MORPHOGENESIS OF THE Simbirskites GROUP

V.V. Drushchits, I.A. Mikhaylova, G.K. Kabanov, and M.V. Knorina
Moscow University

ABSTRACT: Studies have been made of the protoconch and the internal structure of the phragmocone in three Simbirskites genera (Simbirskites, Speetoniceras, Craspedodiscus) and changes occurring in the form of the transverse section, the ornament, the suture, the siphuncle, and the septal necks in the course of ontogeny have been traced in each genus. The points of similarity and difference between these genera are established.

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A thorough study was undertaken of the shells of ammonites of three genera - Simbirskites, Speetoniceras, and Craspedodiscus, belonging to the Simbirskites group, which some authors regard as a family, others as a subfamily. Material for the stusy was provided by a large collection of ammonites made by K. A. and G. K. Kabanov from Hauterivian clays on the right bank of the Volga around Ul'yanovsk.

Some of the shells were uncoiled down to the initial chamber so as to study the protoconch and to trace changes in the cross sectional shape, the ornament and the suture in the course of ontogeny. Longitudinal and, in part, transverse ground sections were prepared for most shells and used to examine the structure and shape of the protoconch, the size of the fixator (of the prosiphon) and the shape and size of the caecum. We also studied the position and measured the absolute and relative dimensions of the siphuncle and its accompanying elements, the structure of the septal necks, variations in the number of septa and the distances between them in each whorl (constructing the relevant curves), and ontogenetic variation in the thickness of the shell wall and the internal height of the whorl. We studied the structure of the nepionic ridge and the nepionic constriction, and measured the angle of the nepionic constriction from a straight line joining the center of the protoconch to the proseptum to a straight line from the center to the middle of the nepionic constriction. This angle was 300° in most specimens, 315° in some. We measured the diameter of the shell of the ammonitella (through the nepionic constriction) and the diameter of the first and subsequent whorls (W_1, W_2, W_3, etc.).

The following abbreviations are used in the description and the figures: H - internal height of whorl, ips - inner prismatic layer, dw - dorsal wall, bc - body chamber, Ch - size of chamber measured from septum to septum along the siphuncle, Cu - cuff, Me - membrane, ops - outer prismatic layer, W_1, W_2, . . . - whorls, nr - nepionic ridge, ll - laminar layer, nc - nepionic constriction, S_1, S_2 . . . - septa, Siph - siphuncle, sn - septal neck, F - fixator (prosiphon), Cae - caecum.

The history of study of the Simbirskites group has been dealt with in detail by Chernova (1952) and Rawson (1971). The internal structure has not previously been studied in detail and is here set out for the first time. Wedekind (1910) described the morphogenesis of the suture for Simbirskites, and it was later examined for Speetoniceras inversum and Craspedodiscus progrediens by Schindewolf (1966).

Prior to re-examination of the boundary between the Hauterivian and Barremian (Drushchits, 1962), the Simbirskites group was assigned to late Hauterivian - early Barremian times; after the Lyon colloquium (Colloque, 1965) had decided to draw the boundary between the Hauterivian and the Barremian along the top of the Pseudothurmannia angulicostata zone, the range of the family described was restricted to the late Hauterivian, although the Speetoniceras versicolor zone continued to be assigned to the top of the lower Hauterivian in some works published at this time and later.

Species of the Simbirskites group developed mainly in the boreal region: in the north of Siberia, in the European regions of the USSR, and in many northwest European countries (Poland, the Federal Republic of Germany and Britain). Outside these regions they are encountered infrequently in the Hauterivian of the Crimea, the North Caucasus, the northeast of the USSR, Spitsbergen, Canada, California and Oregon (USA).

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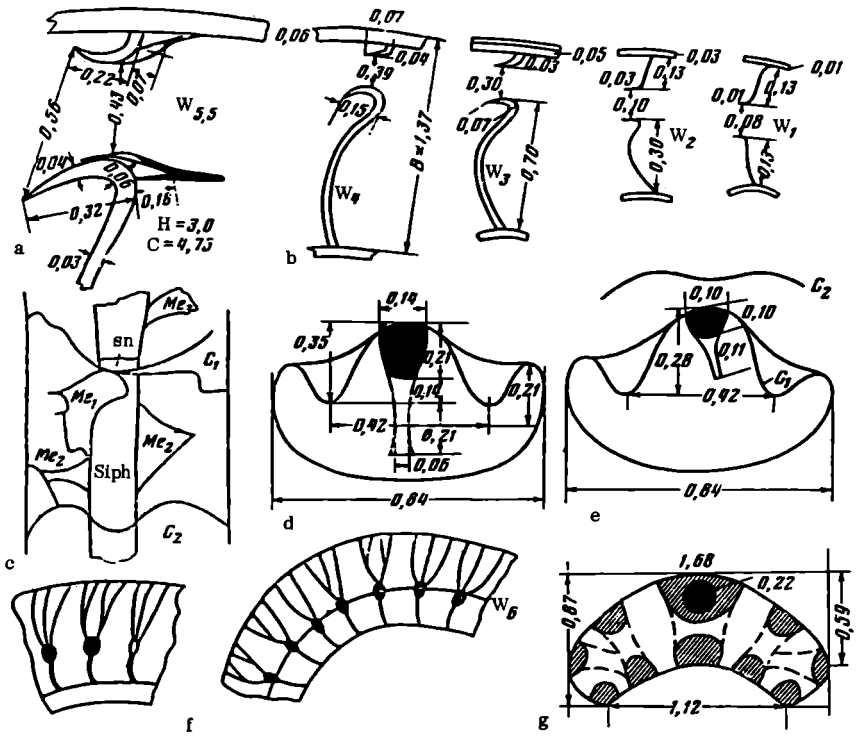


FIGURE 1. Internal structure of the shell and the nature of the ornament in members of the genus Simbirskites; a, b - Simbirskites sp.: a) spec. 17, septal neck, 6th whorl; b) spec. 522, ontogenetic changes in the size of the septal necks and the position of the siphuncle; c, d) S. elatus (Trautschold); spec. 15: c) two pairs of membranes accompanying the siphuncle; d) protoconch, prosuture, caecum and fixator; e-g) S. coronatiformis Pavlow; e) spec. 14, protoconch, prosuture, caecum and fixator; e) spec. 13 (left) and spec. 17 (right), ornament on 6th whorl; g) spec. 14, interrelationship of lobes at 2.75 whorls. Explanations in text.

Most of the specimens described in this paper come from upper Hauterivian clays exposed on the right bank of the Volga north of Ul'yanovsk. The clays contain ankerite-calcite and ankerite-calcite-siderite nodules with a cross section of from 0.2 to 1.5 m. The nodules are dispersed throughout the clays in the lower half of the section (25 m on average), but there is a horizon of large septaria with cross sections of up to 1.5 m in its upper part (about 15 m). The nodules in the lower part of the section contain Speetoniceras versicolor, S. inversum and Simbirskites coronatiformis shells, belemnite rostra, and shells of bivalves, gastropods and brachiopods. The biofossils in the nodules in the upper part, which are more numerous and varied, include Craspedodiscus discofalcatus, C. progrediens, C. speetonensis, Simbirskites decheni and S. umbonatus; in addition to the ammonites there are belemnite rostra, shells of bivalves and gastropods, the tubes of polychaetes, and bone fragments of aquatic reptiles.

A systematic description of the structural features of Simbirskites, Speetoniceras and Craspedodiscus shells is given below and the ontogenetic changes in the various shell characters are considered. All measurements are in millimeters. Membranes attaching the siphuncle to the septum and to the ventral wall of the shell have been found in the genus Simbirskites. V.V. Drushchits was responsible for observations on the membranes and on septal microstructure with the scanning electron microscope (JSM-2), and the photographs were taken by R.A. Konysheva, whom the authors would like to thank.

Simbirskites Pavlow, 1892

Material. Ground sections in the median plane of S. coronatiformis (four spec.), S. elatus (one spec.) and Simbirskites sp. (seven spec.); of these S. elatus (one spec.) and S. coronatiformis (two spec.) were uncoiled down to the protoconch.

Protoconch ridge-like, practically round in section: D^1 = 0.55 to 0.60, D^2 = 0.50 to 0.55, D^1 to D^2 = 0.02 to 0.12 (12 measurements), of which the measurements for one specimen (No. 553) are D^1 = 0.67, D^2 = 0.55, $D^1 - D^2$ = 0.12, while for the other specimens the difference is 0.02 to 0.10. Width of protoconch 0.84 to 0.88, ratio of width to diameter 1.58 (one measurement).

