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THE GENUS TETRACTINELLA BITTNER, 1890: MORPHOLOGY, ULTRASTRUCTURE, AND 3D RECONSTRUCTION

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Riassunto. Sono analizzate le specie *Tetractinella trigonella* (Schlotheim, 1820) e *Tetractinella hexagonalis* (Bittner, 1890). Esemplari della prima provengono dall'Anisico di diverse località del Sudalpino e dall'area-tipo di Tarnowitz (Slesia, Polonia). La seconda è stata studiata su esemplari del Sudalpino. Allo studio tassonomico e all'analisi morfologica e biometrica dei caratteri esterni, è seguita un'analisi morfologica dei caratteri interni, mediante sezioni seriate. Ove possibile, si è condotta un'analisi dell'ultrastruttura dei caratteri interni al microscopio elettronico a scansione (S.E.M.). Tale analisi ha messo in luce nuovi elementi nella struttura delle coste di *T. trigonella* e ha fornito nuovi dati sui caratteri interni di *T. hexagonalis*. Infine, sono state ottenute ricostruzioni in tre dimensioni partendo dai dati ottenuti dalle sezioni seriate, consentendo in questo modo il superamento del limite bidimensionale imposto dai peels.

Abstract. The species *Tetractinella trigonella* (Schlotheim, 1820) and *Tetractinella hexagonalis* (Bittner, 1890) are described. The former has been studied on specimens from several localities of the Anisian of Southern Alps (Italy) and from the type-area of Tarnowitz (Upper Silesia, Poland). The second has been analysed on specimens from the Southern Alps.

Taxonomic description and morphologic and biometrical analyses of external characters were followed by a morphologic analysis of internal structures using transverse serial sections. The ultrastructural analysis of internal characters provided new information about the structure of the ornamentation of *T. trigonella* (the presence of tabulae within costae) and new data about the poorly known *T. hexagonalis*. Finally, the internal characters of *T. trigonella* were re-examined using software for 3-D reconstruction from serial sections to complement the traditional method of study.

Introduction.

The genus *Tetractinella* Bittner, 1890 is a widespread brachiopod genus in the Middle Triassic of the Western Tethys and of the Germanic Basin. Several species have been attributed to this genus, namely *T. trigonella* (Schlotheim, 1820) (type-species), *T. hexagonalis* (Bittner, 1890), *T. cornutula* (Bittner, 1903), *T. biplicatula* (Bittner, 1903), *T. dyactis* Bittner (1890), and *T. cislonensis* (Bittner, 1890). They are most abundant in the Pelsonian substage of the Anisian, from where the first four species have been reported. They gradually vanish through the Illyrian and the genus seems to be represented in the Ladinian only by *T. dyactis*. The enigmatic species *T. cislonensis* could straddle the boundary with the Carnian.

In the present paper, the two most abundant species of the genus *Tetractinella*, *T. tetractinella* and *T. hexagonalis* are described with emphasis on the internal characters and ultrastructure of the shell. *T. cornutula* and *biplicatula* were described only from the area around Sarajevo in Bosnia by Bittner (1903). M. Gaetani (pers. com., 2001) in 1966 spent several days collecting in the Bittner's classical localities of Bosnia, but failed to find specimens of these species. *T. dyactis* was recently redescribed by Siblik (1994) from the Ladinian of Raxalpe (Austria) but specimens are heavy recrystallized (Siblik, pers. com., 2000) and therefore were not further considered for an useful SEM study.

These species were mostly studied towards the end of the nineteenth century (Bittner 1890, 1903; Loretz 1875; Philippi 1896; Tornquist 1898) and no significant advancements were obtained later on.

Some of the specimens here studied originates from Tarnowitz (Upper Silesia, Poland) type-locality of *T. trigonella*, and now are housed in the Muschelkalk Museum (Ingelfingen, Germany). The others specimens, collected by M. Gaetani, A. Tintori, E. Torriani and N. Mantovani, are stored in the Museo di Paleontologia of the Department of Earth Sciences, University of Milan (MPUM).

Systematic description

Classification is according to Alvarez et al. (1998) for the revised edition of the Treatise on Invertebrate

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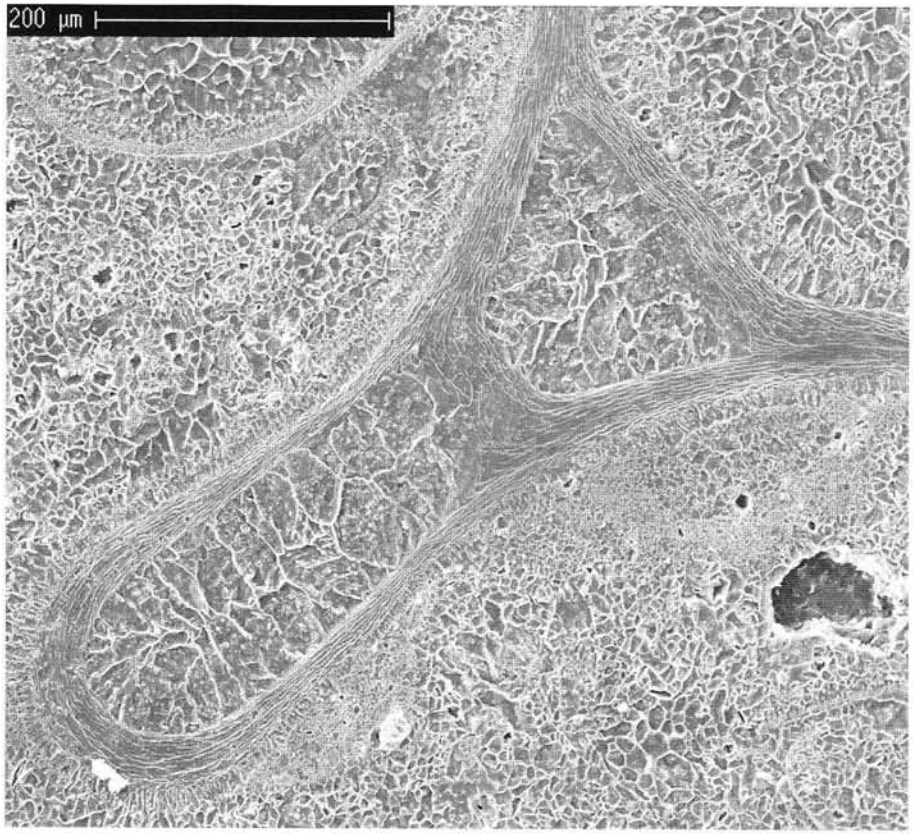

Fig. 1 - *T. trigonella* (specimen MPUM 8440). Detail of a costa with two transverse tabulae, consisting of secondary fibers.

Paleontology.

Order ATHYRIDIDA Boucot, Johnson & Staton, 1964

Suborder ATHYRIDIDINA Boucot, Johnson & Staton, 1964

Superfamily Athyridoidea Davidson, 1881

Family Diplospirellidae Schuchert, 1894

Subfamily Tetractinellinae Grunt, 1986

Genus *Tetractinella* Bittner, 1890

Type-species. *Terebratulites trigonellus* Schlotheim, 1820.

Emended diagnosis. Small to medium sized biconvex shells, commonly with few, high, sub-rounded (in section) costae in corresponding positions on each valve, extending the anterior commissure to variable degrees. Thin but well developed dental plates, usually joined to the lateral walls; very strong articulation consisting of well developed teeth and deep sockets. Jugum joined, forming a rudimentary saddle, jugal stem projecting ventrally, bifurcating to form short accessory lamellae.

