JOZEF MICHALÍK*

TWO REPRESENTATIVES OF STROPHOMENIDA (BRACHIOPODA) IN THE UPPERMOST TRIASSIC OF THE WEST CARPATHIANS

(Fig. 1—11)

Abstract: In the paper the detailed morphology of elements of the outer and inner structure of the species *Thecospira haidingeri* (Suess, 1854) is presented, studied on isolated valves, in sections and on prepared shells. The structure of the brachidium of this species is described, so far insufficiently known (mainly the composition and shape of the jugum). The investigation was based on serial sections and the preparation of three brachiopods. The morphology of the species *Bactrynium bicarinatum* Emmrich, 1855 from the locality Hybe has been discussed. Attention was focused on the external morphology of the so far insufficiently known ventral valve. In the ecological part of the paper the attachment orientation of *Th. haidingeri* shells and the causes of their deformation have been established.

Резюме: В статье подробно разбирается морфология элементов внешней и внутренней формы вида *Thecospira haidingeri* (Suess 1854) изучаемая на отдельных раковинах, в сечениях и на специально оформленных образцах. Описана структура брахидиума этого вида, до сих пор недостаточно изученого (главным образом состав и форма югума). Изучение производилось на образцах серии полированных шлифов и на образцах трех брахидий. Далее в статье описана морфология вида *Bactrynium bicarinatum* Emmrich 1855 из обнажений близ с. Гибе. Внимание было обращено на морфологические особенности до сих пор недостаточно изученой вентральной стороны раковины. В экологической части статьи была определена ориентация прирастающих раковин *Th. haidingeri* и причины их деформации.

Introduction

The species *Thecospira haidingeri* was described by E. Suess (1854) as *Thecidea haidingeri* ("the 12 th Thecidia from the Liassic") without knowing the brachial apparatus structure. After the spiral brachidium of *Thecospira* had been found by H. Zugmayer (1880), was this genus considered as belonging to the order Spiriferida, close to Koninckida, for a long time. A. Williams (1965) considers this genus as related to Davidsoniacea (order Strophomenida).

The systematic appurtenance and functional morphology of both genera was recently dealt with by M. J. Rudwick (1968). On the basis of his studies this author postulated the hypothesis that the order Strophomenida, after a big crisis at the end of the Paleozoic, was represented by three groups in the Triassic: the superfamily Koninckinacea — descendants of Chonetacea, "a group of small Davidsoniacea around the genus *Thecospira*", later included in the superfamily Thecospiracea by A. S. Dagys (1972) and by the superfamily Thecideacea, represented by the genus *Bactrynium*. Development of the spiralium in the genus *Thecospira*, according to M. J. S. Rudwick, does not mean an essential change in the organization of the lophophore in contrast to davidsoniaceid ancestors (probably Schuchertellidae or Orthotetidae).

A. S. Dagys (1972) was mainly dealing with the ultrastructure of thecospirid shells. On the basis of his investigation he came to the opinion that the secretory

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activity of the Thecospirida mantle had been very close to the "s. c. standard" one (A. Williams 1968) but complicated by forming pseudopores, different in the dorsal and ventral valve. The taleolae which probably represent a track of muscle attachment — retractors of the mantle edge, originate directly on the primary shell layer. The pseudopores of the ventral valve have formed by secondary activity modification of outer epithelium cells.

In the year 1855 H. Emmrich described a fossil from the Kössen Beds ("Gervillienbildung") of Jungbad, which he considered as the problematicum *Bactrynium* Heer ("was ich zu *Bactrynium* Heer stellen und *B. bicarinatum* nennen möchte"), with the notice that this "constant accompaniment of the Gervillia Beds" resembles the trilobite *Triarthurus* Green.

C. W. Gümbel (1861) knew the appurtenance of this organism and described it as *Pterophloios Emmrichi*. H. Zugmayer (1880) denied the priority to Emmrich's description because Heer is said not to have described any genus *Bactrynium* and in the description of the new taxon H. Emmrich used the abbreviation "*B. bicarinatum*" only. The author designated the species as *Thecidea Emmrichi*. A. Bittner (1890) described the species as *Thecidium (Pterophloeus) Emmrichi* and noted that the individuals from the Starhemberg Beds are larger than those from the Kössen Beds. W. Goetel (1917) mentioned a "very rare" occurrence of the species *Pterophloios Emmrichi* in the Kössen Beds at the locality Hybe in the West Carpathians.

W. P. Makridin (1960) ranged the genus to the superfamily Thecidacea still under the name *Pterophloios*. On the contrary, A. Williams (1965) used the original name *Bactrynium* and ranged this genus to the monotypic family Bactryniidae, which might be related to Lyttoniacea.

M. J. S. Rudwick (1968) held the opinion of the appurtenance of the genus *Bactrynium* to *Thecidia*. The resemblance of this genus, which is said to be known only from the Rhaetian of Austria, to Lyttoniacea, results from convergency only.

Morphology and systematics

Order Strophomenida Öpik, 1934

Superfamily Thecospiracea Bittner, 1890 (nom. Dagys, 1972)

Including the families Thecospiradae Bittner, 1890, Thecospirellidae Dagys, 1972, Hungarithecidae Dagys, 1972.