Nepionic ridge lenticular, elongated, 0.17 to 0.33 long (12 measurements), 0.03 to 0.05 thick (11 measurements). In only one specimen (No. 2) is the ridge short and swollen, 0.17; in the others it is long, 0.21 to 0.33. Nepionic constriction located at a distance of 300° (11 measurements) and in one specimen (No. 522) at a distance of 315°. Nepionic constriction distinct and well expressed.

Diameter of the shell of the ammonitella 1.05 to 1.12.

Fixator observed in ten specimens: in cross section in eight, within the protoconch cleared in glycerin in two. Length of the fixator 0.15 to 0.40: it is very short, 0.15, in one specimen (No. 6), 0.21 to 0.22 in three and 0.30 to 0.40 in four. When the protoconch was examined in glycerin, the fixator appeared cone-shaped with a ribbon-like stem. In S. elatus (No. 15) the cone is short (0.14), the ribbon-like stem long (0.21) and broad (0.06); total length of the fixator 0.35 (fig. 1, d). In S. coronatiformis the fixator is short, conoid, 0.11 long, displaced to the right of the plane of symmetry (fig. 1, e).

Caecum oval, almost round in some specimens, drop-like (fig. 1, d, e). $Cae_1 > Cae_2$; Cae_1 = 0.13 to 0.21, Cae_2 = 0.10 to 0.14, $Cae_1 - Cae_2$ = 0.01 - 0.07 (eight measurements); the section seen in the proseptum is oval; the major axis located across the width of the whorl is 0.14, the minor axis 0.08.

Siphuncle central in first whorl, located approximately equidistant from the ventral and dorsal surfaces, subcentral at the beginning of the second whorl, approaching the ventral wall from the middle of the second whorl and becoming ventromarginal. In two specimens (2 and 731) the siphuncle is subcentral in the first and second whorls, the ratio of the distance from the dorsal and ventral walls being 12:5 and the diameter of the siphuncle 4 (scale division 0.014). At the end of the second whorl the siphuncle becomes ventromarginal. In the same specimens the siphuncle is outside the plane of symmetry in the first whorls.

The diameter of the siphuncle varies as follows: S_1 = 0.08 to 0;10, $S_{1.5}$ = 0.10 to 0.15, S_2 = 0.13 to 0.18, $S_{2.5}$ = 0.15 to 0.24, S_3 = 0.20 to 0.30, $S_{3.5}$ = 0.38 to 0.40, S_4 = 0.40 to 0.48, $S_{4.5}$ = 0.55, S_5 = 0.70. The ratio of the diameter of the siphuncle to the height of the whorl measured at intervals of half a whorl is respectively 0.23 to 0.36, 0.22 to 0.40, 0.19 to 0.37, 0.30 to 0.36, 0.22 to 0.38, 0.32 to 0.39, 0.27 to 0.31, 0.26, 0.26.

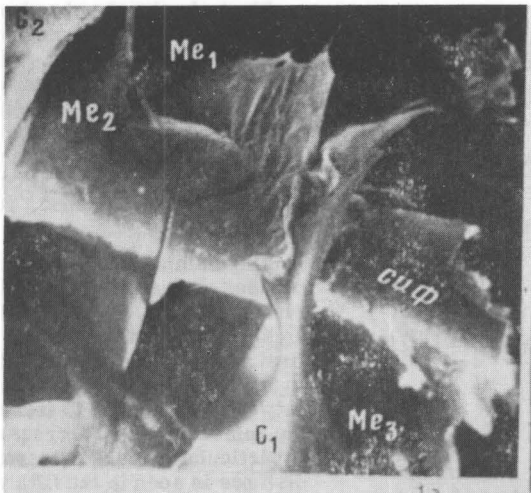
The diameter of the siphuncle in the hydrostatic chamber between the septa is usually considerably greater than the diameter of the septal necks.

In the fourth whorl S. elatus has two pairs of membranes between two septa laterally attached to the siphuncular membrane, to the ventral wall of the shell and to the septum (fig. 1, c). The anterior pair of membranes is relatively short, originating at the anterior margin of the ventral lobe around the median saddle and taking in about 1/5 of the length of the siphuncle, not reaching its dorsal part in the plane of symmetry. The second pair is inserted on the ventral wall of the shell at a distance of (approximately) 0.08 mm; thereafter it is attached to both sides of the siphuncle; the two branches join up around the preceding septum in the plane of symmetry; a strand extends from them to the preceding septum. At the point of insertion on the siphuncle the membrane are slightly undulating, resembling the creases of a badly glued sheet of paper (Pl. VI, fig. 1, a, 1, e).

Septa. There are ten to 13 septa in the first whorl (ten measurements), 12 to 16 in the second (10 measurements), 13 to 18 in the third (11 measurements), 12 to 17 in the fourth (11 measurements), 12 to 14 in the fifth (eight measurements) and nine each in the sixth whorl of spec. 2 and 22, followed by the body chamber. The microstructure of the septa is laminar (Pl. VI, illus. 1f, 1g).

KEY TO PLATE VI

Simbirskites elatus (Trautschold); spec. 15, siphuncle, septa, septal neck and membranes; a-c) dorsal view of siphuncle: a - showing two septa (S_1, S_2), siphuncle (Siph) and accompanying membranes (Me_1, Me_2, Me_3) (x 100); b - showing septal neck (sn), membrane (Me_1) and septum (S_1) (x 170); c - detail from photograph b (x 300); e - membrane (Me_1) attached to siphuncle (Siph) (x 1000); f, g - structure of septum bounded by an organic layer on both sides: f (x 6000), g (x 3000) (photographs taken with a JSM-2 scanning electron microscope).



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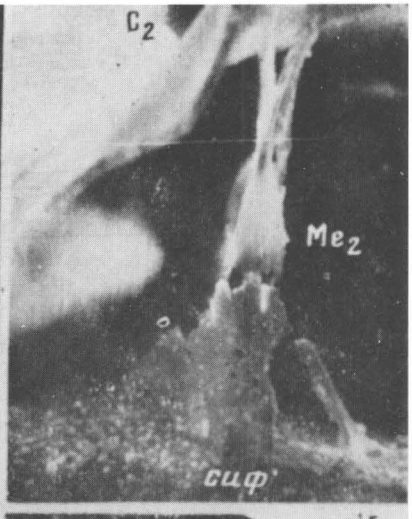

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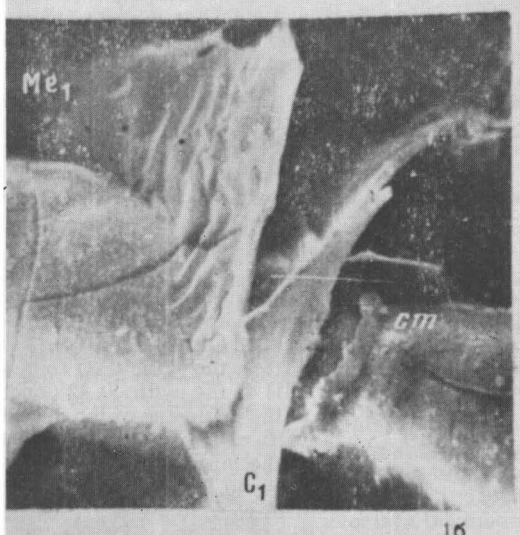

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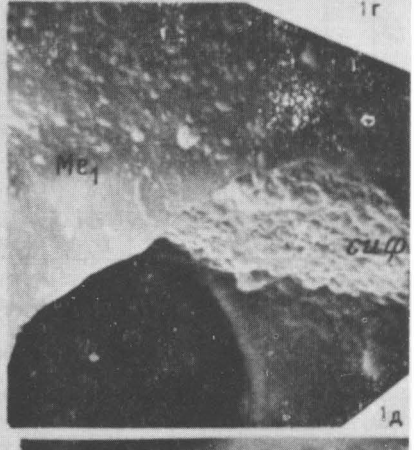

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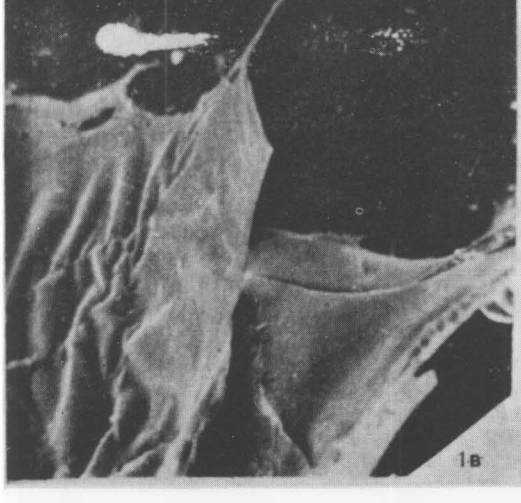