Tetractinella trigonella (Schlotheim, 1820)

Text-figs. 1-12; Pl. 1, figs. 1-6, 9 -12; Pl. 2, figs. 1-6

1820 *Terebratulites trigonellus* Schlotheim, p. 271.
1875 *Rhynchonella tetractis* Loretz, p. 800, pl. 21, fig. 4.
1890 *Spirigera trigonella* - Bittner, p. 17, pl. 36, fig. 8-31.
1896 *Spirigera trigonella* var. robusta Philippi, p. 721, pl. 21, fig. 4 a-c.
1899 *Spirigera trigonella* - Tornquist, p. 256.
1903 *Spirigera (Tetractinella) trigonella* - Bittner, p. 507, 532, 567, pl. 23, fig. 23, ? fig. 24, non fig. 25-26.
1906 *Spirigera trigonella* - Arthaber, pl. 35, fig. 7 a, b.
1906 *Spirigera (Tetractinella) trigonella* - Martelli, p. 117.
1912 *Spirigera trigonella var. tetractis* - De Toni, p. 18, pl. 1, fig. 12 a-d.
1920 *Tetractinella trigonella* - Diener, p. 63.
1938 *Spirigera (Tetractinella) trigonella* - Selli, p. 16, pl. 50, fig. 10-12.
1958 *Tetractinella trigonella* - Pantic, p. 60, pl. 1, fig. 1.
1958 *Tetractinella trigonella* - Sacchi Vialli & Vai, p. 49.
1967 *Tetractinella trigonella* - Speciale, p. 1087, pl. 79, fig. 4 a, e.
1967 *Tetractinella trigonella* - Casati & Gnaccolini, p. 123, pl. 9, fig. 10.
1972 *Tetractinella trigonella* - Siblik, p. 189, text-fig. 14, pl. 61, fig. 1, 7-8, non fig. 6.
1974 *Tetractinella trigonella* - Dagys, p. 159, text-fig. 107, pl. 45, fig. 3 a-d.
1981 *Tetractinella trigonella* - Giovannoni, p. 213, pl. 5, fig. 4-6.
? 1982 *Tetractinella trigonella* - Kochanova & Pevny, p. 34, pl. 7, fig. 2.
1991 *Tetractinella trigonella* - Siblik, p. 168, pl. 1, fig. 6 a, b.
1993 *Tetractinella trigonella* - Iordan, p. 51, pl. 1, fig. 4.
1993 *Tetractinella trigonella* - Angiolini, p. 287, pl. 1, fig. 3-4.
1997 *Tetractinella trigonella* - Torti & Angiolini, p. 158, pl. 1, fig. 14.
1999 *Tetractinella trigonella* - Sulser, p. 116.

Type- locality. Schlotheim based his *Terebratulites trigonellus* on specimens from Stubendorf, Tarnowitz and in the Friedrichsgrube at Tarnowitz. All these localities are in the eastern part of Upper Silesia (Poland).

Material. 967 decorticated specimens, MPUM 8440 (LC/22), MPUM 8441 (TT1/2), MPUM 8442 (TT1/9), MPUM 8443 (CPA/1), MPUM 8444 (CPA/3), MPUM 8445 (VAF/1), MPUM 8446 (VAF/106), MPUM 8447 (VAF/177), MPUM 8448 (G360/2), MPUM 8449 (G223/479), MPUM 8450 (G223/465), MPUM 8451 (G223/481), MPUM 8452 (G223/1-67; G360/1,3; G460/138,152,558-569; G54/60-64) , MPUM 8453 (TT1/1,3-8, 10-28; TT3; CP/1; CPA/1,3), MPUM 8454 (AF/1-13; VAF/ 2-105, 107-176, 178-369),

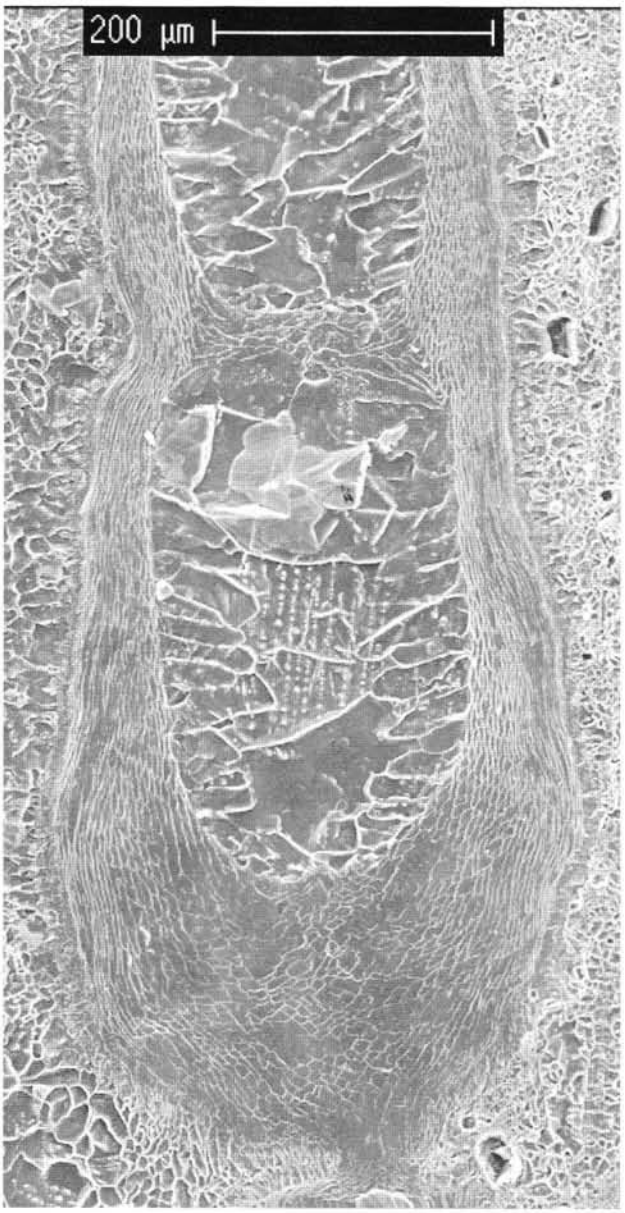

Fig. 2 - *T. trigonella* (specimen MPUM 8440). The roof of a costa with a transverse tabula. The secondary layer thickness is major at the roof of costa.

MPUM 8455 (P/1-2), MPUM 8456 (G67/1-34), MPUM 8457 (G131/1-4; G128/1-4), MHI 1052/2-112, MHI 1581/1-165, MHI 1723/1-22, MHI 1724/1-10, MHI 1725/1-11, MHI 1726/1-42, MHI 1727/1, MHI 1728/1-13, MHI 1729/1-51.

The specimens come from the top of the Calcare di Angolo (Banco a Brachiopodi - Pelsonian, Anisian) of several localities of the Grigna Group (Canalone Porta, Valle dell'Acqua Fredda, Valle dei Grassi Lunghi), from the Pelsonian of Monte Rite (Cadore, Italy), from Rovegliana near Recoaro, and from the Pelsonian - lower Illyrian of Rugialdbach near La Valle (Dolomites). The material at the Muschelkalk Museum (Ingelfingen, Germany) comes from the Anisian of the type-area of Tarnowitz.

Description

External characters. Small to medium sized biconvex shell, outline from sub-pentagonal to sub-oval or sub-triangular. In the sub-pentagonal specimens, width exceeds length and maximum width occurs at about ½ of maximum length. In the sub-oval specimens, length exceeds width and maximum width occurs at about ½-2/3 of maximum length. In the sub-triangular specimens, length exceeds width and maximum width occurs at about 2/3 of maximum length.

Hinge curved and anterior commissure rectimarginate. Flanks usually very steep and sub-orthogonal to the commissural plane. For this reason the lateral commissure is rectimarginate.

Ventral valve, similar in dimensions and in convexity to the dorsal valve, convex near the umbonal area, flattening anteriorly. Short ventral umbo, terminally not pointed and incurved. Foramen medium sized and subcircular in outline. Palintrope reduced. Dorsal valve with a very short umbo. A median sulcus is present in both valves.

Ornamentation. Radial ornamentation consists of 4 costae on each valve. The costae, sub-squared to rounded in section, appear very high, becoming stronger and heavy near the anterior margin. The costae, with very wide interspaces, are in corresponding position on the two valves and they extend the anterior commissure. In several specimens lateral costae define the flanks of the shell, except for the specimens collected at Monte Rite.

In well preserved specimens collected at Tarnowitz (type-area), the costae are very high and reinforced internally by transverse structures (similar to tabulae) (Figs. 1-2). In decorticated specimens the tabulae are lost. Internal tabulae support mainly the higher part of the costa and begin one at a time, at about ½ of the maximum length of shell. The number increases in the direction of the anterior margin and the maximum number occurs anteriorly to the anterior commissure (Figs. 3-4). The ultrastructure of a costa in the specimen (MPUM 8440) was investigated in a transverse section. The primary layer consists of small crystallites oriented perpendicularly to the shell layers. Its maximum thickness is 22.2 μm. The thickness of the secondary layer ranges from 38.1 μm near the transverse tabula to 209.5 μm at the roof of the costa. The secondary layer consists of fibres with a keel and saddle profile. The maximum width of the secondary fibres in transverse section is about 15-17 μm and the thickness is 2-6 μm (Fig. 5A). Transverse tabulae are built up by low density secondary fibres. The last seems to lack the characteristic keel and saddle profile. The thickness of each tabula is variable, ranging from 34.3 μm to 45.7 μm (Fig. 5B).