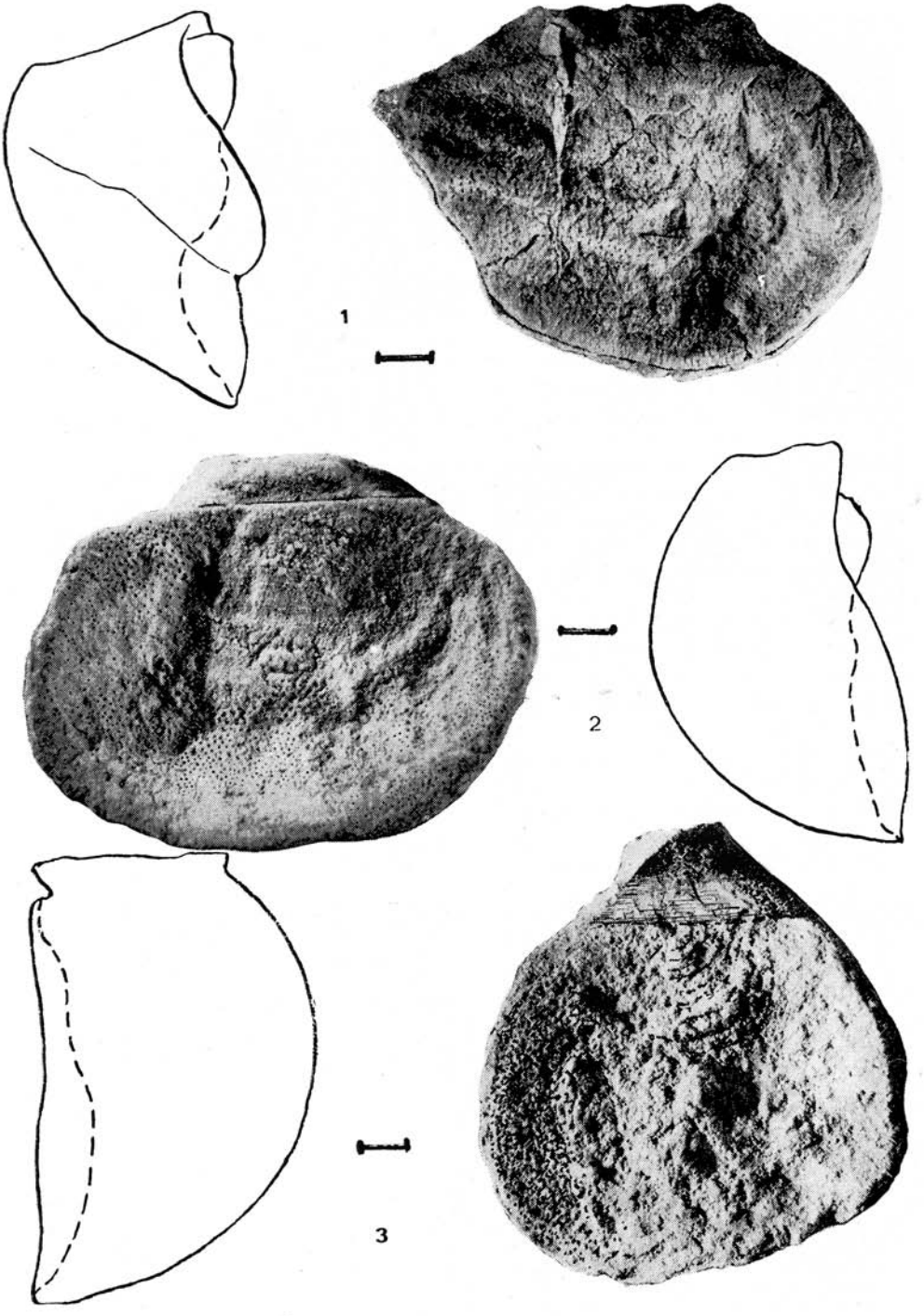
Family Thecospiridae Bittner, 1890

Genus *Thecospira* Zugmayer, 1880

Species typica: *Thecospira haidingeri* (Suess, 1854)

Diagnosis: Concave-convex punctate or pseudopunctate small shell cemented by the umbonal part of the ventral valve. Pseudodeltidium, teeth unsupported, distinct muscle scars separated by the median septum. High bilobate cardinal process, lamellae of flat spiralium cones longitudinally groove-like bent, jugum simple, arcuate.

Fig. 1. Variability of the outline of the species *Thecospira haidingeri* (Suess). 1: Asymmetric individual TH-4, Hybe 1971, Bed XXXII. 2: "Productoid" shell TH-3. Hybe, Kantorská pit. 3: Narrow oval individual TH-2, Hybe-Viper hole. The abscissas (also in other photographic plates) indicate the length of 1 mm before magnification. The dashed line indicates the bottom of the dorsal valve. Photo C. Michalíková.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Species composition:
Thecospira haidingeri (Suess, 1854)
Thecospira davidsoni Bittner, 1890
Thecospira granulata Dagys, 1974.

The species *Th. semseyi* (Bittner, 1900), *Th. arenosa* (Bittner, 1890), *Th. tyrolensis* (Loretz, 1875), *Th. tenuistriata*, Bittner, 1890, *? Th. concentricum* Münster, 1841, *? Th. piestingensis* Bittner, 1890 and *? Th. sturzenbaumi* Bittner, 1890, with a nonporous shell, includes A. Dagys, 1974 under the common genus *Thecospiropsis* Dagys, 1974.

Thecospira haidingeri (Suess, 1854)
(Fig. 1: 1–3; 2: 1–6; 3: 4: 1–6; 5; 6; 7: 3–6; 9; 10; 11)

Thecidia Haidingeri Suess, 1854, p. 15, t. II., f. 16–17
Thecospira Haidingeri Zugmayer, 1880, p. 22, t, II., f. 33–41
Thecospira Haidingeri Goetel, 1917, p. 95, t. 8, f. 1
Thecospira haidingeri Rudwick, 1968, p. 329–360, pl. 65, text-f. 1, 8, 9

Holotype: From the Kössen Beds of the locality Kitzberg bei Pernitz in the Eastern Alps of Austria, the place of its present-day deposition is unknown.

Material: Various horizons of the Hybe Beds of the Kössen Formation at the locality Hybe (northern foothill of the Low Tatra):
Hybe (northern foothill of the Low Tatra):
Hybe 1971-Bed XXXII — 1 shell, 1 ventral valve,
Hybe 1971-Bed XXXIII — 1 ventral valve,
Hybe 1971-Bed XXXV — 4 shells, 2 ventral valves
Hybe-Kantorská pit — 25 shells, 13 ventral valves
Hybe-Viper hole — 5 shells, 8 ventral valves

Description: Small (2–11 mm) calcareous concave-convex punctate strophic shell of rounded oblong to trapezium outline (fig. 1). The surface of valves is smooth, with large (0,01–0,02 mm) pores with intermittent growth lines. Some young individuals have a finely radially striated surface. The commissure is straight in the youth stage, the anterior part is dorsally bent in the adult stage.

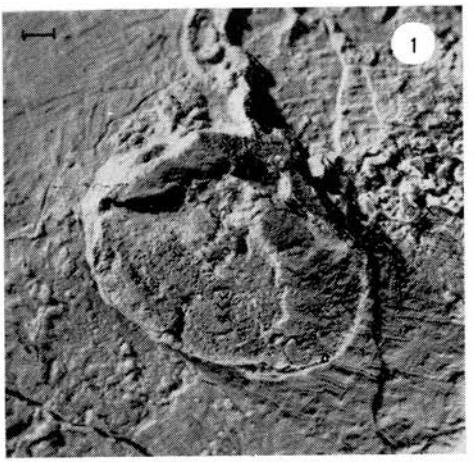
The ventral valve is distinctly convex (in individuals attached with the larger surface of this valve, it is shaped according to the basement). It is attached to the substratum with the area, beak, or the larger part of the posterior surface (fig. 2). In the latter case the valve displays a conspicuous geniculation. The trail has a rugged inner surface. The hinge line is long, often almost equal to the width of the valve.

The pseudodeltidium is separated by fine striae from the remaining area surface. The area displays a fine striation, without pores.

The teeth are distinct unsupported, the muscle scars are oval to triangular, at the anterior margin usually ledge-like raised above the valve bottom. The median septum reaches $^1/_3$ of valve.

The dorsal valve is flat to concave, only in the young stage moderately convex. The interarea is very low, often indistinct. The cardinal process is high, long, bilobate,