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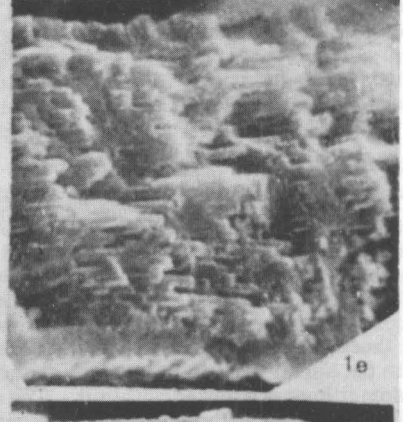

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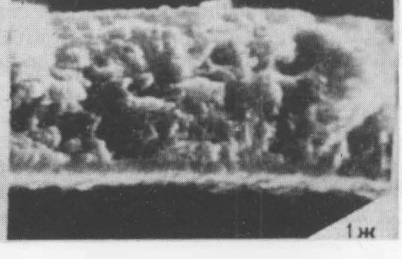

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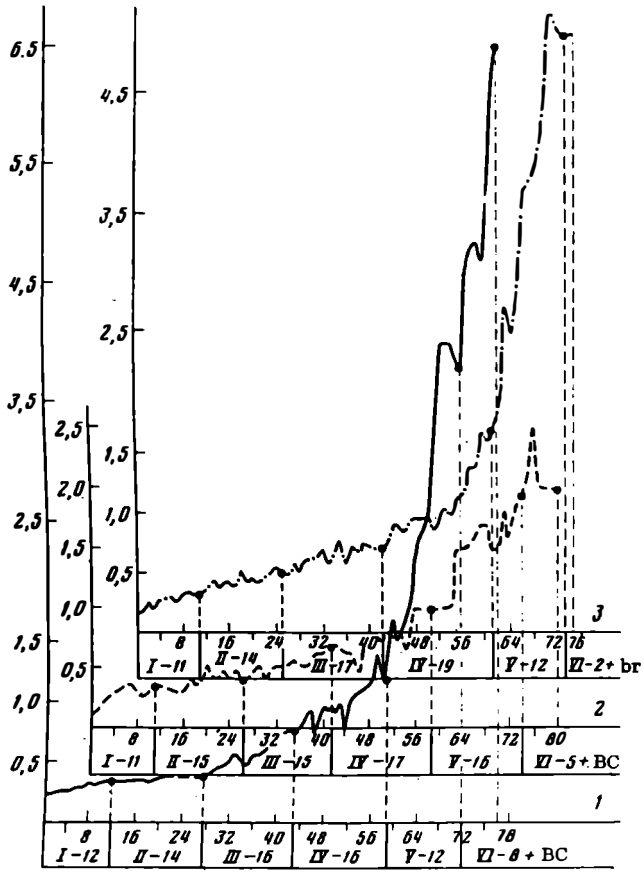

FIGURE 2. Curves of the distances between septa: 1 - Simbirskites sp. (spec. 16), 2 - Speetoniceras sp. (spec. 43), 3 - Craspedodiscus sp. (spec. 993).

BC - body chamber, br - shell broken; the figures indicate the number of septa in a whorl.

The body chamber has been partly preserved in six specimens (2, 3, 6, 16, 17 and 22). In spec. 6 it begins in the fifth whorl (half a whorl preserved), in spec. 2, 3, 16 and 17 in the sixth, in spec. 22 at the beginning of the seventh whorl (half a whorl preserved); in spec. 2 it occupies 3/4 of the whorl, in spec. 16 the entire whorl.

The distance between septa increases very slowly in the first two whorls (fig. 2; spec. 16); the ammonite constructed 12 septa in the first whorl, 14 in the second, while in the third and fourth the distance between septa began to increase and the number of septa increased to 16. A particularly marked increase in distance is seen in the fifth whorl and part of the sixth. The ammonite constructed 12 septa in the fifth whorl and eight in the sixth before dying. The body chamber lies beyond the septa.

No septal necks were found in the first whorl. Starting from the end of the first whorl they are prochoanitic and short (fig. 1). Their length is 0.05 in the second whorl (spec. 6), 0.09 at 2.5 whorls (spec. 6), 0.06 to 0.10 in the third whorl (spec. 6, 17, 49), 0.13 at 3.5 whorls (spec. 6), 0.10 to 0.15 in the fourth whorl (spec. 49), 0.23 (spec. 22) to 0.28 (spec. 49) to 0.30 (spec. 731) in the fifth, 0.21 to 0.45 (spec. 731) in the sixth, 0.42 (spec. 731) at the beginning of the seventh. The ratio of the length of the septal necks to the length of the chamber is as follows: 0.05 for W_2, 0.10 for $W_{2.5}$, 0.07 to 0.10 for W_3, 0.07 to 0.11 for W_4, 0.10 to 0.13 for W_5, 0.08 for W_6.

The length of the septal necks adjacent to the ventral wall is usually less than their length on the dorsal side of the siphuncle. The septal necks are cone-shaped, broadening toward the body chamber. In the middle of the fifth whorl their diameter is 0.25 at the beginning of the neck, 0.32 at the end; the corresponding measurements at 5.5 whorls are 0.43 and 0.56. In the first instance the length of the septal neck is 0.22 on the ventral wall, 0.28 on the opposite side of the siphuncle; the corresponding measurements at 5.5 whorls are 0.22 and 0.32 (fig. 1, a, b). Within the septal neck there are short cuffs that project slightly forward in the first four whorls, are usually located within the septal neck in the fifth to sixth whorls, forming a distinctive coating. Auxiliary deposits are sometimes preserved within it. The organic membrane of the siphuncle is connected to the cuff and calcified at the junction. The organic membrane of the siphuncle extends inward from the septal neck; its beginning is calcified. Hermetic sealing of the chamber was effected by calcification of the anterior and posterior ends of the organic membrane.

Shell wall and ornament. There is a gradual increase in the thickness of the shell wall: T_1 = 0.01 to 0.03; $T_{1.5}$ = 0.01 to 0.03, T_2 = 0.02 to 0.04, $T_{2.5}$ = 0.04 to 0.06, T_3 = 0.04 to 0.08, $T_{3.5}$ = 0.05 to 0.08, T_4 = 0.06 to 0.10, $T_{4.5}$ = 0.06 to 0.10, T_5 = 0.08 to 0.15, $T_{5.5}$ = 0.13 to 0.20. So far as can be assessed from observations under an optical microscope, the shell wall of adult ammonites was three-layered in the fourth-fifth whorls.

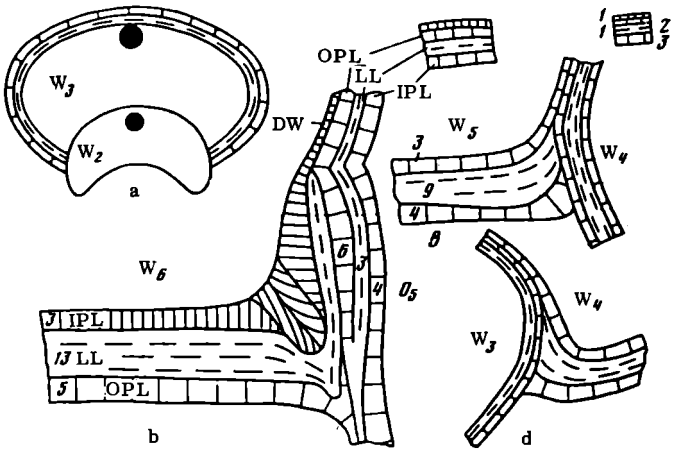

FIGURE 3. Diagram showing the interrelationship between the shell layers of the 3rd-6th whorls and the structure of the ventral wall of Simbirskites elatus (Trautschold); spec. 688. The numerals indicate the number of micrometer divisions, each division measuring 0.014 mm. Explanation in text.

Ridges formed from the nacreous layer are to be seen from the second whorl onward: one to three in the second whorl, one to four in the third, three to five in the fourth, one to two in the fifth, none in the sixth, but the whole of the shell wall is thickened from the middle of the fifth whorl.

The shell is smooth in the first four whorls, with only traces of striation. Thin small tubercles from which ribs gradually form appear in the fifth whorl or at the beginning of the sixth; they terminate as small tubercles on the lateral side and do extend on to the venter. Ventrolateral tubercles are strengthened on the sixth whorl and clusters of ribs extend from them crossing the venter without interruption and bending forward. A cluster consists either of two or three ribs, or of a pair, each of which dichotomizes (fig. 1, f). The ribs from tubercles located on opposite sides of the venter sometimes join up in a zig zag (S. coronatiformis). The ribs are broad and large; the intervals between them are also broad. The tubercles and ribs are made up of three layers of the shell material. In the formation of a new whorl the inner prismatic layer is attached to the lateral wall of the preceding whorl as a broad band, the laminar layer extends along the sides for some distance, and the inner prismatic layer is abruptly thickened at the point of attachment (W_6), and then it narrows and overlays the tubercle and the ventral wall, forming a thin dorsal wall in the new whorl (fig. 3). The tubercles and the ribs are three-layered.

