

CARNIAN *THECOSPIRIDAE* (BRACHIOPODA) FROM SAN CASSIANO FORMATION (CORTINA D'AMPEZZO, ITALY)

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Riassunto. Sono stati esaminati circa 1000 esemplari di Brachiopodi appartenenti a quattro specie del genere *Thecospira* Zugmayer provenienti dalla Formazione di San Cassiano della conca ampezzana (Belluno).

Le analisi effettuate hanno evidenziato quale nuovo carattere diagnostico specifico la morfologia del campo muscolare della valva brachiale; esso risulta chiaramente leggibile sia in esemplari completi (peels) sia in valve disarticolate. La necessità di utilizzare un carattere interno nasce dalla difficoltà di osservazioni della morfologia esterna in esemplari sovente incrostati da organismi epizoi e dalla abbondanza e frequenza di valve brachiali disarticolate. Anche la morfometria ha uno scarso significato, perchè troppo influenzata dalla cementazione della conchiglia di *Thecospira*.

L'analisi della microstruttura del guscio ha evidenziato la presenza di uno strato primario e di uno strato secondario in tutti i taxa; solo in *Thecospira tyrolensis* (Loretz) e *Thecospira semseyi* Bittner è presente uno strato terziario, a livello del campo muscolare della valva brachiale. Tutte le specie esaminate sono pseudopunctate con taleole. Contrariamente a quanto affermato dagli autori precedenti, non sono state osservate punctae in nessuno dei taxa esaminati, ed in particolare in *Thecospira haidingeri* (Suess), specie tipo del genere.

Non vengono quindi accolte le proposte di Dagys (1974), che riserva il genere *Thecospira* per le forme punctate, e istituisce il nuovo genere *Thecospiropsis* Dagys per quelle pseudopunctate.

La famiglia *Thecospiridae* Bittner è stata attribuita all'ordine *Strophomenida*, avallando le ragioni proposte dagli autori precedenti; viene dubitativamente accettata la sua ascrizione alla superfamiglia *Davidsoniacea*, mancando ancora dati sufficienti a convalidare l'istituzione della superfamiglia *Thecospiracea* Dagys, 1974, cui l'autore sovietico ha attribuito la famiglia *Thecospiridae* Bittner.

Summary. Taxa belonging to the genus *Thecospira* Zugmayer, present in the San Cassiano Formation near Cortina d'Ampezzo are reviewed.

The muscle field of the brachial valve is advanced as a diagnostic character, for the reason that the external morphology is not always observable, and often only isolated brachial valves are found.

The microstructure of the shell of these taxa is discussed. This is composed of a primary layer, a secondary layer, and in *Thecospira tyrolensis* (Loretz) and *Thecospira semseyi* Bittner, a tertiary layer only in the muscle field. All the taxa are pseudopunctate with taleolae; in no case were punctae observed.

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The family *Thecospiridae* is ascribable to the Order *Strophomenida*, in accord with several authors, especially Dagys (1974).

Introduction.

The taxa belonging to the *Thecospiridae* Bittner family present in the San Cassiano Formation (Upper Ladinian - Carnian) in the Cortina d'Ampezzo (Belluno) area are, in the light of recent advances in methods of studying Brachiopods, well worth reexamining.

The material was collected and courteously lent by R. Zardini. The species examined were found in association with other shells belonging to the orders *Spiriferida*, *Rhynchonellida*, *Terebratulida*, *Lingulida*.

The large number of brachial valves found against the number of complete specimens prompts us to search for new relevant diagnostic characters.

Previous authors have described for *Thecospira* Zugmayer both pseudopunctate and punctate forms, without specifying what is meant. The problem prompts us to analyze the ultrastructure of this genus.

Moreover, taxonomical problems regarding family *Thecospiridae* Bittner are reviewed.

The specimens were first examined under a light microscope, and their fundamental biometric characters measured: length of brachial valve (L), maximum shell width (W), thickness (T), length of hinge line (HL), and relative ratios (Fig. 1). Examination of internal characters of the complete specimens was done with peels applied to serial transverse sections. The ultrastructure was examined with peels and by scanning electron-microscope. For this examination, the specimens were embedded in plaster and cut both radially and transversally; they were then emery polished (grain 1000) and attacked with 5% HCl. Residual material was stripped off the surface with acetate film applied with acetone, and the surface further cleaned ultrasonically for three minutes.

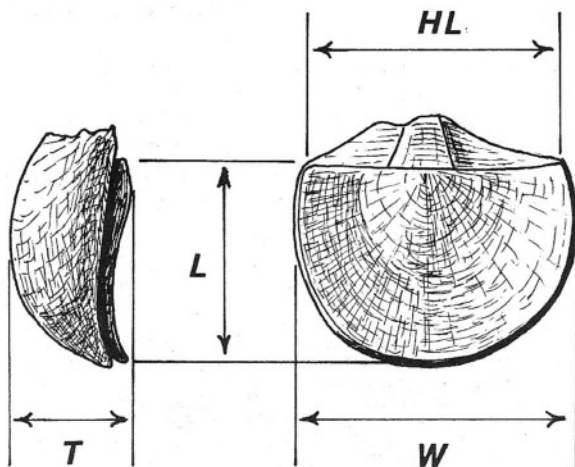


Fig. 1 - Dimensions considered for complete specimens and brachial valves: L) length of brachial valve; W) maximum width; HL) length of hinge line; T) thickness. For complete specimens, only the length of brachial valve is considered, to permit comparison with isolated brachial valves.

The material is currently housed in the "Museo di Paleontologia del Dipartimento di Scienze della Terra", Milan University.

Provenance.

The taxa examined are from the San Cassiano Formation, attributed to the Longobardian - Julic (Urlichs, 1974; Bizzarini et al., 1986). This unit has been well known in the literature since the last century. The most recent studies (Fürsich & Wendt, 1976; Assereto et al., 1977; Wendt & Fürsich, 1980; Wendt, 1982), especially, have put it into thorough paleoecologic and paleogeographic perspective.

Both in the type-locality, i. e., the meadows of Stuores near San Cassiano, as well as in localities near Cortina, sediments of the San Cassiano Fm. correspond morphologically to meadowland, with little outcrop. This is often an obstacle to determining the exact level of provenance of the fossils, the original faunal associations, and the sedimentary characteristics of the matrix; but it does explain the unique conditions in which they are found, which permit the recovery of a very abundant fauna that can be ob-

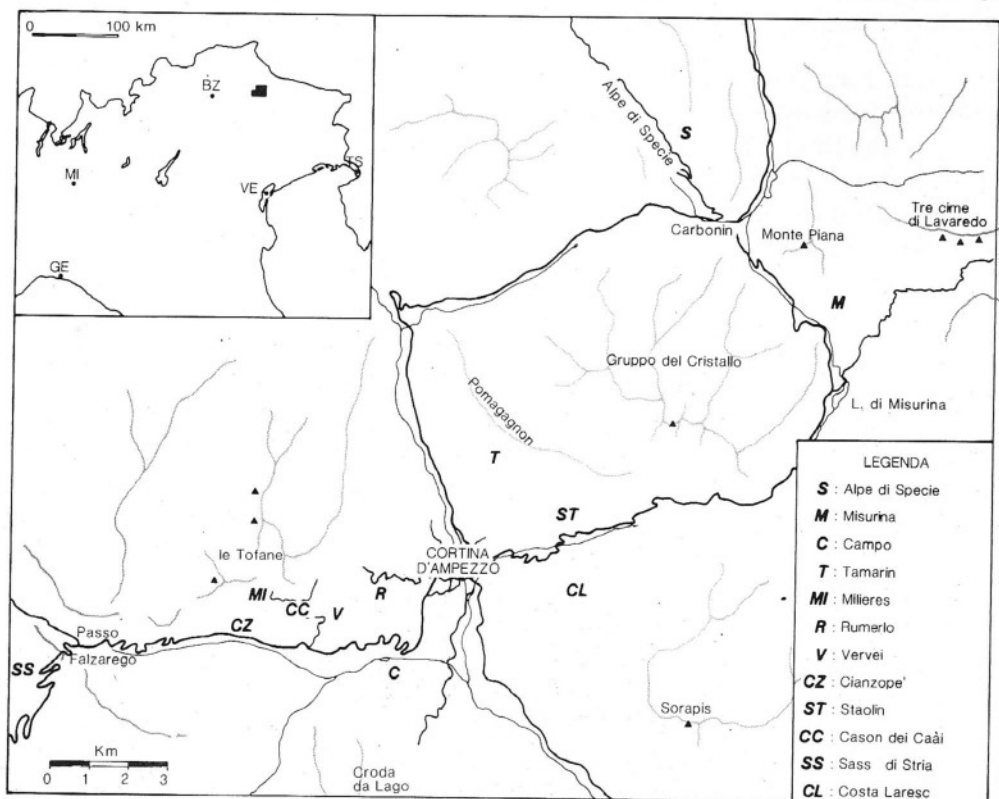


Fig. 2 - Sketch map of the Cortina d'Ampezzo area.

served three-dimensionally, without need of special preparation. Infact, the soil cover supplies the humic acids needed to corrode and dissolve the fossil's calcareous matrix, thus it is found free-lying, already isolated in the ground, conspicuous by its lighter color, or spotted with the aid of a sifter (Zardini, pers. com.).

The material examined in this study comes from localities mostly in and near Cortina d'Ampezzo (Fig. 2):

Tofane area: Rumerlo (1600 m), Milieres (1800-1900 m), Vervei (1700 m), Cason dei Caài (1700 m), Cianzopè (1770 m);

Croda da Lago area: Campo (1200 m);

Pomagagnon area: Tamarin (1550-1600 m), Staolin (1550-1600 m);

Sorapis area: Costalaresc (1450-1600 m).

The following localities outside the Ampezzo valley were also examined:

Sass de Stria (2200-2250 m), within the Cordevole basin;

Alpe di Specie (1900-2000 m);

Misurina - Monte Piana (1800 m), in the Sesto Dolomites.

Considerations on *Thecospiridae* from the Ampezzo area.

The material discussed in this paper consists mainly of isolated brachial valves; complete specimens were fewer in number, whereas there were no isolated pedicle valves at all. This is due to the characteristics of the genus *Thecospira*, which consists of shells cemented to hard substrates by the pedicle valve (Pl. 60, fig. 3), with weak articulation, easily disarticulated postmortem. Their habitat is conducive to disarticulation, as they are forms attached to the patch-reefs of the San Cassiano Fm. (calcareous sponge / coral association, Fürsich & Wendt, 1976), thus typical of high energy environment.

The Ampezzan species are generally cemented to calcareous sponge, rarely to Bivalvia or *Thecospira* shells. The hypothesis that such forms are cemented to small shell fragments only in the youth stages, subsequently growing away from the surface of attachment to lie freely, resting in the soft substratum (Rudwick, 1968), does not appear acceptable in the present instance. It is at variance, in the first place, with habitat, thus with sedimentary characteristics (high energy with abundant production of coarse biogenic detritus). The specimens enclosed in fine argillaceous sediments mentioned by Rudwick (1968) are thus to be considered allochthonous, transported from the edge of the carbonate platform down the slope. This point is further borne out by the large number of specimens extant with cemented surfaces developed also in the adult stage; by the shells, especially frequent for *Thecospira tyrolensis* (Loretz), with reduced convexity, thus subject to rapid burying within the sediment; by the calcareous sponge encrusting the outer surface of the pedicle valve, which cannot have developed within or just above the surface of the sediment itself.

For *Thecospira haidingeri* (Suess), Michalík (1976) suggests commensalism with other Brachiopoda to improve water circulation. This was not observed in the taxa

species -->	tyrolensis		semseyi		tenuistriata		haidingeri		total	
	compl.	b. v.	compl.	b. v.	compl.	b. v.	compl.	b. v.	compl.	b. v.
Alpe Specie	121	180	13	49	4	43	-	-	138	272
Misurina	68	110	7	7	4	10	-	1	79	128
Tamarin	-	51	-	-	-	-	-	48	-	99
Campo	19	48	1	11	-	17	-	14	20	90
Milieres	5	24	-	6	-	-	-	36	5	66
Rumerlo	11	14	-	2	-	-	-	5	11	21
Vervei	5	3	1	-	-	1	-	5	6	9
Cianzope'	6	9	-	-	-	-	-	1	6	10
Costalaresc	-	1	-	3	-	-	-	-	-	4
Cason de Caai	-	5	-	-	-	3	-	-	-	8
Sass di Stria	3	5	-	-	-	-	-	-	3	5
Staoiin	5	4	-	1	-	-	-	2	5	7
Total	243	454	22	79	8	74	-	112		

Tab. 1 - Frequency of taxa collected at different localities. compl.) Complete specimens; b.v.) brachial valves.

under review, probably because of the different habitat providing optimal life conditions.

Of the 17 localities considered by Zardini (1978), the genus *Thecospira* is indicated only in 12. Table 1 shows that the most widespread and frequent species, found in nearly all the sites listed, is *Thecospira tyrolensis* (Loretz) (697 specimens), followed by *Thecospira haidingeri* (Suess), with a total of 112 specimens, indicated in eight sites. *Thecospira semseyi* Bittner and *Thecospira tenuistriata* Bittner are equally frequent, but the former is more widespread (8 sites) than the latter (5 sites).

The sites yielding the most significant number of specimens (>50) were Alpe di Specie, Misurina, Tamarin, Campo, and Milieres. Analysis of these sites shows *Thecospira haidingeri* (Suess) as the most competitive taxon, its frequency being inversely proportional to that of the other species; it is not found wherever the latter are most plentiful (Alpe di Specie).