Fig. 2. *Thecospira haidingeri* (Suess). 1: Individual TH-20, cemented on the valve of *Rh. pyriformis*. Hybe 1971, Bed XXXV. 2: Asymmetric individual TH-30 on the valve of *Rh. hybensis*, Hybe, Kantorská pit. 3: Individual TH-32 on the valve of *Rh. pyriformis*, Hybe-Viper hole. 4: Individual TH-1 from concretions below Bed XXXII, Hybe 1971. 5–6: Dorsal and lateral view of the valve of individual TH-2. Hybe, Viper hole. Photo C. Michalíková.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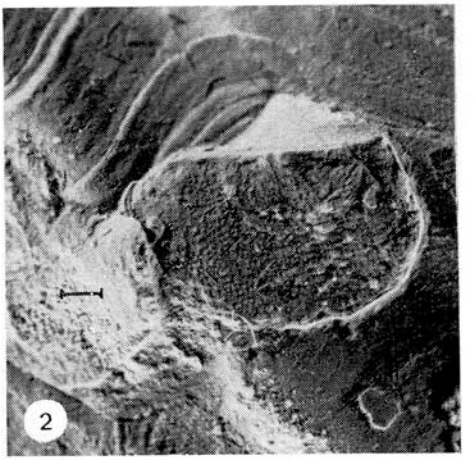
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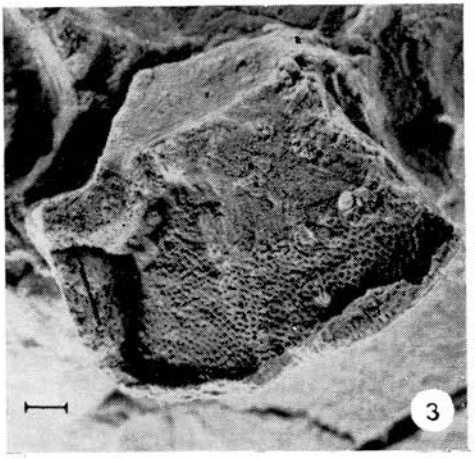
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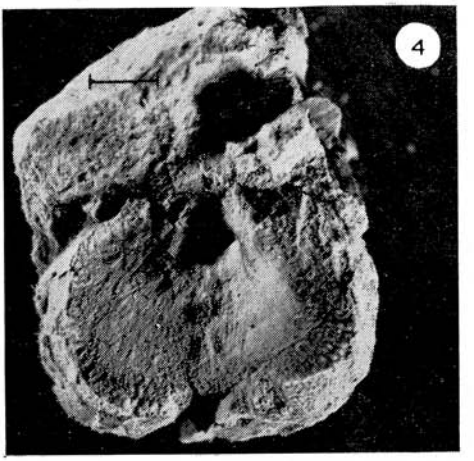
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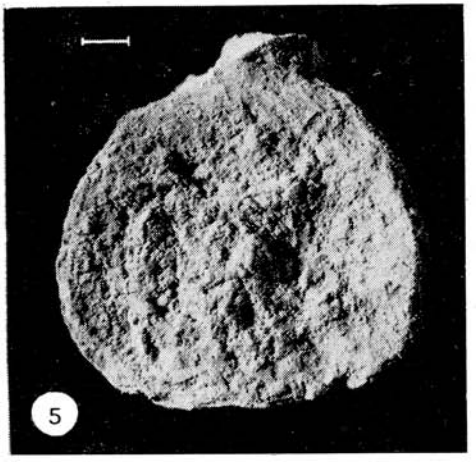
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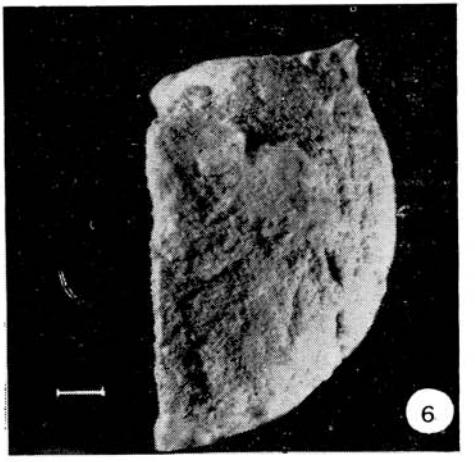
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originating with coalescence of dental sockets margins, hinge plates and the posterior part of crural plates. The diductors were fixed to the posteromedian part of the cardinal process, the adductors anteriorly of them to the valve bottom between the crural plates. The crura are indistinctly separated from the crural plates reaching the valve centre (fig. 3).

They form only minute, subtle projections at the end of the posterior third of crural plates, fixing the primary lamellae of spiralium still before their posterior ending. The primary lamellae are bifurcate at the posterior end. The more posterior projection joins the arcuate jugum connecting the anterior ends of crura. The more anterior projection of the primary lamellae projects into the slender median apophysis connected with the jugum by a spiculose band (fig. 7:5).

The lamellae of spiralium are groove-shaped, finely indented at the margins, forming 4—8 coils. The spiralium cones are oriented ventrally or indistinctly lateroventrally.

Ontogeny and variability

In the time after they were cemented by the beak of ventral valve close behind the area, the individuals had a moderately biconvex semicircular valve. In the neanic stage it acquired a planoconvex to concave-convex shape. In the ephebic stage a geniculation and a more or less distinct median dorsal commissure flexion started to develop. So the anterior growth component was hindered and the shell started to get a rounded oblong outline, which it preserved to the gerontic stage (fig. 4, 5, 8).

Already H. Zugmayer (1882) called attention to frequent deformations of the outline, connected with attachment of shells to a hard substratum. Smaller deformations concern only the ventral valve: shells attached to small hard objects have, according to H. Zugmayer, "a symmetrical, quite productoid shape", i. e. the ventral valve is highly convex, regular. The shells growing on hard even surface (surface of *Rhaetina* valves etc.) are flat: up to the ephebic stage the ventral valve follows the basement surface, after geniculation it forms almost a vertical anterior wall.

From the interior structure elements of valves are subject to variability mainly: the shape and size of teeth, the shape, size and distinctness of muscle scars, length and thickness of the median septum, the number of spiralia coils.

Distribution: Uppermost Sevatian to Rhaetian of the Northern Alps, West Carpathians to the Pamirs. In the West Carpathians this species has so far been found only at the locality Hybe in the Hybe Beds of the Kössen Formation. The shells are here mostly attached to valves of *Rhaetina pyriformis* and *Rhaetina hybensis*.

Thecospira sp. (?)
(Fig. 4:6)

Material: 1 ventral valve attached to the shell of Rhaetina hybensis. Width of valve = 8,2 mm, length = 6 mm.

Description: Small ventral valve, moderately convex. The beak is indistinct, very low. The pseudodeltidium is of the shape of an equilateral triangle. The hinge line is very long, longer than the maximum width of valve. The commissure is nearly straight, slightly dorsally bent. The outline of valve is rounded trapezoid, with the widest part near the hinge line. The shell substance is pseudopunctate (fig. 4:6).

The teeth are minute, rounded, relatively close together. In the posterior part of the valve is a low and short median ridge. The muscle scars are indistinct. The peripheral edge of valve is covered with irregularly distributed minute tubercles.