Shell shape and size. The cross section is low and broad at the beginning of the spiral; its width exceeds its height in all growth stages. Around the nepionic constriction at the end of the first whorl the width is slightly less than at the beginning of the spiral (fig. 4, A).

Changes in the diameter of the protoconch and of the shell of the ammonitella and the corresponding whorls are given below.

Changes in the Diameter of the Protoconch, the Shell of the Ammonitella and the Corresponding Whorls

Spec.	D_1	D_{am}	D_1	D_2	D_3	D_4	D_5	D_6
No. 22	0.55	1.05	1.15	1.95	3.12	5.00	8.50	About 15.0
No. 2	0.56	1.09	1.12	2.00	3.30	5.75	9.70	16.7
No. 3	0.60	1.12	2.00	2.13	3.88	7.15	—	—
No. 78	0.60	1.06	1.19	2.10	3.55	6.00	10.00	—
No. 16	0.56	1.06	1.12	1.90	3.25	5.95	—	—
No. 522	0.56	1.09	1.17	2.05	3.67	7.20	—	—
No. 17	0.57	1.12	1.18	2.05	3.72	6.75	12.00	—
No. 49	0.57	1.05	1.12	1.90	3.25	5.50	10.00	—
No. 6	0.60	1.10	1.15	2.00	3.63	6.50	—	—

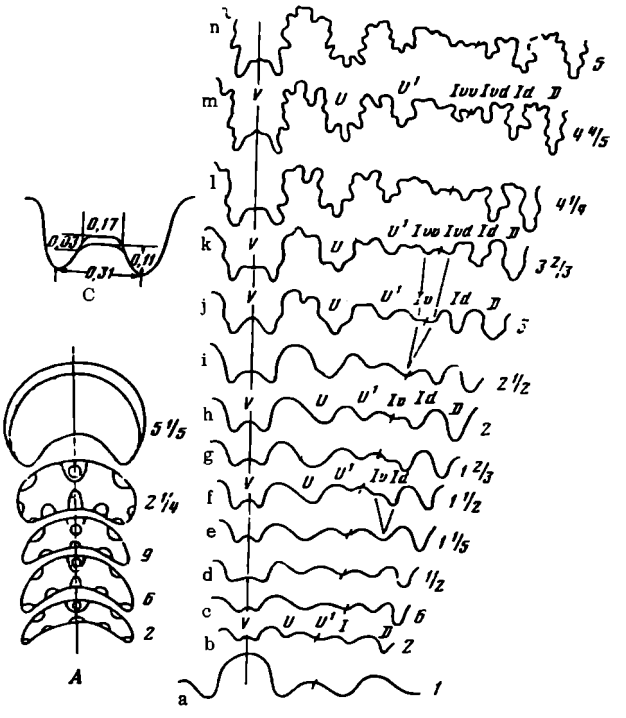

FIGURE 4. Ontogenetic changes in the cross sectional shape of the whorls and in the suture in members of the genus Simbirskites; A - S. elatus (Trautschold); spec. 15, changes in the cross sectional shape of the whorls; B, C - S. coronatiformis Pavlow; spec. 14: B - changes in the suture, C - structure of the median saddle of the ventral lobe (2.75 whorls), showing septal neck.

It is evident from the table that the diameter of the first whorl is slightly greater than 1 mm, that of the second whorl is twice that of the first; the measurements of the third to sixth whorls fluctuate widely, apparently reflecting individual, possibly sexual and specific variability.

At the beginning of the first whorl the internal height of the cross section (measured in the median plane) is on average 0.3 (range 0.28 to 0.33), at the beginning of the second whorl it is 0.38 to 0.53, but at the beginning of the third, fourth and fifth whorls the range is more appreciable (see the table of ontogenetic changes in the internal height of the whorls).

Changes in the Internal Height of the Whorls in the Course of Ontogeny

Spec.	H_1	$H_{1.5}$	H_2	$H_{2.5}$	H_3	$H_{3.5}$	H_4	$H_{4.5}$	H_5	$H_{5.5}$	H_6	$H_{6.5}$
No. 22	0.30	0.45	0.38	0.50	0.60	0.75	1.10	1.60	2.10	2.75	—	4.6
No. 2	0.33	0.40	0.45	0.58	0.75	1.08	1.45	1.85	2.25	2.88	4.0	5.15
No. 3	0.31	0.38	0.50	0.70	0.98	1.38	1.90	2.33	—	—	—	—
No. 78	0.30	0.38	0.48	0.58	0.75	1.08	1.35	1.78	2.20	—	3.65	—
No. 16	0.28	0.34	0.42	0.60	0.77	1.18	1.65	2.38	3.20	3.70	4.30	—
No. 522	0.33	0.38	0.53	0.65	1.02	1.40	2.00	—	—	—	—	—
No. 17	0.30	0.39	0.45	0.66	0.88	1.30	1.70	2.55	3.00	4.15	—	—
No. 49	0.30	0.38	0.43	0.55	0.73	1.03	1.50	2.15	2.70	3.35	—	—
No. 6	0.30	0.39	0.49	0.86	1.28	1.70	1.95	—	—	—	—	—
No. 731	0.30	0.35	0.45	0.50	0.63	0.98	1.20	1.58	2.05	2.70	3.65	—
No. 7	0.30	0.38	0.46	0.60	0.75	1.13	1.60	2.10	—	—	—	—

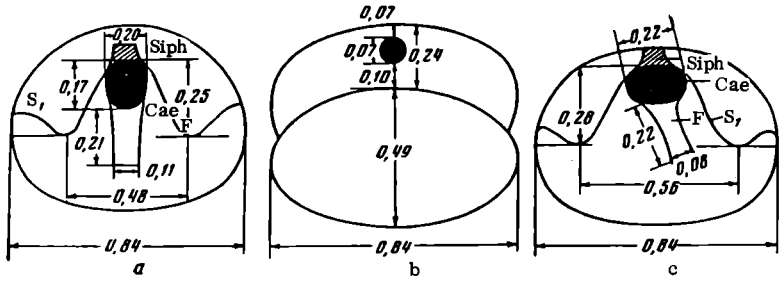

FIGURE 5. Protoconch, ventral saddle of prosuture, caecum and fixator of members of the genus Speetoniceras: a) S. versicolor (Trautschold), spec. 21; b, c) Speetoniceras sp. juv., spec. 19. Expalantions in text.

Suture (fig. 4, B, C). Prosuture angustisellate, bilobed; width of ventral saddle 0.42, height 0.28 to 0.35. Second suture five-lobed. Approximately in the middle of the second whorl the lateral lobe of S. coronatiformis divides into two: $I \rightarrow (I_v, I_d)$. Thereafter the inner branch of this lobe is completely segregated and occupies the place of the inner lateral lobe (fig. 4, B, g); the ventral lobe is connected to the dorsal lobe, the first and second umbilical lobes to the inner branch (I_d), while the outer branch (I_v) is located on the umbilical seam. In the middle of the third whorl the lobe I_v once again divides to form I_{vv} and I_{vd}. In S. elatus the inner lateral lobe divides at the end of the first whorl. Complication of all elements of the suture begins in the middle of the third whorl, when two secondary teeth appear in the umbilical lobe and the ventral saddle divides into two. The ventral and umbilical lobes are practically equal until the third whorl, after which the former deepens and exceeds the depth of the umbilical lobe. All elements of the suture are complicated in the fourth whorl. There is no confirmation of inversion of the suture. The saddles are slightly lower toward the umbilical seam in S. coronatiformis; in S. elatus the ventral saddle and the two subsequent saddles are of approximately the same height, after which the suture descends slightly around the seam.

The genus Simbirskites is characterized by the following features. Protoconch ridge-like, 0.55 to 0.60 in diameter, 0.84 to 0.88 wide; fixator goblet-shaped, with a stalk varying in length from 0.15 to 0.40; caecum ranging from elongate-oval to practically round, varying in size. Siphuncle initially central, ventromarginal at the end of the second whorl, relatively broad (0.31 to 0.33 in the first whorl, 0.36 to 0.39 in the third to fourth, reducing to 0.26 in the fifth). Angle of nepionic constriction about 300°. Diameter of shell of ammonitella 1.05 to 1.12, diameter of first whorl 1.12 to 1.19, of second 1.90 to 2.13; size range of third and subsequent whorls more appreciable. The maximum number of septa reaches 16 to 17 in the second to fourth whorls. Septal necks short, prochoanitic; cuffs short, projecting slightly backward. Thickness of shell wall ranging from 0.01 in first whorl to 0.20 in sixth. Ornament consisting of ventrolateral tubercles from which clusters of ribs extend appears on the fifth or sixth whorl. Prosuture angustisellate and bilobed; second suture five-lobed; the inner lateral lobe divides at the end of the first whorl or in the middle of the second; complication of all elements of the suture begins in the middle of the third whorl. The body chamber occupies approximately one whorl.