Dimensions. The width and thickness parameters are directly proportional to the length of the shell (Fig. 6).

Internal characters: morphology and ultrastructure (Fig. 7). S.E.M. analysis of the internal structures on 12

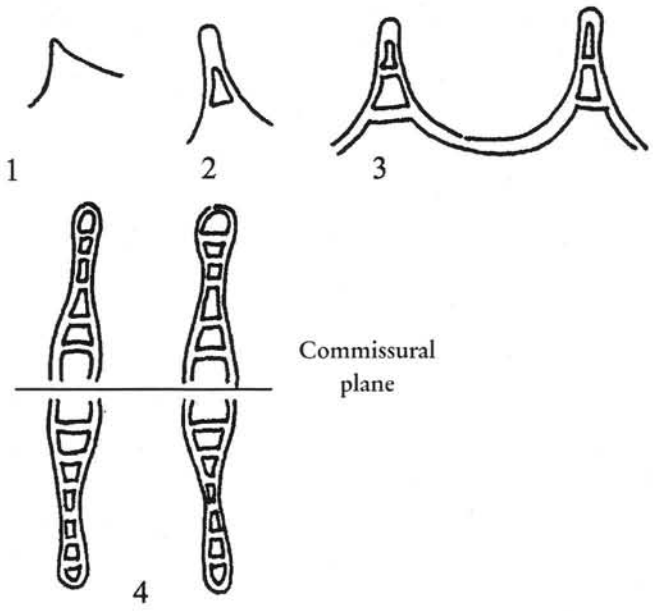

Fig. 3 - The number of tabulae increases towards the anterior margin: near the umbo the transverse tabulae have not been observed (Fig. 3.1); at about ½ of the maximum length of the shell transversal tabulae occur (Fig. 3.2, 3.3); the highest number occurs anteriorly the anterior commissure (Fig. 3.4).

complete specimens (MPUM 8440, MPUM 8441, MPUM 8442, MPUM 8443, MPUM 8445, MPUM 8446, MPUM 8448, MPUM 8449 and MHI 1723/1, MHI 1052/2, MHI 1581/1-2) was performed. The species has shell substance impunctate and it is characterised by the following internal structures:

I. Thin but well developed dental plates weakly curved and partially joined to the lateral walls of the valve (Fig. 8A). Myotest present along the dental plates, from the ventral valve floor to the dorsal part of the valve. Dental plates not very long, disappearing at about 1.9 - 2.5 mm from the umbo. The secondary fibres of the dental plates have a sub-orthogonal trend with respect to the ventral valve floor.

II. Low, short and sub-triangularly shaped dental flanges that disappear at about 2.3 - 3.0 mm from the umbo.

III. Very thick ventral valve floor. The maximum thickness corresponds to the radial ornamentation, where the secondary fibres secretion is greater.

IV. A delthyrial plate is present in the first ontogenetic stages (Fig. 7, sections 5-6), but disappears at about 0.9 - 1.5 mm from the umbo, when the cardinal process begins to enter the central umbonal cavity of the ventral valve.

V. Very wide central umbonal chamber sub-square in shape (Fig. 7, sections 1-15).

VI. Strong and high cardinal process protruding in the ventral central cavity (Fig. 7, sections 9-12). Cardinal plate wide, weakly concave to the dorsal valve floor and composed of parallel secondary fibres (Fig. 7, sections 9-12). A "spherical structure" composed of closed cardinal lamellae is noticeable. At about 1.8 - 2.3 mm from the umbo, cardinal lamellae begin to open allowing the attachment of diductor muscles (lamellae are totally open at about 2.6 mm from the umbo and number about 11 each side). The aperture direction is from the plane of symmetry to the internal walls of the valve (Fig. 8B).

VII. Dorsal central cavity rather wide (Fig. 8C). The interior of the dorsal valve shows a flat high and well developed cardinal plate bearing sockets at its side.

VIII. High, rather long (present at a distance of 3 mm from umbo) sub-triangularly shaped myophragm (Fig. 8D), composed of secondary fibres showing a convex trend towards the ventral part of the dorsal valve.

IX. Articulation composed of a pair of strong

PLATE 1

All x 1.5, except when specified.

Fig. 1 a-b-c - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MPUM 8447 (a, ventral valve; b, dorsal valve; c, anterior commissure with ventral valve below).

Fig. 2 a-b - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MPUM 8444 (a, ventral valve; b, dorsal valve).

Fig. 3 a-b - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MPUM 8451 (a, ventral valve; b, dorsal valve).

Fig. 4 a-b - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MHI 1052/3 (a, ventral valve; b, dorsal valve). Muschelkalk Museum (Ingelfingen, Germany).

Fig. 5 a-b - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MPUM 8450 (a, ventral valve; b, dorsal valve).

Fig. 6 - *Tetractinella trigonella* (Schlotheim, 1820). Ventral valve. Specimen MHI 1727/1. Muschelkalk Museum (Ingelfingen, Germany) (x1).

Fig. 7 a-b - *Tetractinella hexagonalis* (Bittner, 1890). Specimen MPUM 8460 (a, ventral valve; b, dorsal valve).

Fig. 8 a-b - *Tetractinella hexagonalis* (Bittner, 1890). Specimen MPUM 8461 (a, ventral valve; b, dorsal valve).

Fig. 9 a-b - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MHI 1723/2 (a, ventral valve; b, dorsal valve). Muschelkalk Museum (Ingelfingen, Germany) (x2).

Fig. 10 a-b - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MHI 1052/4 (a, ventral valve; b, dorsal valve). Muschelkalk Museum (Ingelfingen, Germany).

Fig. 11 a-b - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MHI 1052/5 (a, ventral valve; b, dorsal valve). Muschelkalk Museum (Ingelfingen, Germany).

Fig. 12 a-b-c - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MHI 1581/3 (a, ventral valve; b, dorsal valve; c, a detail of the flank orthogonal to the commissural plane). Muschelkalk Museum (Ingelfingen, Germany).

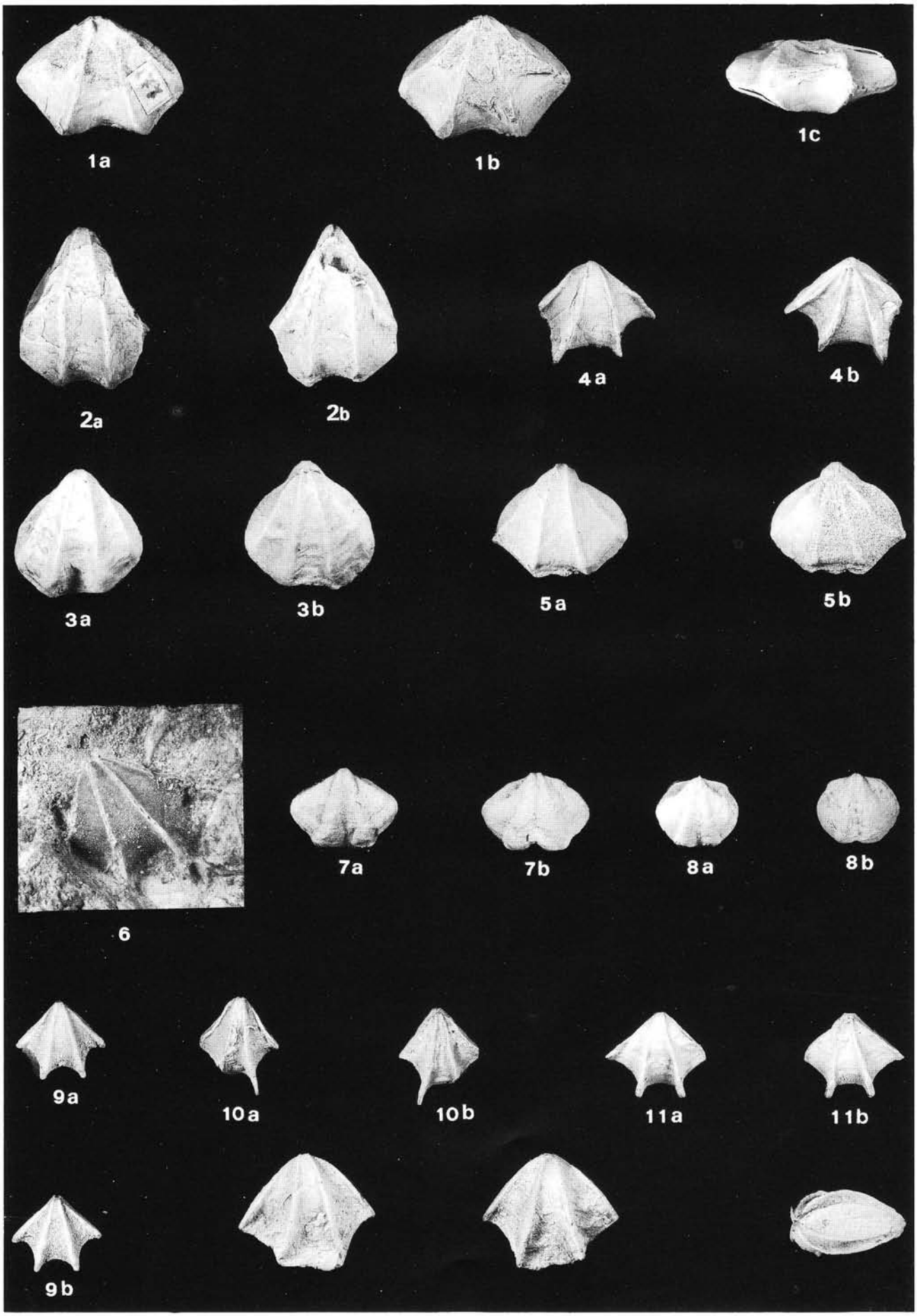
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Fig. 4 - *T. trigonella* (specimen MPUM 8440). The section shows the four median costae in corresponding positions of two valves, anteriorly to the anterior commissure (where the number of tabulae is highest).

