of both ventral and dorsal apophyses. The lateral apophyses do not expand laterally as in *Diplospirella* but point towards the top. The primary lamellae are directly fused to the jugum, therefore the lateral branch

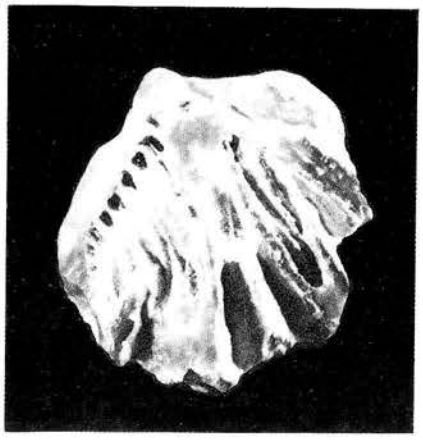


Fig. 14 - *Anisactinella maurensis* Taddei Ruggiero. Specimen with part of the shell missing. The double spiral lamellae of the brachidium fitting into the costae can be observed. Pietra Maura N. 6667.

of jugum in *Anisactinella* is lacking. The whole brachidium is fused to the crura and is not connected to them by organic tissue such as in *Diplospirella.*

The presence of a skeletal welding between crura and brachidium explains the absence of laterally expanded apophyses with stabilizing function which, on the other hand, are necessary in *Diplospirella.*

Functional morphology.

In the present chapter we refer to life strategies already known and well described by Rudwick (1970).

The genus *Anisactinella* shows both internal and external morphological features which are mutually related in order to improve the living strategy of the taxon:

A) Anterior zig-zag deflections in the commissure. A benthic, sessile, suspension-feeder brachiopod must maintain the minimum possible aperture of the valves in order to hinder the passage of large particles that may damage the organism. Furthermore, the edges of the mantle should be kept at close distance. With a given valve anterior gape and the same commissure length, a zig-zag commissure offers a wider section for the inhalant and exhalant fluxes and this represents an advantage favouring the exchanges with the surrounding environment.

B) Costae and furrows that are reversely mirrored in the internal surface. Water circulation in a brachiopod is unidirectional and therefore, it is necessary to separate the inhalant from the exhalant fluxes. This is made possible by the filaments of the lophophore that divide the mantle cavity into exhalant and inhalant chambers.

In *Anisactinella* the costae and furrows of the internal surface (Fig. 15) favour this division of the mantle cavity. In fact, the bases of cones of spiralia fit themselves

into the furrows (Pl. 31, fig. 2) and improve the separation between the two currents the mixing of which is hindered both by the filaments and by the wall of the costa.

These two morphological characters are functional only when the brachiopod also has a limited aperture of the valves. Otherwise the lophophore would not be capable to maintain two separate currents; the zig-zag commissure would not be sufficient to prevent the large particles from entering and the brachidium would be damaged by crushing against the costa if movements were ample.

C) External apophysis of the cardinal process. This morphological character is such to represent a physical obstacle to the valves opening, its presence serves to limit the width of the gape between valves. The genus *Anisactinella* is constrained to develop an external structure with the specific function of blocking the aperture of the valves. In fact, the short cardinal margin as well as the narrow brachial interarea, cannot hinder the aperture of the valves.

The dimensions of the external apophysis are related with the presence (or absence) of internal elements which have an analogous function in blocking the aperture. In fact, in *Anisactinella quadriplecta* the internal structure observed by Dagys (1974) is associated with the small dimensions of the external apophysis of the cardinal process and helps this latter in hindering the width of the aperture of the valves. In *Anisactinella maurensis* the external apophysis is wider and more efficient, therefore the presence of an internal structure with equivalent function is superfluous.

Water circulation in *Anisactinella* is influenced also by an other morphological aspect. The arrangement of the bases of the cone shaped spirals, infact, allows the development of a central cavity with triangular cross-section, the base of which is set in corrispondence with the first two lateral brachial furrows and of the median furrow (Fig. 16). The cones delimit the two small lateral cavities, which develop between the

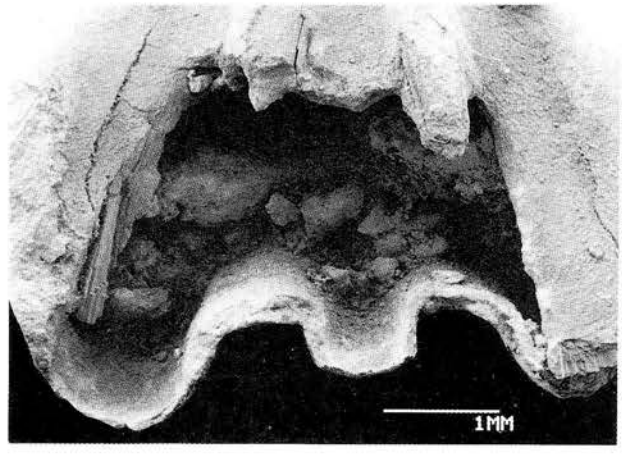


Fig. 15 - *Anisactinella quadriplecta* (Münster). Anterior margin. View of the internal surface which shows costae and furrows as a response to external ornamentation. Milieres N. 5849/11.

Fig. 16 - Scheme showing water circulation within the shell of *Anisactinella*. White) inhalant chamber; dotted) exhalant chamber; broken arrows) inhalant flux; black arrows) exhalant flux.

internal surface of the valves and the external surface of the cone.

A similar internal morphology suggests a straight flux from the small lateral cavities to the spiralia, towards the wide central cavity where a decrease of the pressure is to be expected because of the larger space. Therefore we believe that the two lateral cavities had the function of inhalant chambers, while the central cavity represented the exhalant chamber (Fig. 16).