Speetoniceras Spath, 1924

Material. Ground sections in the median plane of S. versicolor (four spec.), Speetoniceras sp. (eight spec.); Speetoniceras sp. (one spec.) and S. versicolor (one spec.) uncoiled down to the protoconch.

Protoconch urceolate, practically round in section (fig. 5): $D^1 = 0.53$ to 0.63 (eight measurements), $D^2 = 0.50$ to 0.58 (eight measurements), $D^1 - D^2 = 0.03$ to 0.07. Width of protoconch 0.84.

Nepionic ridge lenticular, with long thin initial portion (spec. 43), its length 0.28 to 0.35 (nine measurements), its thickness 0.03 to 0.05 (seven measurements). Nepionic constriction distinct, located at a distance of 300° (nine measurements). In some specimens (1, 42, 71 and 72) it is very deep; the difference between the height of the whorls on and beyond the constriction is in the range 0.03 (spec. 72) to 0.05 (spec. 1). It is less deep in other specimens.

Diameter of shell of ammonitella 1.02 to 1.15.

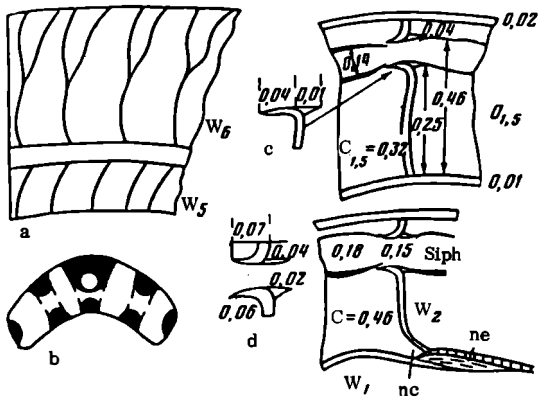

FIGURE 6. Internal structure of shell and nature of ornament in Speetoniceras versicolor (Trautschold): a) spec. 1, nature of ornament; b) spec. 18, interrelationship between lobes at 1.2 whorls; c, d) spec. 72, structure and size of septal necks and location of siphuncle. Explanation in text.

A fixator was observed within the protoconch (spec. 19, 22) cleared in glycerin and in median section. The fixator is tube-like, conically dilated at its point of insertion on the caecum (fig. 5), the length of the tube is 0.21 to 0.22, the width 0.08 to 0.11. The tube is located in the plane of symmetry of the protoconch or displaced to the right (fig. 5, c).

Caecum large, drop-like, 0.17 long, 0.20 to 0.22 wide (fig. 5, a, c); oval or round in section (six measurements): $Cae_1 > Cae_2$, $Cae_1 = 0.10$ to 0.18, $Cae_2 = 0.08$ to 0.14, $Cae_1 - Cae_2 = 0.02$ to 0.05. Membrane of caecum fairly thick in spec. 43.

Siphuncle. Beyond the proseptum the caecum narrows abruptly and gives way to a siphuncular strand, the diameter of which is 0.07 at the third septum (fig. 5). The position of the siphuncle is practically central in the first whorl, but slightly approximated to the ventral wall (fig. 5, b), thereafter it is subcentral and at the end of the second and beginning of the third whorl it becomes ventromarginal (fig. 6c, d). The siphuncle has not been preserved in the first whorl in many specimens or has been greatly distorted (spec. 1, 42, 43).

Siphuncular diameter increases gradually: $S_1 = 0.08$ to 0.13 (two measurements) $S_{1.5} = 0.09$, $S_2 = 0.10$, $S_{2.5} = 0.13$, $S_3 = 0.23$, $C_{3.5} = 0.28$, $S_4 = 0.33$ (spec. 43). Siphuncle relatively broad. Ratio of diameter of siphuncle to whorl height (measured at intervals of half a whorl) respectively 0.25 to 0.37 (two measurements), 0.26, 0.25, 0.28, 0.39, 0.35, 0.30 (spec. 43).

The diameter of the siphuncle in the chamber is usually slightly greater than the diameter of the septal necks; for example 0.15 in the septal neck and 0.18 in the chamber for S_2 (fig. 6d); the corresponding values for spec. 1 are 0.27 and 0.31.

Septa. There are ten to 13 septa in the first whorl (eight measurements), 11 to 15 in the second (ten measurements), 15 to 17 in the third (ten measurements), 12 in one specimen, 15 to 18 in the fourth (eight measurements), 13 in two specimens, 11 to 16 in the fifth (five measurements).

The body chamber has been partly preserved in most specimens. In two (spec. 71, 72) it begins in the fourth whorl, occupying it completely; in spec. 1 the phragmocone occupies 4.25 whorls, in spec. 72 it occupies three whorls, and the fourth whorl has only two chambers; in spec. 43 the phragmocone equals 5.25 whorls. In three specimens (4, 5 and 43) the body chamber begins in the sixth whorl; in spec. 811 the body chamber is at the beginning of the seventh whorl (half a whorl preserved). The distance between septa increases rapidly after the second septum, and then gradually until the end of the third whorl. The distance is variable in the middle of the fourth whorl; a rapid increase that begins at the end of the fourth whorl reaches its maximum at the beginning of the sixth whorl, in which there are six septa; the remainder of the whorl is occupied by the body chamber. A final convergence of the septa is seen in the final whorl (fig. 2).

Septal necks were observed from the second septum (spec. 43); they are prochoanitic and short: 0.04 at $W_{1.5}$, 0.06 to 0.07 at W_2 (fig. 6, c, d), 0.05 to 0.08 at W_3 (spec. 1, 42), 0.10 to 0.13 at W_4 (spec. 4, 43), 0.15 to 0.21 to 0.30 at W_5 (spec. 1, 4, 43). The ratio of the length of the septal necks to that of the chamber is 0.08 to 0.11 at W_3 (two measurements), 0.10 at W_4 (two measurements), 0.09 to 0.10 at W_5 (three measurements). At the beginning of the fifth whorl (spec. 1) the cuff projects slightly rearward; annular deposits are seen on it as a coating; in spec. 4 the cuff projects from the back of the septal neck for 0.05, with a length of 0.07 and a diameter of 0.25. The septal neck, the cuff and the annular deposits probably fuse on the ventral wall to form a small triangular projection.

Shell wall and ornament. The thickness of the shell wall increases gradually (spec. 22): $T_1 = 0.01$, $T_{1.5} = 0.01$, $T_2 = 0.03$, $T_{2.5} = 0.04$, $T_3 = 0.05$, $T_{3.5} = 0.05$, $T_4 = 0.06$, $T_{4.5} = 0.08$, $T_5 = 0.08$, $T_{5.5} = 0.13$. As in the previous genus, the wall is three-layered in the third to sixth whorls.

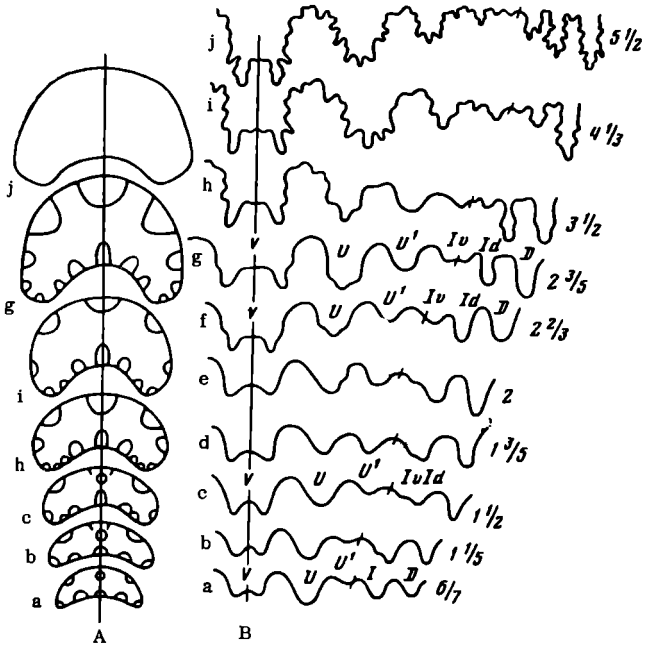

FIGURE 7. Changes in cross-sectional shape (A) and in the suture (B) of Speetoniceras versicolor (Trautschold) in the course of ontogeny; spec. 18. The numerals on the right indicate the position of the suture on the whorl, the letters on the left correspond to the letters for the suture.