teeth, sub-squared in outline, supported by two ventral lateral walls and partially by dental plates. They helps to control torsional movement between the two valves. Dorsal surface of the teeth smooth. Deep and sub-oval shaped sockets (Fig. 7);

X. Internal tabulae ranging in number from one to 5-6, supporting the high part of the costae (Figs. 1-4, 5B).

3-D reconstruction. External and internal structures of a complete specimen from the type-area of Tarnowitz (MHI 1052/2) were reconstructed from serial sections (Figs. 9-11).

Three-dimensional reconstructions are used to complement the traditional method of study, as it was suggested by Sandy (1986). This new perspective allows a better understanding of the main internal characters of ventral and dorsal valves and their evolution from umbo to the anterior margin, overcoming the two-dimensional limitation of peels. The software chosen and the techniques used are described in Mantovani & Olivini (2001, submitted). The three-dimensional reconstruction illustrates the following internal characters:

I. Internal surface of valves (ventral and dorsal valve floor, roof and lateral walls) (Figs. 9-10).

II. Delthyrial plate, present in the first ontogenetic stages as well (Figs. 9-11).

III. Dental plates (adminicula and dental flanges) (Fig. 9).

PLATE 2

Fig. 1 - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MPUM 8446. Section at 0.9 mm from umbo, showing the delthyrial plate.

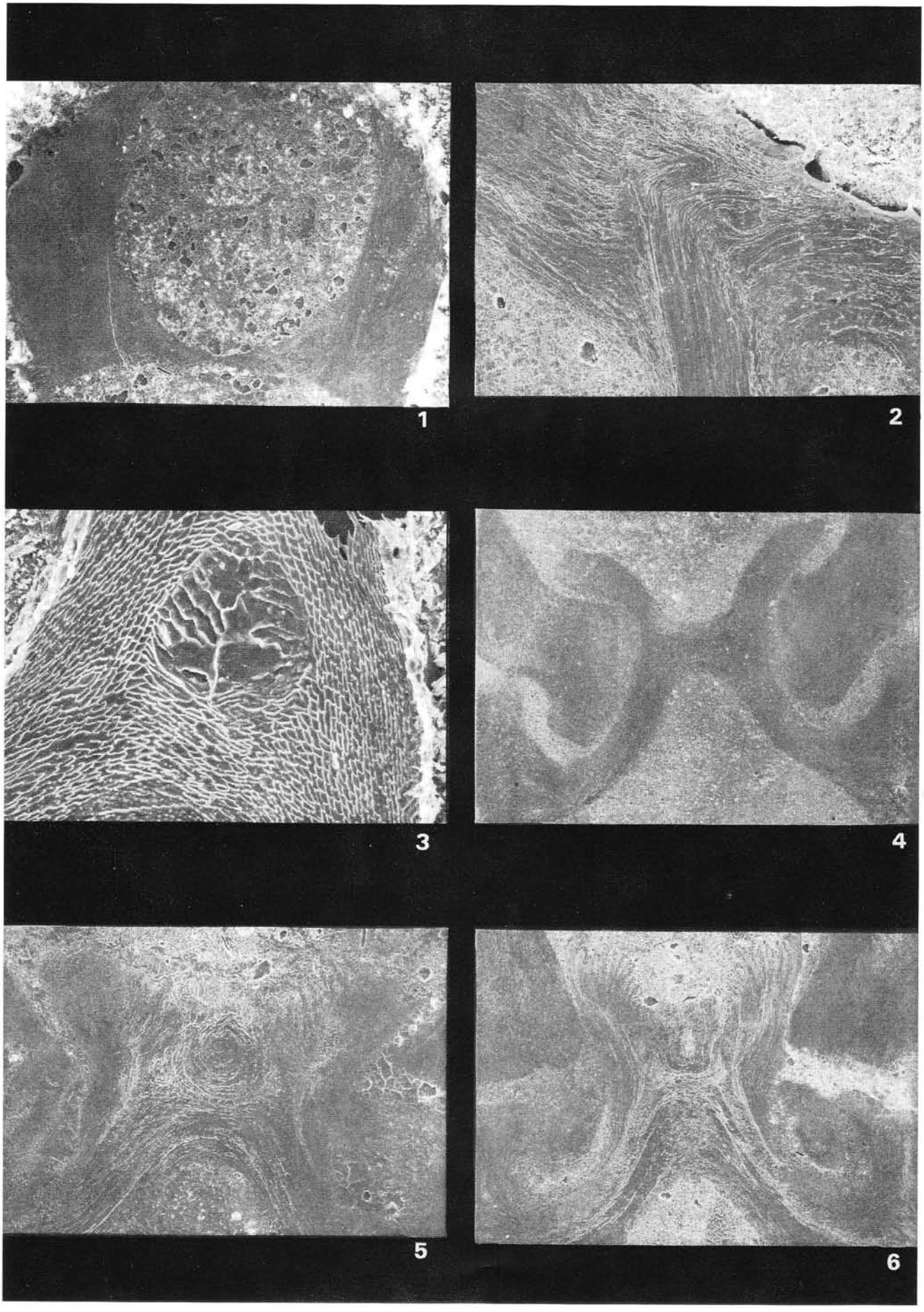
Fig. 2 - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MPUM 8449. Section at 2.3 mm from umbo, showing a detail of an adminiculum.

Fig. 3 - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MHI 1723/1. Section at 3.6 mm from umbo, showing the secondary fibres near the transverse tabula. Muschelkalk Museum (Ingelfingen, Germany).

Fig. 4 - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MPUM 8449. The articulation composed by very strong teeth and deep sockets.

Fig. 5 - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MPUM 8441. Section at 2.15 from umbo, showing the cardinal process with the numerous cardinal lamellae for the attach of diductor muscles.

