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GENUS RHAETINA WAAGEN, 1882 (BRACHIOPODA) IN THE UPPERMOST TRIASSIC OF THE WEST CARPATHIANS

(Fig. 1—23, Pl. I—IV)

Abstract: The paper is dealing with three species of the genus Rhaetina Waagen, 1882: *R. gregaria, R. pyriformis* and a new species, *R. hybensis n. sp.* Attentions is paid in detail to their morphology, inner structure, impressions of soft parts, stratigraphical and geographical distribution, similarities and intraspecies variability. The paper sets out from the results obtained by the study of structures from serial sections of shells and of statistic evaluation of dimensions of hundreds of specimens.

In the chapter on ecology of the representatives of the genus ecological features are discussed, following from morphology, ontogeny, preservation of shells, the occurrence in types of sediments and in associations of other organic remnants, overgrowing of valves by commensalic animals, traces after damaging and healing of valves. These data are used in compiling the picture of general paleogeography of the territory under study.

Резюме: В статье автор рассматривает три вида рода *Rhaetina* Waagen, 1882: *R. gregaria, R. pyriformis* и новый вид *R. hybensis* n. sp. Подробно описана их морфология, внутренное строение, отпечатки мягких частей тела, стратиграфическое и географическое местонахождение, чем похожи и чем отличаются от других брахиопод, и внутривидовая изменчивость. Автор исходит из данных полученных изучением структур серии шлифов раковин и изменчивость по статистическому определению размеров нескольких сотен экземпляров.

В главе об экологии представителей рода разобраны экологические черты, исходящие из морфологии, онтогенеза, сохранения в разных типах седиментов и в ассоциациях других органических остатков, нарастания на створках раковин организмов-комменсалов, следов повреждения и рубцевания. Все эти данные служат для восстановления картины общей палеогеографии области.

The complexes of the uppermost Triassic in the West Carpathians, belonging mainly to the Krížna and Choč nappes, provide for much brachiopod fauna not studied by modern methods so far. In world literature this fauna has been also little treated only. And it is only a thorough knowledge of relationship and affinities of Rhaetian and Norian faunas that can contribute to solving one of the most required problems of Triassic stratigraphy — the question of the Rhaetian — Norian boundary.

An interesting problem is also the interpretation of the regularities of delimitation of living environments of monotypic assemblages of *Rhaetina gregaria:* of the biological, ecological and biogeographical reasons of the existence of so widespread monotonous associations in a wide zone along the northern Tethys coast (Fig. 1).

The genus *Rhaetina* Waagen belongs to the subfamily Dielasmatinae, a blind branch of the family Dielasmatidae, dying out to the end of the Triassic (Fig. 2).

The material studied is derived from bituminous marly limestones, marls, from organodetrital and fine-grained to compact limestones. The brachiopod shells are very well preserved in marly rocks, in rocks with a higher share of calcite recrystallization is more intense, gradually blurring the details of shell wall structures up to a trans-

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formation of the whole shell also with the filling into an aggregate of crystalline calcite.

The material was prepared by an electromagnetic vibrating needle or by common preparation needle under the binocular microscope. The inner structure of the valves and the structures of shell wall have predominantly been observed from celluloid peels of oriented serial sections.

The studied material is deposited in the collection of the author in the Slovak National Museum in Bratislava.

Fig. 1. Schematic representation of the paleobiogeography of brachiopod provinces in the uppermost Triassic (paleogeography according to Smith A. G. et al., 1973, brachiopod provinces of A. S. Dagys (1970), adapted).

I. Systematic part

Order *Terebratulida* Waagen, 1883 (nom. Moore, 1952)
Suborder *Terebratulidina* Waagen, 1883
Superfamily *Dielasmatacea* Schuchert, 1913
Family *Dielasmatidae* Schuchert, 1913
Superfamily *Dielasmatacea* Schuchert, 1913
Genus *Rhaetina* Waagen, 1882
Species typica: *Rhaetina gregaria* (Suess, 1854), Rhaetian of the Eastern Alps.

Diagnosis: Biplicate shell with smooth surface. The loop is short, fixed to the shell bottom by septalial plates, which may but need not form a septalium. The ventral valve is without dental plates.

Description: Small to medium-sized calcareous biconvex punctate nonstrophic biplicate shells with a variable outline (subpentagonal, heart-shaped-oval, elliptical and almost circular). The surface of valves is smooth, covered with indistinct growth-striae. The anterior margin is straight or biplicate, the anterior comissure is straight, deepened, plicate or sulciplicate. The beak of the ventral valve is short, almost upright, revealing

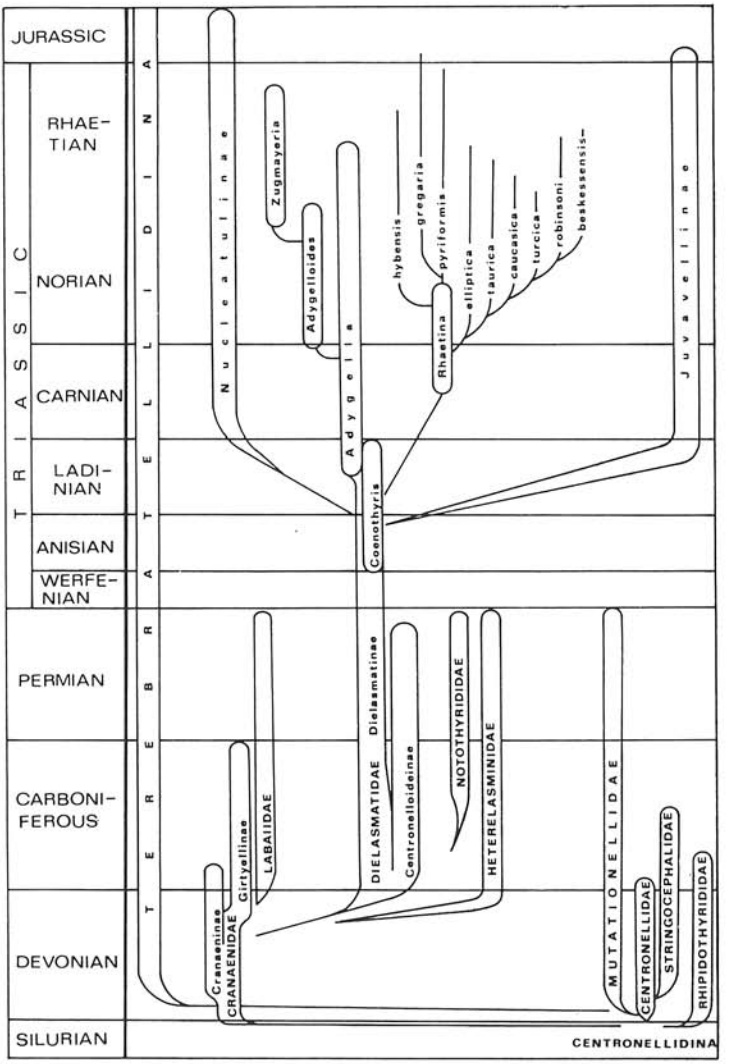


Fig. 2. Schematic representation of development, relationships of Dielasmatidae and composition and position of the genus *Rhaetina* (free according to F. G. Stechli (1965).

the deltidial plates. The beak-ridges are indistinct, the foramen is well developed, permesothyrid to epithyrid.

The ventral valves is distinctly convex, without dental plates in the beak a pedicle collar of up to tubular shape is developed. The muscle scars are not deep, the valve wall is little thickened posteriorly.

The dorsal valve with low septalial plates, linked with the shell bottom (more rarely with a ridge-like septum, forming an indistinct low and wide septalium). The septal ridge is low and short, often present only in the most posterior part of the valve or entirely missing.

The brachial apparatus of early stages is of the shape of a centronelliform loop with a high vertical plate of ventrodorsal direction. Adult individuals have a terebratuliform loop with long crural processes, usually slightly diverging branches and a ventrally strongly bent transversal plate. The anterior part of the branches and of the transverse band is notched with small spines.

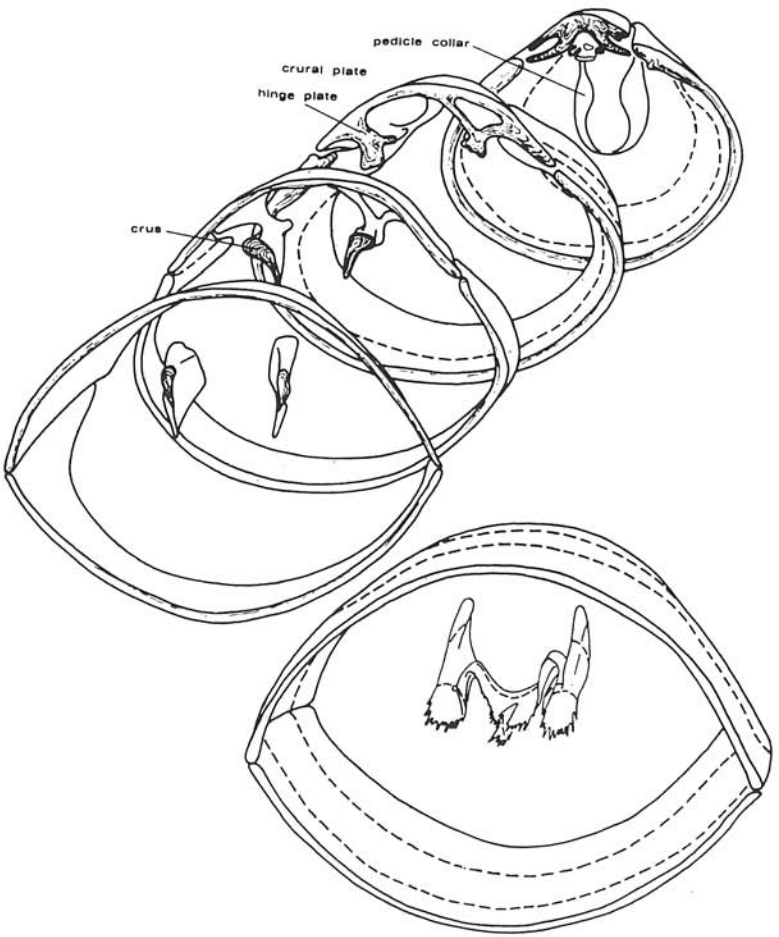


Fig. 3. Spatial representation of serial sections of the shell of *Rhaetina gregaria* (S u e s s) from the locality of Bystrô in the Veľká Fatra. Original.

The genus Rhaetina Waagen includes the following species:
Rhaetina gregaria (Suess), 1854
Rhaetina pyriformis (Suess), 1854
Rhaetina turcica (Bittner), 1891
Rhaetina taurica Moisseiev, 1932
Rhaetina robinsoni Moisseiev, 1947
Rhaetina caucasica Dagys, 1963
Rhaetina beskessensis Dagys, 1963
Rhaetina elliptica Dagys, 1963
Rhaetina hybensis n. sp.

Stratigraphic range: The oldest representative of the genus, *Rh. pyriformis*, has been described from Carnian deposits (e. g. A. S. Dagys, 1963). In the Norian stage it acquired a gradually larger extension, however, reaching the maximum of its development in the Rhaetian. H. Zugmayer (1880), G. F. Parona (1884) and G. Geyer (1889) described representatives of *Rh. gregaria* from the Liassic of the Eastern Alps, which statement, however, has not been confirmed later.

Geographical distribution: In Norian and Rhaetian deposits the genus Rhaetina attained an extension from the Western Alps through the Carpathians, Crimea, Caucasus, Asia Minor as far as the Pamirs.