Ridges are seen on the shell wall from the second whorl onward. The number of ridges per whorl varies: one to two on the second whorl, three to four on the third, three to four on the fourth, one to two on the fifth. The thickness of the ridges is two to three times the normal wall thickness.

The shell is smooth for four whorls and covered in fine striation. Ribs appear in the fifth whorl at the inflection between the umbilical wall and the lateral wall; they slope forward, are prominent, with a broad intercostal space, and disappear on the venter. At the beginning of the sixth whorl in the middle of the lateral side the ribs dichotomize (fig. 6, a), and fine prominent tubercles appear at the branching point. The ribs cross the venter without interruption, forming a broad forward inflection with very broad intercostal spaces. In one specimen (No. 10) ribs appear on the fourth whorl, the phragmocone occupies five whorls, and the body chamber the sixth. In two specimens, in which the body chamber has not been preserved, ornament is well expressed on the sixth whorl (spec. 41), or at the end of the sixth and the start of the seventh (spec. 51).

Shell shape and size. Section low in first two whorls. Umbilical wall weakly segregated. In the third whorl it is fairly steep, merging gradually with the side wall. A distinct umbilical border is seen on the fourth to fifth whorls. Side walls linked to the rounded venter by a smooth transition (fig. 7, a). The changes in the diameter of the protoconch and the shell of the ammonitella and in the corresponding whorls are set out below.

Changes in the Diameter of the Protoconch, the Shell of the Ammonitella and the Corresponding Whorls

Spec.	D^1	D_{am}	D_1	D_2	D_3	D_4	D_5	D_6
No. 43	0.58	1.08	1.15	1.90	3.03	4.90	9.00	—
No. 51	0.60	1.10	1.25	2.13	3.68	6.50	11.7	21.2
No. 1	0.63	1.13	1.20	2.03	4.48	9.05	17.0	—
No. 42	0.53	1.02	1.13	1.98	3.45	6.75	—	—
No. 5	0.55	1.03	1.13	1.98	3.25	—	—	—
No. 811	0.60	1.13	1.23	2.05	3.48	6.90	10.2	—
No. 72	0.63	1.13	1.20	2.23	4.38	—	—	—
No. 71	0.63	1.15	1.20	2.25	4.35	8.15	—	—

Diameter of first whorl 1.13 to 1.25, of second 1.90 to 2.25; shell diameter highly variable in third to fifth whorls.

Changes in the Internal Height of Whorls in the Course of Ontogeny

Spec.	H_1	$H_{1.5}$	H_2	$H_{2.5}$	H_3	$H_{3.5}$	H_4	$H_{4.5}$	H_5	$H_{5.5}$	H_6	$H_{6.6}$	H_7
No. 43	0.31	0.35	0.40	0.45	0.53	0.71	1.05	1.58	2.40	3.0	4.1	—	—
No. 51	0.30	0.35	0.45	0.60	0.80	1.10	1.55	—	2.85	—	4.75	—	—
No. 1	0.33	0.45	0.60	0.90	1.33	1.95	2.70	—	5.30	—	—	—	—
No. 42	0.30	0.38	0.45	0.58	0.88	1.35	2.05	2.82	—	—	—	—	—
No. 5	0.30	0.40	0.45	0.58	0.73	1.00	1.15	—	1.45	—	2.55	—	4.25
No. 811	0.31	0.36	0.46	0.59	0.73	1.00	1.45	1.98	2.40	3.20	—	5.7	—
No. 72	0.35	0.44	0.63	0.93	1.33	2.00	—	—	—	—	—	—	—
No. 71	0.35	0.43	0.63	0.88	1.20	—	—	—	—	—	—	—	—

The internal height of the cross section is on average 0.30 at the end of the first whorl (range 0.30 to 0.35) and 0.45 to 0.60 at the end of the second; the range of variation is very great at the end of the third to fifth whorls (see the table of variations in the internal height of the whorls in the course of ontogeny).

Suture (fig. 7, B). Prosuture angustisellate; width of ventral saddle 0.48 to 0.56, height 0.25 to 0.28 (fig. 5, a, c). At the end of the first whorl the line consists of five lobes: VUU^1ID (fig. 7, B). At the beginning of the second whorl the inner lateral lobe divides into two (I_v, I_d), as in Simbirskites, and the two parts become completely segregated by the middle of the third whorl. At the end of the third whorl I_v once again divides to yield a total of seven lobes (VUU^1I_{vv}. $I_{vd}I_dD$). No new lobes arise thereafter. The umbilical lobe is initially the largest; thereafter the ventral lobe becomes larger. Complication of all elements of the suture commences in the third whorl. With the exception of the ventral lobe, all the lobes are tripartite with weakly developed lateral teeth, and the saddles are finely dissected.

Speetoniceras has the following characteristic features. Protoconch urceolate, 0.53 to 0.63 in diameter, 0.84 wide. Fixator conoid, appearing as a tube 0.21 to 0.22 long at a diameter of 0.08 to 0.11. Caecum drop-like. Siphuncle initially central, thereafter subcentral, ventromarginal and relatively broad at the end of the second and beginning of the third whorl (0.35 of the height in the third whorl, 0.22 in the middle of the fifth). Angle of nepionic constriction 300°. Shell diameter of ammonitella 1.02 to 1.15, of first whorl 1.13 to 1.25, of second 1.90 to 2.25; whorl diameter highly variable in third to sixth whorls. There are ten to 13 septa in the first whorl, up to 18 in the third to fourth, 11 to 16 in the fifth. Septal necks short, prochoanitic; cuffs also short, projecting slightly backward. Wall thickness of shell ranging from 0.01 in the first whorl to 0.13 in the sixth. Ornament, consisting of dichotomously branching ribs, appears in the fifth whorl. Prosuture angustisellate; suture five-lobed at the end of the first whorl. Complication of the suture occurs by repeated division of the inner lateral lobe and the dissection of all elements. All lobes, apart from the ventral lobe, are tripartite.

Craspedodiscus Spath, 1924

Material. Ground sections of C. discofalcatus in the median plane (nine spec.); C. progrediens (one spec.) and C. discofalcatus (one spec.) uncoiled to the protoconch.

Protoconch ridge-like, practically round in section: $D^1 = 0.55$ to 0.70, $D^2 = 0.53$ to 0.63, $D^1 - D^2 = 0.02$ to 0.10 (eight measurements); in one specimens measured (No. 992) $D^1 = 0.55$, $D^2 = 0.53$, $D^1 - D^2 = 0.02$. Width of protoconch 0.84 to 0.91 (fig. 8, c, d). Ratio of width to diameter 1.41 (one measurement).

Nepionic ridge lenticular. Its length is 0.21 to 0.45 (eight measurements) for a thickness of 0.03 to 0.05 (six measurements). Angle of nepionic constriction 300° (seven measurements), 315° in one specimen; the constriction is clearly expressed in two specimens (36 and 37), indistinct in the others.

Shell diameter of ammonitella 1.13 to 1.20 (eight measurements).

Fixator well preserved in five specimens (28, 36, 37, 38 and 993), indistinctly expressed in one specimen (34). A single strand, varying in length from 0.25 (spec. 34, 993) to 0.45 (spec. 37) is seen in median section. In one specimen placed in glycerin (spec. 11) the fixator in the protoconch appears as a goblet on a long stem; the height of the conical goblet is 0.28, the length of the terminally bifurcating stem (fig. 8, d) is the same; the two branches (0.07) of the bifurca-