Fig. 6 - *Tetractinella trigonella* (Schlotheim, 1820). Specimen MPUM 8442. Section at 2.1 mm from umbo, showing the cardinal process. The cardinal lamellae are completely open.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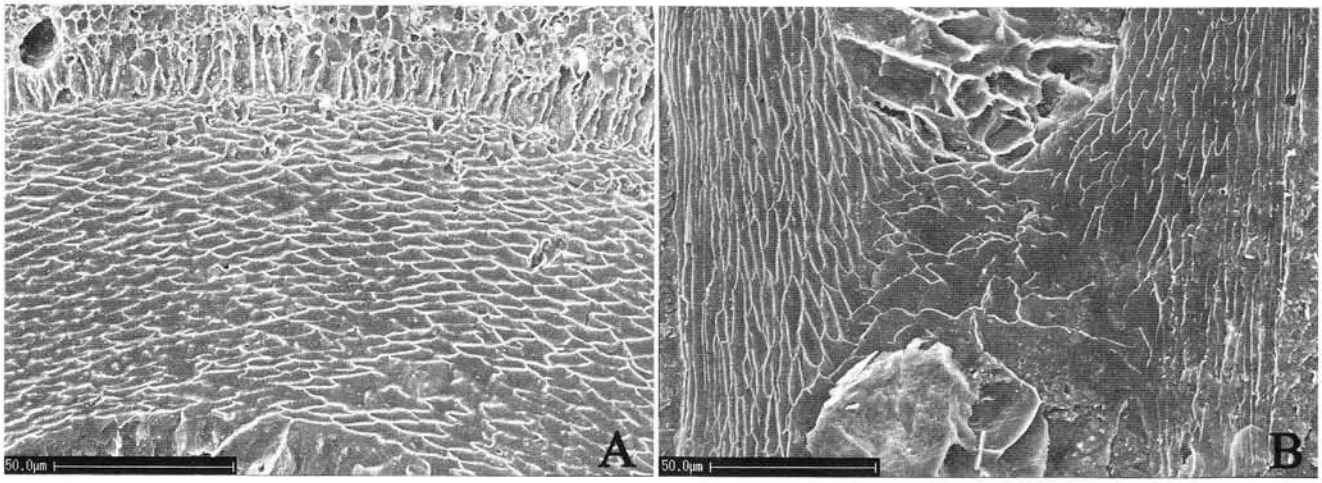

Fig. 5 - *T. trigonella* (specimen MPUM 8440). A - transverse section of a costa showing the primary and secondary layers. The secondary fibres show the keel and saddle profile; B - detail of a transverse tabula showing uncompacted secondary fibres.

IV. Myophragm (Figs. 9-11).

V. Cardinal process with cardinal plate (Figs. 9-11).

VI. Articulation between valves (Fig. 11).

Intraspecific variability. Intraspecific variability was observed in the outline (sub-pentagonal or sub-triangular), depending on the length/width ratio; in the maximum length and width of the shell; in the lateral costae position (lateral costae may or may not underlie the flanks of the shell); and in the flank inclination with respect to the commissural plane (from about 90° to about 40°-45°). Specimens collected from Monte Rite are characterised by variability in outline (from sub-pentagonal to sub-oval) and lateral costae not underlying flanks. The last are not inclined and not orthogonal with respect to the commissural plane.

Discussion. *T. trigonella* is probably the most widespread brachiopod species of the Anisian of the Western Tethys and Germanic Basin. Loretz (1875) erected the new species *Rhynchonella tetractis* from Ausserprags (Braies Dolomites). De Toni (1912), preferred to consider *tetractis* as a variety of *Spirigera trigonella*. The analysed specimens from Monte Rite are very similar to specimens illustrated by Loretz (1875) and De Toni (1912). The general morphology and the internal structures of two specimens (MPUM 8448 and MPUM 8449) does not show significant difference in comparisons to the other analysed specimens. Therefore the species *Rhynchonella tetractis* Loretz, 1875 is considered as synonym of *T. trigonella*.

The specimens illustrated by Bittner (1903, pl. 23, fig. 24-26) and collected from Studenkovic (Sarajevo

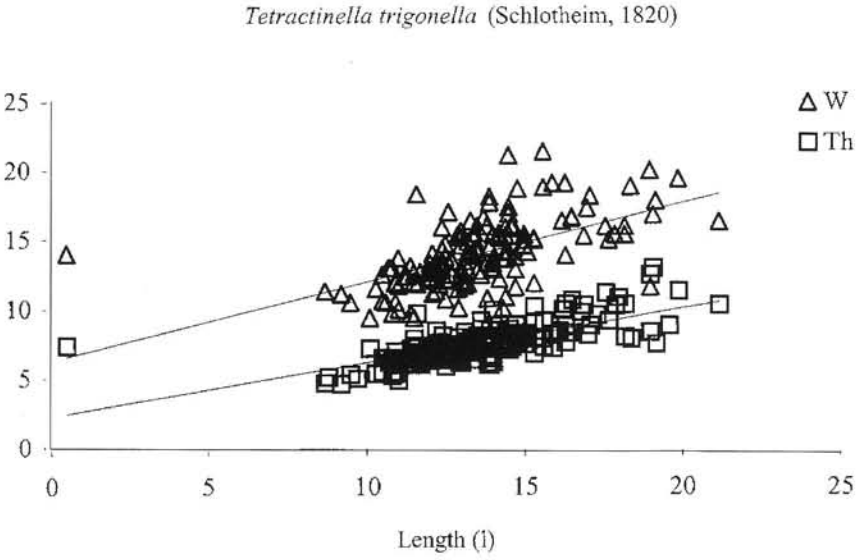

Fig. 6 - *T. trigonella*. Constant relationship between width, thickness and length of the shell.

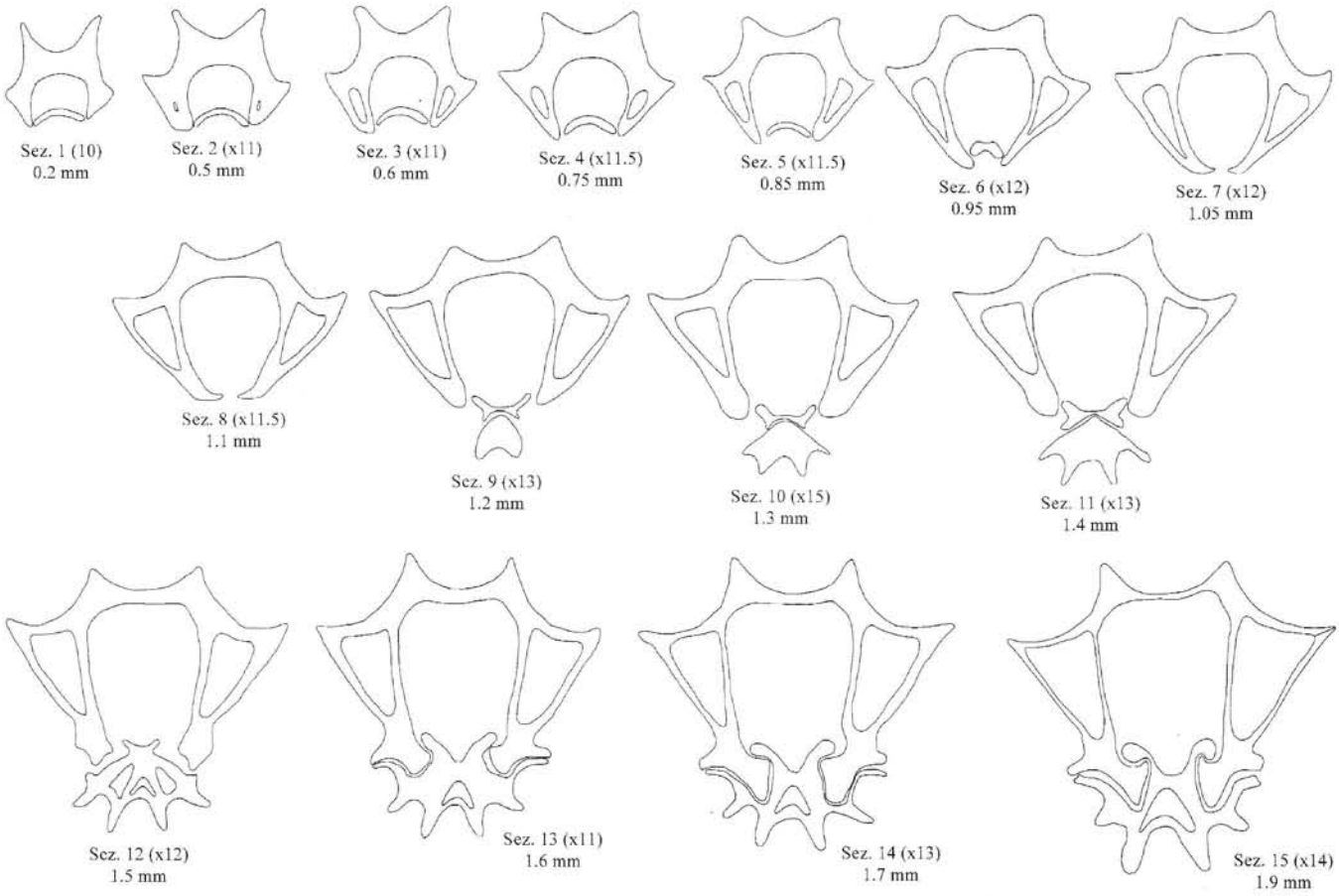

Fig. 7 - Serial sections of *T. trigonella* (specimen MHI 1052/2 from the type-locality of Tarnowitz). Distance from the umbo in mm