The characteristics described are the result of adaptative solutions which exaggerate some morphological elements normally present in most *Spiriferida*, such as the presence of alternating costae and furrows (reflected also on the internal surface of the shell) and the presence of a spiral-shaped brachidium with the apex of the cones pointing laterally. The enhancement of both furrows and costae resulting in the reduction and modification of the internal space is connected with the fitting of the spiralia into the internal furrows, as well as with the necessity of having a minimum width of valve aperture in order to obtain the maximum efficiency. Therefore, it is also linked to the presence of an external apophysis of the cardinal process blocking the aperture.

Paleontological description

Taxonomic classification of the species is based on proposal of Dagys (1974).

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 *Anisactinella* Bittner, 1890

Type-species: *Terebratula quadriplecta* Münster, 1841 (in Wissman & Münster, 1841)

Anisactinella quadriplecta (Münster, 1841)

Pl. 28-30; Text - fig. 1, 2, 6-13, 15, 18-20

1841 *Terebratula quadriplecta* Münster, in Wissmann & Münster, p. 58, pl. 6, fig. 9a,b, 10a,b.
1865 *Retzia quadriplecta* - Laube, p. 22, pl. 13, fig. 6a-f, j (non g-i).
Non 1871 *Terebratula quadriplecta* - Quenstedt, p. 178, pl. 41, fig. 95, 96.
1890 *Spirigera quadriplecta* - Bittner, pp. 84, 91, 113, 157, pl. 37, fig. 22-24 "var." *euplecta*; pl. 38, fig. 4, 5 "var." *euplecta;* fig. 6 "var." *obliterans* (? pl. 2, fig. 19 "var." *costosa*)(non pl. 2, fig. 20, 21 "var." *confluens*).
1895 *Spirigera (Didymospira) quadriplecta* "var." *confluens* - Salomon, p. 82, pl. 2, fig. 24.
1895 *Spirigera (Didymospira) quadriplecta* "var." *tenuicostata* Salomon, p. 90, pl. 2, fig. 25-28.
1900 *Spirigera (Anisactinella) quadriplecta* - Bittner, p. 34, pl. 3, fig. 25, 26; fig. 27 "var." *euplecta;* fig. 28 "var." *costosa;* fig. 29 "var." *obliterans;* fig. 30 "var." *subconfluens.*
1902 *Spirigera (Anisactinella) matutina* Bittner, p. 521, pl. 24, fig. 21, 22.
1903 *Spirigera (Didymospira) quadriplecta* - Broili, p. 159, pl. 18, fig. 3.
1903 *Spirigera (Anisactinella) quadriplecta* "var." *tenuicostata* - Waagen, p. 447, text-fig. 4.
1903 *Spirigera (Anisactinella) quadriplecta* "var." *bicostosa* Waagen, p. 448, text-fig. 5.
1974 *Anisactinella quadriplecta* - Dagys, p. 163, pl. 45, fig. 5a-d; text-fig. 111.
1974 *Anisactinella quadriplecta* - Mackinnon, pl. 15, fig. 2; pl. 30, fig. 5.

Material. 130 specimens, 26 measured. Campo N. 5847/1-49; Tamarin N. 5848/1-41; Milieres N. 5849/1-15; Vervei N. 5850/1-9; Staolin N. 5851/1-3; Rumerlo N. 5852/1-2; Cason dei Caài N. 5853; Sass de Stria N. 5854/1-5; Alpe di Specie N. 5855/1-3; Giau N. 5856; Misurina N. 5857.

Description.

External characters. Biconvex shell with subpentagonal shape, generally longer than large. The maximum width is reached near the anterior region. Short and straight cardinal margin with narrow interarea. Wide flanks, a little sunken and formed by the pedicle valve. Lateral commissure with sinuous course. Convexity more pronounced in the pedicle valve than in the brachial one. In the pedicle valve the umbo is cross-cut by a supra-apical foramen and the delthyrium partially occluded by atypical pseudodeltidium. Brachial valve with maximum convexity in the umbonal region. Pointed and arcuate umbo, semicircular and small external apophysis of the cardinal process.

The ornamentation consists of marked costae with acute profile that develop from the umbo: 5 on the brachial valve and 4 on the pedicle valve. The brachial valve costae are thus arranged: a median costa flanked by two lateral ones. Furthermore there are two more distant external lateral costae. The median costa is thinner and less pronounced with respect to the two lateral costae. On the pedicle valve the costae of central region are one very near to the other and separated from the lateral costae by large and deep furrows (Fig. 17).

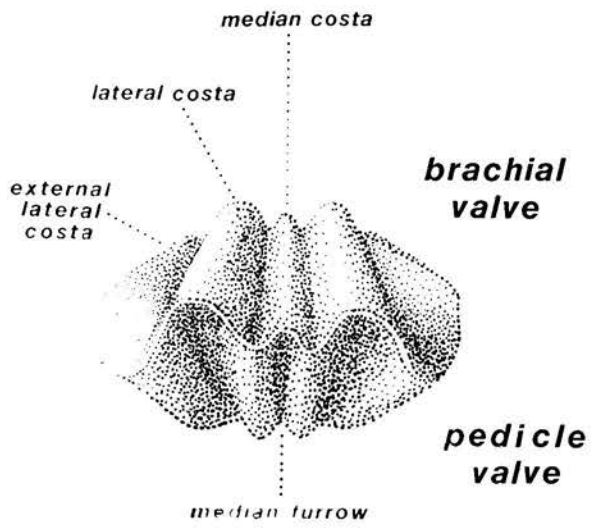


Fig. 17 - Scheme showing the arrangement of the costae in *Anisactinella quadriplecta* (Münster) as well as their nomenclature.