1. *Rhaetina gregaria* (Suess), 1854
(Fig. 3-10, 22, Pl. 1-6)

Terebratula gregaria Suess 1854, p. 42, t. II, f. 13-15
Ooster 1863, p. 5, t. I, f. 1-6
Terebratula dipla Schafhäutl 1863, p. 348, t. LXX, f. 67-69
Terebratula gregaria Quenstedt 1871, p. 418, t. 50, f. 67-69
Zugmayer 1882, p. 10, t. I, f. 1-11
Haas 1885, p. 23, t. I, f. 1-16
Trauth 1909, p. 66, t. II, f. 3-4
Goethel 1916, p. 111-116, t. VII, f. 6-8
Rhaetina gregaria Dagys 1963, p. 143, t. XXI, f. 14-19.

The holotype of the species is from the Eastern Alps, the place of its deposition, however, is unknown at present.

Material: 2212 individuals from various localities of the Krížna and Choč nappes and the Klippen Belt.

Diagnosis: Subpentagonal, smooth shells, usually with an elongated posterior part. The length of the ventral valve is mostly 25—30 mm, the maximum width approximately in the middle. The anterior margin is biplicate, the plicae reach the first third of dorsal valve, often also more posteriorly.

Description: The small to medium-sized biconvex shells have a pear-shaped to oval, rounded heart-shapped outline in the young age, later a subpentagonal one. The maximum width of the shells is in the anterior third, later roughly in the half of the shell. At the surface of shell, covered only with fine growth-lines, one ventral and two dorsal plicae appear in the adult stage, usually distinct in the anterior third only. The ventral valve is as much convex as the dorsal one, the transversal deflection is always larger than the longitudinal one.

In ephebic individuals the comissure is four times dorsally deflected: on the sides of the shell there are two insignificant lateral dorsal bends, after their termination in narrow ventral bends the comissure line gradually rises towards sharp bendings

Fig. 4. Spatial representation of serial sections of the shell of another individual of *Rhaetina gregaria* from the locality of Bystrô with a spicular partition closing the septalial cavity. Original.

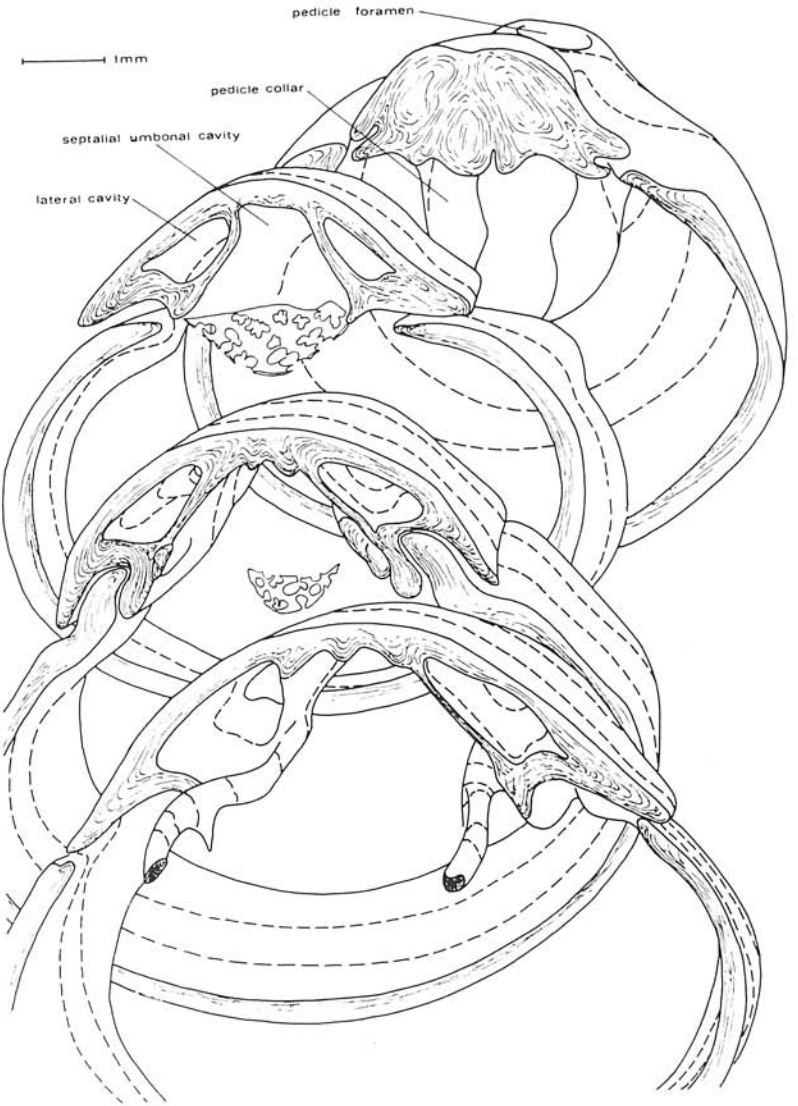
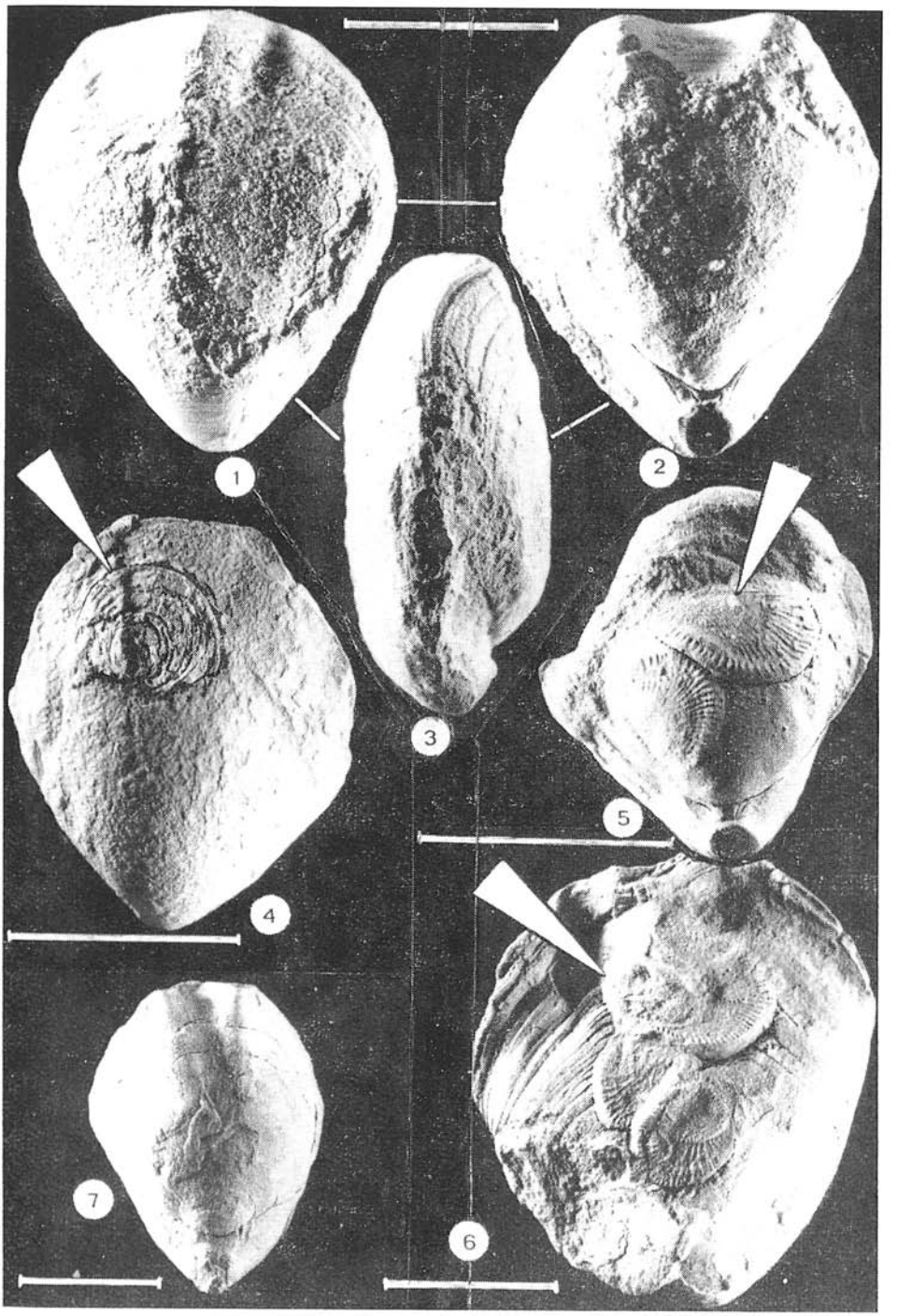


Plate I.

Fig. 1—3. Ventral, dorsal and lateral view of the shell of *Rhaetina gregaria* (S u e s s) from the locality of Bystrô in the Veľká Fatra. — Fig. 4. Ventral valve of *Rh. gregaria* with attached shell of *Discina sp.* Locality of Bystrô. — Fig. 5—6. Dorsal and ventral valve of individuals of *Rh. gregaria* with attached valves of *Atreta intusstriata.* Locality of Bystrô. — Fig. 7. Dorsal view of the shell of *Rh. gregaria* from the surroundings of Vienna. The distance on the abscissa at all individuals = 1 cm.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of the markedly sulciplicate sinus. The whole line of the comissure runs dorsally above the hinge margin plane.

The sinus appearing at the beginning of the ephebic stage has first the shape of a dorsal plicate deflection; however, very soon a medial ventral deflection develops and the sinus is getting a characteristic sulciplicate shape: Only seldom the sinus remains uniplicate up to adult age or does not develop at all.

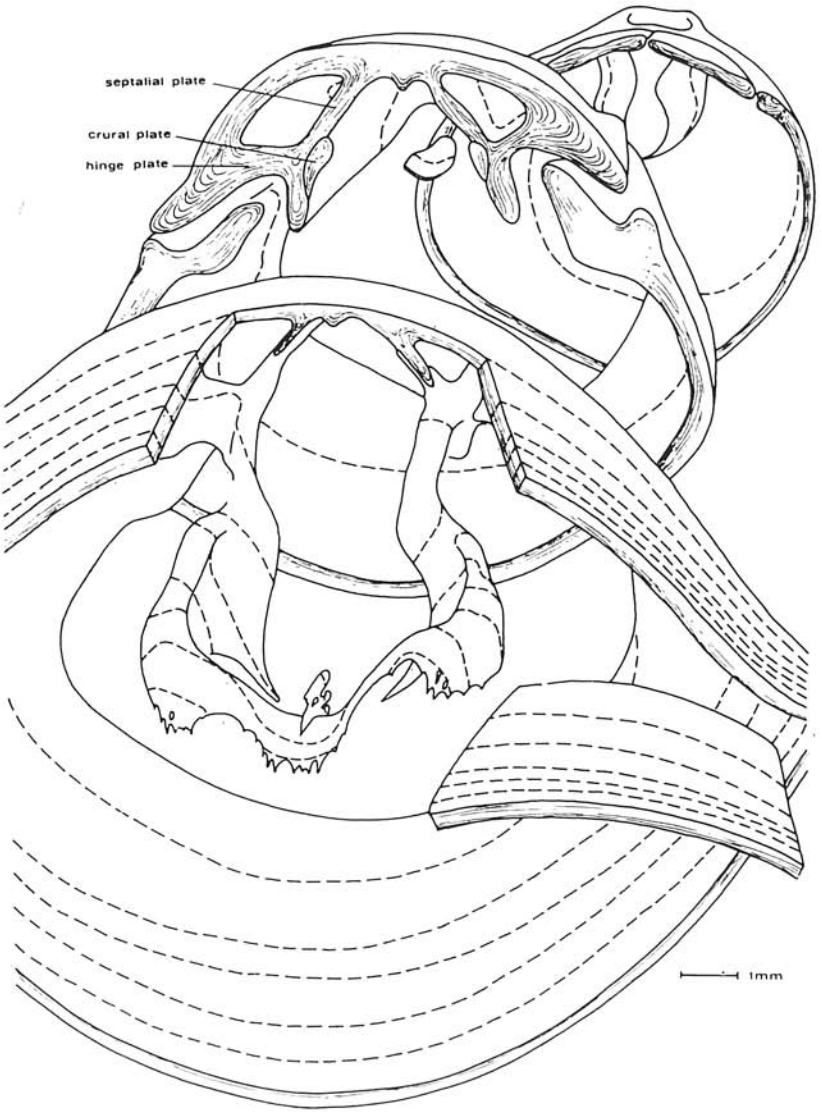


Fig. 5. Spatial representation of serial sections of the shell of the species *Rhaetina gregaria* from the locality of Havranský žľab in Zadné Meďodoly (Belianske Tatry). Original.