The material is relatively well preserved, considering the large number of determinable specimens. Further, there is no trace of diagenetic processes, such as to cancel the delicate inner structure (spiralium are clearly seen in sections of closed specimens), and, often, also the ultrastructure of the shells. In this connection, it is to be noted that nearly all SEM examined specimens were devoid of primary layer. Finally, resistance of the shell to corrosion by humic acids enables them to be easily isolated.

Ultrastructure.

Previous research.

In the last fifty years, study of the genus *Thecospira* Zugschmayer, 1880 has been focused especially on two strictly correlated problems: the ultrastructure of the shell, and the systematic position of the genus itself.

When Suess (1854) erected the species *Thecidea haidingeri* (= *Thecospira*), he pointed out the presence of punctae. In describing species belonging to the genus *Thecospira*, Bittner (1890) mentioned both punctate and impunctate shells.

Williams (1968) examined specimens of the genus *Thecospira*, recognizing a pseudopunctate shell, with tubercles "deposited in evaginations of the outer epithelium which caused an inward deflection of adjacent fibres".

Rudwick (1968), having examined a large number of specimens from Alpe di Specie, confirmed substantial differences in the ultrastructure of the genus under review: for a few specimens of *Thecospira* sp., in fact, he described the punctuation as numerous, unusual and fairly closely spaced in the external shell layers, coalescing into comparatively few, more widely spaced punctae, as they crossed the shell thickness. He believed the structure was the same as that described by Bittner (1890) for *Thecospira davidsoni* Bittner. *Thecospira tyrolensis* (Loretz), instead, is described as impunctate, with a complex shell structure due to the presence of small pustules on the inner surface of the valve, which are incorporated in the secondary layer during growth. *Thecospira guembeli*

Pichler has a pseudopunctate shell. Finally, the specimens examined by Zugmayer (1880) ascribed to *Thecospira haidingeri* (Suess) and reillustrated by Rudwick (1968), are described as having a clearly punctate shell.

McKinnon (1974), considering a few specimens from Alpe di Specie attributed to *Thecospira* sp., gives a full description of the ultrastructure, and especially of the primary layer. He identifies both punctate and pseudopunctate shells, but is unable to say whether or not they are variants of the same species. Further, he discusses the presence and appearance of the tubercles on either valve, and identifies a series of micritic bands in the secondary layer, which he attributes to successive levels of organic layers sandwiched within the normal calcareous succession.

Dagys (1972) (1), working on upper Triassic specimens from Pamir and the Caucasus, clearly recognized a primary layer of microcrystalline calcite, a secondary layer, and pseudopunctae arranged differently in the pedicle valve and in the brachial valve, with taleolae of microcrystalline calcite not unlike that of the primary layer. Later, Dagys (1974) (1), besides confirming the above, observed that for some species punctae and pseudopunctae are found on the same specimen, whereas in other taxa only pseudopunctae occur. The punctae cross both the primary and secondary layers, with a variable diameter in the same specimen. He attributes punctate species to the genus *Thecospira* Zugmayer, ascribing forms lacking punctae, characterized only by pseudopunctae, to the new genus *Thecospiropsis* Dagys. According to the original attribution by Dagys (1974) the following taxa are to be regarded as belonging to the genus *Thecospira* Zugmayer:

"*Thecospira haidingeri* (Suess, 1854)
Thecospira davidsoni Bittner 1890
Thecospira granulata Dagys, 1974
Thecospira sp. Rudwick, 1968"

whereas the following are included in the genus *Thecospiropsis* Dagys:

"*Thecospira semseyi* Bittner, 1900
Thecospira arenosa Bittner, 1890
Thecospira tyrolensis (Loretz, 1875)
Thecospira tenuistriata Bittner, 1890
Thecidium concentricum Münster, 1841
Thecidium piestingensis Bittner, 1890
Thecidium sturzenbaumi Bittner, 1890"

New data.

The ultrastructure of the species in this paper has been examined primarily on brachial valves. As the number of pedicle valves isolated was insufficient to permit a full or documented study of their ultrastructure, our data for the latter are based on analysis

(1) Italian translation of the original work by G. Ferliga.

of peels of serial transverse sections, and refer only to *Thecospira tyrolensis* (Loretz) and *Thecospira semseyi* Bittner.

Primary layer.

In the Ampezzan specimens examined, there nearly always occurs slight corrosion of the external shell surface, allowing the fibres of the secondary layer to show through without, however, completely erasing the ornamentation of the shell. Only in a few brachial valves was it possible to observe a thin continuous layer, external to the secondary layer, consisting of microcrystalline calcite, in a state of alteration or in the stages of subsequent re-crystallization, which can be construed as the primary layer (Fig. 3). From the size of the structure, and the fineness of the ornamentation which is still preserved over the secondary layer, visible through corrosion, it can be inferred that the primary layer is extremely reduced in thickness. For *Thecospira tyrolensis* (Loretz), in particular, a thickness of about 76 μm was measured in the muscle field of the brachial valve of specimen N. 5784/60 from Alpe di Specie (L = 8.85 mm, W = 12.80 mm).

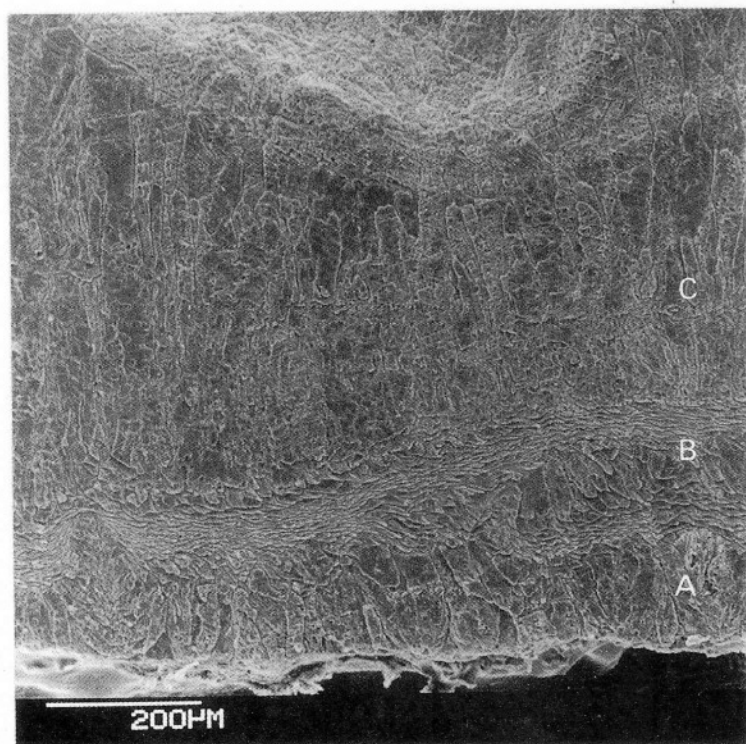


Fig. 3 - *Thecospira tyrolensis* (Loretz). Brachial valve, transverse section through muscle field. A) Primary layer; B) thin secondary layer deformed by taleolae; C) thick tertiary layer. Alpe di Specie; N. 5784/150.

Secondary layer.

The secondary layer is compact, composed of numerous imbricated fibres, having a flattened, diamond-shaped transversal section (Fig. 4). They appear longitudinally very elongated, subparallel to the valve surface (Fig. 5). Within the scope of the four species examined, no noteworthy morphological variations in the secondary layer were observed (Tab. 2).

In a few specimens, sections through the secondary layer revealed some alteration and corrosion, with the formation of a series of levels of microcrystalline calcite modifying the bands of fibres. These structures appear to correspond to the "micritic bands" described by McKinnon (1974, pl. 27, fig. 6). In the case under review, we rule out any organic origin, as they are clearly due to alteration (Fig. 6).

In the brachial valve, the fibres of the secondary layer are deflected inwardly, forming pseudopunctae (*sensu* Williams & Rowell, 1965). Occupying the inside of these structures is a calcitic core (taleola *sensu* Williams & Rowell, 1965), composed of crystals of irregular outline, of identical size, neither elongated nor preferentially oriented (Fig. 7, 8). This can be observed in well preserved specimens, free from alteration, whereas in the remaining specimens this core appears transformed into calcite granules of the size of micrite, with an appearance similar to the one defined by McKinnon (1974) as

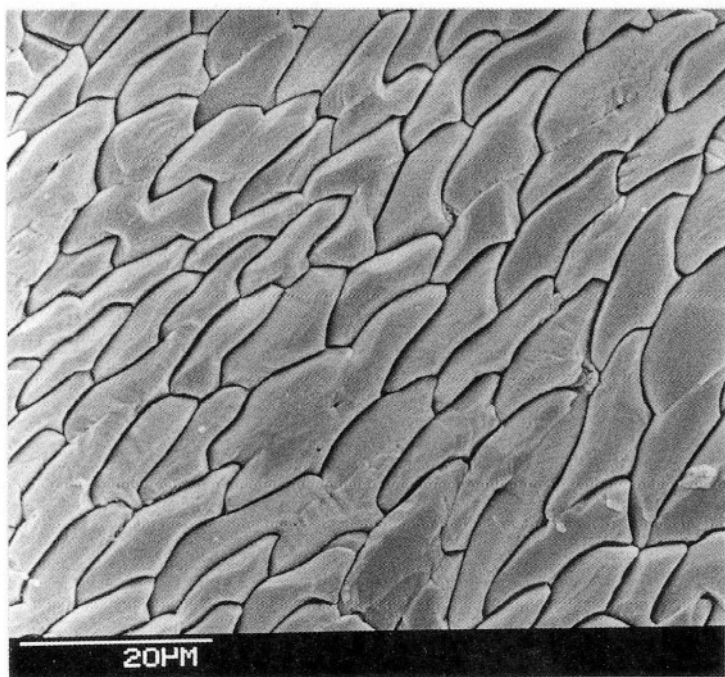


Fig. 4 - *Thecospira semseyi* Bittner. Brachial valve, radial section through muscle field (internal surface to the top). Cross-section view of secondary fibres composing the muscle field peripheral ridge. Alpe di Specie; N. 5796/19.

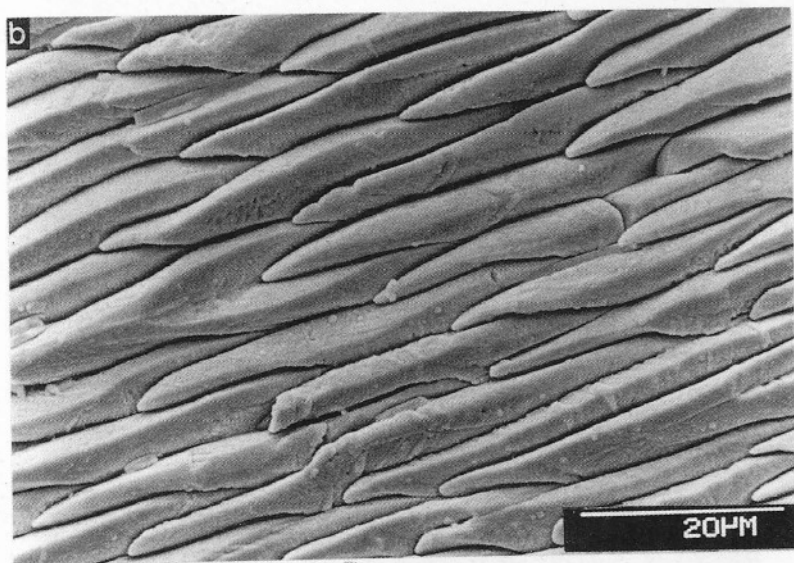


Fig. 5 - *Thecospira tenuistriata* Bittner. Brachial valve, radial section (internal surface to the top). a) Longitudinal view of secondary fibres at muscle field level; b) detail of the fibres. Alpe di Specie; N. 5804/40.

species	primary: thickness	secondary				tertiary: thickness (only in mf.)
		thickness		fibres in mf.		
		mf.	ext.	w	h	
<i>Th. tyrolensis</i>	76	100	-	30	10	200-250
<i>Th. semseyi</i>	?	235	-	20	5	175
<i>Th. tenuistriata</i>	?	-	-	-	-	absent
<i>Th. haidingeri</i>	?	-	725	22	3	absent

Tab. 2 - Average dimensions (in μm) of brachial valve shell layers in the taxa considered. mf) Muscle field; ext.) muscle field external area; w) secondary fibre section width; h) secondary fibre section height.

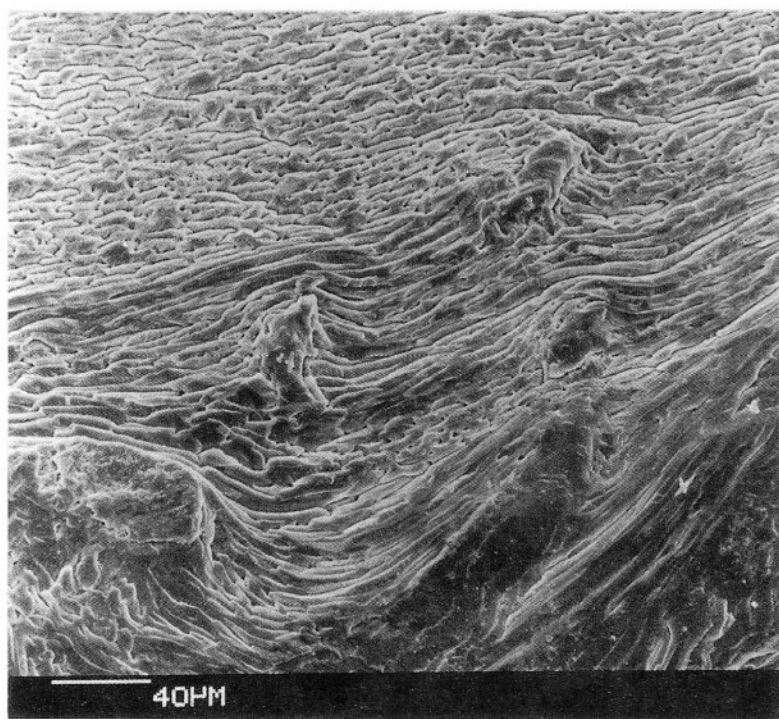


Fig. 6 - *Thecospira haidingeri* (Suess). Brachial valve, radial section (internal surface to the top). Exterior of muscle field. The beginning of alteration of secondary fibres is visible at several levels (thin layer in centre of photo, thick layer at the top), as small, closely spaced dissolution pores among the fibres. As the process continues, the outline of the fibres is destroyed and they take on a micritic look. Tamarin; N. 5810/20.