Biometric characteristics:

	L	W	T	W/L	T/L	T/W	N.sp
$\bar{x}$	0.66	0.63	0.37	0.97	0.59	0.61	26
s	0.33	0.31	0.16	0.11	0.12	0.12	26
sm	0.12	0.12	0.06	0.04	0.04	0.04	26

Internal characters. Pedicle valve with subrectangular deltyrial cavity, triangular massive teeth devoid of dental lamellae. Median septum not elevated, projecting from the umbonal cavity towards the anterior region where, at 1/3 of the total length of the valve thickens and stops (in some cases it makes a pronounced protrusion) branching into two elevated lateral septa and a little median septum (Fig. 18, a, b).

Brachial valve with high cardinal process composed of two lateral ridges (Fig. 11, c) extending beyond the inner socket ridges and an accessory ridge in median position (Fig. 11, b). Deep dental sockets, thin crura and weakly impressed muscle field divided by a median septum which is thin, hinted and extends from the umbo up to 1/3 of the total length of the valve (Fig. 19). Brachidium consisting in a double spiral lamellae, jugum composed of a rectangular saddle into which fit the two primary lamellae. Outside the muscle field it is possible to observe costae and furrows that represent the negative of the external ornamentation.

Ultrastructure. The primary layer has not been observed in the studied specimens. However, Mackinnon (1974), in Pralongià specimens, described and showed (pl. 15, fig. 2) a primary layer consisting of vertical crystals of calcite about 8 μm long.

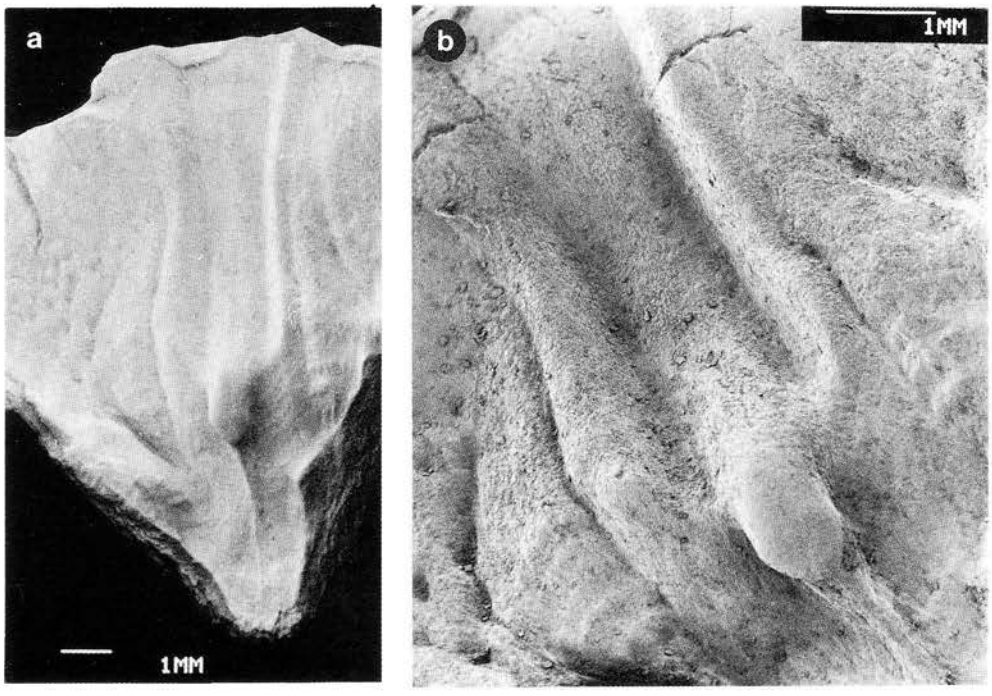


Fig. 18 - *Anisactinella quadriplecta* (Münster). Internal surface of broken pedicle valve. a) General view; b) detail of median septum. It is possible to see its thickening and its extention in lateral septa. Campo N. 5847/43 (a, b).

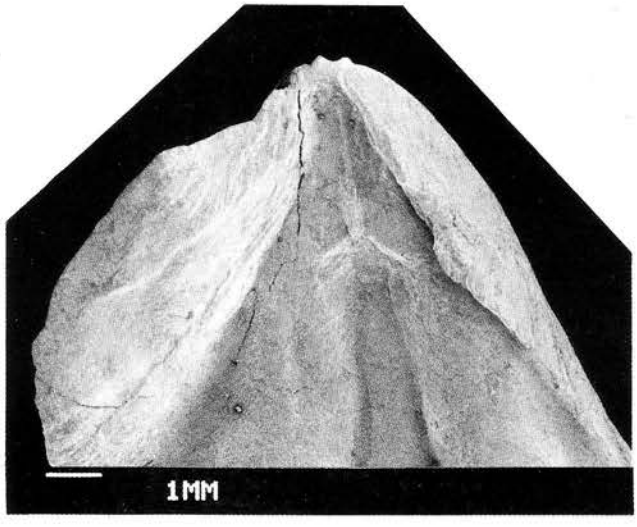


Fig. 19 - *Anisactinella quadriplecta* (Münster). Internal surface of the brachial valve. Muscle field and thin median septum. Campo N. 5847/44.