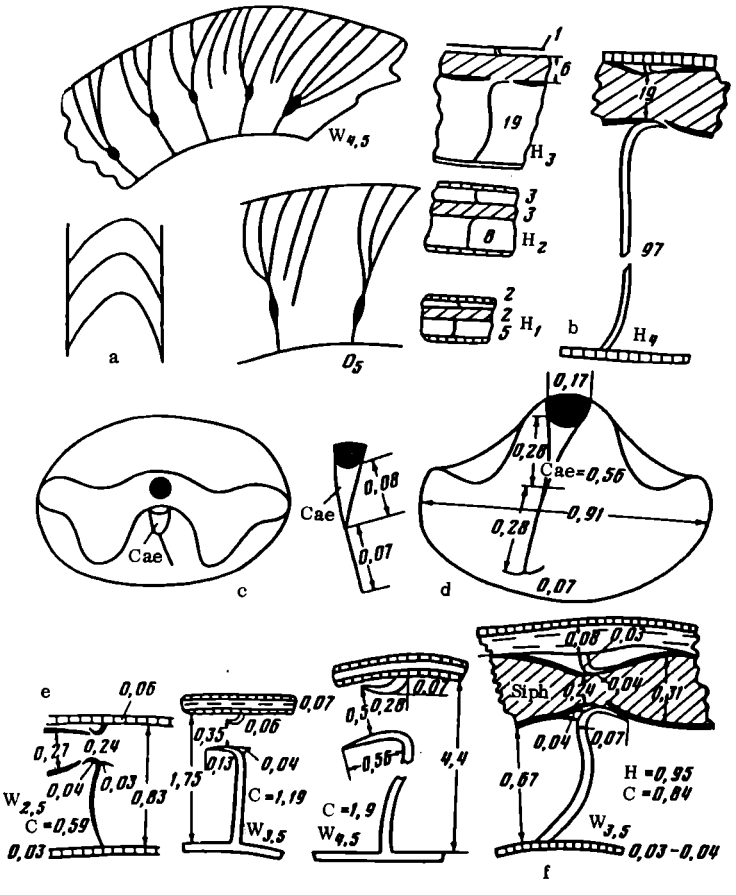

FIGURE 8. Internal structure of the shell and the nature of ornament in members of the genus Craspedodiscus; a, d - C. discofalcatus (Lahusen); a - spec. 991, nature of ornament, d - spec. 12, protoconch, ventral saddle of prosuture, caecum and fixator; c - C. progrediens (Lahusen); spec. 11, protoconch on side of proseptum, shape and size of fixator; b, e, f - Craspedodiscus sp.; b - spec. 36, change in the position and size of the siphuncle in the course of of ontogeny; the numerals indicate the number of divisions of the measuring scale at a scale division of 0.014; e - spec. 38, structure and size of septal necks and position of siphuncle; f - spec. 28, interrelationship of siphuncle and septal neck at 3.5 whorls.

tion are attached to the protoconch. In a second specimen the goblet is small, the height of the cone is 0.08 and the length of the stem 0.07, i.e. about a quarter the size in the previous specimen (fig. 8, c).

Caecum oval in section (four measurements) or round (one measurement); as a rule $C_1 > C_2$, $C_1 = 0.13$ to 0.20, $C_2 = 0.10$ to 0.18, $C_1 - C_2 = 0.02$ to 0.07 (spec. 38); in spec. 993 $C_1 = C_2 = 0.13$; in one specimen (36) $C_1 < C_2$, $C_1 = 0.14$, $C_2 = 0.18$. The section of the caecum is round in the proseptum.

Siphuncle central in first half of first whorl, subcentral approximately to middle of second whorl, becoming ventromarginal thereafter (fig. 8, b). The state of preservation of the siphuncle

varies. For example, the siphuncle is heavily ferruginized in the first two whorls in spec. 34 and lies outside the plane of symmetry; in spec. 991 it is greatly crumpled in the first two whorls, and its thickness in the chambers is reduced to approximately a third of the diameter of the septal neck. It is usual for the diameter of the siphuncle between septa to be considerably greater than in the septal neck (fig. 8, f).

Siphuncular diameter varies as follows: S_1 = 0.08 to 0.10, $S_{1.5}$ = 0.08 to 0.15, S_2 = 0.15 to 0.20, $S_{2.5}$ = 0.18 to 0.25, S_3 = 0.25 to 0.33, $C_{3.5}$ = 0.33 to 0.50, C_4 = 0.48 to 0.58, $C_{4.5}$ = 0.55 (one measurement). Siphuncle relatively broad. Corresponding ratios between siphuncular diameter and whorl height 0.21 to 0.29, 0.33 to 0.40, 0.27 to 0.37, 0.23 to 0.33, 0.23 to 0.27, 0.20 to 0.25, 0.16 to 0.21, 0.12.

Septa. There are ten to 11 septa in the first whorl (three measurements), 12 to 15 in the second (seven measurements), 16 to 20 in the third (six measurements), 14 in one specimen (spec. 992), 16 to 20 in the fourth (five measurements), 13 in one (spec. 992), 12 to 13 in the fifth (three measurements). In only one specimen was a body chamber seen, preserved for half a whorl at the beginning of the sixth whorl.

The distance between septa increases gradually up to the end of the third whorl (spec. 993); it increases more rapidly in the fourth whorl and most intensively in the fifth whorl (fig. 2).

Septal necks prochoanitic, short: their length is 0.04 to 0.08 in the third whorl (three measurements), 0.13 to 0.21 in the fourth (four measurements), 0.35 at the end of the fourth (one measurement), 0.35 to 0.67 in the fifth (four measurements), 0.84 at the end of the fifth (one measurement). Septal necks cone-shaped, with the anterior end broadened; the part adjacent to the ventral wall is usually shorter than the opposite part, sometimes half its length (fig. 8, e in fifth whorl). Cuffs short, rarely preserved. The length of their posterior end is 0.03 to 0.04. The organic membrane of the siphuncle gives way to a calcified cuff (third whorl, spec. 34, 38). Annular formations are preserved in some forms. In one specimen a membrane extending from the septum to the siphuncular membrane has been preserved in the middle of the fourth whorl (fig. 8, f).

Shell wall and ornament. The thickness of the shell wall varies as follows: T_1 = 0.01 to 0.03, $T_{1.5}$ = 0.03 to 0.05, T_2 = 0.04 to 0.05, $T_{2.5}$ = 0.04 to 0.08, T_3 = 0.05 to 0.08; $T_{3.5}$ = 0.06 to 0.10, T_4 = 0.10 to 0.13.

Ridges are seen on the shell wall from the second whorl onward; their number differs from whorl to whorl: one at the end of the second whorl (four measurements), two in the third (three measurements), four in the fourth (one measurement).

The shell is smooth for the first three whorls. Lateral tubercles appear in the middle of the fourth whorl. Weak costation begins to appear from the end of the third whorl (spec. 993) or the beginning of the fourth (spec. 37, 991). Ribs, initially weak and indistinct, appear at the end of the fourth whorl. Clusters of ribs (three to four), some of which branch dichotomously, extend from the tubercles in the middle of the fifth whorl; one to two intercalary ribs are to be seen between the main clusters (fig. 8, a).

Shell shape and size. The transverse section is low and ellipsoidal throughout the first three whorls; at the end of the first whorl (at the tenth septum) the width is slightly less than at the fifth septum (fig. 9, A). An appreciable increase in cross-sectional height occurs in the fourth whorl and the section becomes high-oval by the end of the fifth whorl.

The changes in the diameter of the protoconch, the shell of the ammonitella and the corresponding whorls are given below.

Changes of the Diameter of the Protoconch, the Shell of the Ammonitella and the Corresponding Whorls

Spec.	D^1	D_{am}	D_1	D_2	D_3	D_4	D_5
No. 992	0.55	1.13	1.30	2.33	4.45	9.45	—
No. 37	0.60	1.15	1.25	2.23	4.25	8.90	19.5
No. 28	0.63	1.15	1.23	2.55	—	—	—
No. 36	0.64	1.18	1.28	2.53	4.75	10.55	—
No. 34	0.65	1.19	1.28	2.33	4.38	9.10	—
No. 993	0.65	1.18	1.30	2.35	4.45	9.20	20.5
No. 38	0.68	1.20	1.25	2.15	4.03	8.10	—

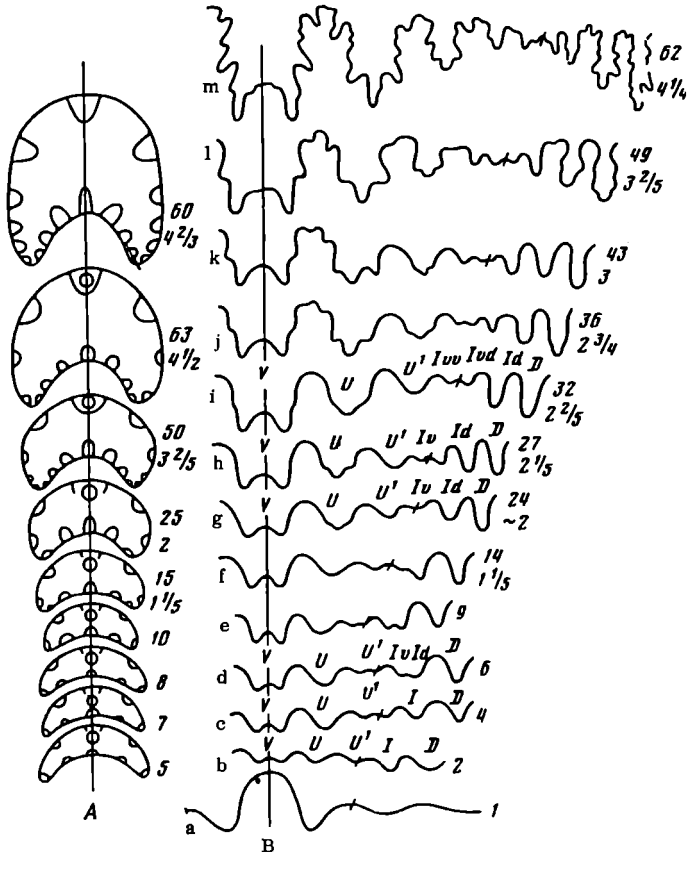

FIGURE 9. Changes in the cross-sectional shape (A) and suture (B) of Craspedodiscus progrediens (Lahusen) in the course of ontogeny; spec. 11.