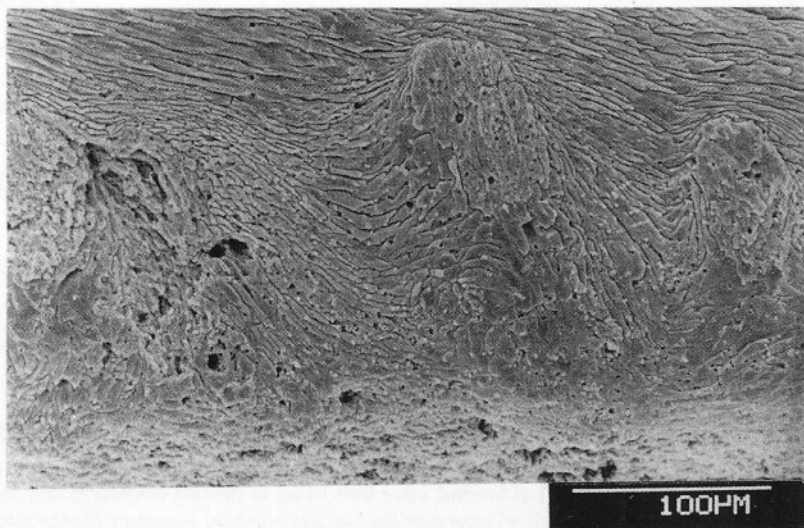


Fig. 7 - *Thecospira semseyi* Bittner. Brachial valve, radial section (internal surface to the top). Buried taleolae in the muscle field. Secondary fibres clearly overlap them. In the centre, corrosion of the calcitic crystals of the taleolae is seen starting.

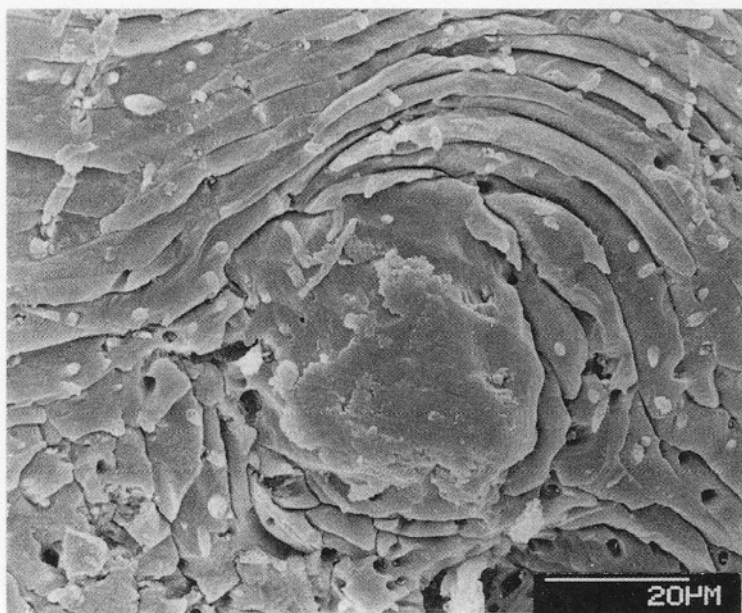


Fig. 8 - *Thecospira semseyi* Bittner. Brachial valve, transverse section (internal surface to the top). Transverse section of a small taleola, showing one of the calcitic crystals which constitutes the core of the structure. Alpe di Specie; N. 5796/19.

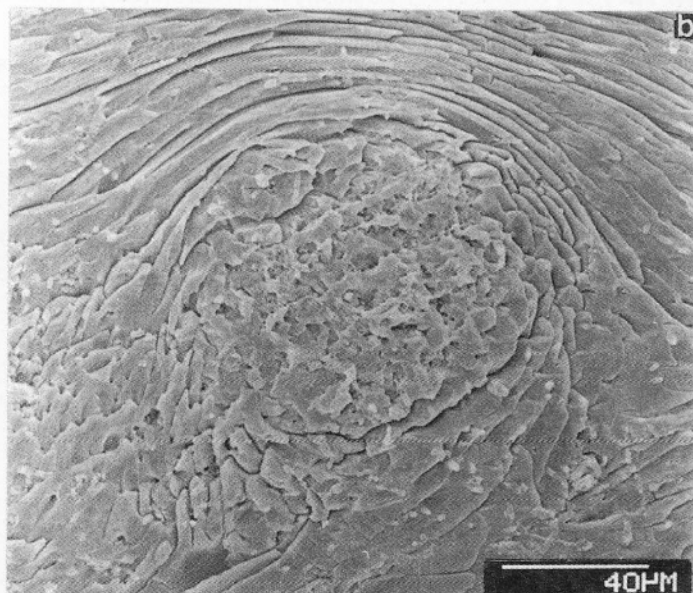
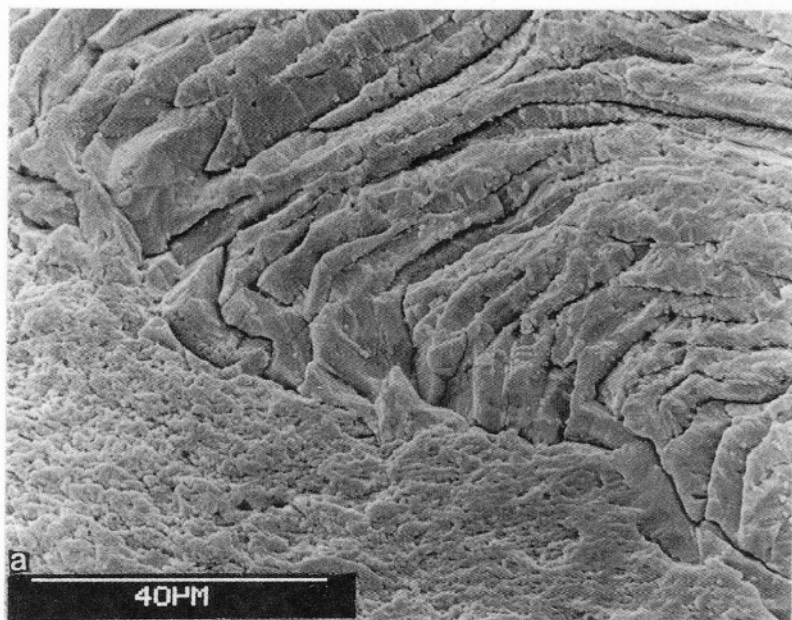


Fig. 9 - *Thecospira semseyi* Bittner. Brachial valve, transverse section through muscle field (external surface to the top). a) Contact between secondary fibres and a corroded taleola. Compare with Fig. 7. b) Transversal section of taleola, with corrosion of the core. The result is a porous, microcrystalline appearance. Compare with Fig. 8. Alpe di Specie; N. 5796/34 (Fig. 9a), N. 5796/19 (Fig. 9b).

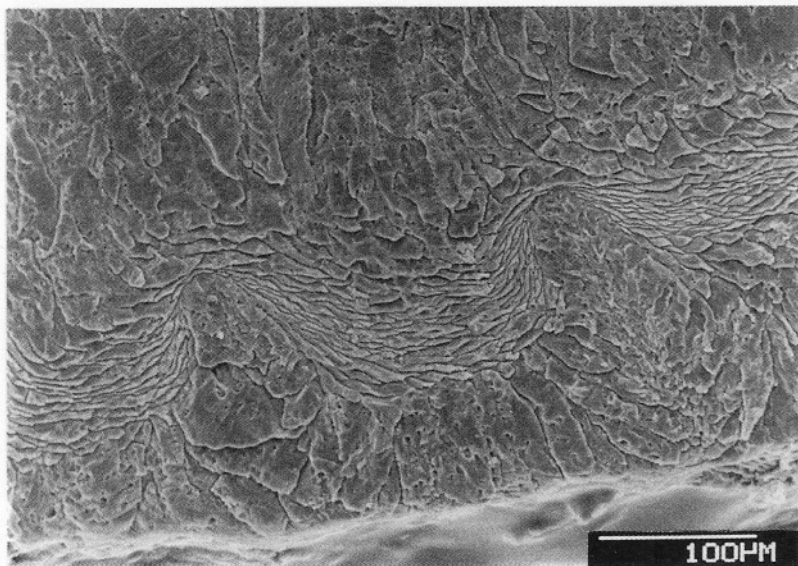


Fig. 10 - *Thecospira tyrolensis* (Loretz). Brachial valve, detail of Fig. 3: small taleolae buried in the secondary layer, their base visibly continuous with the primary layer. Alpe di Specie; N. 5784/150.

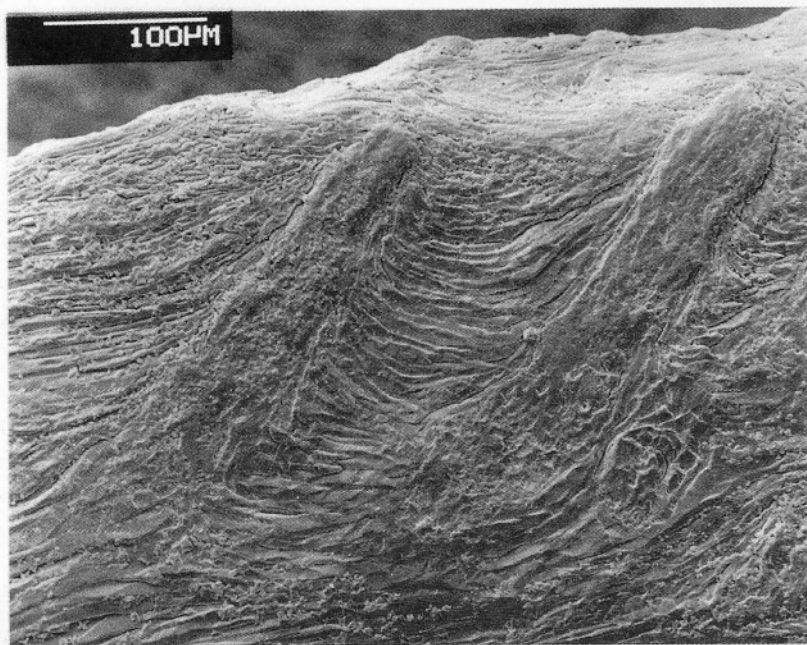


Fig. 11 - *Thecospira tenuistriata* Bittner. Brachial valve, radial section (internal surface to the top). Taleolae at the periphery. Alpe di Specie; N. 5804/40.

Species	mf.		ext.		pm.		density	aspect
	ϕ	h	ϕ	h	ϕ	h		
<i>Th. tyrolensis</i>	45*- 85*	95	45 - 65		90	1100	Loosely spaced, secondary fibres little disturbed	Low and conic shaped in mf., cylindrical at p.m
<i>Th. semseyi</i>	60 - 90	148	40 - 90				Loosely spaced, secondary fibres little disturbed	cylindric shaped
<i>Th. tenuistriata</i>	70 - 100				50 - 60	270	Loosely spaced, secondary fibres little disturbed	cylindric shaped
<i>Th. haidingeri</i>			40 - 50		55 - 70	290	Very closely disposed, fibres deviated	subspherical

Tab. 3 - Average dimensions (in μm) of brachial valve taleolae in the taxa considered. Difficulties in diameter evaluation of taleolae are due to orientation of section, often hardly deviating from direction of taleolae. mf) Muscle field; ext.) muscle field external area; pm.) peripheral margin; ϕ diameter of taleolae; h) height of taleolae; *) at the top; ●) at the base (conic shape).

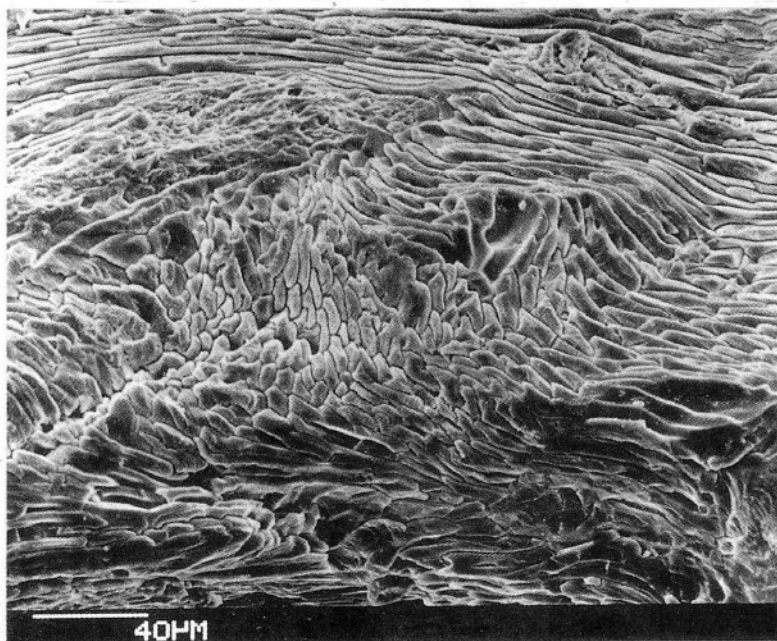


Fig. 12 - *Thecospira haidingeri* (Suess). Brachial valve, transverse section through muscle field (internal surface to the top). Secondary fibres near the periphery, showing chaotic patterns, due to presence of very closely spaced taleolae. Campo; N. 5811/12.