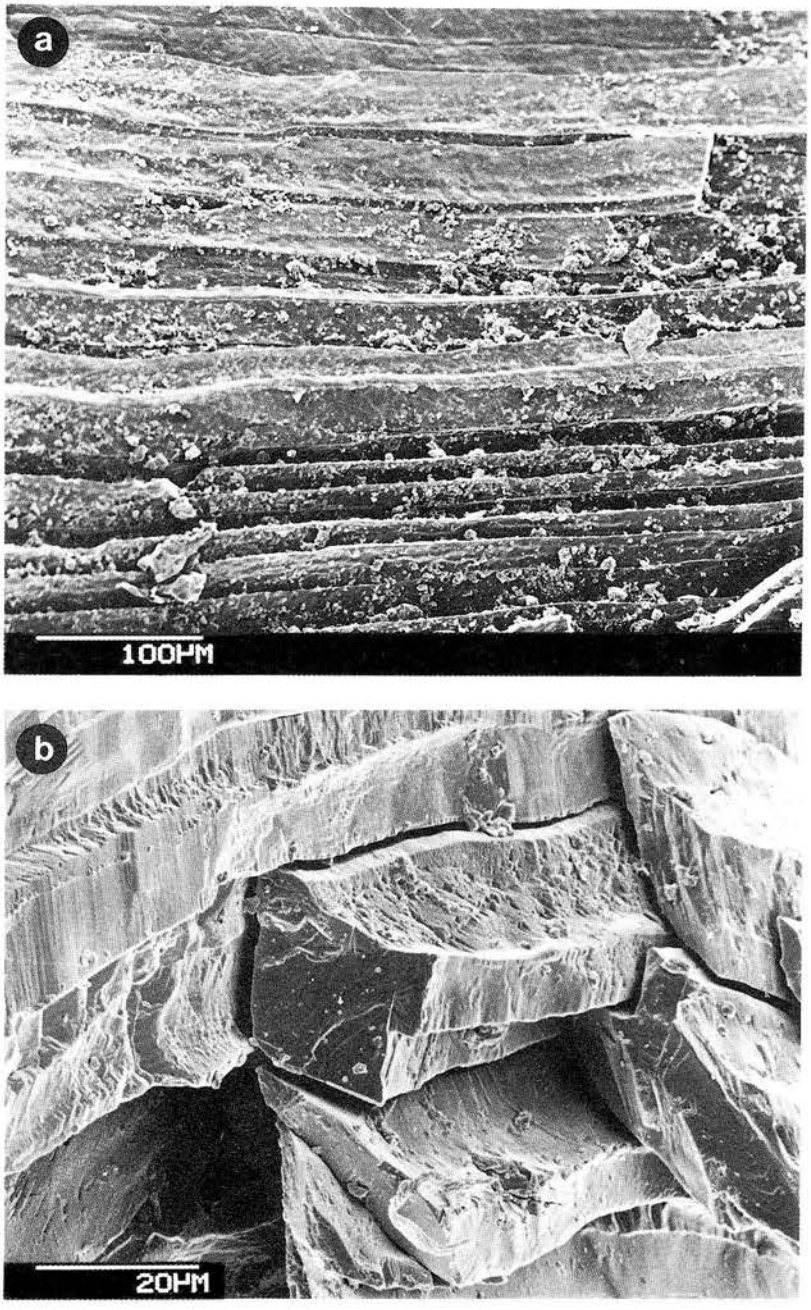


Fig. 20 - *Anisactinella quadriplecta* (Münster). a) Longitudinal section through the pedicle valve; note the arrangement of the fibres in the secondary layer. b) Pedicle valve, transversal section; detailed view of the shape of the fibres of the secondary layer. Campo N. 5847/41 (a). Vervei N. 5850/7 (b).

Our specimens coming from other areas underwent a higher degree of diagenetic alteration and therefore it is possible to observe only a multistriated, compact secondary layer with imbricated lamellae, quadrangular in outline (Fig. 20, a, b). The lamellae of the secondary layer show differentiated thicknesses: those making up the most external layer are thinner with respect to the internal ones (Pl. 28, fig. 1). There is no change in both thickness and arrangement of the lamellae in correspondence with the costae, unlike what observed in *Anisactinella maurensis* (Taddei Ruggiero, 1981).

Remarks. *Anisactinella quadriplecta* (Münster, 1841) shows a high degree of variability mostly related to the ornamentation. The basic scheme consists of 5 costae on the brachial valve and 4 on the pedicle one. This basic pattern can be varied because of the different development of the costae. In particular, on the brachial valve, that of the median costa.

This morphological character, which has been already observed by other Authors, led to the distinction of at least 7 "varieties" that, in most cases, can be considered morphotypes of *Anisactinella quadriplecta*. Therefore, a critical reapprisal is necessary.

In erecting the species Münster (1841) already shows two specimens which differ because of the development of the costae. However, he did not distinguish any "varieties".

Bittner (1890, 1900) introduces several "varieties":

- *euplecta* (1890): adult specimens with thin median brachial costa. In our opinion this definition corresponds to the type-species described by Münster (1841) and, therefore, it is redundant to distinguish a "variety" which actually coincides with adult form of the species;

- *costosa* (1890): specimens with equally developed costae. We consider this morphology as a morphotype (Fig. 21);

- *obliterans* (1890): forms with a reduced development of the costae, particularly regarding the median costa on the brachial valve. This "variety" is a morphotype of the species *Anisactinella quadriplecta* (Fig. 21);

- *confluens* (1890): the median costa of the brachial valve and the furrow of the pedicle one disappear, with a change in the number of costae: only 4 on brachial valve and 3 on the pedicle one. This brings also an inversion in the ornamentation of the valves because there is a median furrow in the brachial valve instead of a costa and vice versa in the pedicle valve. The phenomenon is reflected by the internal morphology of the shell and possibly responded to different functional meaning. Therefore, we consider this "variety" a different taxon (Fig. 21);

- *subconfluens* (1900): specimens with a very thin median costa on the brachial valve and shallow corresponding furrow in the pedicle valve. We consider this "variety" a morphotype of *Anisactinella quadriplecta* (Fig. 21).