The ventral valve is most convex in the posterior half. The delthyrium is not large, the deltidial plates are partly concealed by the umbo of the dorsal valve, the cardinal area is indistinct. The beak-ridges are rounded, the beak projected, of various length, however, in the most cases relatively short. The apical angle is 70—95°. The foramen is circular, permesothyrid to epithyrid. From the inner side it is rimmed by an arch-like pedicle collar. The teeth are supported by massive bases, however, never by dental plates (Fig. 3—6).

The narrow and long field of adductor muscle scars in the middle of the valve is deepened into the surface. It lies at the anterior end of long furrow-like tracks of muscle scars, only little smoothed by callus filling. The medial ridge separating both

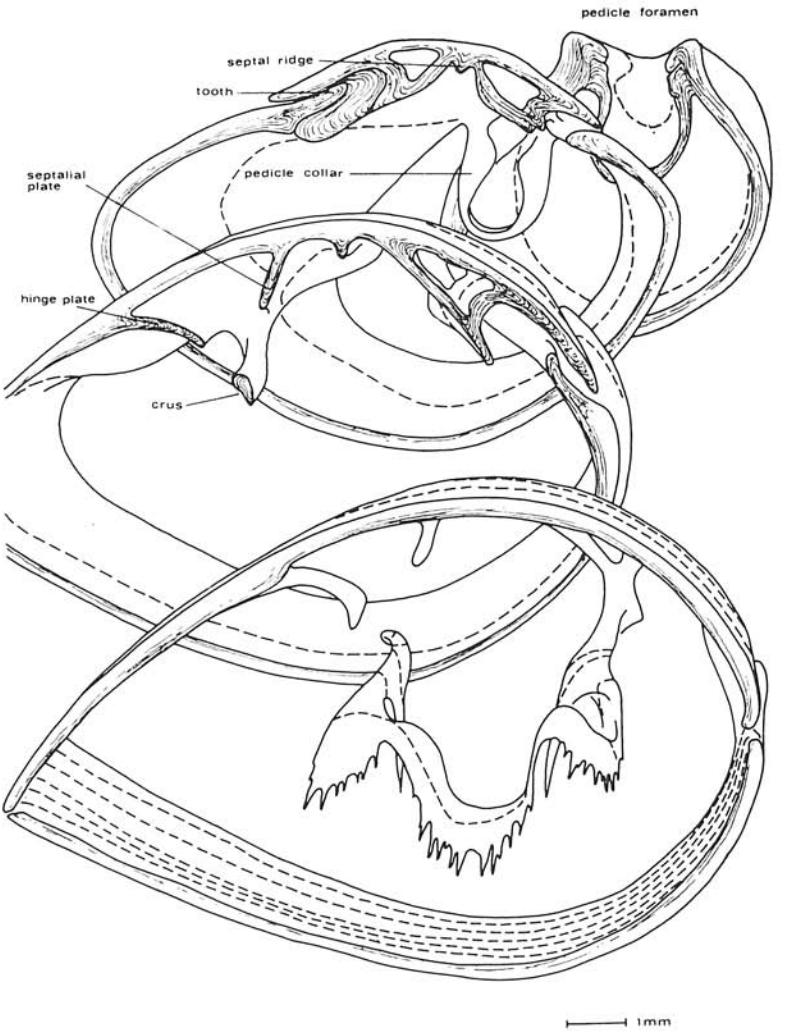


Fig. 6. Spatial representation of serial sections of the shell of *Rh. gregaria* from the foothill belt of the Alps near Vienna. Original.

scars continues sometimes farther anteriorly and may be mistaken for a remnant of the ventral median septum (H. H a a s, 1885). In the posterior part of the valve, on the sides of the adductor scar tracks, are found triangular diductor scars, laterally from them are indistinct gonoglyphs. The pallioglyphs are little distinct, the branches of vascula media are usually marked anteriorly from the adductor scars.

The dorsal valve is most convex approximately in the middle, its width is nearly as great as its length. The hinge plates are narrow, indistinctly separated from the inner socket ridges and crural bases. The hinge plates are high, of lateral direction, merging with the margins of dental sockets into small bodies of the shape of isosceles triangles. The median septum of juvenile shells attains half the length of the valve, in older individuals getting gradually less distinct, changes into a short, indistinct ridge and sometimes almost disappears below a cover of deposited secondary material. The septalial plates are low, oblique to the central part of the valve. Their length does not exceed 1/5 of the valve length, sometimes they extend on the valve as inconspicuous, low ridges, they are fixed to the valve bottom usually at a certain distance from the medial line. I have not observed the presence of a septalium in adult individuals of my material.

The crural bases are low, in the posterior part resembling indistinct ribs at the surface of septalial plates, becoming more distinct anteriorly. The crura are relatively wide and flat plates, directed ventrodorsally. After a short anteriorly running section they are bent ventrally, forming long, hook-shaped processes. The branches of the brachial apparatus are much thinner, running almost parallelly in anterior direction nearly to the beginning of the second third of the valve; here they turn into postero-ventral direction and converge towards the transverse band. The latter carries in the

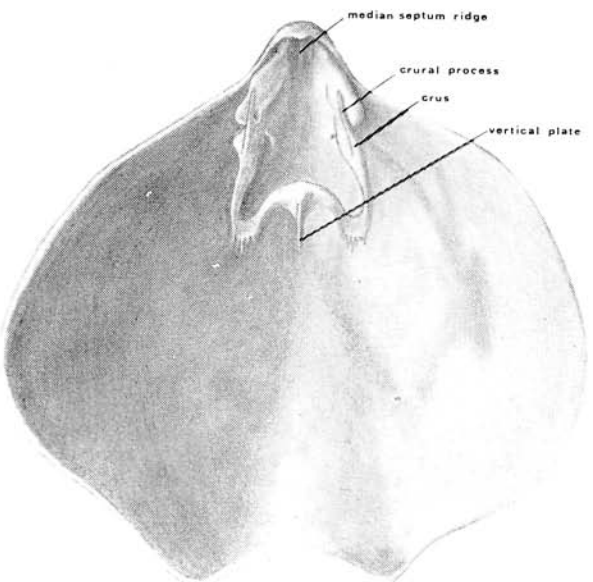


Fig. 7. Reconstruction of the cardinalia and brachial apparatus of a young individual of the species *Rhaetina gregaria* (S u e s s) from the locality of Bystrô according to serial sections. Actual length of the dorsal valve is 16 mm. Original.

middle a ventrodorsally oriented vertical small plate, distinct mainly during the young growth stages. At the anterior edge of the bendings of the brachial apparatus branches and on the transverse band the are small spine-like needles (Fig. 7).

In the middle of the posterior half of the dorsal valve there is a variously distinct field of aductor scars: being rounded heart-shaped, divided by the median septum. Distinct is sometimes also the diductors scar between the dental plates. On the sides of the muscle scars field two crescent-shaped areas of ovarian markings are found. From the pallial grooves only the branches of vascular media are mostly conspicuous (Fig. 8).

Distribution: Rhaetian of the Northern and Southern Alps. West and East Carpathians, Corsica, Apennines, "Rhaetonorian" of the Northwestern Caucasus, Afganistan . . . In the West Carpathians the material was collected at localities in the Klippen

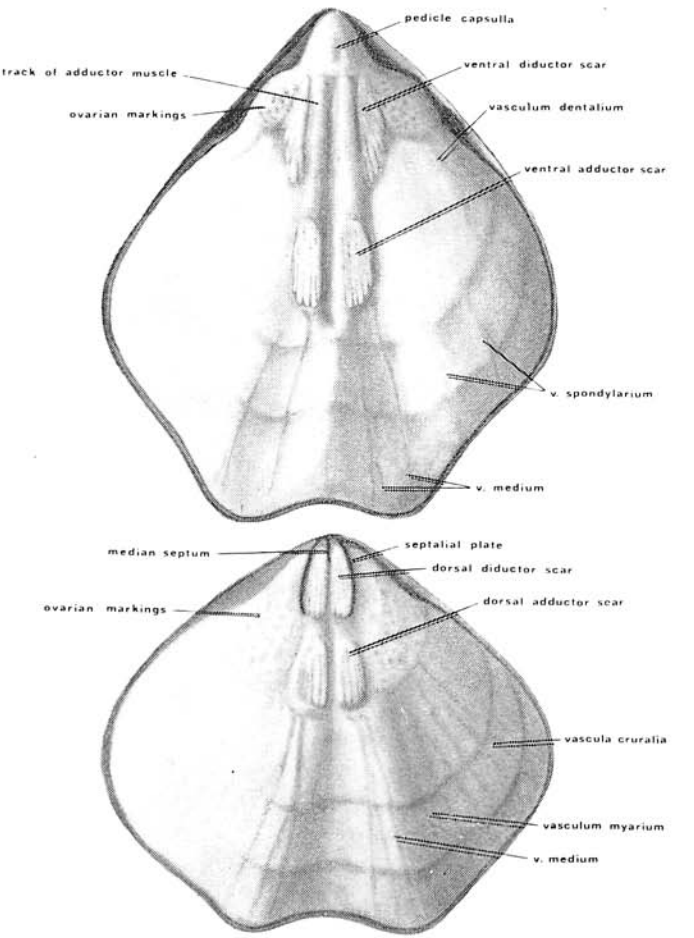


Fig. 8. Idealized representation of impressions of soft parts (myoglyphs, pallioglyphs, gonoglyphs) on cores of the ventral and dorsal valve of *Rh. gregaria* (Suess). Original.