"porous", or by Dagens (1972, 1974) as "mielkocristallin" (= cryptocrystalline) (Fig. 9a,b).

The taleolae extend inwardly and radially to the periphery of the valve. In at least one specimen (*Thecospira tyrolensis*, Fig. 10) they are visibly continuous with the primary layer. This contrasts with Dagens (1972, 1974) and McKinnon (1974) who claim they originate inside the secondary layer. This impression may be due to slight deviations of the section from the axis of the taleolae, as observed in other specimens. Williams (1968, p. 39), on the other hand, described the taleolae of other *Strophomenida* as "extending inwardly from the laminar primary layer".

As already observed by Dagens (1972), taleolae give rise to functional tubercles along the valve periphery and are buried gradually under the secondary layer during growth (Fig. 11). They can be recognized from the first stages of ontogeny, in the muscle field, as relatively not very elongated bodies, covered in variable thicknesses of secondary layer (Fig. 7, 10).

A comparison of the four species examined did not reveal such differences in the ultrastructure of the brachial valve as to permit a distinction at species level. Infact, no marked variation in the size of the tubercles occurs from one species to the other (Tab. 3). On the contrary, marked variability in the size of these structures can be observed in the same individual, related to the different ontogenetic stages.

Tab. 3 shows how *Thecospira haidingeri* (Suess) differs from the others, the tubercles being short, of rounded contour. The tubercles of this taxon are more numerous, thus closer together. This is reflected on the fibres of the surrounding secondary layer, which show a chaotic pattern (Fig. 12). Further, it was observed that the longest tubercles on the periphery occurred for *Thecospira tyrolensis* (Loretz); moreover, this taxon is the one attaining the greatest size.

The fibres of the secondary layer of the pedicle valve have a more regular trend, because there are fewer taleolae. The density of taleolae is, anyway, greater in *Thecospira semseyi* Bittner than in *Thecospira tyrolensis* (Loretz). In the specimens examined, the pseudopunctae of the pedicle valve are also provided with taleolae. This is at variance with Dagens (1972).

Tertiary layer.

The tertiary layer, in the muscle field of the brachial valve, was observed only in two species: *Thecospira tyrolensis* (Loretz) and *Thecospira semseyi* Bittner. It is more developed in the former, where it extends outside the muscle field, to form its bulging border (Fig. 3, 10, 21). In *Thecospira semseyi* Bittner, the tertiary layer is restricted to the muscle field, not reaching the ridge which demarcates it laterally and anteriorly. Further, its thickness is smaller than that of *Thecospira tyrolensis* (Loretz). There was no tertiary layer in the other two taxa examined.

The tertiary layer would seem to be related to the accentuation of the structures of the muscle field of the brachial valve. It can thus be inferred that the adductor muscles are more developed, in line with the greater size of the two taxa considered. In-

fact, in more minute and lighter shells (*Thecospira tenuistriata* Bittner and *Thecospira haidingeri* (Suess)) these characteristics were not observed.

As the tertiary layer is limited to the structure of the muscle field of the brachial valve, it is not regarded as a diagnostic character significant enough to constitute a distinction between the two genera.

The problem of punctae.

In none of the specimens examined were structures found comparable to punctae. In particular, in *Thecospira haidingeri* (Suess), indicated by Dagys (1974) as punctate, no punctae were observed in the transverse or longitudinal sections, nor in those tangential to the surface of the valve. A large number of taleolae can be seen on the tangential section, more or less corroded, and with a variable diameter according to the stage of development, whereas there are no visible gaps in the secondary layer which could be interpreted as punctae (Fig. 13). Their appearance is comparable to the photograph published by the Soviet author (Dagys, 1974, pl. 14, fig. 5, 6) showing the "punctae" of *Thecospira davidsoni* Bittner.

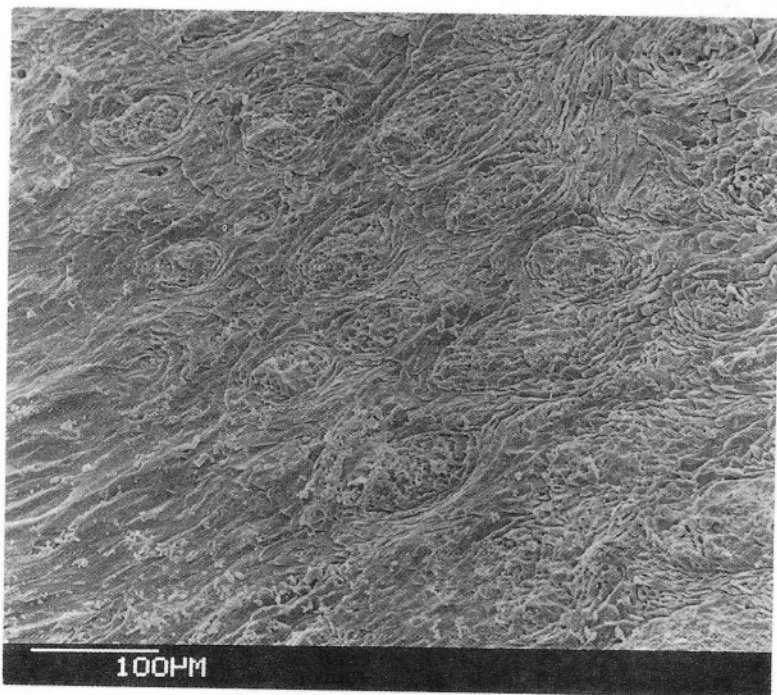


Fig. 13 - *Thecospira haidingeri* (Suess). Brachial valve, external surface tangential section. Very closely spaced taleolae (diameter wider than space between them), and compact secondary fibres inflexed towards the internal surface. No punctae or perforate structure are visible. Campo; N. 5811/12.

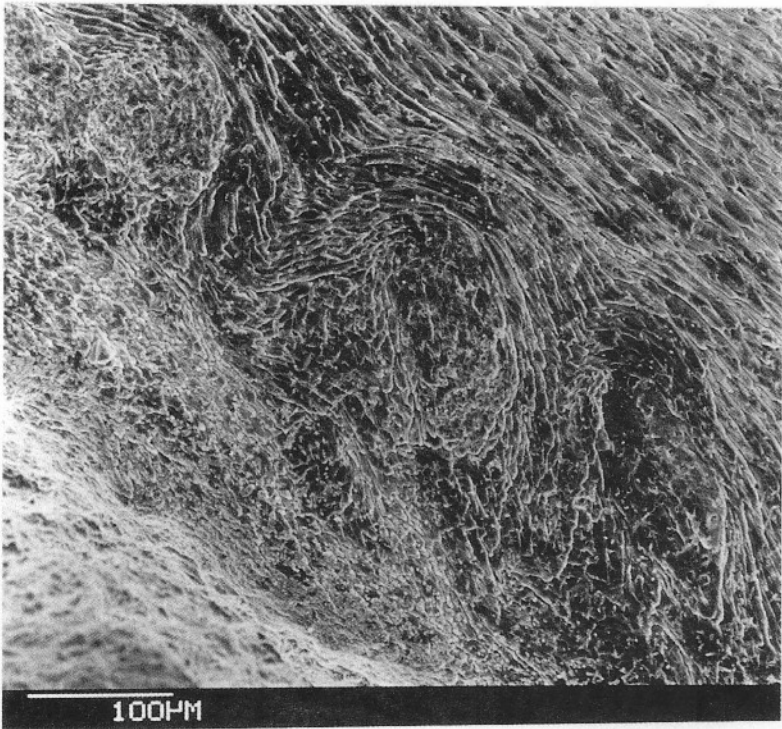


Fig. 14 - *Thecospira haidingeri* (Suess). Brachial valve, transverse section through muscle field (internal surface to the top). "Inflexion" of fibres toward the external surface, due to closely spaced taleolae near the periphery. The structure may resemble a puncta, but no perforation is present. Tamarin; N. 5810/40.

In the transverse and radial sections, in the sector between the muscle field and valve periphery, the taleolae are closely spaced, so cramping the fibres of the secondary layer that they cannot re-arrange in regular fashion. The fibres are thus apparently warped outwardly, although this cannot be mistaken for a perforated puncta-like structure (Fig. 14). Similar "inflexions" can be observed in some specimens also for *Thecospira semseyi* Bittner, whose taleolae are, however, more widely spaced (Fig. 15, 16).

The possibility of there being at the same time, and on the same specimen, both punctae and pseudopunctae, as affirmed by Dagys (1974) and McKinnon (1974), must be ruled out for the taxa under review.

In view of the foregoing, as the Suess taxon is the type-species for *Thecospira* Zugmayer and, in the light of our observations, pseudopunctate, it follows that the generic name *Thecospira* is attributable to pseudopunctate forms. This conflicts with Dagys (1974), when he ascribes to this genus only forms with punctae and pseudopunctae on the same specimen, and attributes specimens with only pseudopunctae to his new genus *Thecospiropsis* Dagys (1974). According to the present authors, therefore, the taxa classified by the Soviet author as *Thecospiropsis tyrolense*, *Thecospiropsis semseyi* and *Thecospiropsis tenuistriatum*, retain their ascription to the genus *Thecospira* Zugmayer, in accord with the classification by Loretz (1875) and Bittner (1890, 1900).

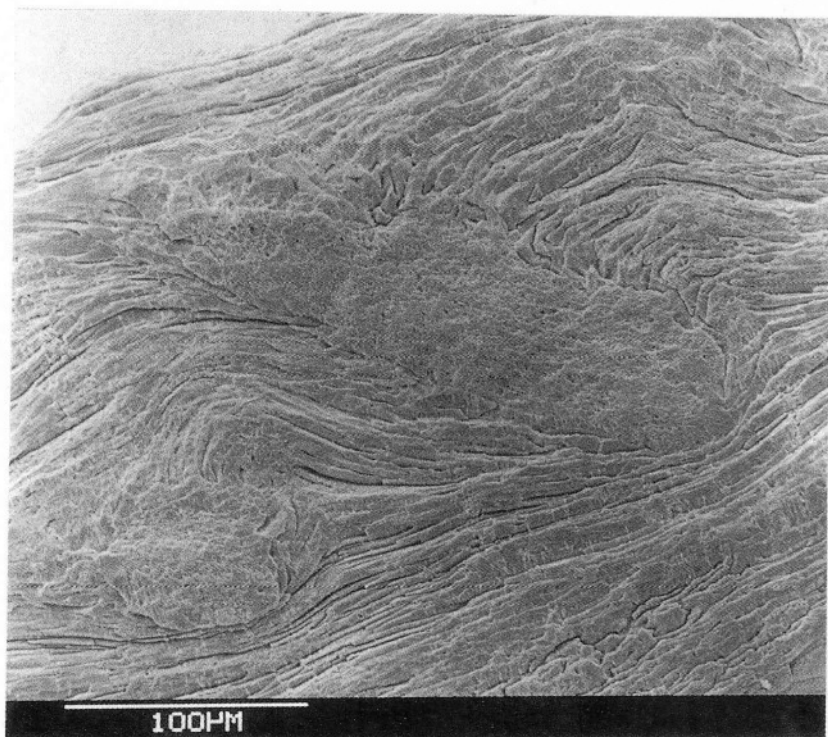


Fig. 15 - *Thecospira semseyi* Bittner. Brachial valve, transverse section through muscle field (external surface to the top). Taleolae buried into the secondary layer, outside the muscle field. The strong dipping of secondary fibres towards external surface may suggest a puncta, but no perforation is present. On the left of the photo the true picture is obscured by beginning of micritization which, continuing, could simulate the filling of a perforation. Alpe di Specie; N. 5796/34.

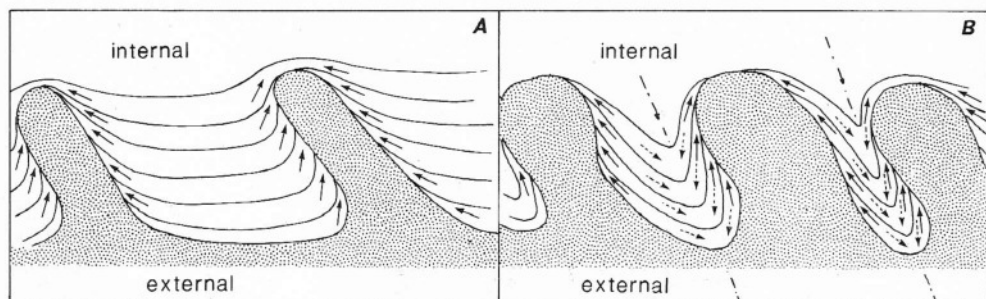


Fig. 16 - Interpretative sketch of pseudopunctate structure. A) Spaced taleolae: fibres can rearrange in regular fashion. B) Very closely spaced taleolae: black arrows show the real inflexions of the fibres; dashed arrows show their apparent inflexion, which may simulate a puncta. Compare with Fig. 14, 15.

Classification criteria: a proposal.