Salomon (1895) describes the new "var." *tenuicostata*. He does not underestimate the development of the costae, however, he considers as diagnostic character the morphology of the lateral-posterior region, which actually does not represent a significant feature. According to the description and the figures a clear identification of this "va-

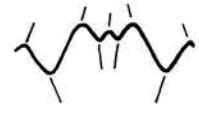
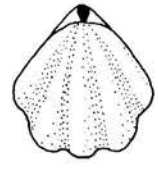
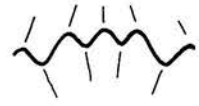
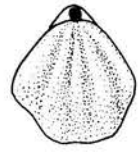
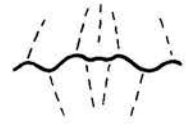
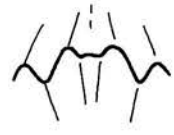
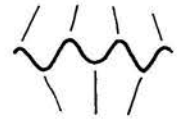
Species	Morphotype	Dorsal view	Anterior commissure	Number of costae	
A. QUADRIPLECTA	(euplecta)			brach. / ped.	5 / 4
	costosa			brach. / ped.	5 / 4
	obliterans			brach. / ped.	5 / 4
	subconfluens			brach. / ped.	5 / 4
?	confluens			brach. / ped.	4 / 3

Fig. 21 - Summary of the morphotypes of *Anisactinella quadriplecta* (Münster). The "variety" *euplecta*, which coincides with the typical form, is put at the beginning for comparison though it is not a morphotype.

riety" does not emerge. In fact, the "var." *tenuicostata* (Salomon, 1895) results to be based on specimens belonging to varieties already described by Bittner (1890) and, consequently, cannot be regarded as a distinct morphotype.

Waagen (1903) describes the new "var." *bicostosa*: specimens where the median brachial costa does not reach the anterior commissure and the lateral costae develop as in *tenuicostata* (Salomon, 1895). The explanatory pictures do not shows these characteristics because the median costa reaches the anterior commissure and the specimen can be considered *Anisactinella quadriplecta* sensu strictu. We believe that the description and the figures show considerable discrepancy and does not allow a clear identification of the "variety". In any case the specimens belong to Münster's (1841) taxon.

In synthesis we consider *Anisactinella quadriplecta* morphotypes only the following "varieties": *costosa, obliterans* and *subconfluens* (Fig. 21).

The comparison between the figures allows to consider as lectotype the specimen represented in Münster's (1841) pl. 6, fig. 10 as already suggested by Bittner (1890).

We do not accept the forms indicated by Laube (1865) in pl. 13, fig. 6 g-i for their subovoidal shape, the reduced number and arrangement of the costae. We also point out that figures 6a and 6b, as already observed by Bittner (1890) with respect only to figure 6a, show the pedicle valve of *Anisactinella quadriplecta* incorrectly.

We do not consider *Anisactinella quadriplecta* the specimen in Quenstedt's (1871) pl. 41, fig. 95 because it shows opposite costae, and fig. 96 because the ornamentation is totally different from that of *Anisactinella quadriplecta.*

We consider doubtfully the attribution to the "var." *costosa* by Bittner (1890) of specimen in pl. 2, fig. 19 because of the absence of the interarea, the subquadrangular shape, the rectimarginate anterior commissure and the rounded costae separated by deep furrows.

We believe that the new species "*Spirigera*" (*Anisactinella*) *matutina* Bittner (1902) which Author distinguished from similar forms on the basis of the dimensions (in particular the width) is co-specific to *Anisactinella quadriplecta.* In fact, both from the description and the figures, it is impossible to see any difference.

In Ampezzan area all morphotypes of *Anisactinella quadriplecta* are present. The careful observation of some juvenile forms puts to evidence that in the first growth stages all the costae, well marked and subequivalent, are already present. At a juvenile stage (Pl. 28, fig. 4) all the specimens of *Anisactinella quadriplecta* correspond to the definition given for the "variety" *costosa* and this justifies Bittner's (1890, 1900) remark. Only afterwards, during ontogeny, there can be a different development of the costae with the progressive thinning of the median brachial one (*euplecta*) up to its almost total disappearance near the anterior edge (*subconfluens*). Even in this extreme case there is a faint groove in the median position of the pedicle valve. The number of costae and furrows, which is characteristic for the species, remains therefore unchanged.

Distribution. *Anisactinella quadriplecta* (Münster) is reported from Anisian? of Dinarides, Ladinian of Southern Alps, Carnian of Bakony Mt. and Southern Alps.

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PLATE 28

Fig. 1 - *Anisactinella quadriplecta* (Münster). Brachial valve. Detail of the lateral costa. The lamellae in the most external secondary layer are thinner with respect to the internal ones. In the costa the thickness of the lamellae does not change. Tamarin N. 5848/2; X 32.

Fig. 2 - *Anisactinella quadriplecta* (Münster). a-e) Ventral, dorsal, lateral, anterior, posterior views. Campo N. 5847/9; X 6.

Fig. 3 - *Anisactinella quadriplecta* (Münster) (Morphotype *costosa*). a-c) Ventral, dorsal, anterior views. Milieres N. 5849/7; X 6.

Fig. 4 - *Anisactinella quadriplecta* (Münster) (Juvenile specimen). Pedicle valve. Median furrow well developed (as in morphotype *costosa*). Tamarin N. 5848/6.

PLATE 29

Fig. 1 - *Anisactinella quadriplecta* (Münster) (Morphotype *obliterans).* a-e) Ventral, dorsal, lateral, anterior, posterior views. Staolin N. 5851/2; X 4.

Fig. 2 - *Anisactinella quadriplecta* (Münster) (Morphotype *subconfluens*). a-c) Ventral, dorsal, posterior views. Tamarin N. 5848/12; X 3.