Belt (Branč), in the Vysoká unit of the Malé Karpaty Mts. (Mt. Vysoká near Vývrat), Krížna unit of the Strážovská hornatina Mts. (Híreška, Vysoká near Gápel, Nožové near Čičmany), the Malá Fatra Mts. (Lesnianska dolina valley, Tržinovo near Zázrivá), Veľká Fatra Mts. (Revúcky mlyn below the Mt. Borišov, Vôdky near Jasenovo, Turecký salaš Chalet near Turecká, Bystrý potok near Hubová), Western Tatra Mts. (W slope of the Veľká Furkaška near Oravice) in the Havran unit in the Belianske

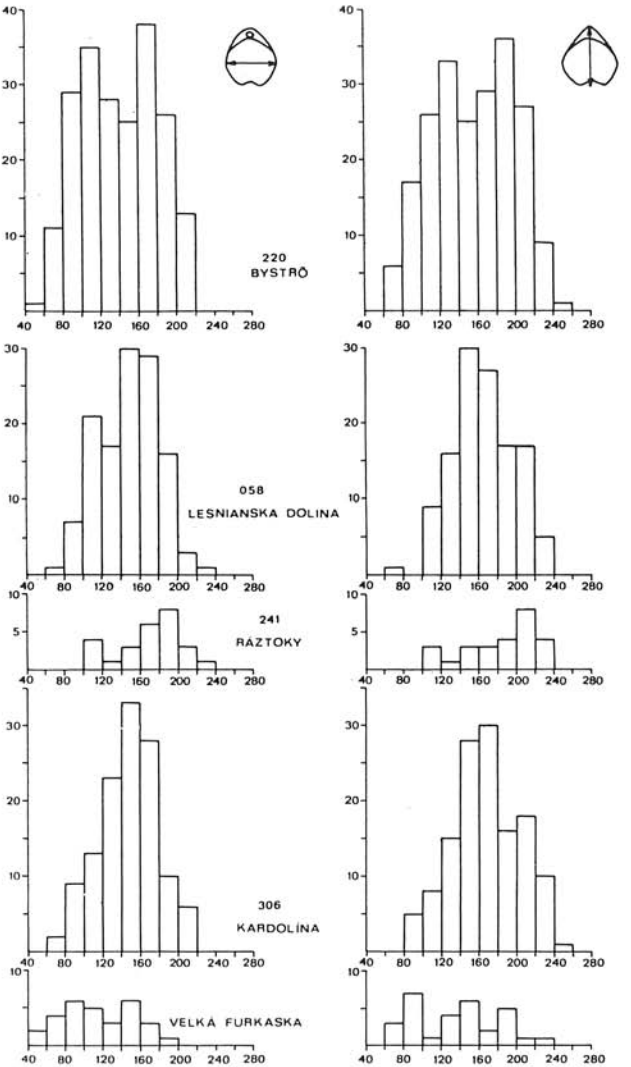


Fig. 9. Graphs of quantitative representation of the width and length of the species *Rh. gregaria* from various localities of the Krížna nappe (on the vertical coordinate the number of individuals, on the horizontal one the size in tenths of milimeters. The graphs of monotypic assemblages (loc. 058, 306) distinctly differ from the populations of lagoonar areas, assemblages richer in species (loc. 220, 241).

Tatry Mts. (groove W below the Havran, groove W below the Ždiarska Vidla), in the unit of Bujačí of the Belianske Tatry Mts. (Kardolina) and in the Humenské pohorie Mts. (Porúbka, Okor.) W. G o e t e l (1917) mentioned rich localities of this species from the northern slopes of the High Tatras. Isolated valves and rare transported shells of this species are not uncommon practically within the whole area with Fatra beds of the Krížna nappe although the zones of the original biotop were obviously narrow (Fig. 9, 10).

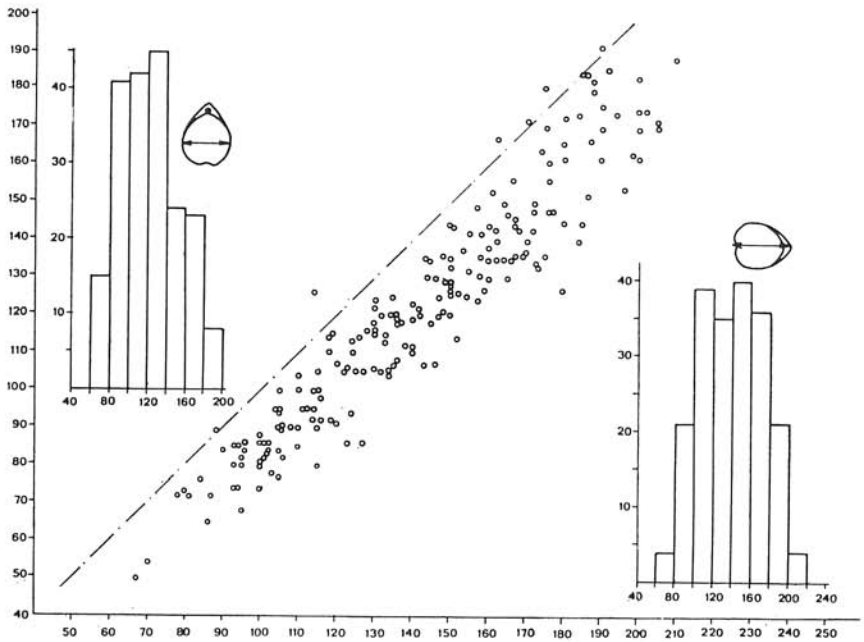


Fig. 10. Qualitative and quantitative graphs of the width and length of shells of *Rhaetina gregaria* from the locality Groove below the Ždiarska Vidla in the Belianske Tatry. Dimensions in tenths of milimetres.

D i s c u s s i o n: The individuals from the observed material agree with the specimens from the foothill-belt of the Alps near Vienna, which were sent to me for comparison kindly by Prof. H. Z a p f e. *Rhaetina turcica* (B i t t n e r) with an almost identical appearance and character of plication has a wider anterior margin, less distinct sinus and much smaller dimensions in the adult age. *Rhaetina taurica* M o i s s e i e v differs in having a less distinct sinus and a plica developed on the dorsal valve only. From the species *Tradithyris gregariaeformis* (Z u g m a y e r) the described species differs in the outline (development of lateral lobes, posterior shift of maximum width, shorter and broader beak), size and a different structure of the cardinalia and brachial apparatus.

2. *Rhaetina hybensis n. sp.*
(Fig. 11, 12, 23. Pl. II 1-6. III 1. IV 1-5)

Terebratula gregaria G o e t e l 1917, p. 116, pl. VII, f. 5

H o l o t y p e: Specimen no. 48 (Pl. IV 1-5) m width 26.3 mm, length of ventral valve 91.3 mm, thickness 15.4 mm.

Locality: The classical locality of Hybe on the right concave bank of the meander of the Biely Váh river 2 km SE of the community Hybe, "Kantorská pit".

Stratum typicum: Rhythmical complex of black marls and blackish-grey organodetrital limestones, beds with the conodont *Misikiella hernsteini* (uppermost Sevatian — Lower Rhaetian?).

Material: 137 individuals from the locality of Hybe.

Diagnosis: Relatively large elliptical shells, higly biconvex, with a distinct sinus. Maximum width in the middle of the shell. The plicae reach almost the half of the dorsal valve, the ventral plica as high as the posterior third of the ventral valve.

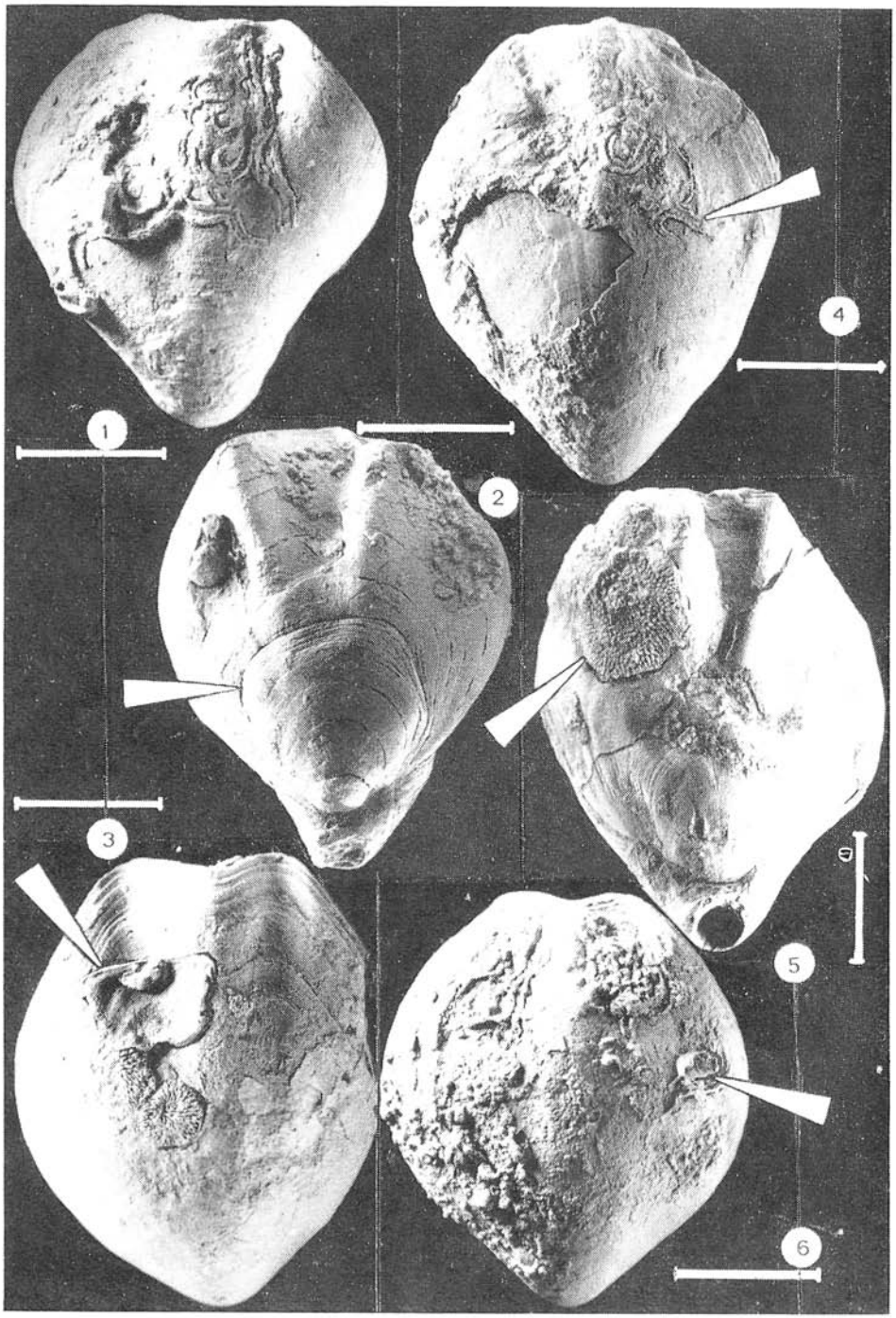
Description: Medium-sized to large shells (30—40 mm long, i. e. nearly 2.5 times larger than *Rhaetina gregaria* from the Krížna nappe), distinctly biconvex to globular, the outline is subpentagonal, oval, sometimes to nearly circular. The maximum width is in the middle of the shell, only sometimes indistinctly shifted anteriorly. The surface of the valves is smooth, with to a various degres conspicuous growth-lines, often overgrown with commensalic organisms. On ephebic shells there are two dorsal and one ventral plica, separated by two deep furrow-like sulci from the other surface of the valve. The plicae usually begin from the middle of the shell (the ventral plica even more posteriorly) but as distinct ridge-like forms they are to be seen in the anterior third only. Sometimes they are poorly visible also in the posterior half of the shell.

The ventral valve is as much convex as the dorsal one; the impression of flatness of the dorsal valve is caused by the strong development of sinus. The transversal deflection of valves is always larger than the longitudinal deflection. The comissure of adult individuals is only twice markedly bent dorsally. The lateral bendings are only insignificantly indicated in best case, the comissure line is only slightly dorsally raised above the hinge margin plane. In the anterolateral region it sinks moderately and then it immediately starts to rise steeply dorsally. At the top of rising at the anterior margin it forms sharp dorsal sinuses, separated by a median deep fold. The sinus is thus of a distinctly sulciplicate shape, entirely lying relatively high above the hinge margin plane.

The ventral valve is deepest approximately in the middle, its convexity is uneven. The delthyrium is not large, the deltidial plates are uncovered, the cardinal area is only little distinct. The beak-ridges are indistinct, more pronounced on the sides of the apex only. The beak is short, flat and low, the apical angle 80—100°. The foramen is circular, epithyrid. The pedicle collar is collar-shaped to tubular, on the posterior side of the foramen often appearing from the inner valve surface (Fig. 11). The teeth

Plate II.