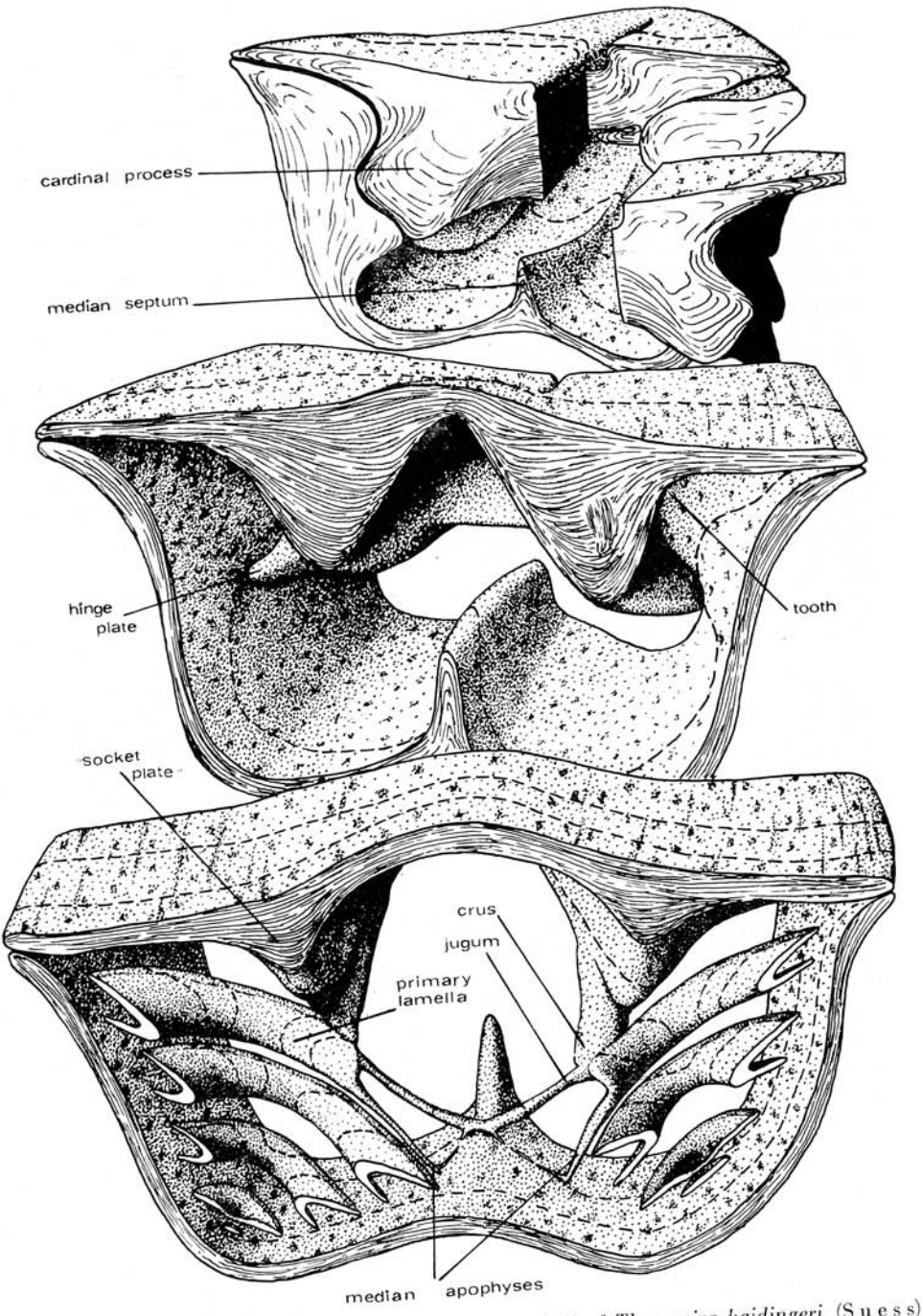


Fig. 3. Special representation of serial sections of the shell of *Thecospira haidingeri* (S u e s s) from the locality Hybe-1971, Original.

Occurrence: Hybe Beds of the Kössen Formation at the locality Hybe (together with *Thecospira haidingeri*).

Superfamily Thecideacea Gray 1840
Family Bactryniidae Williams 1965
Genus *Bactrynium* Emmrich 1855

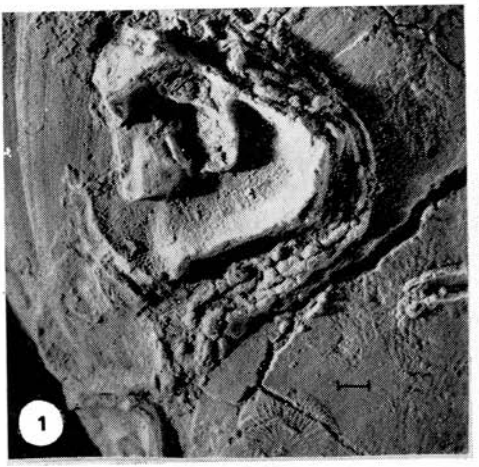
Species typica: *Bactrynium bicarinatum* Emmrich 1885
Diagnosis: A distinctly concave-convex calcareous pseudopunctate strophic small shell, cemented to the substratum by the ventral apex. The hinge apparatus in subtle, the brachia fixed to the lobate apparatus, consisting of paired 5—10 lobate bendings of the ribbon at the inner dorsal valve surface. So far the genus includes one species only.

Bactrynium bicarinatum Emmrich 1855
(fig. 7:1—2)

Bactrynium bicarinatum Emmrich 1855, p. 449, f. 1
Pterophloios Emmrichi Gümbel 1861, p. 411
Thecidea Emmrichi Zugmayer 1880, p. 19, f. II., f. 17—32
Thecidium (Pterophloeus) Emmrichi Bittner 1890, p. 311, t. XXVI, f. 18—19
Thecidea (Pterophloeus) Emmrichi Goetel 1917, p. 94—95
Bactrynium bicarinatum Williams 1965, p. 521, f. 397
Bactrynium bicarinatum Rudwick 1968, p. 329—360, pl. 66, 67, 68, text. fig. 2, 4, 5, 6, 7, 10.
Holotype: From the Kössen Beds of Jungbad in the Eastern Alps, the place of its deposition is not known (the originals of the figures in Zugmayers's work (1880) are deposited in the collections of the Paläontologisches Institut der Universität, Wien).
Material: 1 shell and 1 dorsal valve from the Hybe Beds of the Kössen Formation at the locality Hybe-Kantorská pit.
Description: A small (width = 5—6 cm) concave-convex pseudopunctate shell with oval, slightly lengthened outline. The valve surface is smooth, provided with indistinct growth lines and small tubercles. The hinge line is straight, approaching the maximum width of shell. The commissure is straight.

The ventral valve is markedly convex, the beak is low, pointed, without foramen. The pseudodeltidium is missing, the interarea only with fine growth lines. In the individual, attached with the larger valve surface to the flat substratum, the ventral valve is flat, the geniculation indistinct. An interesting fact, however, is that the geniculated margin of the ventral valve tends to follow the lobate apparatus bendings at the dorsal valve; at the margin of the dorsal valve these bendings are indicated only indistinctly (fig. 7:2). Due to the lacking material the elements of internal valve structure have not been investigated.