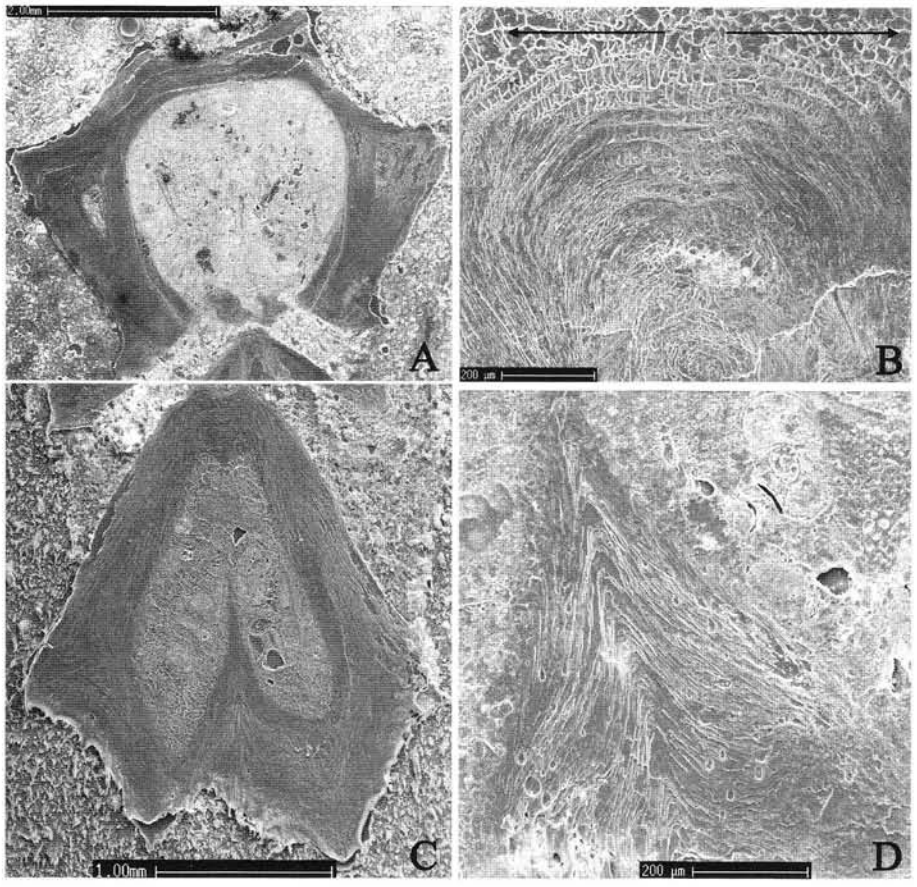

Fig. 8 - *T. trigonella*. A (specimen MPUM 8445). Dental plates weakly curved and partially joined to the lateral walls; B (specimen MPUM 8443). Detail of the cardinal process: the black arrows indicate the opening direction of the cardinal lamellae; C (specimen MPUM 8441). Dorsal valve with very high myophragm; D (specimen MPUM 8441). Detail of the myophragm formed by secondary fibres.

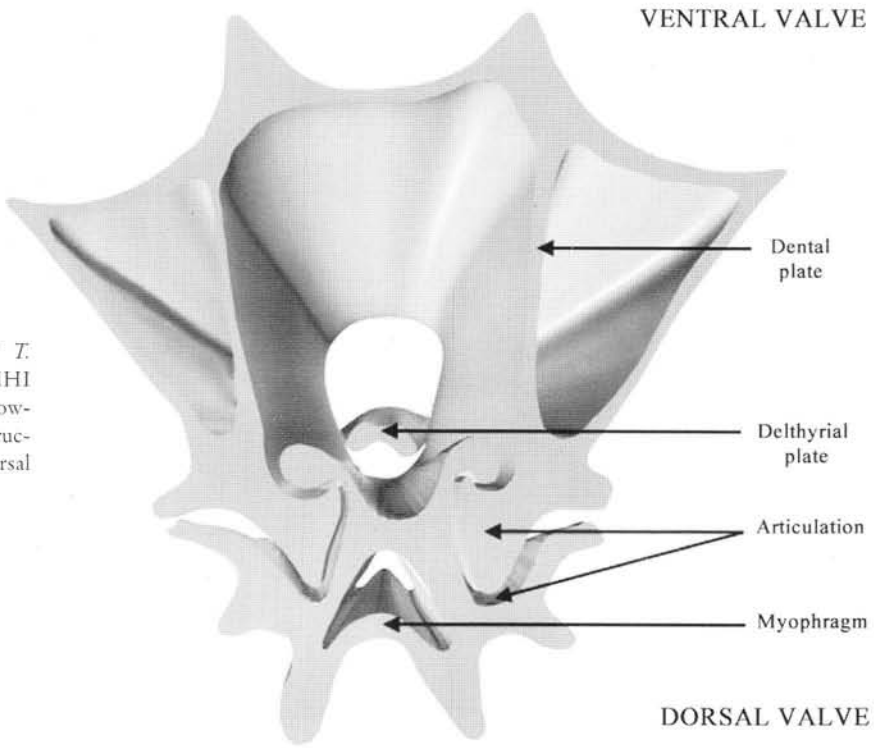

Fig. 9 - 3D reconstruction of *T. trigonella* (specimen MHI 1052/2). Frontal view showing the main internal structures of ventral and dorsal valves.

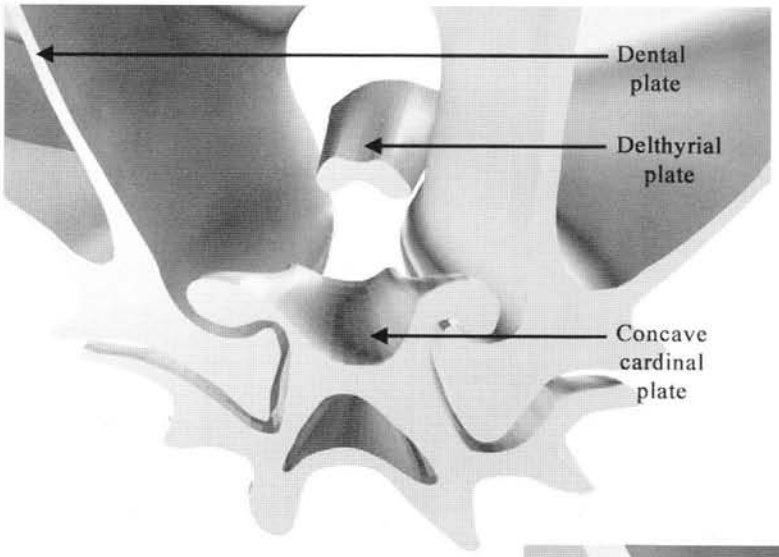

Fig. 10 - 3D reconstruction of *T. trigonella* (specimen MHI 1052/2). A detail of delthyrial plate, concave cardinal plate, articulation and dorsal valve.

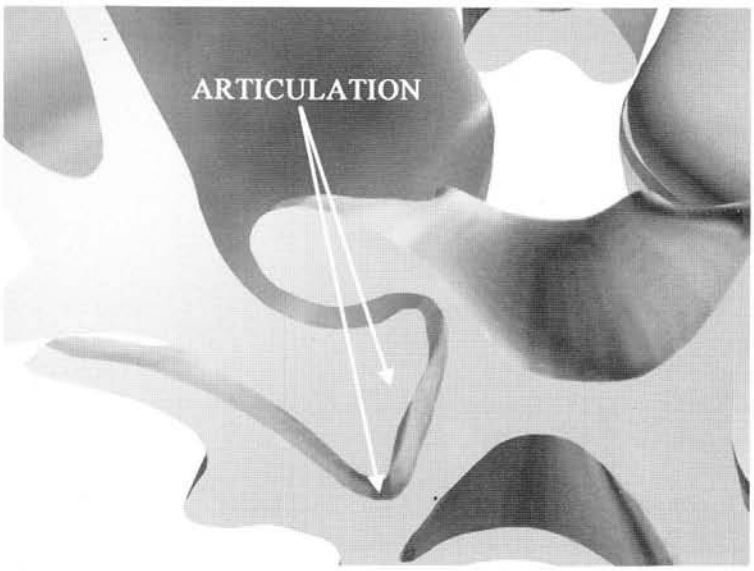

Fig. 11 - 3D reconstruction of *T. trigonella* (specimen MHI 1052/2). Frontal view showing detail of the articulation between the valves.