Fig. 1. Ventral valve of *Rh. hybensis* sp. n. with attached worm tubules. Locality "Viper pit", Hybe, individual no. 25. — Fig. 2. Dorsal view of an individual of *Rh. hybensis* sp. n. with teratological damaging of shell, indicated in a distinct growth interval. Locality "Viper pit", Hybe, individual no. 21. — Fig. 3. Ventral valve of *Rh. hybensis* sp. n. with an attached valve of *Rh. pyriformis* with cemented worm tubules and zoaria of bryozoan. Individual no. 37. — Fig. 4. Ventral valve of *Rh. hybensis* sp. n. with attached worm tubules. Locality "Viper pit", Hybe individual no. 15. — Fig. 5. Dorsal valve of *Rh. hybensis*, sp. n. with a bryozoan zoarium in the anterolateral part. Hybe, "Viper pit", individual no. 36. — Fig. 6. Ventral valve with attached worm tubules and cemented valve of a small brachiopod. Locality "Viper pit", Hybe, individual no. 35.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are big and massive, with strong teeth-bases, however, always without dental plates. The field of muscle scars is conspicuous and long, essentially similar to these of *Rh. gregaria*. The adductor scars are lying before the half of the ventral valve, more anteriorly than in the foregoing species.

The dorsal valve is deepest in the middle, often laterally extended, its width is greater than the length. In the interior of the valve there are strong narrow hinge plates, coalesced with crural bases into long plate-like triangular bodies, very extended at the anterior margin. The septalial plates are fixed to the bottom of the valve relatively far away from each other and from the septal ridge: a development of the septalium I have not observed at my material. The median septal ridge is indistinct, wide, low and short.

The crural bases are low, projecting from little distinct ribs on the surface of the hinge plate. The crura are wide and massive, rising hook-shaped into long apparatus diverge arch-like (in contrast to the narrow loops of other representatives of the genus) and converge again towards a long and thin transverse band. On its anterior edge and on the anterior edge of the bending of loop branches are small, anteriorly projecting spines (Fig. 12).

Discussion: The new species differs from the species *Rh. gregaria* in the size of shells, in having a more distinct and narrower sinus, in the outline of shells, development of the pedicle collar and position of the foramen, the shape of cardinalia and a different course of the loop. W. Goetel (1917) also noticed these differences: he even pointed to "numerous transitions to *Terebratula pyriformis*". Beside the similar shape of outline of some individuals, however, there is a great difference between the described species and *Rh. pyriformis* and many similarities originated due to the wide variability of the species *Rh. pyriformis* at the locality of Hybe (shape of the anterior margin, width of the hinge line, etc.).

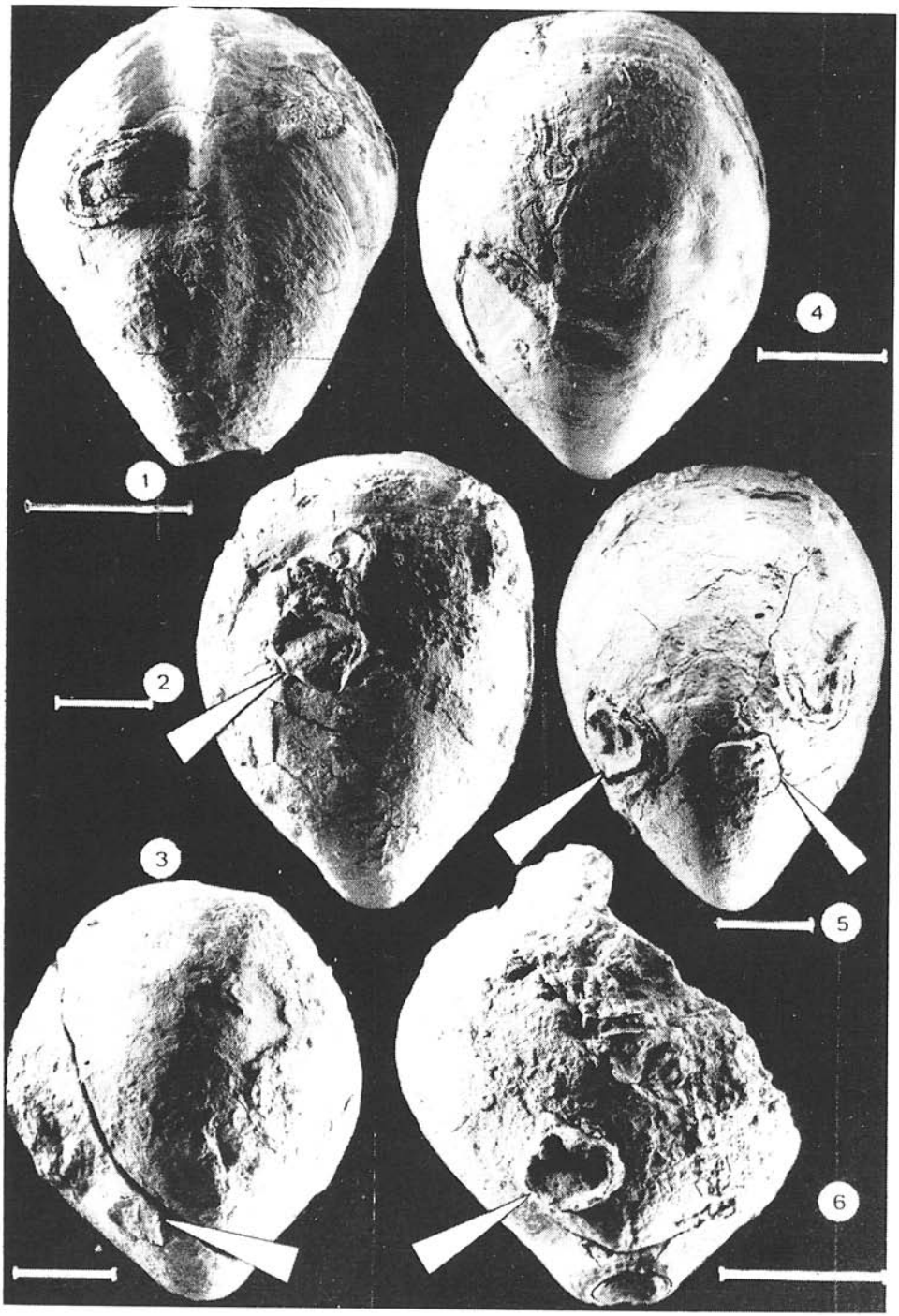
3. *Rhaetina pyriformis* (Suess) 1854
(Fig. 13-18, Pl. XXXXX)

The holotype of the species came from the Eastern Alps, the place of its deposition, however, is not known at present.

Terebratula pyriformis Suess 1854, p. 41, t. III, f. 6-8
Terebratula horia Suess 1854, p. 42, t. III, f. 9
Terebratula pyriformis Ooster 1863, p. 6, t. I, f. 7-8
Zugmayer 1882, p. 11, t. I, f. 12-21
Bittner 1890, p. 278, t. XXVI, f. 1
Goetel 1917, p. 117, t. III, f. 9
Rhaetina skirdaensis Moisseiev 1947, p. 79, t. IX, f. 3
Rhaetina pyriformis Dagys 1963, p. 145, t. XXII, f. 1-5.

Plate III.

Fig. 1. Ventral valve of *Rh. hybensis* sp. n. with attached worm tubules aud a bryozoan zoarium. Locality "Kantorská pit", Hybe, individual no. 33. — Fig. Ventral valve of *Rh. pyriformis* (Suess) with cemented shells of *Thecospira haidingeri* Suess. Locality "Viper pit", Hybe, individual no. 2. — Fig. Ventral valve of *Rh. pyriformis* with a cemented valve of *T. haidingeri* and worm tubules from the locality "Viper pit", Hybe. — Fig. 4. Ventral valve of *Rh. pyriformis* with cement worm tubules and zoaria of bryozoan. Locality "Viper pit", Hybe. — Fig. 5. Ventral valve of *Rh. pyriformis* with cemented worm tubules and valves of *T. haidingeri*. Locality "Kantorská pit", Hybe. — Fig. 6. Dorsal view of a shell of *Rh. hybensis* sp. n. with a cemented valve of *T. haidingeri*. Locality "Viper pit", Hybe.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Material: 1232 individuals from the locality of Hybe. 18 individuals from localities of the Krížna nappe.

Diagnosis: Large biconvex shell with elliptical outline and a flattened anterior margin. The sinus is flat, plicate or indistinctly sulciplicate, sometimes absent. The dorsal valve is often flattened in the median region.

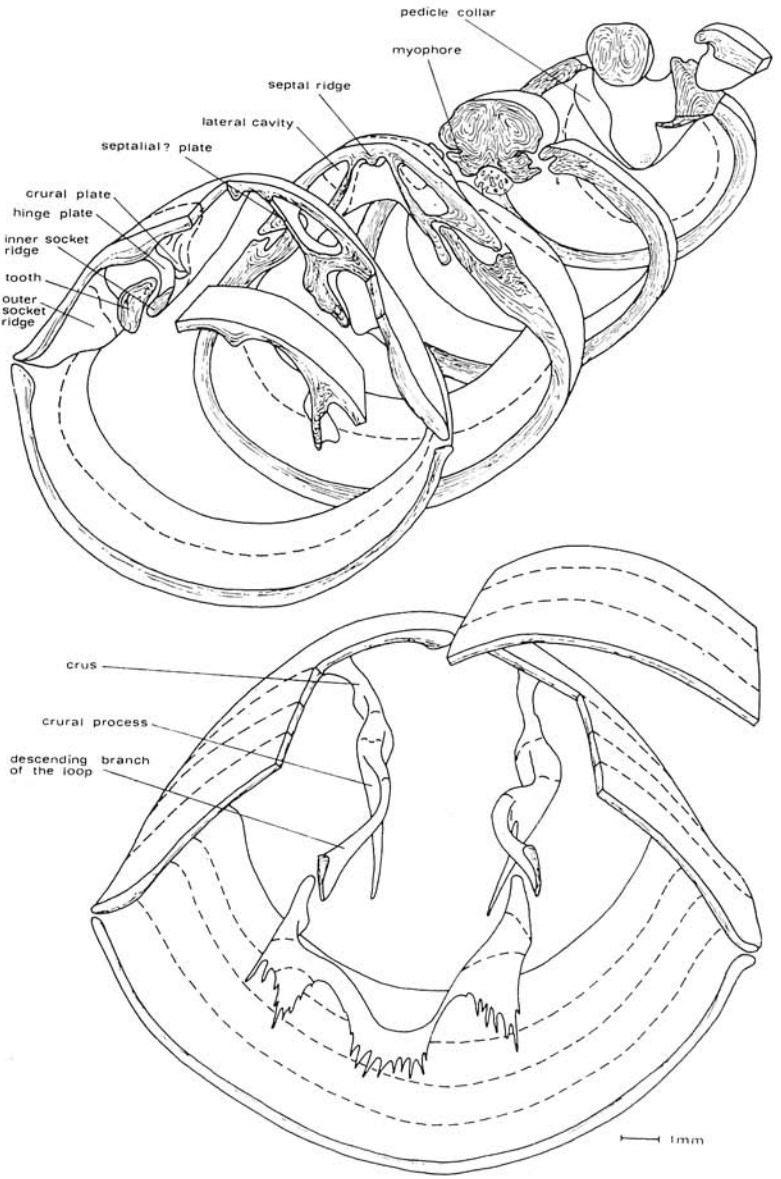


Fig. 11. Spatial representation of serial sections of the shell of *Rh. hybensis* sp. n. from the locality of Hybe. Original.

Description: Large biconvex shell (length 30—40—50 mm, width 35—40 mm) with a subpentagonal, more often, however, almost oval elliptical outline, with a rounded trapezium-shaped or circular, moderately flattened anterior margin. The maximum width of shells is in the middle or shifted slightly anteriorly. The surface of the shells is smooth, the growth-lines indistinct: only in the gerontic stage more conspicuous. Remarkable is often their equal distance and correlability of their distances from the beak of the valve of various individuals from the locality of Hybe: the cause of the origin of intervals in the growth of shell must obviously have been common for all individuals. There could have been inner causes (achieving of ontogenetic development stages, breeding seasons . . .), or of external character (alternation of cyclic annual seasons?) or a combination of both factors: a similar regularity may be observed also on the shells of other larger smooth brachiopods from the Hybe locality (*Rhaetina hybensis, Zeilleria norica, Oxycolpella oxycolpos* . . ., Fig. 13).