The authors who in the past have dealt with the taxa under review (Bittner, 1890; Laube, 1865; Dagens, 1972, 1974) stress the importance of external shell morphology and, sometimes, ornamentation (*Thecospira tenuistriata* Bittner, 1890), for the purpose of species determination. Internal brachial valve morphology is described in detail only for *Thecospira tyrolensis* (Loretz) by Bittner (1890). On the contrary, in the material examined, noteworthy differences were observed in the internal characters of the brachial valve of individual species, especially as regards structure of the adductor muscle field,

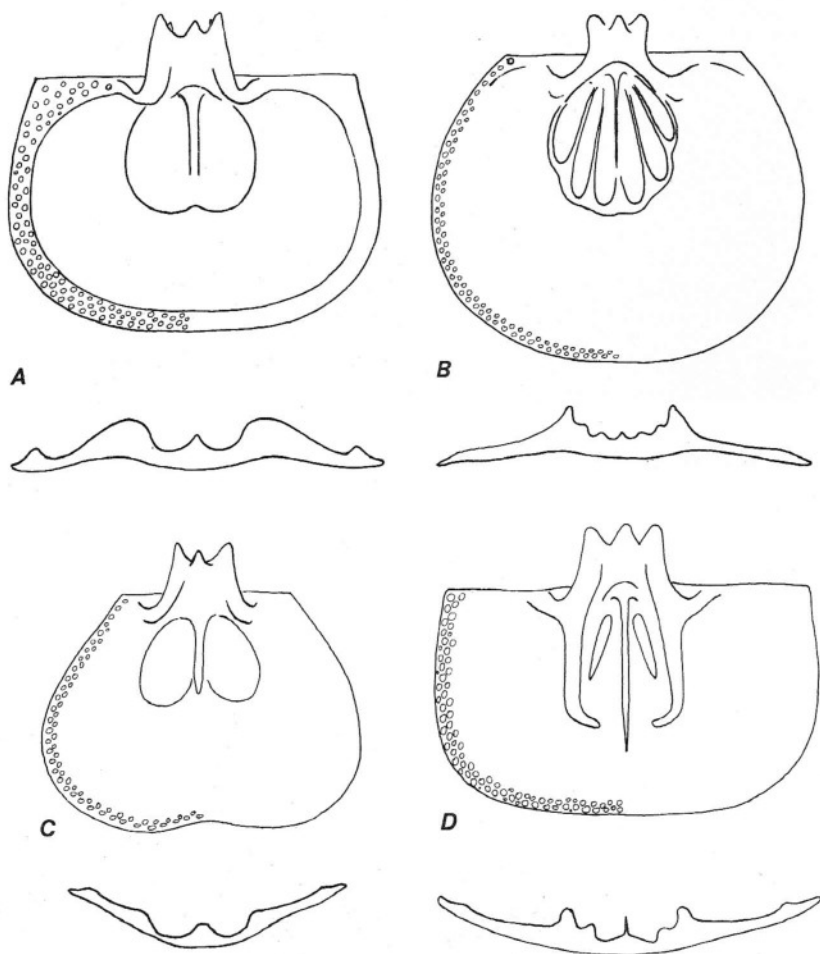


Fig. 17 - Schematic representation patterns of brachial valve adductor muscle field in the taxa examined (plant view and transverse section). A) *Th. tyrolensis* pattern. B) *Th. semseyi* pattern. C) *Th. tenuistriata* pattern. D) *Th. haidingeri* pattern.

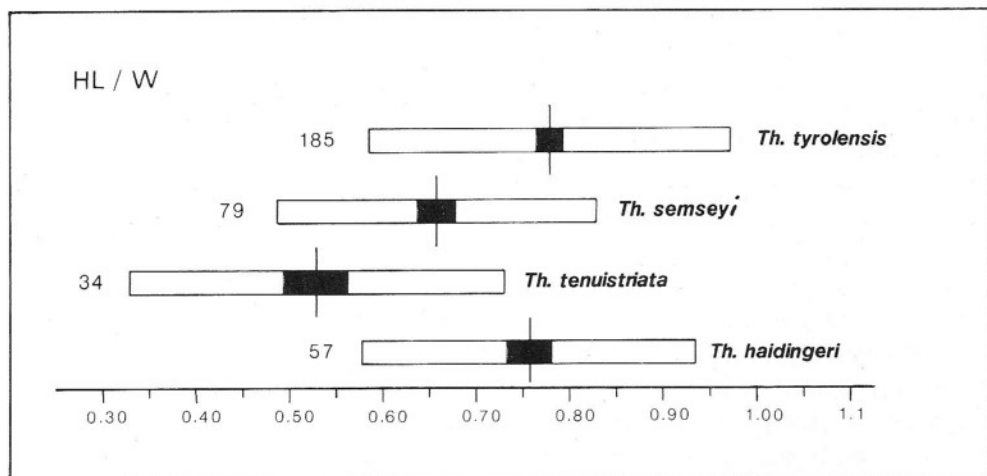


Fig. 18 - Diagram to show hinge line length (HL) / max. width (W) ratio average, fiduciary intervals and $\bar{x} \pm 5\% \text{ sm}$, for the taxa considered. Values on the left indicate the number of specimens considered for each interval.

hence their relationship to the rest of the valve surface.

As a result, outline and profile of the periphery of the adductor muscle field, as well as morphology of the median septum, are advanced as diagnostic characters for species. On this basis, the adductor muscle fields can be grouped under four models, each of which characteristic for one of the species described:

- A) W-shaped outline, raised margin with swollen section continuous with surrounding surface (Fig. 17 A). This is characteristic of *Thecospira tyrolensis* (Loretz), and is accompanied by a marked median septum having a triangular section.
- B) Sub-circular outline, distinctly demarcated by a raised, scalloped ridge (Fig. 17 B; Pl. 57, fig. 4). The median septum tends to merge with the ridges separating the grooves within the muscle field. This is characteristic of *Thecospira semseyi* Bittner.
- C) Distinctly bilobate and depressed, demarcated by a step (Fig. 17 C). The median septum ranges from thin and sharp to a low, wide platform separating the two lobes. This is characteristic of *Thecospira tenuistriata* Bittner.
- D) Subrectangular outline, open anteriorly and demarcated only laterally by raised, sub-parallel ridges (Fig. 17 D). This is characteristic of *Thecospira haidingeri* (Suess), and is accompanied by a thin sharp median septum.

These differences in the adductor muscle field conflict with the variations in the external morphology, which do not appear to follow the same schemes.

The length/width ratio (L/W), for instance, varies greatly within each species, especially for *Thecospira tyrolensis* (Loretz), as seen clearly in Bittner's pictures (1890,

1900). The thickness of the complete specimens is likewise variable. This is because the shells are cemented. Depending on the type of substrate (bryozoans, corals, weakly convex valves), and especially on its shape and extent, cementation surfaces vary in size and this affects valve growth. Extreme cases, characterized by shell deformation, are well documented by Michalík (1976).

The length of hinge line/width ratio (HL/W) appears to be less sensitive to the environment, and on this basis it is possible to differentiate *Thecospira semseyi* Bittner fairly well from *Thecospira tyrolensis* (Loretz) and *Thecospira haidingeri* (Suess) (Fig. 18). In isolated brachial valves, however, the hinge line is not always well preserved and thus limits the validity of this morphometrical criterion.

Ornamentation appears to be diagnostically significant. Bittner (1890) pointed out the closely spaced radial costae observed in *Thecospira tenuistriata* Bittner, which markedly differentiates it from *Thecospira tyrolensis* (Loretz), characterized by few, well spaced costae. It must be noted, however, that in the taxa under review the costae are thin and not very marked, thus unlikely to be preserved. Furthermore, Cassian fauna frequently has epizoic organisms, and specimens are often encrusted by sediment, all factors obscuring ornamentation.

It follows that the internal surface of the brachial valve, and especially the adductor muscle field, appears to be the most valid diagnostic criterion for distinguishing species belonging to the genus *Thecospira* Zugmayer. Infact, it has the following characteristics:

- 1) Practicality: there was a prevalence of isolated brachial valves in the material examined. Only for *Thecospira tyrolensis* (Loretz) were a large number of complete specimens available; very few those ascribable to *Thecospira semseyi* Bittner and *Thecospira tenuistriata* Bittner. Last, not one complete specimen of *Thecospira haidingeri* (Suess) was identified.
- 2) Legibility: this diagnostic character was observed not only in individual brachial valves, but also in serial sections through complete specimens.
- 3) Preservation: this is furthered by the robust structure of the adductor muscle field; only rarely is the internal surface encrusted with organisms.
- 4) Correspondance: the four different aspects of this character correspond perfectly to the four species under review, as identified by previous authors.

Taxonomical considerations.

The systematic classification of the genus *Thecospira* Zugmayer at Order level is still highly argued.

The presence of a spiral brachidium has induced several authors to attribute this taxon to the *Spiriferida* order (Schuchert, 1893 fide Dagys; Schuchert & Le Vene, 1929; Williams, 1968; McKinnon, 1974). Others (Williams, 1953; Muir Wood & Williams, 1965; Cowen & Rudwick, 1967; Rudwick, 1968; Dagys, 1974; Michalík, 1976) attribute

this genus to the *Strophomenida* order. Dagys (1974) substantiates this claim most fully by reverting to the arguments partially expounded by the authors mentioned above; they are:

- ultrastructure: the taleolae of *Thecospiridae* are comparable with those of *Strophomenida*;
- plano-convex or concavo-convex shape, typical of all *Strophomenida*, which conditions the type of brachidium;
- ventral interarea with complete pseudodeltidium and reduced dorsal interarea;
- cementation to substrate;
- cardinal process comparable with that of *Strophomenida*;
- spirolophe analogous to that of *Strophomenida*.

With regard to the brachidium, Dagys (1974) observed how the spiralia of *Thecospiridae* differ from those of *Spiriferida*, "thus constituting independent structures, not comparable with other types of known brachidia". In fact, the brachidium of *Thecospiridae* consists of two ventrolaterally directed spiralia.

The same characteristics were observed in our specimens, and it is for this reason that we endorse attribution of the *Thecospiridae* family to the *Strophomenida* order.

The brachidium is not examined in detail here as it has been amply illustrated and discussed elsewhere (Rudwick, 1968; McKinnon, 1974; Dagys, 1974), and was observed only occasionally in the Ampezzan material. The pseudodeltidium is composed of a single plate, as in the majority of *Strophomenida*. The chilidium was not sufficiently well preserved to permit a more thorough analysis of its structure.

Furthermore, Dagys (1974) suggests introducing a superfamily, *Thecospiracea*, comprising the families *Thecospiridae* Bittner, *Thecospirellidae* fam. nov., *Hungaritecidae* fam. nov. The Soviet author believes the above superfamily evolved in the Triassic from paleozoic *Davidsoniacea*, through the development of a calcareous structure (spiralia) supporting the lophophore. Our data cannot endorse this hypothesis, at least, until a detailed re-examination is undertaken of the other taxa found in the Ampezzan fauna and ascribed by Dagys (1974) to that superfamily. Attribution to the superfamily *Davidsoniacea* is thus dubitatively maintained.

Paleontological description

The determined species have been classified on the lines proposed in "Treatise on Invertebrate Paleontology", part H, Brachiopoda, 1965.

As regards the diagnosis suggested in "Treatise" for the family *Thecospiridae* Bittner, the following amendments were thought necessary:

- 1) the presence of a differentiated pseudodeltidium;
- 2) the presence of a chilidium;

3) the peculiar feature of the brachial valve described as a "pair of subparallel ridges containing dorsal adductor field...", is characteristic only for *Thecospira haidingeri* (Suess). The margin of the muscle field of the brachial valve is different in the other species examined. The above definition thus appears reductive. With regard to the muscle field of the brachial valve, our suggestion for the diagnosis of *Thecospiridae* family is, simply: "well demarcated adductor muscle field, divided by a poorly developed median septum". So, the amended diagnosis is:

"Cemented by ventral umbo, ventral interarea with pseudodeltidium; dorsal interarea vestigial, chilidium present; teeth unsupported, ventral muscle scar small, divided by low median septum; cardinal process high, functionally bilobed but united medianly to form tripartite structure, socket plates recurved; well demarcated adductor muscle field, divided by a poorly developed median septum; cardinal process bases prolonged into two short processes supporting pair of spirally coiled calcareous ribbons, directed ventrolaterally; brachial ribbons sharply folded throughout length to give V-shaped cross section; shell substance pseudopunctate".

Further, the assertion "without radial ornamentation" is reductive for the genus *Thecospira* Zugmayer. Infact, this genus includes species having a distinct sculpture.

The four species determined here are: *Thecospira tyrolensis* (Loretz, 1875), *Thecospira tenuistriata* Bittner, 1890, *Thecospira semseyi* Bittner, 1900, *Thecospira haidingeri* (Suess, 1854).

Phylum **Brachiopoda**

Class **Articulata**

Order **Strophomenida** Opik, 1934

Suborder **Strophomenidina** Opik, 1934

Superfamily ?*Davidsoniacea* King, 1850

Family *Thecospiridae* Bittner, 1893

Genus *Thecospira* Zugmayer, 1880

Type-species *Thecospira haidingeri* (Suess, 1854)

Thecospira tyrolensis (Loretz, 1875)

Pl. 57, fig. 1-3; Pl. 58, fig. 1-3; Pl. 59, fig. 1-3; Pl. 60, fig. 1-4;

Text-fig. 3, 10, 17A, 19-22

1865 *Thecidium concentricum* - Laube, p. 11, pl. 11, fig. 1.

1875 *Thecidium tyrolense* Loretz, p. 820, pl. 21, fig. 6-8.

1890 *Thecospira tyrolensis* - Bittner, p. 114, pl. 38, fig. 14-18.

1890 *Thecospira* aff. *tyrolensis* - Bittner, p. 152.

1892 *Thecospira tyrolensis* - Bittner, p. 9.

- 1900 *Thecospira tyrolensis* - Bittner, p. 40, pl. 4, fig. 24-39.
1903 *Thecospira tyrolensis* - Waagen, p. 443, text-fig. 1.
1968 *Thecospira tyrolensis* - Rudwigh, pl. 65, fig. 12,13; text-fig. 1B.
1974 *Thecospiropsis tyrolensis* - Dagens, p. 75.