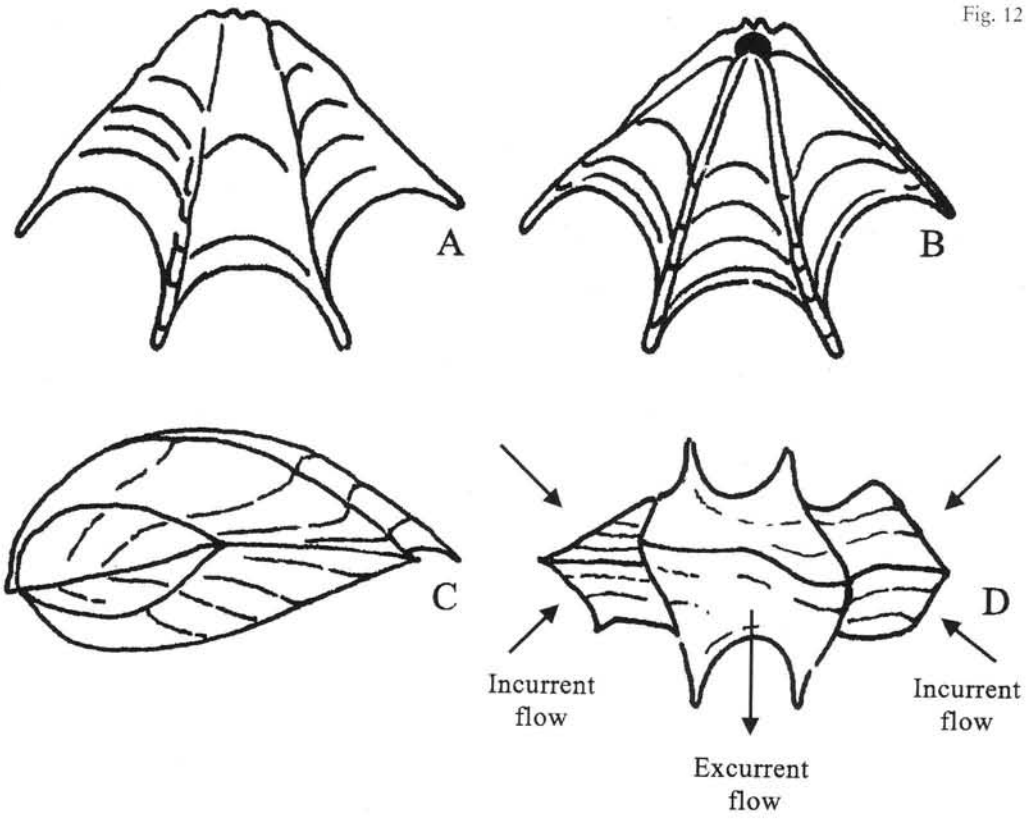

Fig. 12 - *T. trigonella*: the separation between excurrent and incurrent flows.

area, Bosnia) differ from the analysed specimens for different number of costae. Especially the specimen of fig. 26 seems to be more similar to *T. dyactis*. In the present paper, the *robusta* variety erected by Philippi (1896, pl. 21, fig. 4) from M. Cavallo (Grigna Group) is considered to enter into the intraspecific variability. The specimen of Siblik (1972, pl. 61, fig. 6) is rejected because, more similar to *T. dyactis*. The single specimen described and illustrated by Kochanova & Pevny (1982, pl. 7, fig. 29) is most probably a pathogenic specimen.

Remarks on the functional morphology of costae. A peculiar feature of the species are the internal transversal tabulae of the costae. I suggest the interpretation that they have the function to stabilize and reinforce the very high costae in medium energy environments where ornamentation is likely to collapse. In fact, the number of tabulae increases progressively in the direction of the anterior margin, reaching the maximum number (5-6) beyond the main anterior commissure, where the costae appear weakest.

Rudwick (1965, 1970), pointing out the resemblance between *Tetractinella trigonella* and *Cheirothyris fleuriausa* (d'Orbigny), suggested costae are used as sensory "antennae" which carried the sensitive mantle edges, and hence provided the brachiopods with early warning. The presence of the internal tabulae void the hypothesis proposed by Rudwick. I suggest that the costae extend the anterior commissure, having a similar function to the median sulcus and dorsal fold in some Spiriferids. In these Spiriferid brachiopods, the ventral sulcus and dorsal fold are thought to separate the plane of anterior excurrent flow from the plane of lateral incurrent flow, increasing the efficiency of the current in the lophophore (Emig 1992). In *T. trigonella*, the incurrent flow is thought to be separated from the excurrent flow by the median costae on the two valves. The couple of the median costae defines the excurrent flow area and the lateral costae the incurrent flow areas (Fig. 12).

The flanking position of the lateral costae (suborthogonal to the commissural plane) reduced the aperture degree of the shell opening, allowing the selection of particle-size that in other brachiopods was obtained by a "zig-zag" commissure as shown by Rudwick (1970).

Occurrence. *Tetractinella trigonella* occurs in the Anisian (Pelsonian and lowermost Illyrian) of the Southern Alps. It is frequent in the "Banco a brachiopodi" of Calcare di Angolo from the Grigna Group in the West to the Giudicarie in the East, in Lombardy and Trentino. Occasionally a few specimens may be collected in the lower part of the Calcare di Prezzo. It is also abundant in the Recoaro Limestone of the Recoaro area, in the uppermost part of the Serla Fm. in the M. Rite (Dolomites), in the Dont/Braies Fms. of the Eastern (Dolomites), in the Anisian of the Northern Alps of Germany and Austria, in the Lower and Upper Muschelkalk of the Germanic Basin, in the Anisian of Hungary (Balaton Highland), Dinarides, Balkanides and in the Upper Ladinian of Aghdarband (Iran) (Siblik 1988).

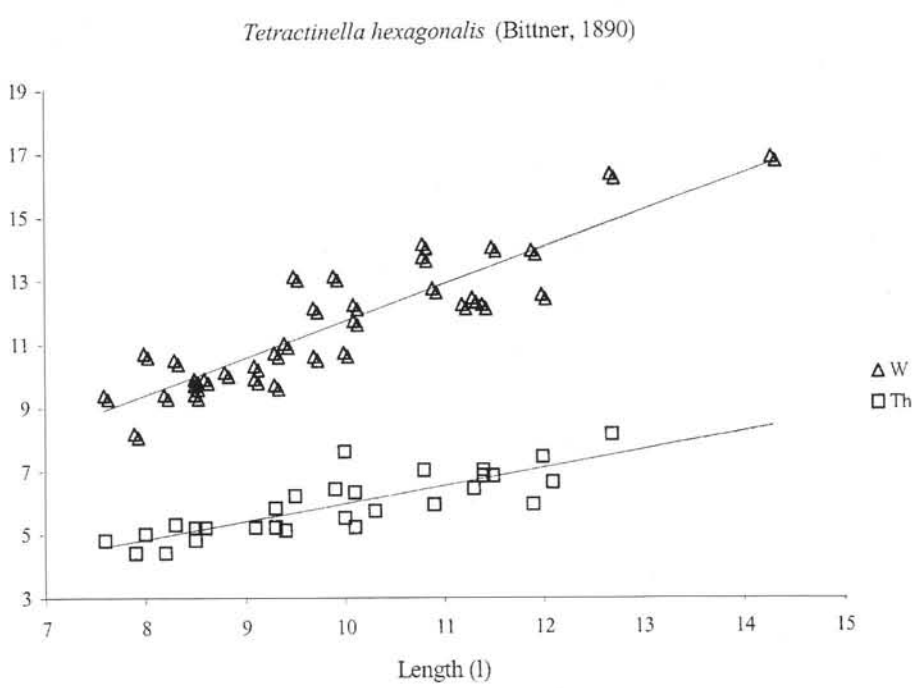

Fig. 13 - *T. hexagonalis*. The diagram shows the constant relationship between width, thickness and length of the shell.