Fig. 4. 1—5: *Thecospira haidingeri* (Suess. 1: Individual TH-37 of *Rh. pyriformis*, Hybe—Kantorská pit. Left other two individuals, below is *Atreta sp.*, above it a worm tubule. 2: Individual TH-19 on *Rh. hybensis*, Hybe-Viper hole. 3: Individual TH-28 on *Rh. pyriformis*, Hybe 1971, Bed XXXII. 4: Individual TH-23 on *Rh. cf. hybensis*, Hybe-Viper hole. 5: Individual TH-40 with worm tube on the dorsal valve, cemented on *Rh. pyriformis*, Hybe-Viper hole. 6: Ventral valve of *Thecospira* sp. on *Rh. hybensis*, Hybe-Viper hole. Photo C. Michalíková.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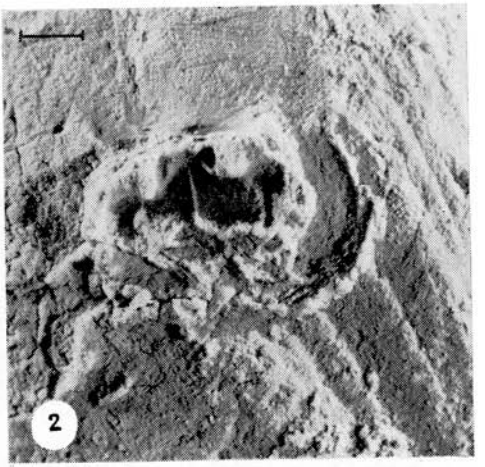
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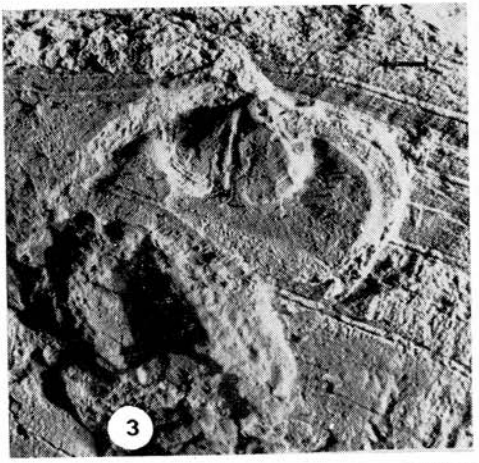
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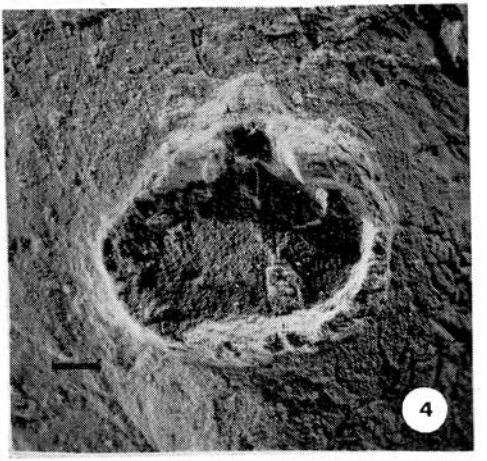
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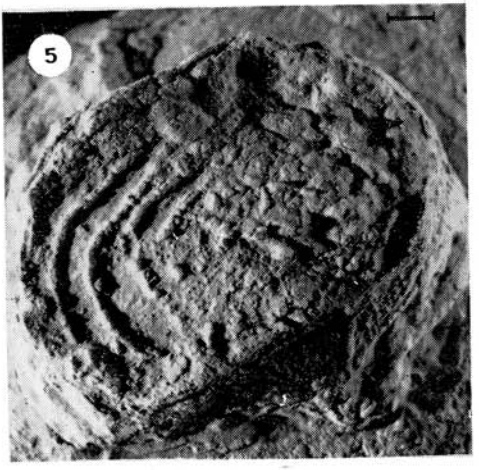
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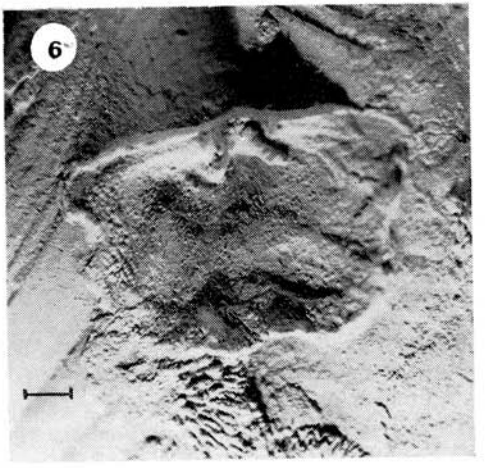
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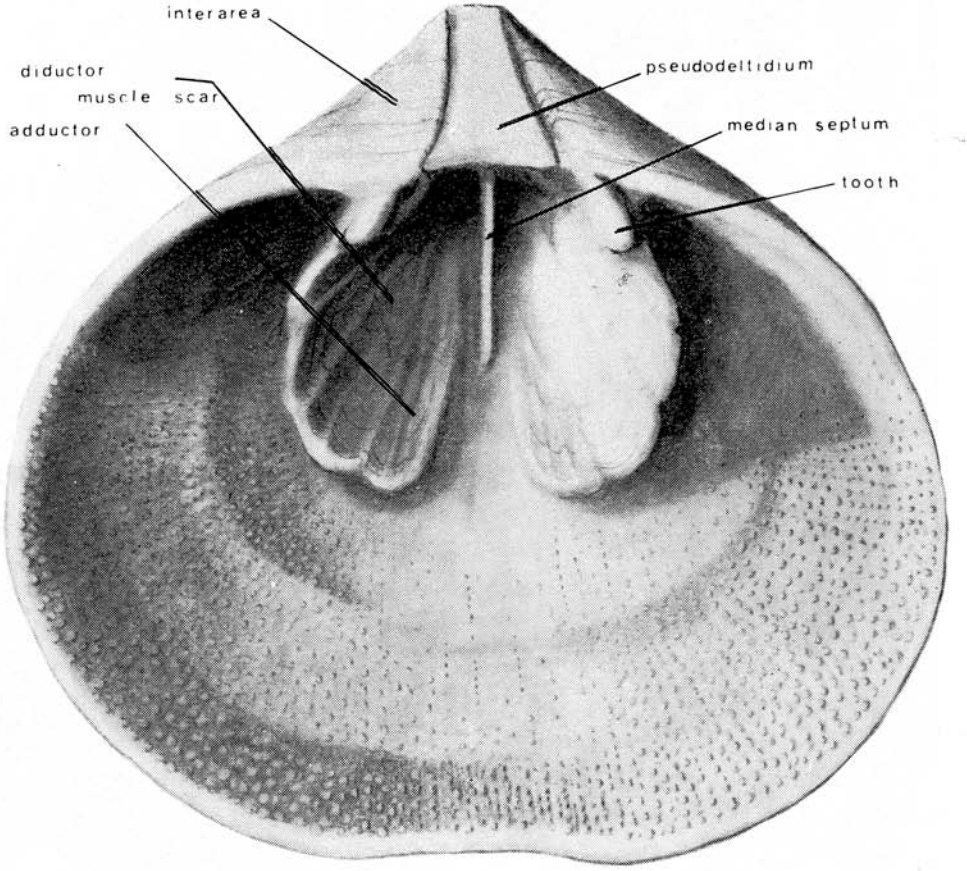

Fig. 5. Idealized representation of the internal structure of the ventral valve of *Thecospira haidingeri* (S u e s s) from the locality Hybe with indicated individual morphological elements. Original.

The dorsal valve is flat to concave. The interarea is low. The cardinal process is small, short, bilobate, on its sides are small, shallow dental sockets. The lobate apparatus consists of 6 bendings (fig. 7:1).

O c c u r r e n c e: Rhaetian of the Eastern Alps and West Carpathians. In the West Carpathians the species is found in the Hybe Beds of the Kössen Formation at the locality Hybe. W. G o e t e l (1917) described a find of two individuals from the northern slopes of the High Tatra (Lejowa dolina valley).

Ecology

A t t a c h m e n t c o n d i t i o n s. The individuals of the species *Thecospira haidingeri* (S u e s s) grew in 61,5 % on *Rhaetina pyriformis*, in 7,5 % on *Rhaetina hybensis*, in 0,5 % on shell fragments of larger bivalves and in 30,5 % on coarse organodetrital frag-

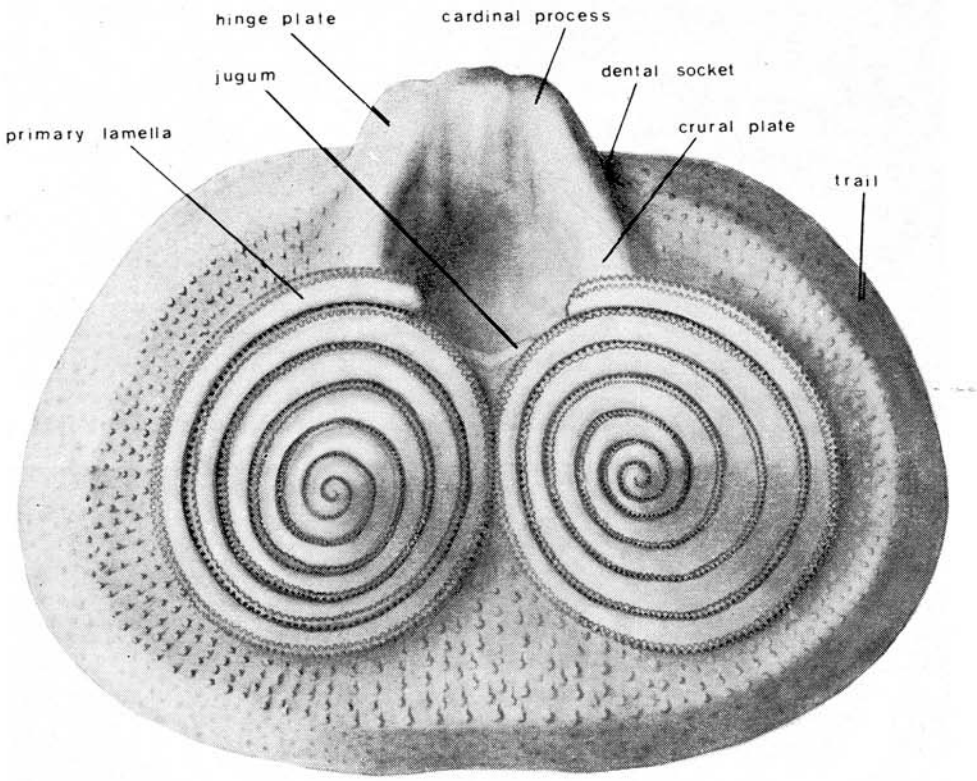

Fig. 6. Idealized representation of the internal structure of the dorsal valve and brachidium of *Thecospira haidingeri* (S u e s s) from the locality Hybe with indicated individual morphological elements. Original.