The low plica is distinct only near the anterior margin of the dorsal valves of ephebic and gerontic individuals. More rarely it is divided by a shallow median sulcus. The plica never exceeds the anterior third of the dorsal valve, is usually shorter. The anterior part of the ventral valves of individuals with a sulciplicate sinus has two short, shallow furrows.

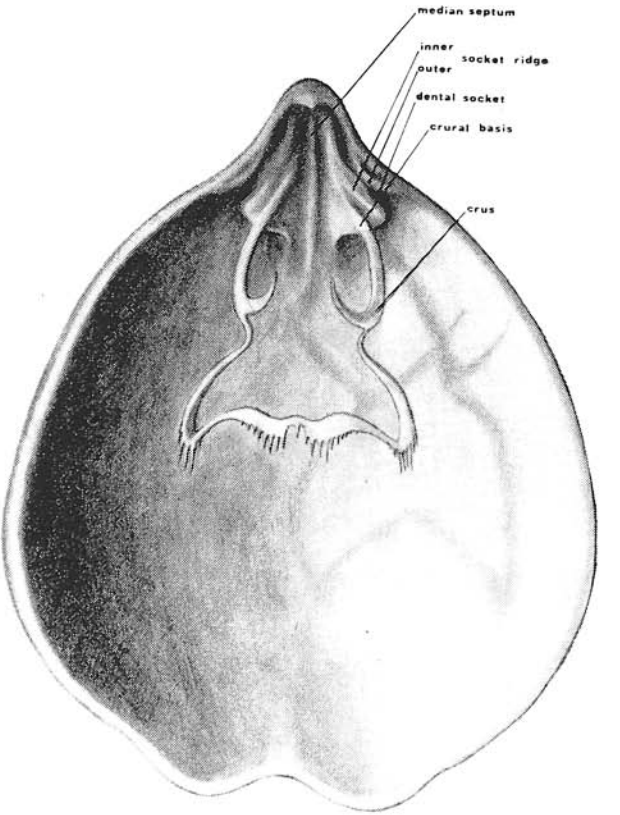


Fig. 12. Reconstruction of the cardinalia and brachial apparatus of *Rh. hybensis* sp. n. from the locality of Hybe according to serial sections. Original.

The ventral valve is a little more convex than the moderately flattened dorsal valve. The comissure can be in the posterior part slightly ventrally bent, from about the half length of the plicate or slightly sulciplicate sinus, which is situated highly dorsaly above the hinge margin plane. Even those adult shells, which are apparently without sinus, have the anterior part of the comissure highly dorsally convex (Fig. 15, 16).

The ventral valve is most convex nearly at the beginning of the posterior third of length. The delthyrium is not large, the deltidial plates are concavely arched, overhanging the umbo of the dorsal valve. The beak-ridges are rounded, the cardinal area is indistinct. The beak is thick, rounded, short, gently curved, the apical angle is variable: 70—90°. The foramen is large, circular, permesothyrid to epithyrid, rimmed by a pedicle collar from the inner side, particularly distinct on the dorsal side of the margin. The relatively long teeth are supported by strong teeth bases only.

The dorsal valve is less convex than the ventral one, its transversal deflection is larger than the longitudinal deflection. The narrow septalial plates are fixed to the valve bottom at a relatively great distance from each other. The lateral umbonal cavities are narrow, slot-shaped. The hinge plates coalesce with inner socket-ridges.

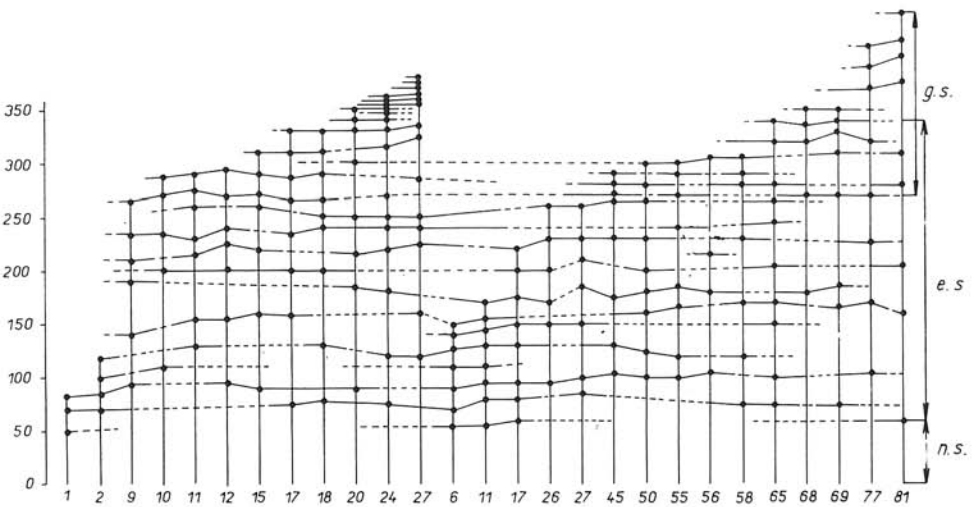


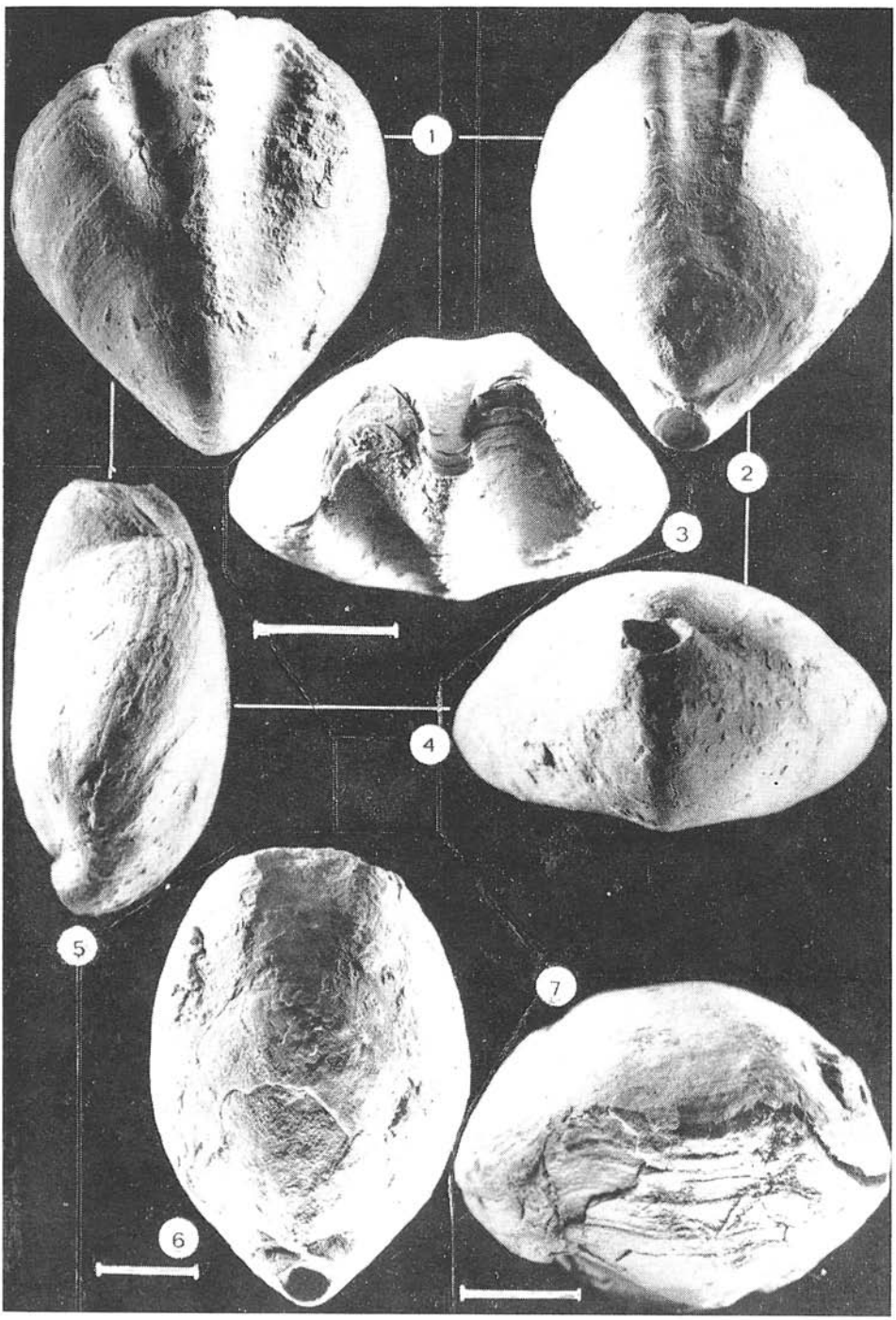
Fig. 13. Correlation of growth intervals on shells of *Rh. pyriformis* (S u e s s) from beds. No. XXXV and XXXII at the locality of Hybe according to the width of shell, indicated on the vertical coordinate in tenths of mm. The numbers on the horizontal coordinate are inventory numbers of individuals. Abbreviations: n. s. neanic stage, e. s. ephebic stage, g. s. gerontic stage.

Plate IV.

Fig. 1—5. Ventral, dorsal, anterior, posterior and lateral view of the holotype of *Rhaetina hybensis* sp. n. (individual no. 48, "Kantorská pit", Hybe). — Fig. 6—7. Dorsal and anterior view of an individual of *Rhaetina pyriformis* (S u e s s) from the locality "Kantorská pit", Hybe.

The photographs of the individuals were taken in biological orientation.

All the photographs by C. Chladová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with crural bases and septalial plates. The adductor muscle scars on the dorsal valve are drop-shaped in outline, long (about one third of valve length) and relatively distinct.

The crura are strongly curved ventrally, massive. The brachial apparatus is relatively small, the loop is short and wide: the short branches gently converge towards a markedly bent transverse band (Fig. 19).

Discussion: The species *Rh. caucasica*, similar in size of the shell differs from the described species in the presence of a groove in the posterior part of the dorsal valve. *Rh. elliptica* with relativelly large elliptical shells with a plicate sinus has a wider umbonal part of the comissure. The forms which seem to be „transitional" to the species *Rh. gregaria* cannot be separated objectively from the range of variability of the species, which is very wide in this species: varying the shape of the sinus (plicate to sulciplicate), the shape of outline (pentagonal-oval to almost circular), the size of shell of adult individuals and other features.

Distribution: The oldest finds are described from the Upper Carnian of the Northwestern Caucasus, in the Norian and Rhaetian the species is widely spread in the Caucasus, Crimea, Carpathians and Alps.