Fig. 3 - *Anisactinella quadriplecta* (Münster) (Morphotype *subconfluens*). a-e) Ventral, dorsal, lateral, anterior, posterior views. Campo N. 5847/10; X 6.

PLATE 30

Anisactinella quadriplecta (Münster). Serial transverse sections (acetate peels). Tamarin N. 5848/2. Length 4.9 mm, width 5.1 mm, thickness 3.8 mm; X 6.

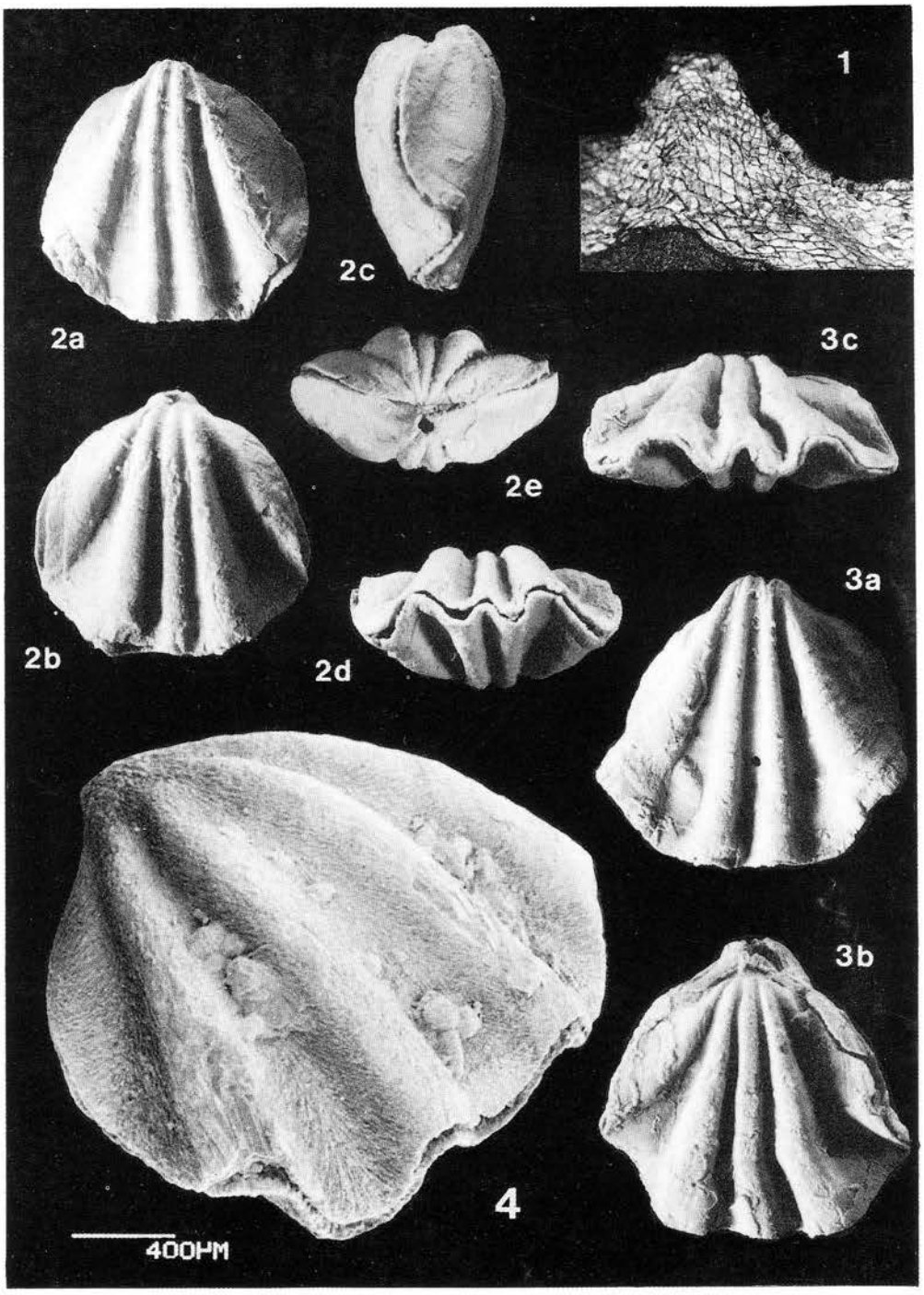
PLATE 31

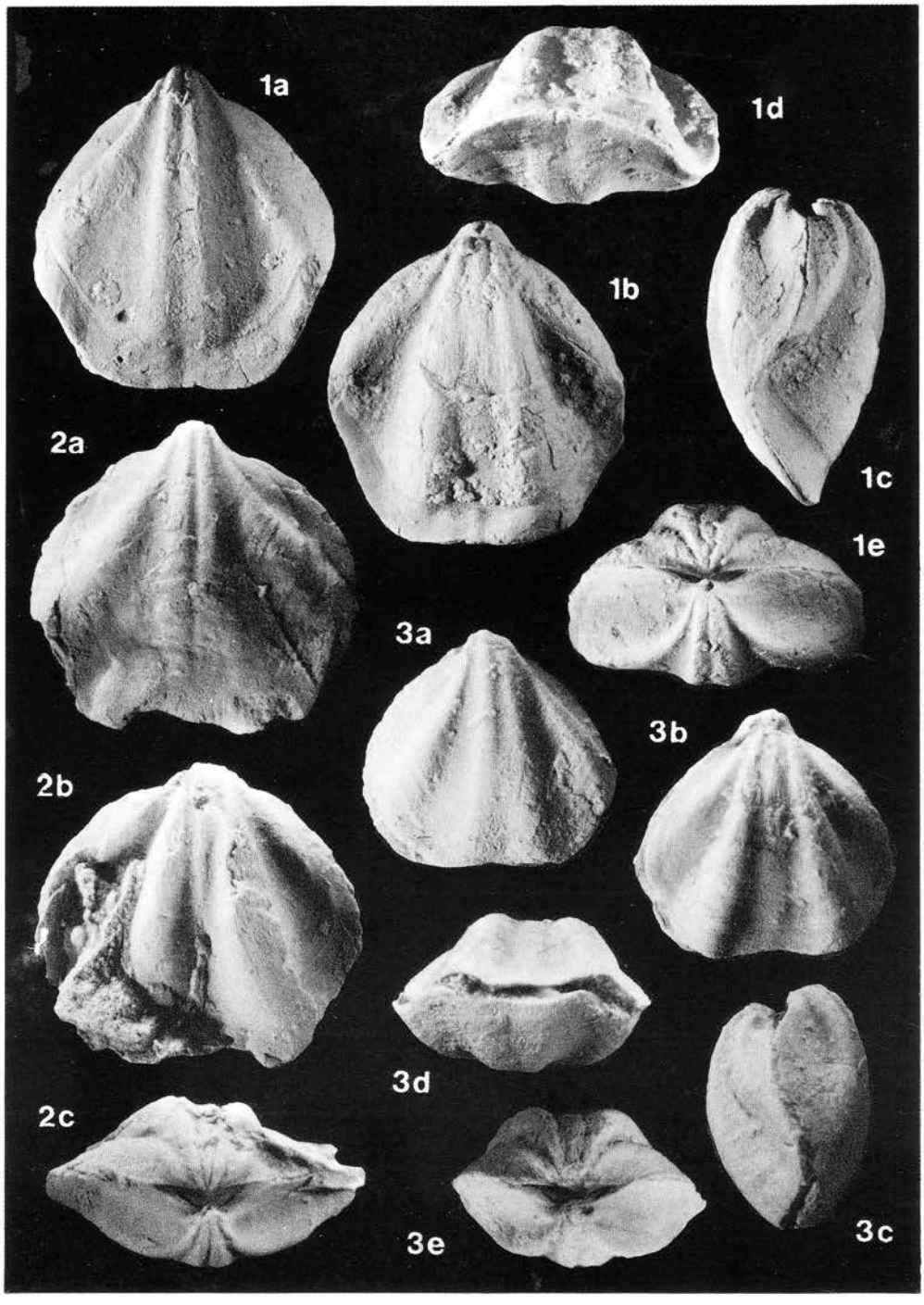
Anisactinella maurensis Taddei Ruggiero. Serial transverse sections (acetate peels). Pietra Maura.

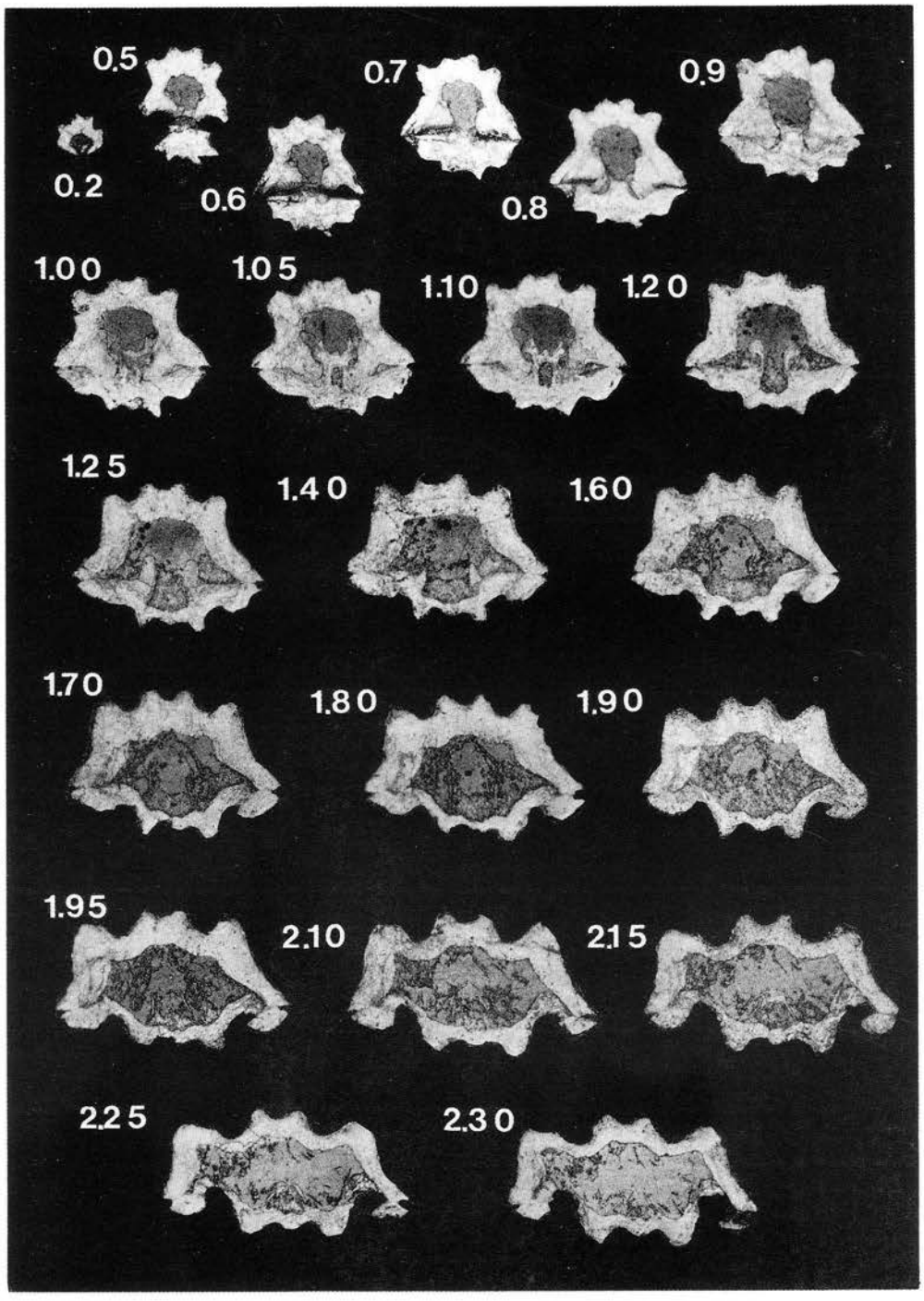
Fig. 1 - Length 7.8 mm, width 8.2 mm, thickness 6.1 mm. N. 6645; X 4.