ments not determined closer. In shells of *Th. haidingeri* cemented to valves of the genus *Rhaetina* a distinct oriented attachment may be observed (fig. 9). Provided that there was a natural orientation of shells of the genus *Rhaetina* in an almost vertical position with the beak directed downwards (J. M i c h a l í k 1975), the sessile *Thecospira* shells took a position with the umbo of the dorsal valve upwards (fig. 10). With a relatively highly raised trail of the peripheral edge this position assured the possibility of washing out accidentally penetrated detrital fragments from the shell interior. When plotting the attachment directions in a diagram (fig. 9) it may be seen that the symmetry plane of attached valves is in no case coincident with the symmetry plane of "host" shells of *Rhaetina* but turned under a certain angle to it (usually 30—40 %). In most cases young individuals of *Thecospira* were attached on the ventral valve of the genus *Rhaetina;* in every case, however, to the peripheral zone of valves at some distance from the opening. Such an attachmet assured to the fixed individuals a food supply by still not utilized suspension currents (fig. 10).

I n t e r p r e t a t i o n o f a s y m m e t r i c g r o w t h. The shells of the species *Thecospira haidingeri* from the locality Hybe are very often asymmetric (about 30 % of


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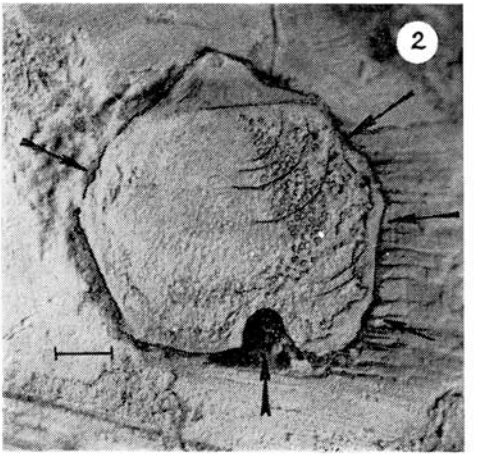
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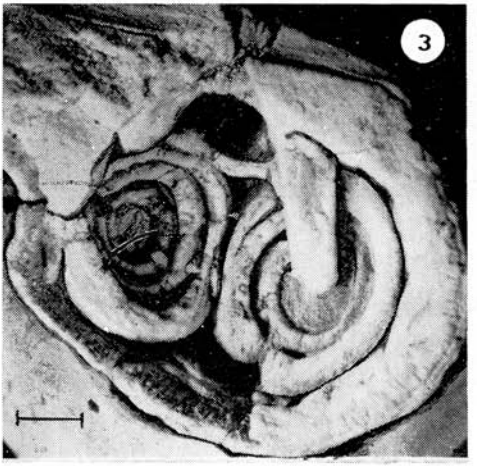
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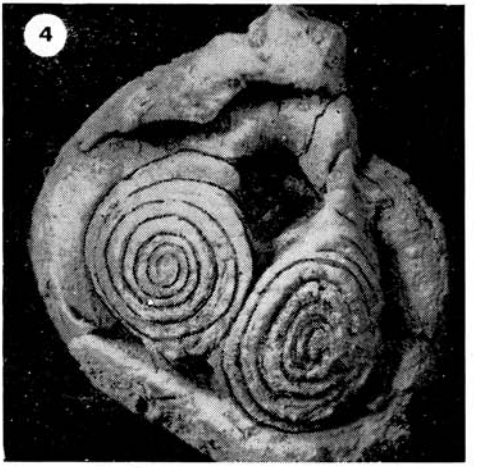
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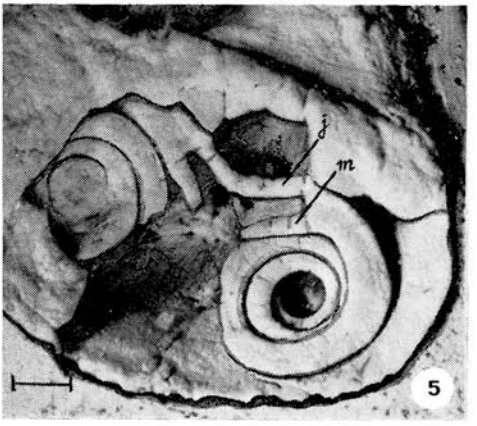
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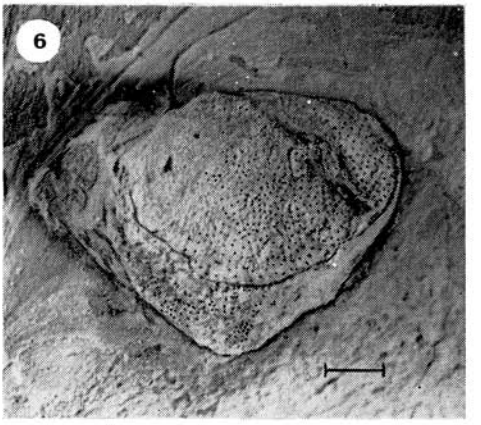
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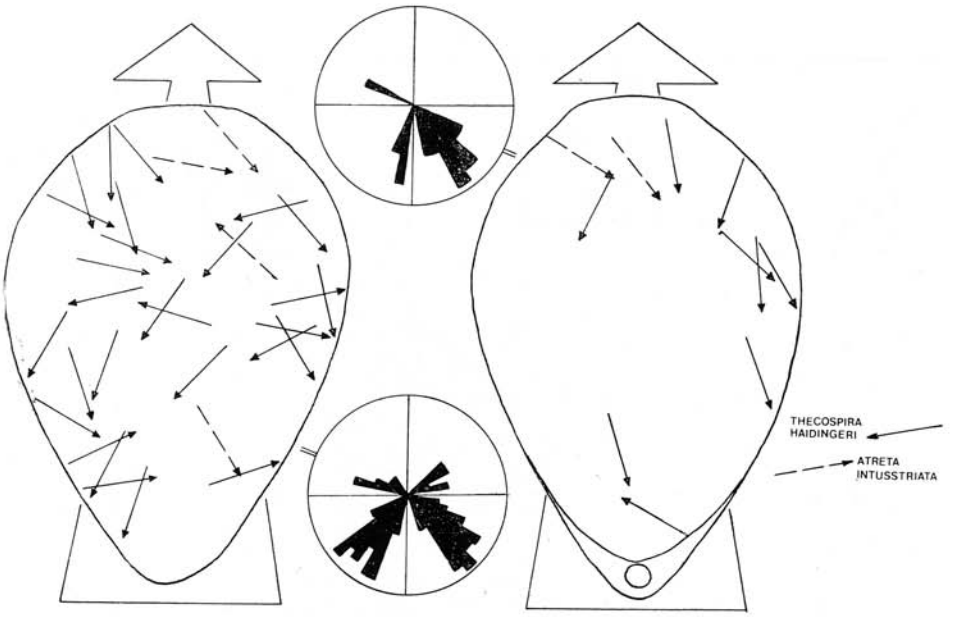

Fig. 9. Schematic evaluation of attachment direction of *Thecospira haidingeri* (S u e s s) shells on *Rhaetina* valves. The obtained values are also plotted in rosette diagrams (in the middle). The arrows are directed toward the anterior margin of valves.

cases of the studied material). When searching for the origin of this asymmetry it has turned out that there were obviously several reasons combining mutually in many cases. Among the investigated material I have distinguished four most abundant types of asymmetry:

a) Type concerning shells cemented in immediate proximity of the active opening of the host shell. The shells cemented in this part of the margin are distinctly asymmetric, stretched along the opening. The shell margin adjacent to the opening (double line right in fig. 11 a) is distinctly geniculated. When tracing the ontogenetic growth of the geometric shell outline, we see that as a matter of fact gradual turning of the anterior margin into a position parallel to the opening of host shell proceeds (fig. 11 e). For the normal action of organism functions it was important that distribution of exhalant and inhalant openings in relation to the active inhalant opening of the host should be oriented. From the observation of mutual interaction between the host and guest organism according to the growth of shells results that the growth of *Thecospira* was probably slower than in *Rhaetina* shells.