In the West Carpathians the species is sporadically found in the Fatra Beds ("Carpathian facies" of the Rhaetian) of the Krížna nappe associated with Rhaetina gregaria together with the rare *Austrirhynchia cornigera* (Rusnáci near Valaská Belá in the

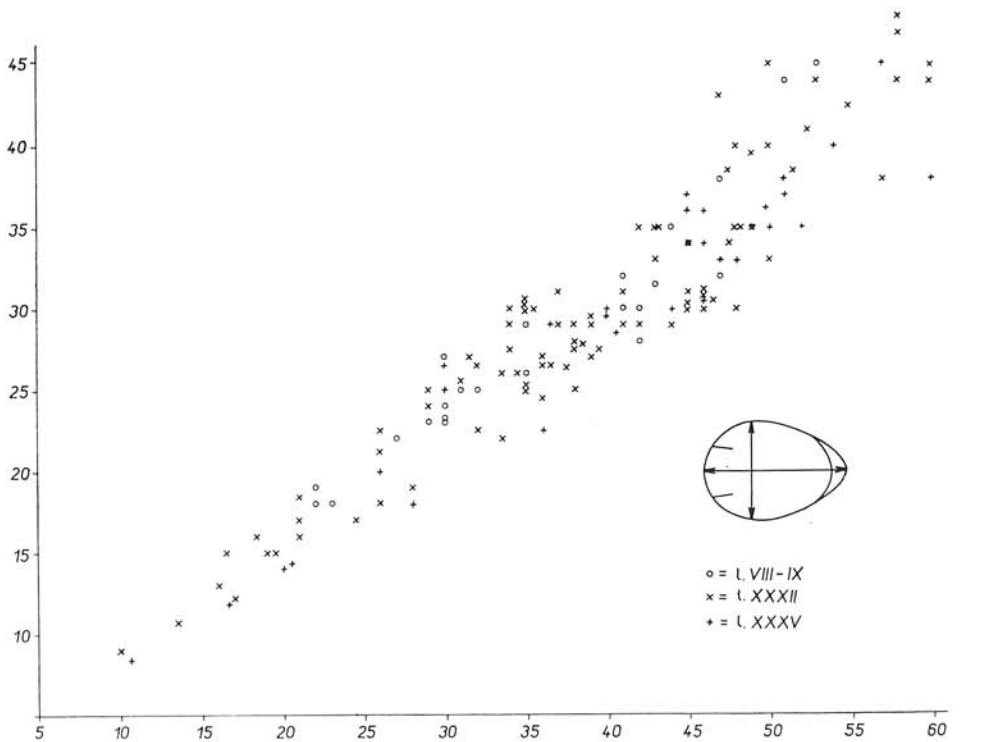

Fig. 14. Graph of width — length ratio of shells of individuals of *Rh. pyriformis* from three intercalations of marls at the locality of Hybe.

Strážovská hornatina Mts., Bystrô in the Veľká Fatra Mts., at the northern slopes of the High Tatras . . .). These individuals are characterized by small dimensions (length 25—35 mm) and a simple, plicate sinus. On the contrary, in the Hybe Beds (so called "Kössen facies" of the Rhaetian near the community of Hybe) of the Choč nappe the individuals of this species are very abundant: their shells are large, with an uniplicate and sulciplicate sinus (Fig. 20).

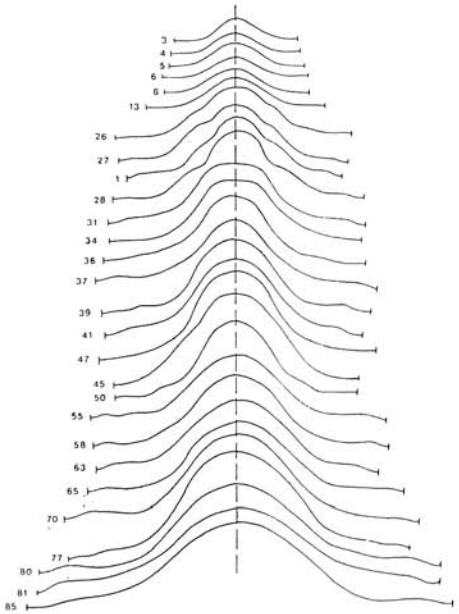

Fig. 15. Unfolded commisures of the species *Rhaetina pyriformis* from bed XXXII at the locality of Hybe. The individuals have a typical plicate sinus.

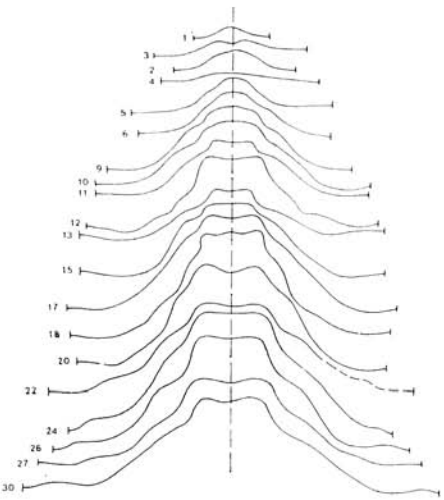

Fig. 16. Unfolded commissures of *Rh. pyriformis* from bed XXXV at the locality of Hybe with an abundant occurrence of *Rh. hybensis*. A trend towards development of a sulciplicate sinus.

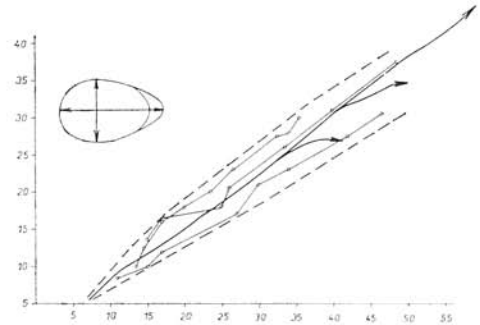

Fig. 18. Ontogenetic development of length — width ratio of shells of *Rh. pyriformis* from bed XXXV at the locality of Hybe. Generalized.

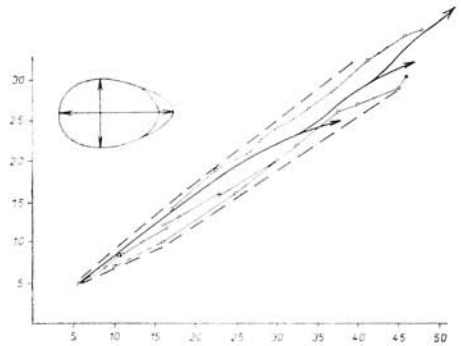

Fig. 17. Ontogenetic development of length — width ratio of shells of *Rh. pyriformis* from bed XXXII at the locality of Hybe. Generalized.

II. Ecology

1. Remarks to the paleobiogeography of the region

The region of the West Carpathians was much diversified to the end of the Upper Triassic. Alhough our knowledge of the conditions in the Flysch Belt and Klippen Belt is only fragmentary, it should be supposed that they formed together a region with predominating continental sedimentation. Terrigenous sedimentation was predo-

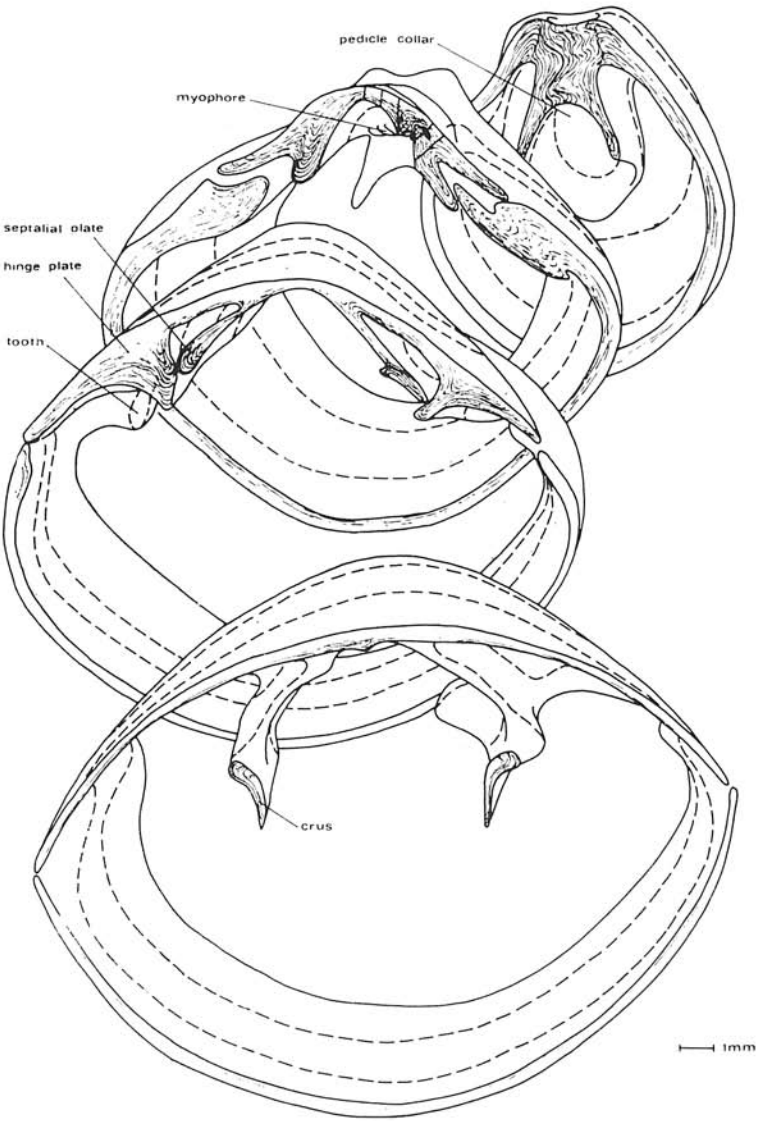

Fig. 19. Spatial representation of serial sections of the shell of *Rh. pyriformis* (S u e s s) from the locality of Hybe. Original.

minantly also in the larger part of the area of the Tatrides and Krížna unit — a terrestrial, bolson-like area with deposition of the Carpathian Keuper. The influences of this extensive arid zone were manifested also in the shallow-water near-shore zone of the more southern zone, the Choč unit, with a sedimentation of shallow-water (to supratidal) dolomites. Only in the southernmost, Gemeride area a typical marine sedimentation dominated (Fig. 21).

The Rhaetian transgression, distinctly manifested in the zone of the Krížna unit, caused extensive changes in paleogeographical conditions of the region. According to up to present knowledge we may conclude that it proceeded gradually, with a strong influence of the relief configuration, in the shape of shallow basins and ridge-like elevations already formed during sedimentation of the Carpathian Keuper. From the beginning so conditions were created for a rich dissection of facies and development of faunistic assemblages in this region. The flat, elevated, not flooded areas, according to the depth of water horizon, were flat plains, on which dolomitic crusts formed, or near-shore marshes. (In inland, higher lying areas sedimentation of bolson type could have continued.)

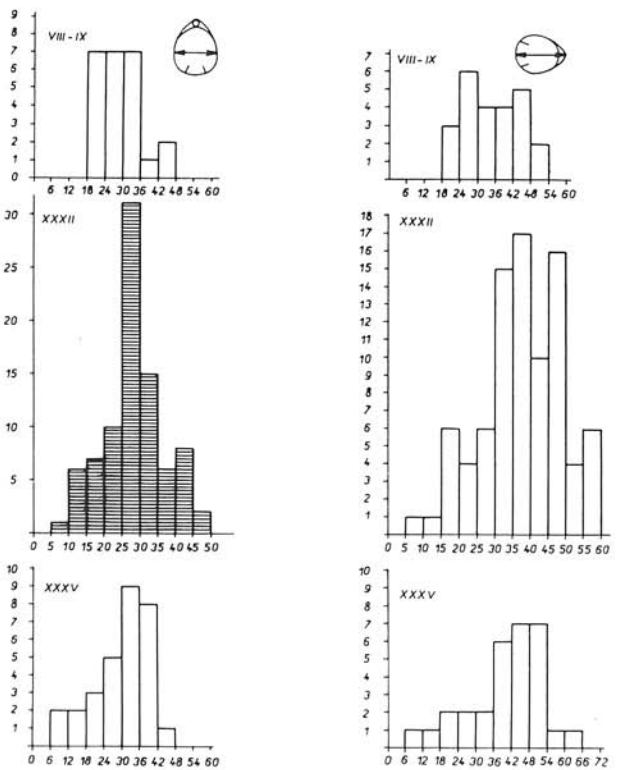

Fig. 20. Variation graphs of width and length of the shell of *Rh. pyriformis*. It is obvious that the first case represents an allochtonous accumulation of shells, the other two ones show a distinct distribution of autochtonous populations. Locality of Hybe (the Roman figures indicate the bed numbers).