Material. 243 complete specimens and 454 isolated brachial valves. 80 complete specimens and 201 brachial valves measured. N. 5784/1-301; N. 5785/1-178; N. 5786/1-51; N. 5787/1-67; N. 5788/1-29; N. 5789/1-25; N. 5790/1-8; N. 5791/1-15; N. 5792; N. 5793/1-5; N. 5794/1-8; N. 5795/1-9.

Description.

External characters. Average size shell, rectimarginate, plano-convex, in some cases (30%) concavo-convex, greater in width than in length; maximum width in proximity of hinge line, not much greater than its length. Shell generally subrectangular in outline; long, straight hinge line, lateral and anterior commissure with blade-like profile. Lateral commissure more or less at right angles to hinge line, continuous with anterior commissure.

Pedicle valve with very variable convexity, affected by extent of surface of attachment. Umbonal region affected and modified by cementation; very well developed interarea, large, complete pseudodeltidium. Brachial valve with reduced interarea, sharp umbo, chilidium (Fig. 19).

Ornament observable only on a few specimens, consisting, on the pedicle valve, of numerous, small, evenly distributed tubercles; on the brachial valve, of thin, widely spaced radial costae (Pl. 60, fig. 1).

Internal characters. Pedicle valve with deep delthyrial chamber; massive oval shaped teeth; muscle field weakly depressed, expanding into posterior area of the valve, distinctly bilobed. Sharp median septum originating in the umbonal region, breaking off where the two lobes separate (Fig. 20). Outer periphery with extensive band of small, radially aligned tubercles.

Brachial valve with high cardinal process, extending to the pedicle valve, where it is prolonged for two-thirds of the length of the pseudodeltidium; cardinal process with sharp median ridge and two massive lateral lobes; there is also a short, sharp apophysis on the distal end of each lobe towards the median ridge and outwardly displaced (Pl. 58, fig. 1). Deep dental sockets, elongated, circumscribed by a well developed inner socket ridge. Thin, short crura at the base of the cardinal process; cone shaped spiralia, composed of 6-7 convolutions, with apex directed towards pedicle valve (Pl. 60, fig. 4; text-fig. 21, 22). Internal surface of brachial valve subdivided in three distinct parts (Pl. 57, fig. 1): muscle field, surface outside the muscle field, periphery. Muscle field not very large, depressed, with W-shaped outline, divided by a clearly visible median septum (Fig. 17 A). Surface outside the muscle field swollen, demarcated towards the periphery by a sulcus. The periphery of the valve consists of a variably raised band extending to the hinge line, covered with very small tubercles, closely and unorthodoxly packed (Pl. 59, fig. 3).

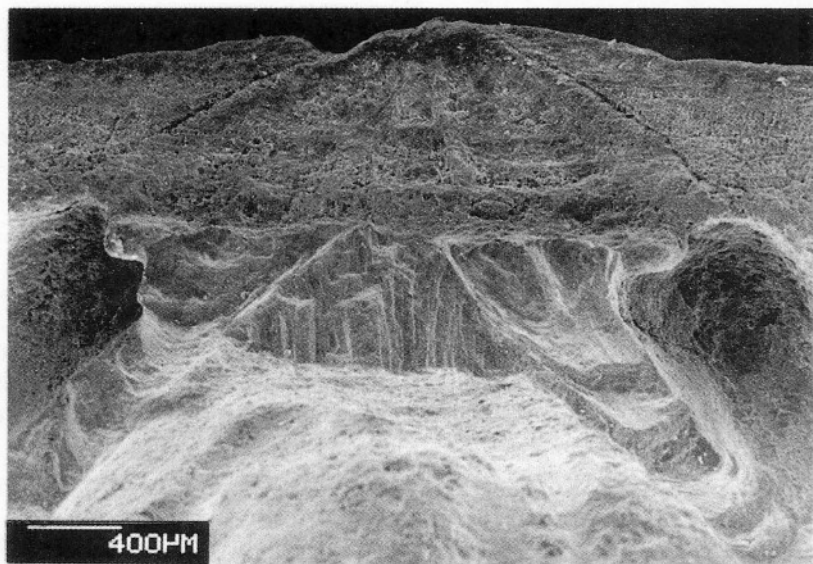


Fig. 19 - *Thecospira tyrolensis* (Loretz). Brachial valve with broken cardinal process. View of the chidium. Misurina; N. 5785/80.

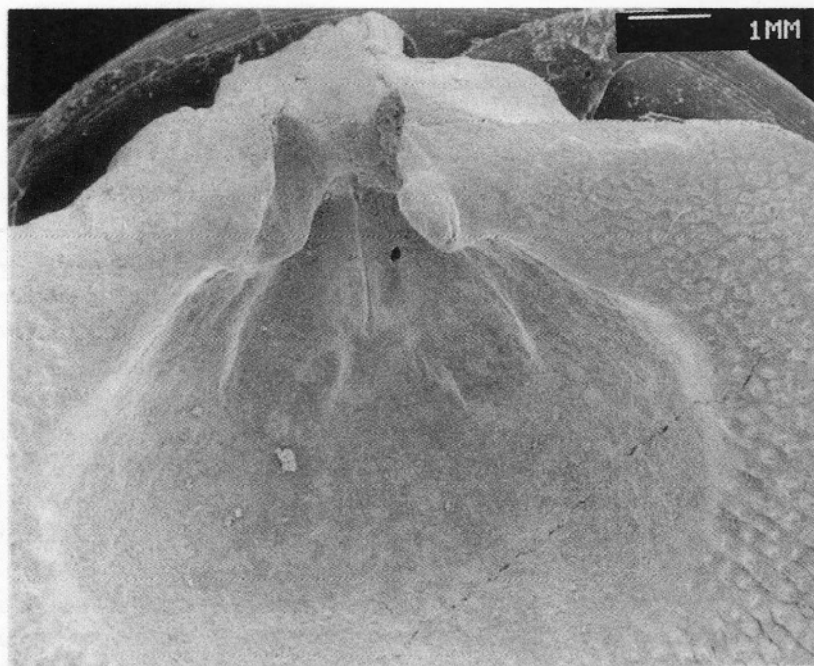


Fig. 20 - *Thecospira tyrolensis* (Loretz). Pedicle valve. View of internal surface, with median septum and muscle scars. Alpe di Specie; N. 5784/50.

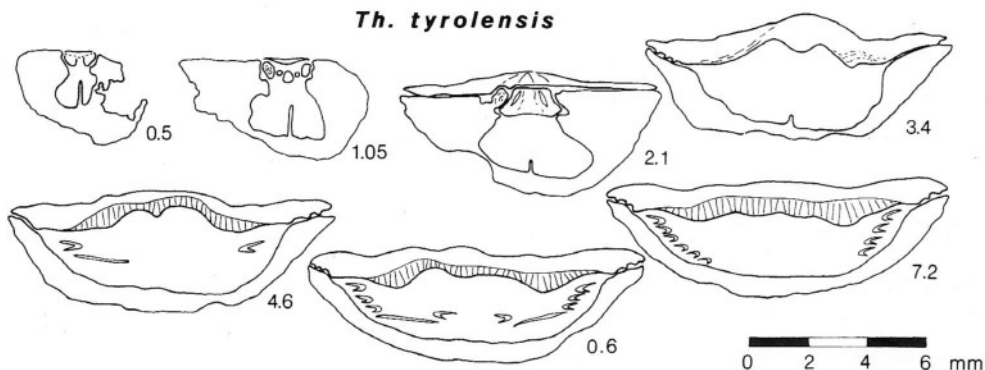
Th. tyrolensis

Fig. 21 - *Thecospira tyrolensis* (Loretz). Serial transverse sections through the posterior part of the shell. Alpe di Specie; N. 5784/43.

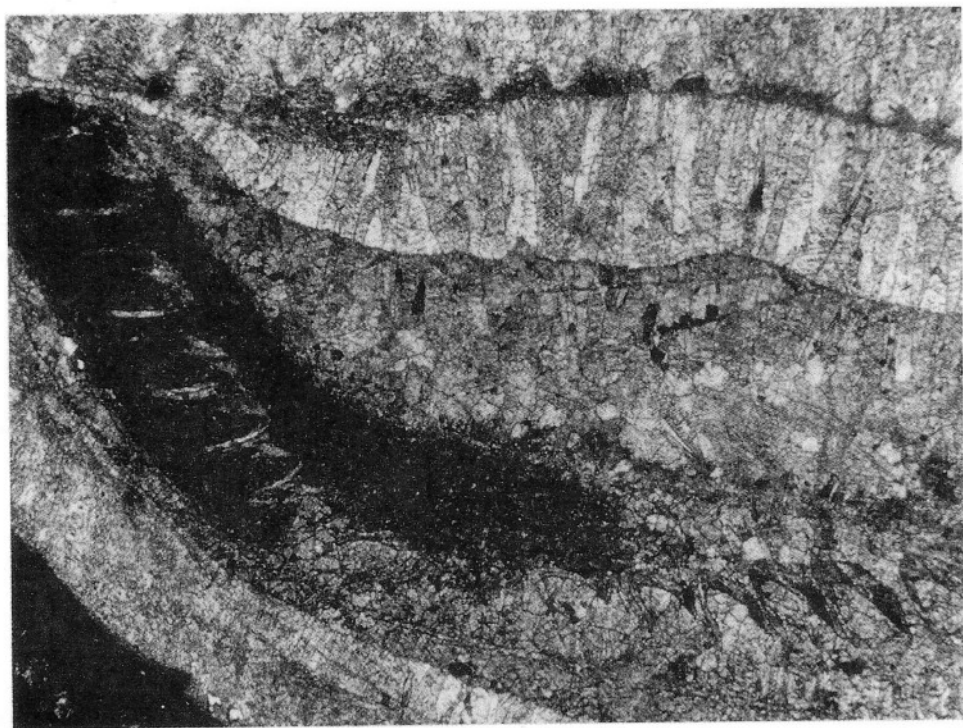


Fig. 22 - *Thecospira tyrolensis* (Loretz). Transverse section through muscle field, showing one of the spiralia. Tertiary layer visible on top; x 15. Alpe di Specie; N. 5784/43.

Biometric characteristics.

	L	W	T	HL	L/W	HL/W	T/W
N. sp.	281	281	80	185	281	185	80
x	7.0046	9.8883	4.1831	8.29	0.7093	0.7796	0.388
s	1.7360	2.5406	1.235	2.397	0.0731	0.0990	0.0932
sm	0.1035	0.1515	0.138	0.176	0.0043	0.0072	0.0104

Remarks.

Variability in thickness (T) and outline (L/W) of shell was noted. Thickness is affected by mode of cementation to substrate: large areas of attachment, involving the entire umbonal region, point up convexity of pedicle valve, hence, thickness of the entire specimen; with a reduced area of attachment, involving only the apex of the umbo, convexity of the pedicle valve is less pronounced, hence thickness of specimen is reduced.

The outline is subrectangular, but shells of greater length can be distinguished (longitudinally elongated) (Pl. 57, fig. 1) from those of smaller length (transversally elongated) (Pl. 57, fig. 3). This variability was already observed in the specimens illustrated by Bittner (1890).

The cardinal process differs in the two lateral lobes, at times partly separated by a wide groove (Pl. 58, fig. 3), and in the median ridge, which can be as robust as the lobes (Pl. 58, fig. 2); in some cases, median ridge and lateral apophysis of the lobes tend to be the same size (Pl. 58, fig. 3).

The surface surrounding the muscle field of the brachial valve of several specimens has numerous, minute circular cavities; it is probably this structure to which Bittner (1890) refers in describing a punctate shell for *Thecospira tyrolensis* (Loretz). SEM examination shows they are clogged by microcrystalline calcite; we thus infer they are connected with preferential solution of some calcite crystals in the tertiary layer.

Juvenile specimens do not yet show the characteristic tripartition of the internal surface of the brachial valve. Further, in the early growth stages there is no marked development of the hinge line, which is relatively short, giving rise to a subcircular outline. They could thus be mistaken for the shells attributed to *Thecospira tenuistriata* Bittner. As regards affinities and differences, the remarks made in respect of the latter taxon apply.

Distribution. The species has been recorded from Carnian of Southern Alps and Bakony Mt.

Occurrence. Alpe di Specie, Misurina, Tamarin, Campo, Milieres, Rumerlo, Vervei, Cianzope', Sass di Stria, Staolin, Costalaresc, Cason dei Caài.

***Thecospira tenuistriata* Bittner, 1890**

1884 *Thecidium* sp. Penecke, p. 383 (fide Bittner).

1888 *Thecospira* sp. Bittner, p. 128.

1890 *Thecospira tenuistriata* Bittner, p. 143, pl. 38, fig. 27-31.

1974 *Thecospiropsis tenuistriata* - Dagys, p. 75.

Material. 8 complete specimens and 74 isolated brachial valves. 34 brachial valves measured. N. 5804/1-47; N. 5805/1-14; N. 5806/1-17; N. 5807; N. 5808/1-3.

Description.

External characters. Small, uniplicated, bi-convex shell, generally subtrapezoidal in outline; maximum width at two thirds of length of brachial valve. Short, straight hinge line, smaller than maximum width of the shell. Lateral commissure and hinge line at obtuse angles.

Pedicle valve more convex than brachial valve; umbonal region modified to provide a cementation surface as broad as the hinge line. Poorly developed interarea; pseudodeltidium. Wide, shallow sulcus developed from the cementation surface, expanding towards anterior margin, flanked by two weak folds.

Brachial valve weakly convex, with only a hint of interarea; small sharp umbo, very reduced chilidium. Anterior commissure with slight fold flush with sulcus of pedicle valve.