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Fig. 7. 1—2: *Bactrynium bicarinatum* E m m r i c h 1855. 1: Core of the dorsal valve. Hybe-Kantorská pit. 2: Individual cemented to *Rh. pyriformis*. Hybe-new pit. The arrows indicate the bendings of the ventral valve edge. 3—6: *Thecospira haidingeri* (S u e s s). 3: Prepared brachidium of individual from fig. 1 : 1. Dorsal view. 4: Ventral view of the prepared brachidium of individual from fig. 1 : 3. Dorsal view of the prepared brachidium of individual TH-44 from the locality Hybe-Kantorská pit. J = jugum, m = median apophysis. 6: Individual TH-10 on *Rh. pyriformis*. Hybe-Kantorská pit. Photo F. Martančík.

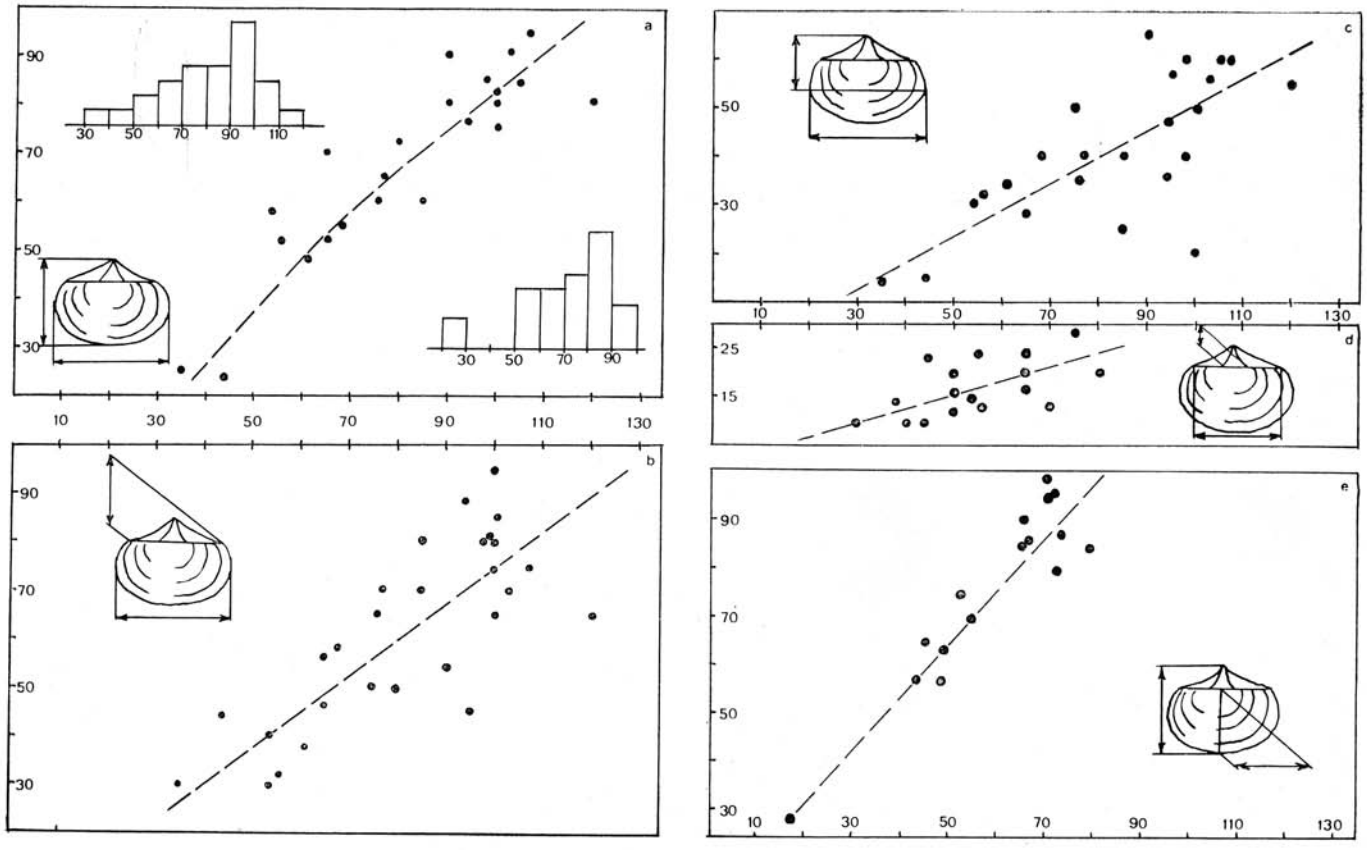


Fig. 8. Graphs of variability of dimensions of Thecospira haidingeri (S u e s s) a: Graph and histograms of shell width and length from the locality Hybe-Kantorská pit. b: Graph of the ratio of width and hinge line of shells from the locality Hybe-Kantorská pit. c: Graph of the ratio of shell width to the distance of the place of maximum width from the ventral valve beak. Hybe-Kantorská pit. d: Graph of the ratio of hinge line length to the length of the lower pseudodeltidium margin. Kantorská pit. e: Graph of the ratio of ventral and dorsal valve lengths. Kantorská pit. All dimensions in tenths of mm.