It is evident from the table that the diameter of the first and second whorls (1.23 to 1.30) is greater than the corresponding diameters in the genera Simbirskites and Speetoniceras. However, the difference is particularly apparent from the third whorl onward; the diameter of the fourth whorl is twice that of the third, the diameter of the fifth twice that of the fourth.

It is evident from the table below, which shows the changes in the internal height of the whorls in the course of ontogeny, that the internal height is already slightly greater than in the two preceding genera in the first whorl (0.33 to 0.35, compared with 0.28 to 0.33). The increase in internal height is particularly great from the fourth whorl onward.

Changes in the Internal Height of Whorls in the Course of Ontogeny

Spec.	H_1	$H_{1.5}$	H_2	$H_{2.5}$	H_3	$H_{3.5}$	H_4	$H_{4.5}$	H_5
No. 992	0.33	0.40	0.50	0.75	1.13	1.70	2.88	4.13	—
No. 37	0.33	0.40	0.53	0.78	1.05	1.68	2.50	4.25	6.38
No. 28	0.33	0.38	0.40	0.63	—	1.23	—	2.60	5.80
No. 36	0.35	0.45	0.65	0.90	1.20	2.05	3.10	4.60	—
No. 34	0.35	0.40	0.55	0.80	1.15	1.75	2.40	—	—
No. 993	0.33	0.45	0.55	0.75	1.18	1.80	2.73	4.25	6.50
No. 38	0.35	0.38	0.55	0.75	1.18	1.63	3.00	—	—

Suture (fig. 9, B). Prosuture angustisellate (fig. 8, c, d). Second suture five-lobed. Fourth line six-lobed, the sixth lobe arising by division of the first umbilical lobe (U^1), but by the

beginning of the second whorl this lobe once again becomes entire. At the same time, in the sixth line (earlier than in the genera considered above) division of the inner lateral lobe into independent lobes I_{vv} and I_{vd} begins. In the two species investigated (C. discofalcatus and C. progrediens) the formation of a sutural lobe resembling that found in the Hoplitoidea and Desmoceratoidea is seen during ontogeny. The inversion of the suture, which is sometimes referred to, was not observed. Lowering of all the elements of the suture on the dorsal side is seen in the last suture drawn (64) in C. discofalcatus.

The genus Craspedodiscus is characterized by the following features. Protoconch ridge-like, 0.55 to 0.70 in diameter, 0.85 to 1.02 in width. Fixator 0.25 to 0.45 long. Caecum ranging from oval to round (0.13 to 0.20). Siphuncle initially central, ventromarginal from the middle of the second whorl, relatively broad (0.20 to 0.37) in the first two whorls, 0.16 to 0.25 in the fourth, much reduced to 0.12 in the fifth. Angle of nepionic constriction about 300°, 315° in one specimen. Shell diameter of ammonitella 1.13 to 1.20, of first whorl 1.28 to 1.30, of second 2.15 to 2.55, of third 4.03 to 4.75, with a sharp increase in the fourth to fifth. There are ten to 11 septa in the first whorl; the number of septa is greatest (16 to 20) in the third to fourth whorls. Septal necks short, prochoanitic; cuffs short, slightly projecting backward. Thickness of shell wall ranging from 0.01 in the first whorl to 0.10 to 0.13 in the fourth, where tubercles appear. In the fifth to sixth whorls clusters of three to four ribs, with one to two intercalary ribs between them, originate from the tubercles. Prosuture angusticellate; division of the inner lateral lobe begins in the sixth line concurrently with division of the first umbilical lobe, which subsequently again becomes entire. A sutural lobe is formed in the fifth to sixth whorls. Complication of all elements begins in the third whorl.

* * *

Comparison of all the observed characters of the genera investigated, reveals a number of differences, as well as many features in common.

Superficially the protoconch has the same urceolate shape, with the width considerably exceeding the diameter; width is 0.84 to 0.88 in Simbirskites, 0.84 in Speetoniceras and 0.85 to 0.91 in Craspedodiscus for corresponding diameters of, respectively, 0.55 to 0.67, 0.53 to 0.63 and 0.55 to 0.70. The fixator resembles a goblet on a long or short stem, or is tube-like, giving way to a narrow cone joining up with the caecum. The overall length of the fixator is very variable in all genera (ranging from 0.11 to 0.38) and is not characteristic for any particular genus.

The shape of the caecum is also variable, ranging from drop-like to cup-like, with a length of between 0.10 and 0.21. The cross section of the siphuncle in the proseptum is round or oval with the long axis situated along the width of the whorl. The position of the siphuncle varies uniformly: central in the first half of the whorl, subcentral in the second half, becoming ventromarginal in the middle or at the end of the second whorl. Siphuncle broad; its relative dimensions (ratio of siphuncular diameter to height) increase to 0.35 in the third to fourth whorl), but thereafter gradually decrease to 0.22, and in two genera to 0.12 in the middle of the fifth whorl. The absolute diameter of the siphuncle increases approximately in the same way to reach 0.5 to 0.6 mm in the fifth whorl.

The minimum number of septa (10 to 11) is seen in the first whorl, increasing to 16 on average, although there may be 17 or 19, in the second to fourth whorls, and again decreasing to 12 to 13 in the fifth. It may be deduced that the ammonite advanced its body along the arc for 36° when constructing the septa in the first whorl, but for only 18 to 21° in the fourth whorl (assuming that 17 to 19 septa were constructed), i.e., that construction of the shell proceeded more rapidly in the first whorl than in the fourth, on the assumption that the intervals between the construction of septa were identical (lunar rhythm, according to Ivanov, 1971). Graphs based on the change in the distance between septa indicate considerable increases in these distances in the fourth and especially the fifth whorl. Consequently there was a correlation between the increase in shell diameter and in the internal height of the whorls. The difference between the three genera is here very apparent. As a rule, the diameter of the first whorl is slightly greater in Craspedodiscus than in the other two genera. An appreciable difference in shell diameter is to seen in the fourth and fifth whorls.

There is a direct correlation between the size of the protoconch (D^1), and the shell diameter of the ammonitella (D_{am}) and the first whorl. The greater the diameter of the protoconch, the greater are the corresponding diameters. For example, $D^1 = 0.55$, $D_{am} = 1.05$; $D^1 = 0.60$, $D_{am} = 1.10$ in Simbirskites, $D^1 = 0.48$, $D_{am} = 0.88$; $D^1 = 0.55$, $D_{am} = 1.03$; $D^1 = 0.63$; $D_{am} = 1.15$ in Speetoniceras, $D^1 = 0.55$, $D_{am} = 1.13$; $D^1 = 0.64$, $D_{am} = 1.18$; $D^1 = 0.70$, $D_{am} = 1.18$ in Craspedodiscus.

The body chamber occupies up to one whorl. The phragmocone equals three whorls in one specimen of Speetoniceras, but it more often occupies four or five whorls.

Judging from ground sections, the septal necks are prochoanitic and cone-like in all whorls. Their absolute length increases from whorl to whorl, reaching 0.49 in the dorsal part and 0.35 on the ventral wall at 5.5 whorls in Simbirskites, and correspondingly 0.42 and 0.24 in Craspedodiscus. The relative length of the septal necks (the ratio of the length of the septal neck to the length of the hydrostatic chamber) is 0.08 to 0.19. The structures accompanying the septal necks are identically constructed: there are short cuffs directed backward and annular deposits appearing as small raised areas within the septal neck.

All three genera differ considerably in the character of the ornament, but the protoconch and the first three whorls are smooth. Ornament appears from the middle of the fourth whorl in Craspedodiscus and in the fifth whorl in Speetoniceras and Simbirskites.

The last two genera are similar in the mode of development and complication of the suture, while Craspedodiscus differs in having a sutural lobe.

The data obtained on the morphogenesis of the three genera constitute initial information on the various characters and on the changes that they undergo during ontogeny, but are still insufficient for determination of independence of the genera and their generic relationships. Further investigations of the assumed ancestors and of members of the subgenus Milanowskia may possibly yield something more definite.

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