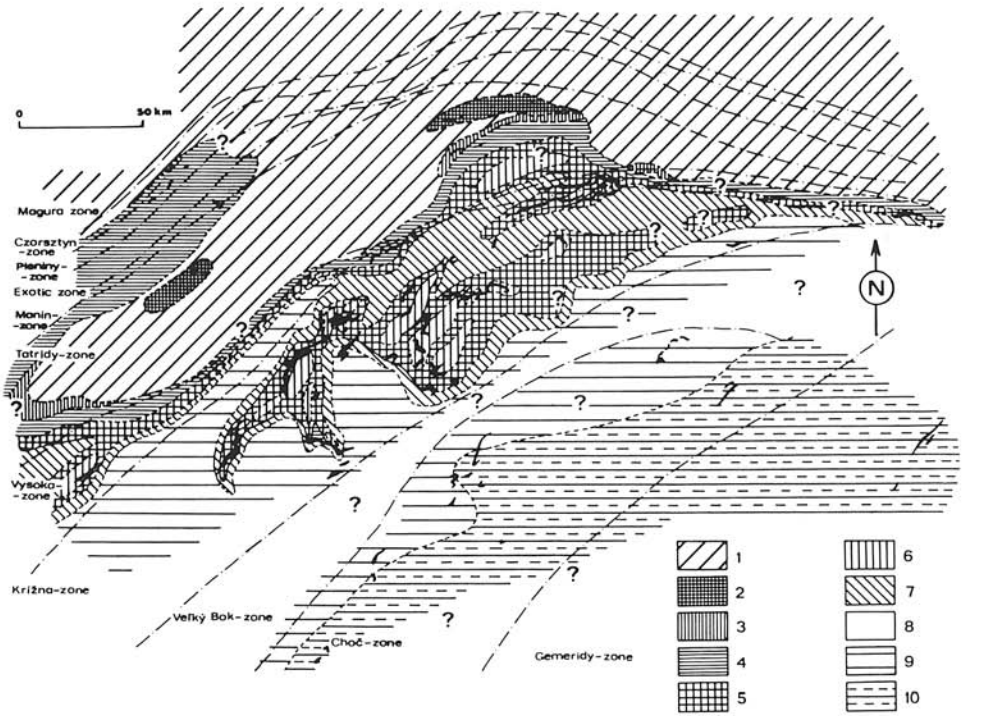

Fig. 21. Scheme of the paleogeographical situation of the West Carpathians of the uppermost Triassic. The black spots are nowadays preserved occurrences of „Rhaetian" rocks in various tectonic units. 1. Emerged areas, 2. Terrigenous (limnic?) facies, 3. Facies of the brackish zone, 4. Near-shore (littoral) facies, 5. Facies of biostromatic plains formed by coral, sponge and algal covers, 6. Lagoonar facies in biostromes, 7. Detrital facies of biostrome slopes, 8. Area without data on the type of sediments, 9. Basin facies, 10. Shallow-water facies with influences of open sea. Original.

The areas bordered upon extensive plains with unstable water regimen (thin bed of water driven by wind), where a detritus of sea animals was ejected by waves. In permanently inundated small depressions assemblages of lamellibranchs, gastropods and calcareous sponges were living. At the margin of the plain assemblages of corals, hydrozoans and calcareous sponges developed in the form of unequable biostromatic covers. Only a few of the isolated small platy and lenticular bodies could have preserved until present: the waving energy brought about breaking and washing away of their material on the adjacent slope inclined towards a deeper basin. At the deeper outer margin of the coral zone and on more protected surfaces inside of it a brachiopod assemblage of *Rh. gregaria* was living. The relatively high energy of the environment caused scattering of the valves of perished individuals over a much wider area than they originally lived in. At the detrital slope inclined towards the bottom of the basin with muddy sedimentation crinoids were living in discontinuous zones, in places where superficial waving did not reach and where they were supplied with nutrition by currents descending from the water level (also the depth of these bottom parts, however, could not have been more than a few tens of meters). The relatively great

mobility of the bottom did not permit here attachment of such animals as brachiopods. Finally, the muddy bottom of deeper depressions was obviously not suitable for the life of larger benthonic animals.

The data on living conditions in the region of the Choč unit are fragmentary only. Also here shallow areas existed, alternating with areas of depressions. As the study of the Hybe profile testifies, conditions for the life of the benthos were changing with time. In the area of this locality an extremely shallow-water area may be supposed, however, which was exposed to influences of the open sea more than the region of the Krížna unit (occurrences of nautiloid cephalopoda).

The occurrence of Uppermost Triassic deposits at the Goštanová near Tisovec in the Gemeride Triassic rather resembles shallow-water deposits with a fauna similar to that from Hybe, washed down in to deeper parts.

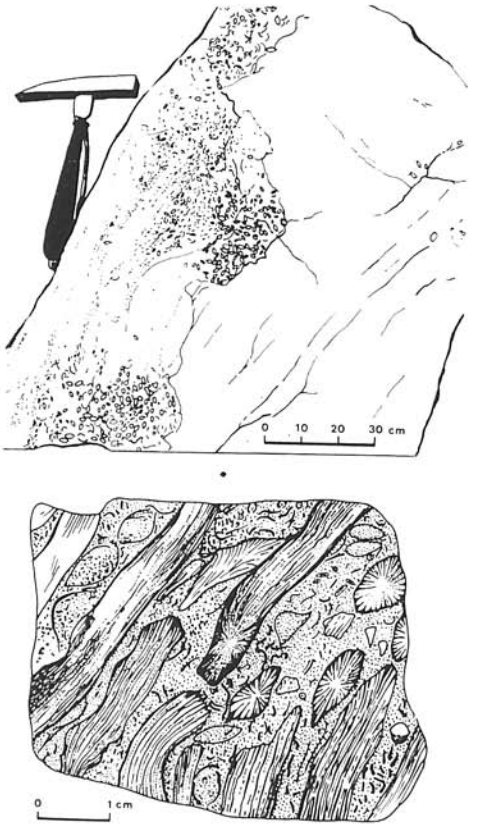

Fig. 22. Types of the primary occurrence of shells of *Rh. gregaria:* in nest-like clusters in sea-floor depression (loc. 119 Hireška in the Strážovská hornatina Mts., bed 7) and in interstices of coral bunches (locality 108 in the valley of Potok near Istebné in the Malá Fatra Mts.).

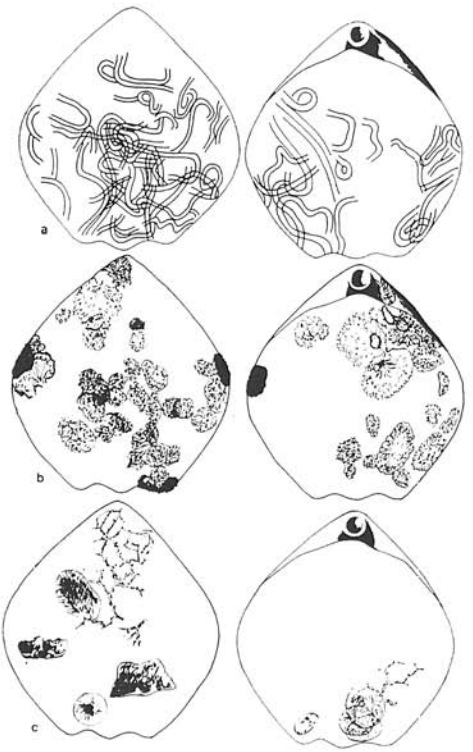

Fig. 23. Comparison of places of the growth of commensalic organisms on shells of *Rhaetina hybensis* sp. n. from the locality of Hybe. a = worms, b = bryozoans, c = brachiopods *(Thecospira haidingeriana),* lamellibranchs (mainly *Atreta intusstriata* and bryozoans. Original.

2. *Ecological characteristics of Rhaetina gregaria* (Suess)

Small to medium-sized shells of the basic ecological subtype, attached to the substratum for the whole time of life by a distinctly developed pedicle. This species therefore needed an environment with a hard substratum or at least with objects providing the possibility of a stable and fixed attachment. The environment of formation of the Fatra Beds with a mobile detrital bottom provided such a possibility only in the near vicinity of the coral zone and on the bottom of more protected lagoons in the zone of biostromes. These areas, where possible, were densely populated by a monotypic assemblage of *Rhaetina gregaria*. The density of population required an economically operating current system of feeding the organism: this requirement was fulfilled by separating the inhalant and exhalant opening and development of a distinct sinus. At individuals from dense populations of *Rh. gregaria* there are usually non commensalic organisms: the organic suspension was completely utilized. Commensalic organisms on shells of *Rh. gregaria* are found on individuals from lagoonar areas (Bystrô), where the population was thinner, its composition more variegated and the substratum provided less possibilities for attachment (Fig. 22).

On shells of the individuals of the described species sometimes traces of damaging or irregular growth may be observed, evoked by being packed in dense groups of shells, which often hindered one another from gaining nutrition also under normal conditions.

Rhaetina hybensis n. sp.

The shells, although differing from individuals of the foregoing species in size, in having a strongly developed foramen and pedicle collar, prove that they also were firmly attached to the substratum for the whole life: in the oldest stage they were obviously leaning on the umbonal region as testified by the absence of commensalic organisms in this part of the valves. The individuals of this species were living on a relatively soft but stabilized bottom with many possibilities of attachment to solid objects, which, however, were gradually covered by sediment. Such a possibility of attachment was suitable for brachiopods with a long, strong pedicle, however, but not for animals directly cemented to the hard substratum. Such animals often grew on the valves of the species *Rh. hybensis,* always sufficiently high above the sediment. Frequent oriented growing (bryozoans, worms . . .), concentrated to the proximity of inhalant openings in the anterolateral parts of the comissure and to the proximity of the exhalant opening in the medial part of the sinus, indicates currents, evoked by activity of the lophophore of the brachiopod (Fig. 23).

Rhaetina pyriformis (Suess)

The similar mode of life of this species to that of *Rh. hybensis* resulted in an approached external shape of their shells. Interesting is, that the forms, the shells of which resemble most the shape of *Rh. hybensis* (mainly a sulciplicate sinus), are found in the bed with the abundant occurrence of the species (Fig. 15, 16). The larger and heavier shells of the species *Rh. pyriformis* required more often leaning on the umbonal part of the ventral valve. Some older shells could have been plunged also more into the sediment: they acquired then a broad shape with a low, angular sinus and a smooth

surface without the growth of commensalic organisms. The primary attachment by the pedicle, however, remained undisturbed.

III. Conclusions

1. A material was examined, including representatives of the genus Rhaetina Waagen, 1882, coming from various localities of the uppermost Triassic in the West Carpathians.

2. Beside the species *Rh. gregaria* (Suess) and *Rh. pyriformis* (Suess) a new species of the genus, *Rh. hybensis* sp. n., was described, found at the locality of Hybe. In the descriptions of the species the morphology, internal structure, impressions of soft parts, similarities and differences from other brachiopods, inner-species variability and the sites and horizons of occurrence are discussed in detail. The description sets out from the results of observation of shell wall structures based on serial sections and from observation of variability according to the statistic evaluation of their dimensions. More in detail was examined the material from 1 locality in the Klippen Belt, 16 localities in the Krížna unit, 2 localities in the Choč unit and 1 locality in the Gemerides.

3. The chapter on ecology of the described species sets out from information, following from the study morphology, ontogeny, preservation of shells, the occurrence in various types of sediments and growth of commensalic organisms on shells and traces after damaging and healing of valves. The information obtained with application of these data is used in compiling the picture of paleobiogeography of the region of the West Carpathians in the uppermost Triassic. The description of the paleobiogeography is completed by a sketch map of the paleogeography of this region.

Translated by J. PEVNÝ

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Review by M. SIBLÍK