Tetractinella hexagonalis (Bittner, 1890)

Text-figs. 13-14; Pl. 1, figs. 7-8

1890 *Spirigera hexagonalis* Bittner, p. 156, pl. 37, fig. 27-28.
1903 *Spirigera (Euractinella?) hexagonalis* - Bittner, p. 510, pl. 24, fig. 13-18, non fig. 19.
1904 *Spirigera hexagonalis* - Martelli, p. 116, pl. 5, fig. 7a, b.
1912 *Spirigera hexagonalis* - De Toni, p. 334.

Holotype. Not selected.

Type-locality. The original material described and illustrated by Bittner (1890) comes from Nagy-Vászony in Hungary. Bittner reported it as originating from the Tridentinus beds. This stratigraphic position is questionable, because in the Southern Alps the species is exclusively Pelsonian.

Material. 201 specimens decorticated and deformed, MPUM 8458 (G460/475), MPUM 8459 (G460/491), MPUM 8460 (G460/435), MPUM 8461 (G54/99), MPUM 8462 (G460/426-434, 436-474, 476-490, 492-546; G54/84-98, 100-165).

Occurrence. All specimens come from the topmost part of the Serla Formation (Anisian, Pelsonian substage) of Monte Rite (Cadore, Veneto, Italy) (Farabegoli & Guasti 1980, fig. 1, for the location).

Description

External characters. Small biconvex and sub-hexagonal shell in outline. Width exceeds length and maximum width occurs at about 1/3-1/2 of maximum length. Short and straight hinge sometimes with weakly winged and angular (obtuse angle) cardinal extremities. Anterior commissure more or less uniplicate. Fold semi-circular in profile.

Median sulcus in the ventral valve, starting near the umbo and becoming larger and deeper towards the anterior margin. Small ventral umbo not pointed terminally and not incurved. The Medium sized foramen, sub-circular to sub-oval in outline. Very reduced ventral palintrope.

Dorsal valve more convex than ventral valve in particular near the umbonal region. Small sized dorsal umbo. Fastigium weak.

Ornamentation. The radial ornamentation consists of four low and rounded costae in corresponding position on the two valves. The costae begin at the umbones and become larger and heavier near the anterior margin. The lateral costae, less strong than the central costae, underline the flanks only in some specimens. The presence of transversal tabulae like in *Tetractinella trigonella* was not observed.

In some specimens, an ornamentation consisting of weak growth lamellae occurs in the anterior half of the shell. The growth lamellae are denser near the anterior commissure. Micro-ornamentation not observed.

Dimensions. Width and thickness parameters are directly proportional to length (Fig. 13).

Internal characters: morphology and ultrastructure (Fig. 14). Shell substance impunctate. S.E.M. analysis of internal structures on 2 complete specimens (MPUM 8458 and MPUM 8459) was performed. The species is characterised by the following internal structures:

I. Very thin and short dental plates (they disappear at 0.9 mm from the umbo) that are completely fused to the lateral walls. A myotest along dental plates is observable.

II. A delthyrial plate is present at a distance of about 0.1 mm - 0.3 mm from the umbo.

III. Strong and high cardinal process protruding in the ventral central cavity.

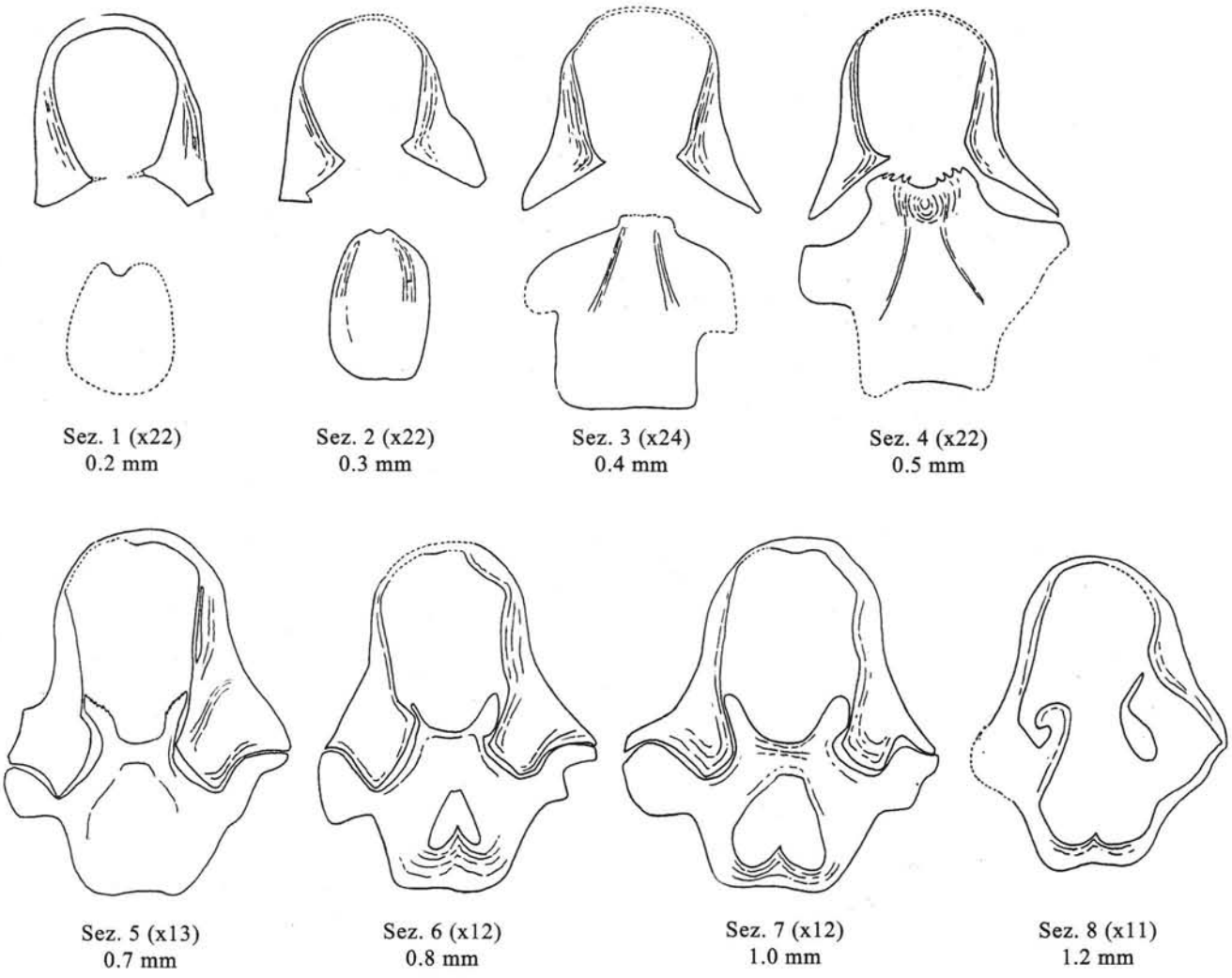

Fig. 14 - *T. hexagonalis* (specimen MPUM 8459): internal characters of ventral and dorsal valves. Distance from the umbo in mm.

IV. Articulation between the valves very strong, like in *T. trigonella*.

V. Low and sub-triangularly shaped myophragm.

Intraspecific variability. *Tetractinella hexagonalis* shows intraspecific variability in the outline, sub-hexagonal to sub-hexagonally extended along the plane of symmetry; in the hinge length, which is longer in the specimens sub-hexagonal along the transverse direction; in the median sulcus, deeper in the specimens with stronger central costae.

Discussion. The specimen illustrated by Bittner (1903, pl. 24, fig. 19) is rejected because of the presence of small fastigium. The specimens analysed are very similar to specimens described by Martelli (1906) and collected from Skala Vucetina (Montenegro) in shell length and width but are thicker. The specimens described by De Toni (1912, p. 334) are put doubtfully in synonymy because they are not illustrated.

Occurrence. *Tetractinella hexagonalis* beyond the type-locality occurs in the Middle Pelsonian of Monte Rite (this paper) and of Monte Cucco and Monte Tersadia (Friuli, Italy) (Metzeltin, 1973), in the Anisian stage of Studenkovic and Blizanac (Sarajevo area, Bosnia), Pocmin (Dalmatia), and Skala Vucetina (Montenegro).

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