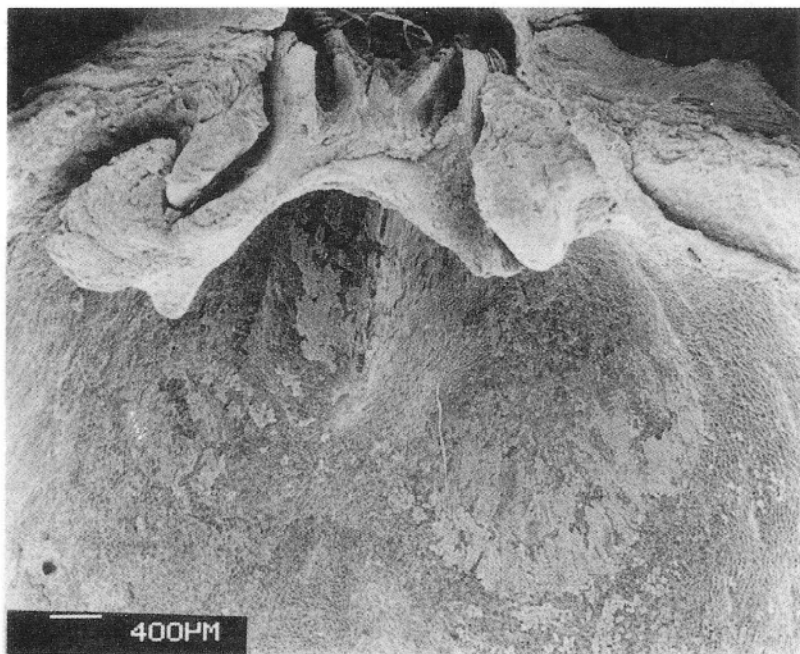


Fig. 23 - *Thecospira tenuistriata* Bittner. Pedicle valve. Detail of muscle scars and median septum. Broken cardinal process is also visible. Misurina; N. 5805/3.

Ornamentation only on brachial valve, composed of numerous, slender costellae, bifurcating at one-third of the beak.

Internal characters. Pedicle valve with large, rounded, not very protruding teeth. Deep muscle field, expanding to half the length of the valve, bilobed. In the first third of the posterior region, wide base median septum, narrowing towards the top (Fig. 23). Peripheral rim with rows of tubercles, subparallel to the internal surface of the valve (Pl. 61, fig. 4).

Brachial valve with high cardinal process, bilobate, extending into the pedicle valve, under the pseudodeltidium; minute median ridge, flanked by two short apophyses emerging from the lobes (Pl. 58, fig. 4). Deep dental sockets, suboval in outline. Subrectangular muscle field with two depressed areas (Fig. 17C), suboval in outline, separated by a low, wide plate, comparable to a median septum (Fig. 24); in some cases, a true median septum, thin and not very high.

Along the periphery of the valve, starting from the hinge line, three - four rows of rounded tubercles, closely and irregularly spaced (Pl. 61, fig. 3).

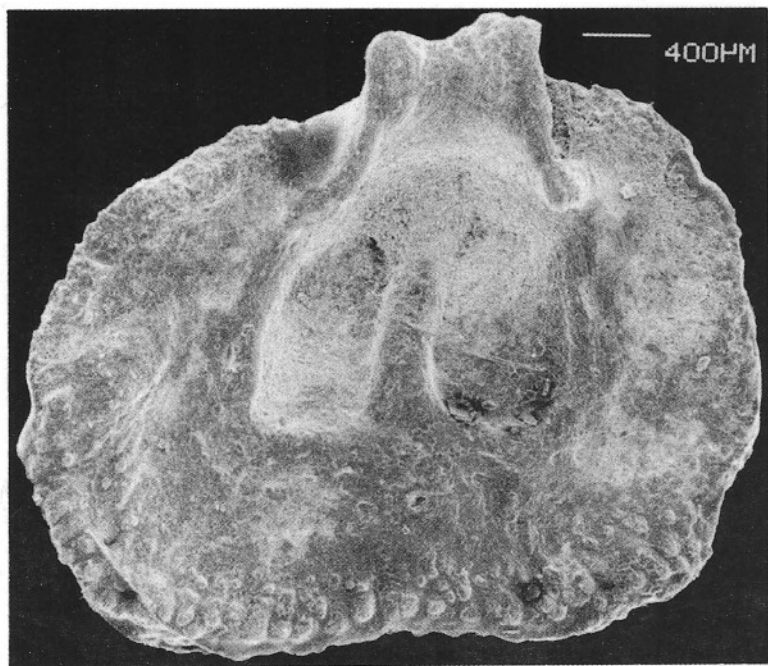


Fig. 24 - *Thecospira tenuistriata* Bittner. Internal surface of brachial valve, with median septum transformed into a low plate. Alpe di Specie; N. 5804/9.

Biometric characteristics:

	L	W	HL	L/W	HL/W
N. sp.	34	34	34	34	34
\bar{x}	3.6324	4.8941	2.6662	0.7332	0.5291
s	0.9581	1.3977	1.1402	0.0830	0.0996
sm	0.1643	0.2397	0.1955	0.1424	0.0170

Remarks.

The only taxon-specific character pointed out by Bittner (1890) is the ornamentation of the brachial valve. In the Ampezzan specimens examined, however, other taxon-specific features occur, such as: subtrapezoidal outline; hinge line smaller than the maximum width of the shell; sulcus on the pedicle valve, thus uniplication in the anterior commissure; muscle field of the brachial valve separated into two hollowed lobes.

The brachial valve of *Thecospira tenuistriata* Bittner, as mentioned earlier, has affinities to the juvenile shells of *Thecospira tyrolensis* (Loretz) on account of its small size and ornamentation, consisting in both taxa of slender radial costae. In *Thecospira tenuistriata* Bittner, however, the costae are less widely spaced, the outline is subtrapezoidal rather than subcircular, the brachial valve is slightly convex, the anterior commissure is uniplicate, the muscle field is sharply defined instead of almost indistinct.

Distribution. This species is recorded from Carnian of Southern Alps.

Occurrence. Alpe di Specie, Misurina, Campo, Vervei, Cason dei Caài.

***Thecospira semseyi* Bittner, 1900**

Pl. 57, fig. 4-7; Pl. 58, fig. 6; Pl. 62, fig. 1-3; Text-fig. 4, 7, 8, 9, 15, 17B, 25

1900 *Thecospira Semseyi* Bittner, p. 41, pl. 4, fig. 40-65; pl. 5, fig. 1.

1910 *Thecospira* aff. *Semseyi* Scalia, p. 23, pl. 2, fig. 19, 20.

1972 *Thecospira semseyi* - Dagys, pp. 90, 91, 96; text-fig. 2.

1974 *Thecospiropsis semseyi* - Dagys, p. 75, pl. 27, fig. 1-5; text-fig. 28, 46.

Material. 22 complete specimens and 79 brachial valves, all measured. N. 5796/1-62; N. 5797/1-14; N. 5798/1-12; N. 5799/1-6; N. 5800/1-2; N. 5801; N. 5802/1-3; N. 5803.

Description.

External characters. Average size shell, rectimarginate, in general plano-convex, with few concavo-convex specimens. Subcircular outline; short hinge line, less than maximum width of shell, straight, forming an obtuse angle with lateral commissure.

Pedicle valve strongly convex, umbonal region affected by cementation. Well-developed interarea with complete pseudodeltidium. Brachial valve with reduced inter-

area, pointed umbo; chilidium.

Both valves distinctly show concentric growth lamellae.

Internal characters. Pedicle valve observed only on acetate peels of transverse serial section (Fig. 25). Massive teeth, protruding, elongated in outline. Muscle field not extending beyond one-third of the length of the valve, raised over the floor of the valve, well demarcated laterally by a raised rim, apparently open anteriorly. Presence of a thin median septum with sharp outline, high and distinct in the umbonal region, gradually reduced towards the anterior margin of the field, where it is implanted in a broad, flat base. This structure separates the two lobes, each with three-four large radial grooves, intercalated by rounded ridges of equal width, whose relief gradually tapers off at the anterior margin of the field. Valve periphery with a row of tubercles subparallel to its internal surface.

Brachial valve with high cardinal process, composed of two massive lateral lobes, with thin terminal apophysis and a well-developed median ridge (Pl. 58, fig. 6). Deep egg-shaped dental sockets. Two short crura at base of cardinal process, supporting the spirally coiled brachidium. Cone-shaped spiralia with ventrolaterally directed apexes, composed of 5 - 6 convolutions. Muscle field subcircular in shape, broad, expanding to about half the length of the valve, clearly demarcated by a continuous, raised ridge (Pl. 57, fig. 5, 6, 7; Fig. 17B), with acute angled section and often scalloped course (Pl. 57, fig. 4). Presence of a thin, slightly raised median septum, extending to the outer edge of the field, and of a few, wide grooves, separated by radially inclined thin ridges, connected to the scalloping of the rim. Periphery pointed up by a band of cylindrical tubercles, irregularly disposed, tending to overlap (Pl. 62, fig. 3).

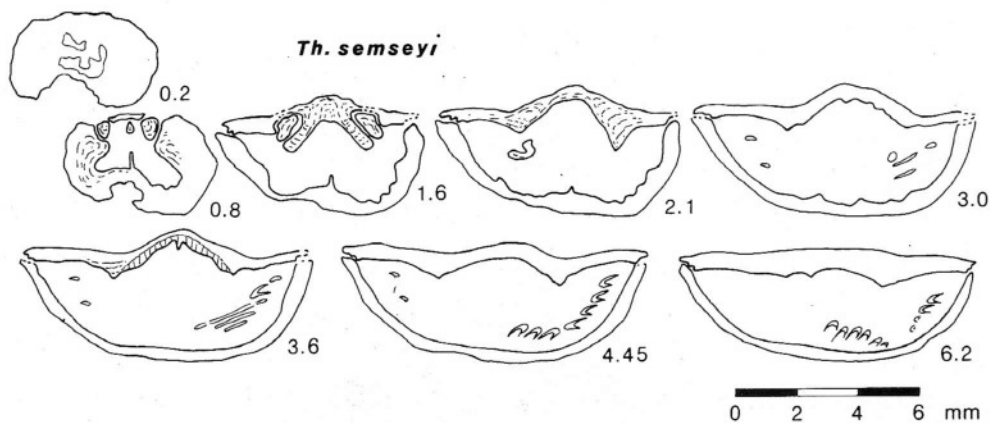


Fig. 25 - *Thecospira semseyi* Bittner. Serial transverse sections through the posterior part of the shell. Alpe di Specie; N. 5796/37.

Biometric characteristics:

	L	W	T	HL	L/W	HL/W	T/W
N. sp.	100	100	21	79	100	79	21
\bar{x}	6.6840	8.7325	3.8595	5.9551	0.7622	0.6582	0.4514
s	1.7004	2.1682	1.5731	1.3950	0.0867	0.0862	0.0848
sm	0.1700	0.2168	0.3432	0.1569	0.0086	0.0097	0.0185

Remarks.

The specimens examined correspond, even in size, to the primary types described by Bittner (1900). However, that author only illustrated shells with a broad area of attachment, where the umbo is distinctly truncated; whereas in our Ampezzan material numerous specimens were also found with a smaller cementation surface, and the umbo well defined.

From a pictorial comparison alone, the attribution of Scalia's shells (1910) to the species under review remains dubitative, insofar as they are not very clearly illustrated and only briefly described.

Distribution. *Thecospira semseyi* Bittner is recorded from Carnian of Bakony Mt., Caucasus and Pamir. Dubitatively, it occurs in the Carnian of Sicily.

Occurrence. Alpe di Specie, Misurina, Campo, Milieres, Rumerlo, Costalaresc, Vervei, Staolin.

***Thecospira haidingeri* (Suess, 1854)**

Pl. 57, fig. 10, 11; Pl. 58, fig. 5; Pl. 63, fig. 1-3; Text-fig. 6, 12, 13, 14, 17D

1854 *Thecidea Haidingeri* Suess, p. 43, pl. 2, fig. 16,17.

1880 *Thecospira haidingeri* - Zugmayer, p. 22, pl. 2, fig. 33- 41.

1917 *Thecospira haidingeri* - Goetel, p. 95, pl. 8, fig. 1.

1968 *Thecospira haidingeri* - Rudwick, pp. 329-360, pl. 65, fig. 1, 11; text-fig. 1 A, C-E.

1974 *Thecospira haidingeri* - Dagys, p. 73, text-fig. 44.

1976 *Thecospira haidingeri* - Michalik, p. 80, fig. 1: 1,2 (non 3); 2: 1-4 (non 5, 6); 3; 4: 1-5; 5; 6; 7: 3-6; 8; 9; 11.

Material. 112 isolated brachial valves; 58 measured. N. 5809; N. 5810/1-48; N. 5811/1-14; N. 5812/1-36; N. 5813/1-5; N. 5814/1-5; N. 5815; N. 5816/1-2.

Description.

External characters. Small valves, weakly convex, subrectangular in outline, greater in width than in length. Straight, long hinge line, slightly smaller than maximum width of valve. Reduced interarea, with chilidium. External surface with irregular growth lines.

Internal characters. High cardinal process, bilobate, with developed median ridge and minute lateral ridges, not always observable (Pl. 58, fig. 5). Deep dental sockets, demarcated by a well-developed inner socket ridge. Depressed muscle field, subrectangular, narrow and anteriorly elongated (Fig. 17D); laterally distinctly demarcated by two raised ridges, rectilinear, subparallel, extending from the base of the cardinal process, under the crura, to about two-thirds of the length of the valve; anteriorly incurving towards the plane of symmetry to become totally flat (Pl. 57, fig. 10, 11; Pl. 63, fig. 3). Muscle field open anteriorly, continuous with valve surface. Presence of a thin, distinct median septum, extending to the outer margin of the muscle field, flanked by two broader, diverging, rounded ridges extending to half the length of the septum. Surface surrounding the muscle field weakly concave, more rarely plane. Valve periphery pointed up by a raised border, externally densely covered by small, rounded tubercles, unorthodoxly arranged (Pl. 63, fig. 1).