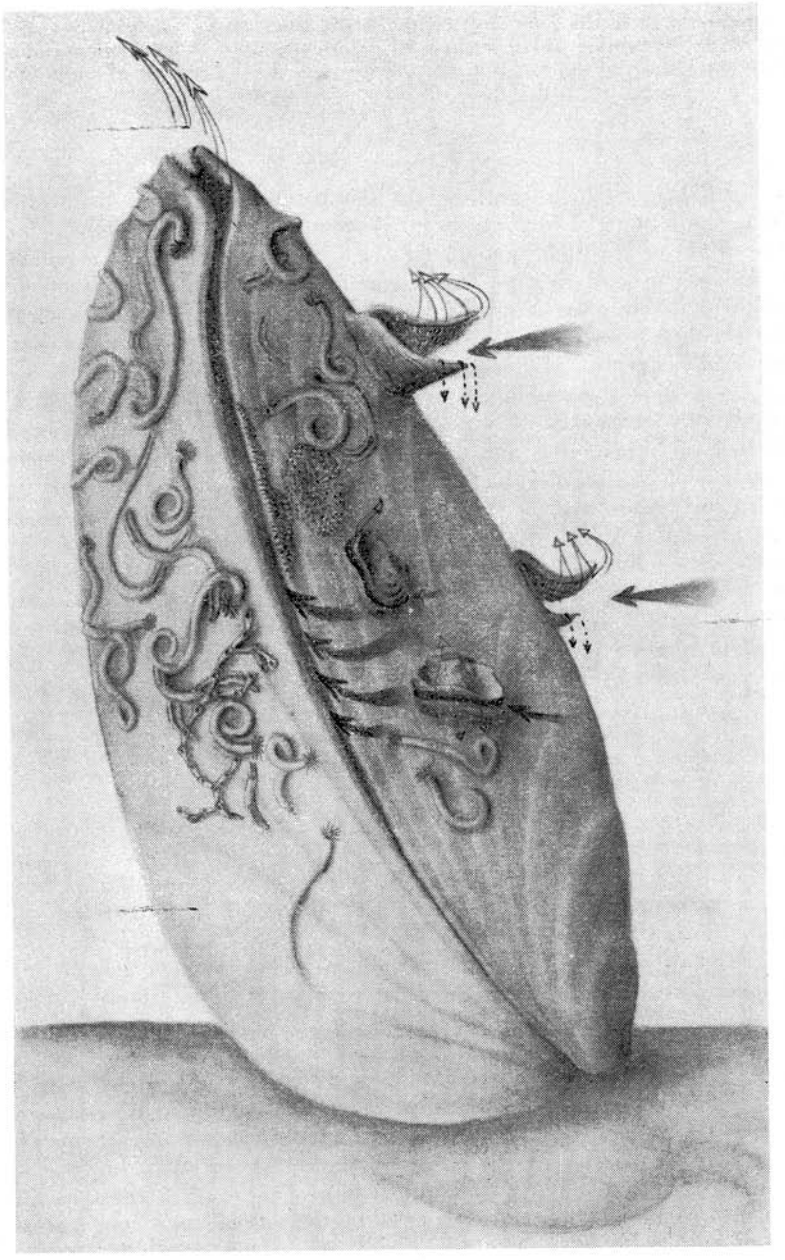


Fig. 10. Schematic representation of attachment of commensals on *Rhaetina* shells in relation to suspension currents. Worms, bryozoans, *Thecospira*. Black arrows-not utilized, white-utilized suspension current. Original.

Fig. 11. Interpretation of the four most characteristic ways of shell deformation of *Thecospira haidingeri*. a—d: Illustration of the outlines of deformed shells. e—h: Schematic interpretation of the individual ways of deformation and their origin. i—j: Location of individual cases of deformed shells. a—d: Original.

b) Type concerning shells cemented to the bottom of narrow depressions. Shells cemented to the bottom of furrows (e. g. on *Rh. hybensis*) are spirally deformed (fig. 2—2). The origin of this deformation (fig. 11 b) proves that it was inevitable for the organism to keep a constant ratio of the length of the lateral parts of opening to the length of the anterior part. A growth under conditions of a reduction of the lateral growth by pressing from the sides was only possible with a contemporaneous rotation of the whole dorsal valve, also with the hinge line (fig. 11 f).

c) Type, present in shells obliquely attached to a flat surface (fig. 11 c). Such shells were affected by a steady strong one—sided resistance (small triangles), which prevented normal articulation and growth. As a consequence, in the course of the growth rotation of the dorsal valve took place (fig. 11 g). The actual hinge line can be concealed in such cases—see the dashed line in (fig. 11 c).

d) Type present in shells attached in the region of the posterior commissure part. These shells were subject to (intermittent) pressure from one side (from the left lower corner in fig. 11 d) induced by the pressure of the adjacent host valve with its articulation in this case (the host valves were permanently closed in this part). This hindrance caused a slight rotation of the dorsal valve during growth (fig. 11 h). A similar effect had also other hard objects in proximity of the place of cementing of *Th. haidingeri* shells.

Conclusions

1. On the contrary to the statement of A. Williams (1965) *Th. haidingeri* has a distinct pseudodeltidium.

2. The jugal apparatus of *Thecospira haidingeri* has a complicated structure: it consists of a jugal arch, fixed to the crura and of median apophyses projecting from the ends of primary lamellae.

3. The ventral valve of *Bactrynium bicardinatum* follows sometimes with the bendings of its peripheral edge the bends of the lobate apparatus of the dorsal valve.

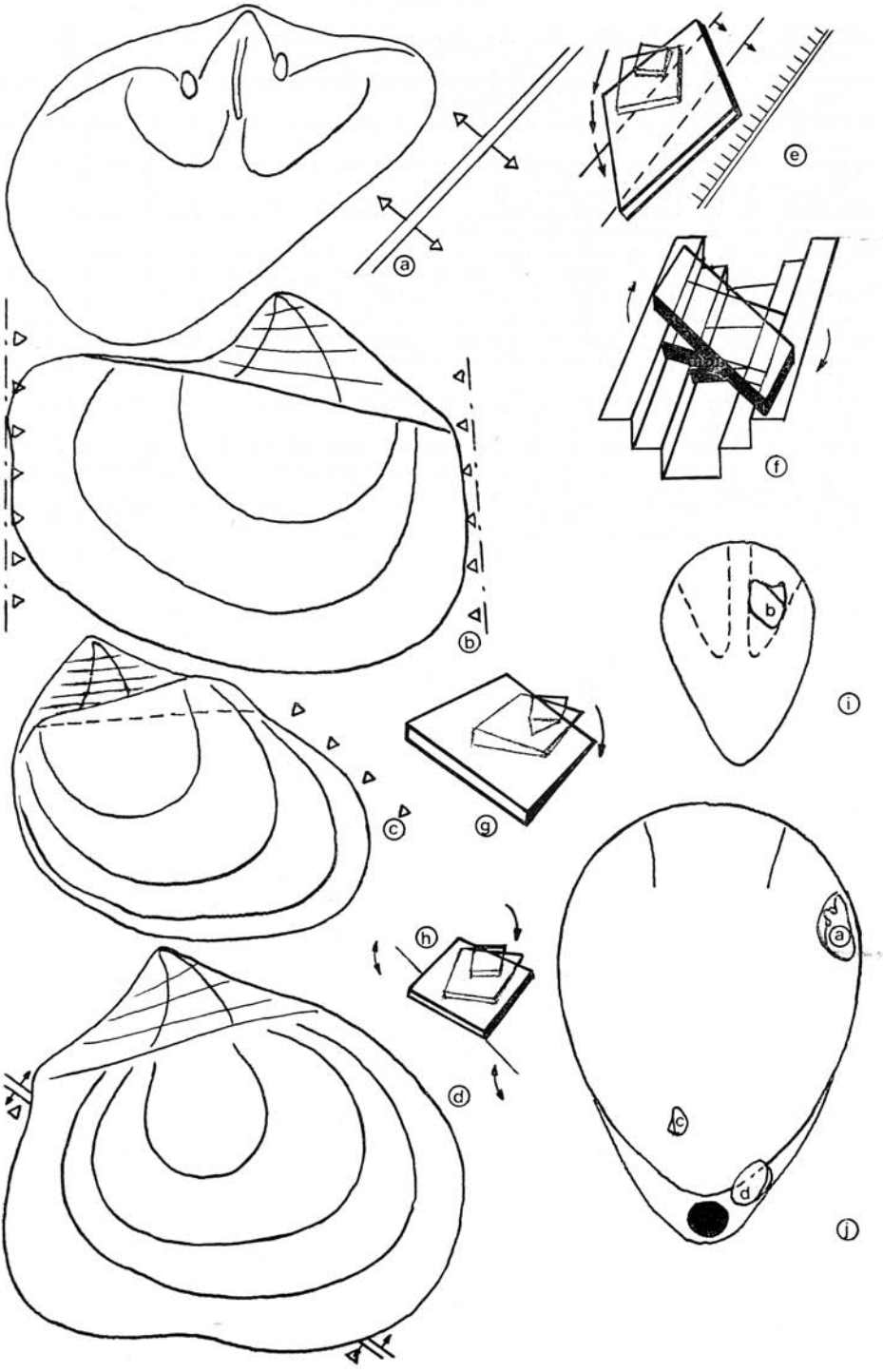
4. The shells of *Th. haidingeri* are attached on *Rhaetina* valves mostly in postero-lateral orientation.

5. The asymmetry of *Th. haidingeri* shells is caused in most cases: a) by the food-supplying current of the host, b) by lateral reduction of growth in the furrows of the substratum, c) by oblique cementing, d) by objects in proximity of the cementing place.

6. The growth of *Thecospira* shells was obviously slower than in *Rhaetina* shells.

7. For a normal action of organism functions of *Thecospira* a constant ratio of the magnitude of the lateral and anterior parts of the commissure was necessary more than a constancy of angles.

Translated by J. PEVNÝ.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