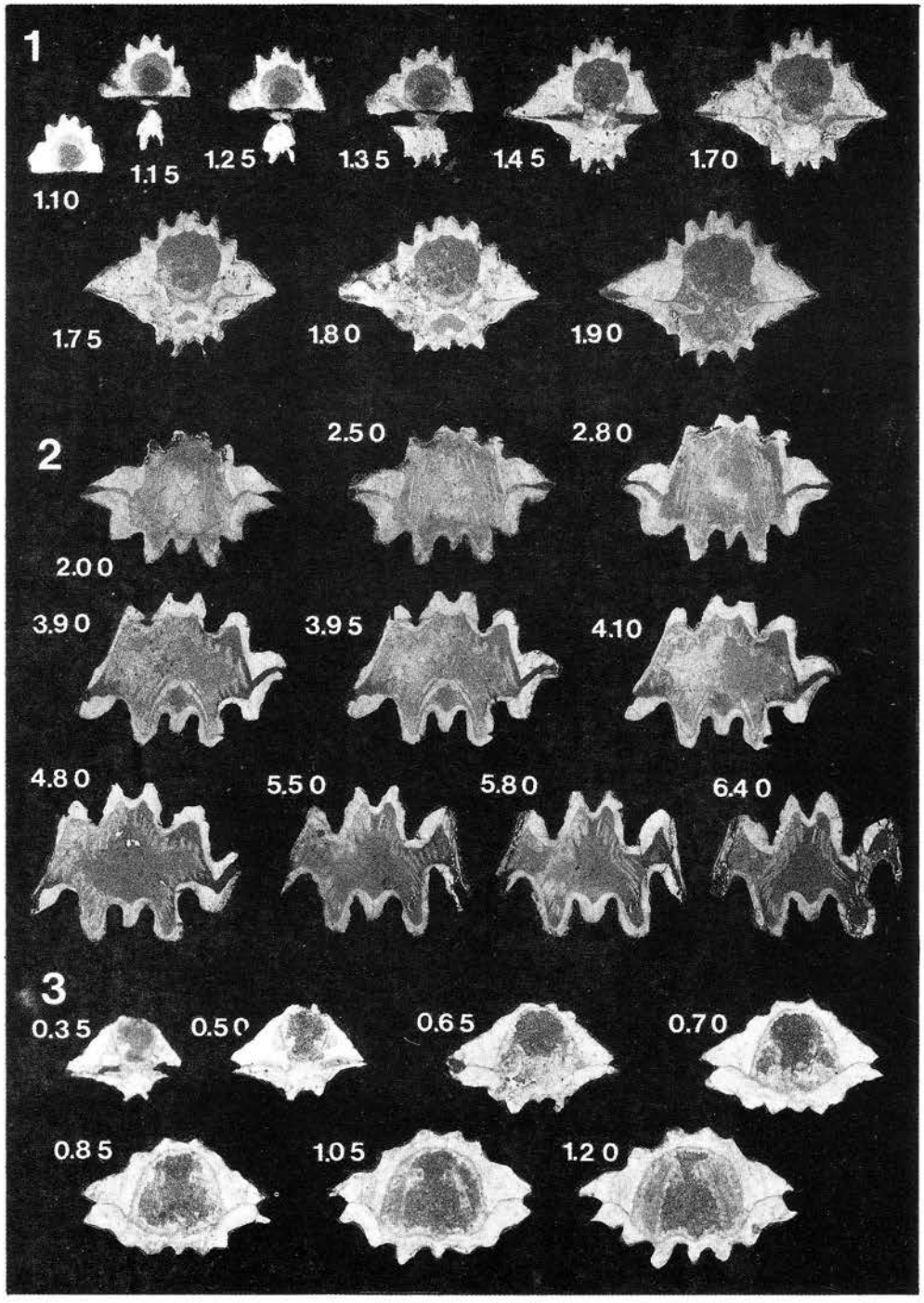
Fig. 2 - Length 9.8 mm, width 10.3 mm, thickness 5.5 mm. N. 6646; X 4.

Fig. 3 - Juvenile specimen: length 3.6 mm, width 3.8 mm, thickness 2.40 mm. N. 6648; X 10.


1
2a
2c
2b
2d
2e
3a
3b
3c
4
400μm


1a
1d
1b
1c
1e
2a
3a
3b
2b
3d
2c
3e
3c


0.5
0.7
0.9
0.2
0.6
0.8
1.00
1.05
1.10
1.20
1.25
1.40
1.60
1.70
1.80
1.90
1.95
2.10
2.15
2.25
2.30


1
1.10
1.15
1.25
1.35
1.45
1.70
1.75
1.80
1.90
2
2.00
2.50
2.80
3.90
3.95
4.10
4.80
5.50
5.80
6.40
3
0.35
0.50
0.65
0.70
0.85
1.05
1.20