Biometric characteristics:

	L	W	HL	L/W	HL/W
N. sp.	58	58	58	58	58
\bar{x}	4.8388	6.8698	5.2621	0.7078	0.7565
s	1.0719	1.6930	1.6461	0.0737	0.0895
sm	0.1407	0.2223	0.2161	0.0096	0.0118

Remarks.

Our isolated brachial valves are comparable with Suess's complete specimens (1854), as far as concerns the external characters. According to the present authors, the perforations observed by Suess (1854) and successively interpreted as punctae, are to be considered structures due to solution of taleolae.

The examined material corresponds well to isolated brachial valves depicted by Zugmayer (1880) and reillustrated by Rudwick (1968).

In many of the valves examined, numerous small pointed dents were noted in the area between the muscle field and the periphery of the valve. They do not continue within the secondary layer as true perforations. They are therefore construed as related to preferential dissolution of some fibres of the secondary layer, to the point of corroding the tubercles below.

Attribution of some of Michalík's specimens (1976) to the species under review is dubitative. In particular, specimens in Fig. 1.3, 2.5, 2.6 would seem to be attributable to *Thecospira semseyi* Bittner.

Distribution. The species is recorded from Rhaetian of Northern Alps and Carpathians.

Occurrence. Misurina, Tamarin, Campo, Milieres, Rumerlo, Vervei, Cianzope', Staolin.

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PLATE 57

Brachial valves.

- Fig. 1 - *Thecospira tyrolensis* (Loretz). Misurina; N. 5785/90; x 5.
 Fig. 2 - *Thecospira tyrolensis* (Loretz). Alpe di Specie; N. 5784/130; x 5.
 Fig. 3 - *Thecospira tyrolensis* (Loretz). Misurina; N. 5785/95; x 5.
 Fig. 4 - *Thecospira semseyi* Bittner. Brachial valve adductor muscle field, view from cardinal process. Alpe di Specie; N. 5796/36.
 Fig. 5 - *Thecospira semseyi* Bittner. Costalaresc; N. 5802/2; x 5.
 Fig. 6 - *Thecospira semseyi* Bittner. Alpe di Specie; N. 5796/32; x 5.
 Fig. 7 - *Thecospira semseyi* Bittner. Alpe di Specie; N. 5796/35; x 5.
 Fig. 8 - *Thecospira tenuistriata* Bittner. Alpe di Specie; N. 5804/24; x 7.
 Fig. 9 - *Thecospira tenuistriata* Bittner. Alpe di Specie; N. 5804/27; x 7.
 Fig. 10 - *Thecospira haidingeri* (Suess). Milieres; N. 5812/4; x 6.
 Fig. 11 - *Thecospira haidingeri* (Suess). Milieres; N. 5812/9; x 6.

PLATE 58

Cardinal process.

- Fig. 1 - *Thecospira tyrolensis* (Loretz). Normal pattern. Alpe di Specie; N. 5784/128.
 Fig. 2 - *Thecospira tyrolensis* (Loretz). Normal pattern. Alpe di Specie; N. 5784/124.
 Fig. 3 - *Thecospira tyrolensis* (Loretz). Normal pattern. Misurina; N. 5785/70.
 Fig. 4 - *Thecospira tenuistriata* Bittner. Alpe di Specie; N. 5804/20.
 Fig. 5 - *Thecospira haidingeri* (Suess). Milieres; N. 5812/10.
 Fig. 6 - *Thecospira semseyi* Bittner. Alpe di Specie; N. 5796/31.

PLATE 59

- Fig. 1 - *Thecospira tyrolensis* (Loretz). a-e) Ventral, dorsal, lateral, anterior, posterior views. Misurina; N. 5785/12; x 4.
 Fig. 2 - *Thecospira tyrolensis* (Loretz). a-e) Ventral, dorsal, lateral, anterior, posterior views. Misurina; N. 5785/11; x 4.
 Fig. 3 - *Thecospira tyrolensis* (Loretz). Brachial valve. Tubercles on peripheral margin. Misurina; N. 5785/98.

PLATE 60

- Fig. 1 - *Thecospira tyrolensis* (Loretz). Dorsal view. Specimen with preserved pseudodeltidium and ornamentation. Rumerlo; N. 5789/2; x 4.
 Fig. 2 - *Thecospira tyrolensis* (Loretz). Dorsal view. Misurina; N. 5785/9; x 4.
 Fig. 3 - *Thecospira tyrolensis* (Loretz). Specimen in life position. Alpe di Specie; N. 5784/8; x 3.
 Fig. 4 - *Thecospira tyrolensis* (Loretz). Pedicle valve. Internal model of spiralia. Alpe di Specie; N. 5784/45.

PLATE 61

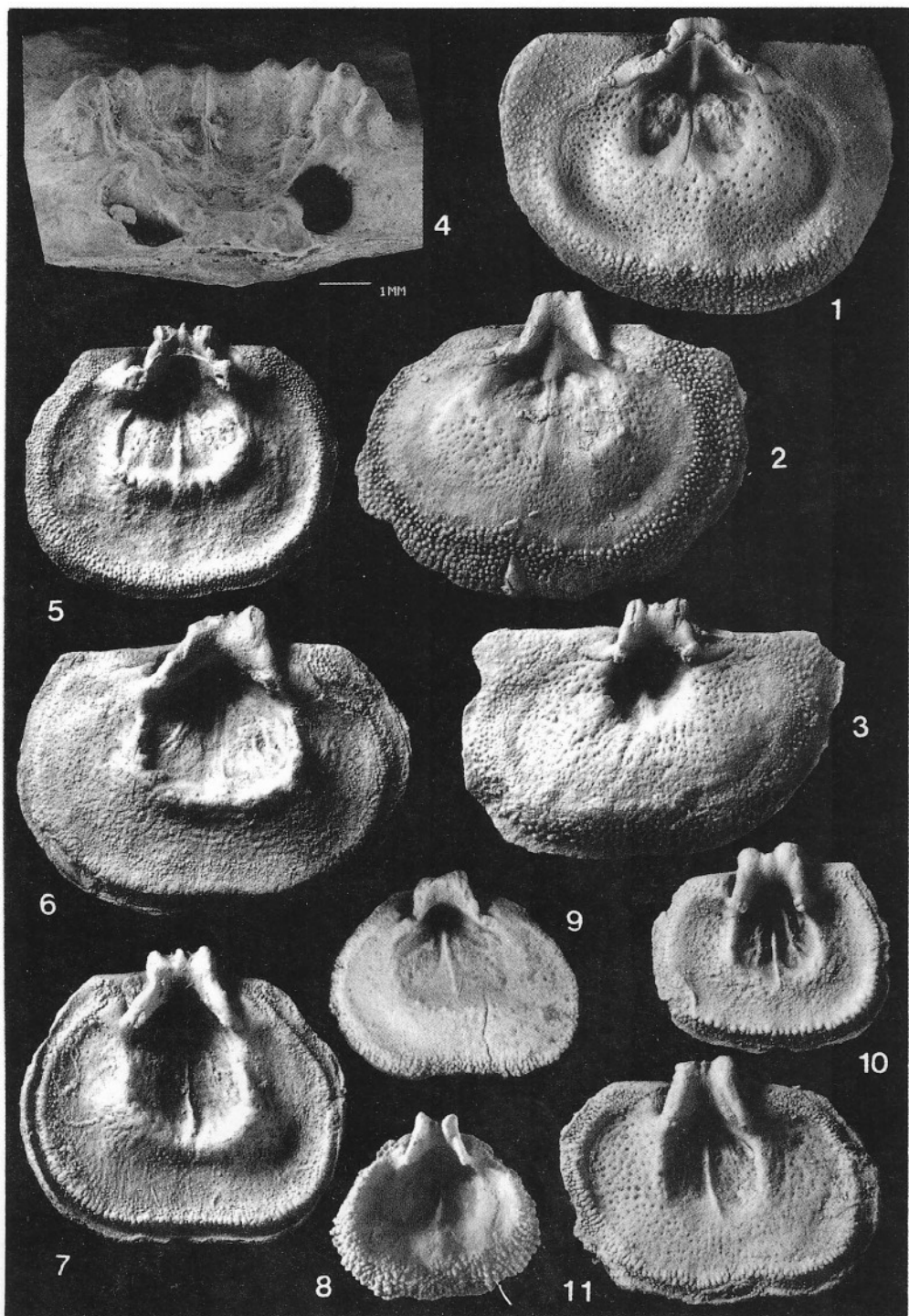
- Fig. 1 - *Thecospira tenuistriata* Bittner. a-e) Ventral, dorsal, lateral, anterior, posterior views. Misurina; N. 5805/2; x 7.
- Fig. 2 - *Thecospira tenuistriata* Bittner. a-e) Ventral, dorsal, lateral, anterior, posterior views. Alpe di Specie; N. 5804/3; x 7.
- Fig. 3 - *Thecospira tenuistriata* Bittner. Brachial valve. Tubercles on peripheral margin. Alpe di Specie; N. 5804/22.
- Fig. 4 - *Thecospira tenuistriata* Bittner. Pedicle valve, internal surface. Misurina; N.5805/3.

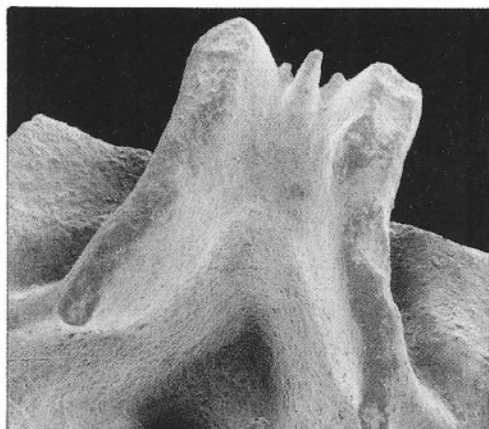
PLATE 62

- Fig. 1 - *Thecospira semseyi* Bittner. a-e) Ventral, dorsal, lateral, anterior, posterior views. Alpe di specie; N. 5796/10; x 3.5.
- Fig. 2 - *Thecospira semseyi* Bittner. a-e) Ventral, dorsal, lateral, anterior, posterior views. Misurina; N. 5797/7; x 3.5.
- Fig. 3 - *Thecospira semseyi* Bittner. Brachial valve. Tubercles on peripheral margin. Alpe di Specie; N. 5796/38.

PLATE 63

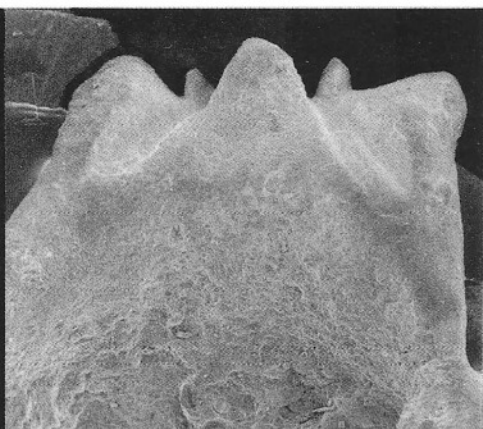
- Fig. 1 - *Thecospira baidingeri* (Suess). Brachial valve. Tubercles on peripheral margin. Campo; N. 5811/5.
- Fig. 2 - *Thecospira baidingeri* (Suess). Brachial valve, dorsal view. Milieres; N. 5812/8; x 6.
- Fig. 3 - *Thecospira baidingeri* (Suess). Brachial valve. Particular of muscle field. Milieres; N. 5812/10.





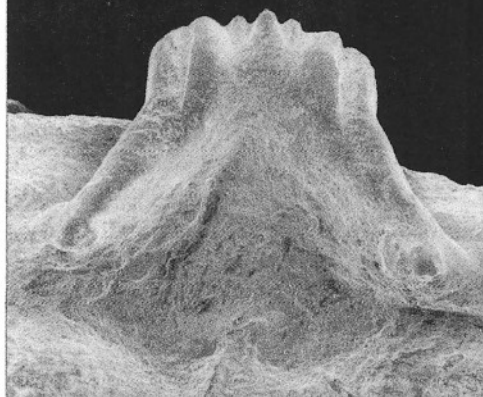
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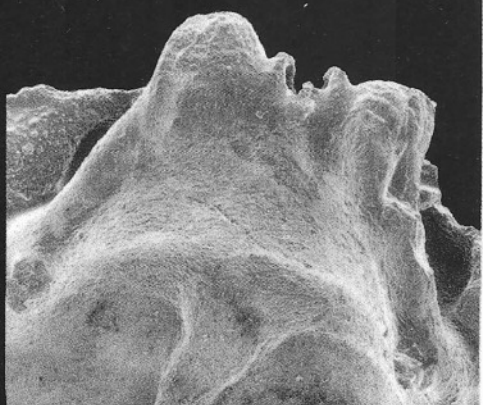
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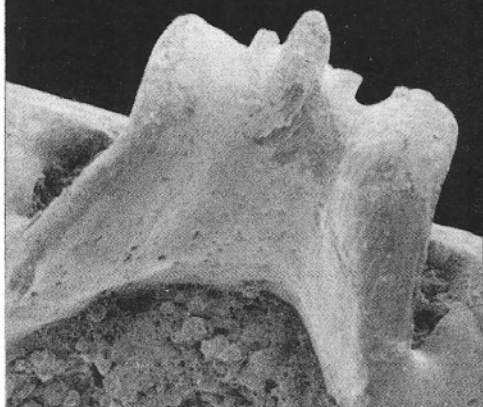
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3



200µm

4



400µm

5



1mm

6

