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MIDDLE DEVONIAN ORTHOIDEA OF THE HOLY CROSS MOUNTAINS AND THEIR ONTOGENY

(ORTHOIDEA ŚRODKOWO-DEWOŃSKIE Z GÓR ŚWIĘTOKRZYSKICH I ICH ONTOGENEZA)

BY

GERTRUDA BIERNAT

(WITH 23 TEXT-FIGURES, 8 TEXT-PLATES AND 12 PLATES)

WARSZAWA 1959

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PREFACE

The ontogeny of Middle Devonian brachiopods has so far been inadequately studied. There is little on this subject in the world literature mainly because of the difficulties in collecting well preserved material representing the various growth stages.

The Middle Devonian brachiopods from the Givetian shales of the Grzegorzowice-Skały section in the Holy Cross (Święty Krzyż) Mountains are of particular interest. These shales are crowded with fossils especially brachiopods, many species being represented by numerous individuals showing all the different growth stages.

The orthids described in the present paper constitute the largest group, both numerically and generically, of brachiopods from these deposits. Further material from the same deposits, collected during 1947—1952 by Professor R. Kongiel, the writer and students, has been made available to the present author.

The writer's studies have been carried out in the Palaeontological Institute of the Polish Academy of Sciences in Warsaw, under the guidance of Professor Dr. Roman Kozłowski, to whom most sincere gratitude is due for his helpful advice and valuable criticism. The writer is also deeply indebted to Professor R. Kongiel for the gift of material collected from Skały in the Holy Cross Mountains.

Comparative studies of material in the collection of the Palaeontological Museum of the Humboldt University in Berlin were made during the writer's visit there, in 1955 and 1956, and in this connection she is indebted to Professor W. Gross, Director of the Institute of Palaeontology, for making accessible the necessary material and literature and for providing the indispensable facilities.

Palaeozoological Laboratory
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MATERIAL

The present material from one Givetian horizon at Skały in the Holy Cross Mountains is preserved in shales, referred by J. Czarnocki (1950) to the so-called «Skały series». These shales, known in the Polish literature as «brachiopod shales», are argillaceous and marly with fine intercalations of marl. They are 12 m thick, unconformably overlaying limestones with *Calceola sandalina* and themselves covered by marls and limestones, containing corals and brachiopods (M. Pajchlowa, 1957, p. 152, fig. 3). The outcrop of this brachiopod horizon is on the eastern slope of the valley of the Dobruchna stream, at the village of Skały.

A rich fauna of tetracorals, bryozoans, ostracods and trilobites occurs within these shales. Brachiopods are the dominant group, representing few genera and species, but very many individuals. In the writer's collection most species are represented by hundreds and even thousands of specimens at different growth stages. The most abundant are mature and old specimens. Nearly all major brachiopod groups have their representatives here, but most of the genera have only one species. The dalmanelloids especially appear more important because of their great abundance and better generic differentiation. The six species identified belong to the following 6 genera and 5 families:

1. Skenidiidae Kozłowski, 1929 (*Skenidium* Hall, 1860),
2. Dalmanellidae Schuchert, 1929 (*Aulacella* Schuchert & Cooper, 1931),
3. Mystrophoridae Schuchert & Cooper, 1931 (*Kayserella* Hall & Clarke, 1892),
4. Onniellidae Öpik, 1933 (*Phragmophora* Cooper, 1955),
5. Schizophoriidae Schuchert, 1929 (*Schizophoria* King, 1850; *Isorthis* Kozłowski, 1929).

All these species with the exception of *Kayserella lepida* (Schnur) were already known in the Holy Cross Mountains (G. Gürich, 1896; D. Sobolev, 1904, 1909). Some of them such as *Phragmophora schnuri* Cooper and *Kayserella lepida* (Schnur) are rather important index fossils.

All the material, with few exceptions, was beautifully preserved and thus suitable for studying both the external and internal structures. Besides closed shells, there were also abundant isolated ventral and dorsal valves mostly of mature individuals. Minute specimens of immature individuals with very delicate shell are complete, sometimes being only slightly damaged. Young but large specimens of *Schizophoria striatula* Schlotheim are very badly preserved. Isolated ventral or dorsal valves are represented chiefly by fragments. Also many closed shells are crushed and damaged centrally and anteriorly.

METHODS

The preliminary preparation of the shells was accomplished in the field. Large quantities of shale were washed in the nearby stream, in sieves with mesh diameters ranging from 1 to 4 mm. The washed material was thus separated into several fractions. For rapid cleansing all the specimens were boiled in Glauber's salt. Matrix still adhering to the specimens was removed with needles of various sizes. Cleaned shells were slightly coated with dissolved wax or paraffin.

The material thus obtained of the identified species was suitable for studying the shell structure, external and internal morphology, ontogeny and individual variation.

In order to investigate the microstructure of the shell, in particular its punctation, numerous thin sections were made from various parts of the valves belonging to both mature and young individuals. The purpose of sectioning was to determine differences of size and density of the punctae in a particular species as well as changes connected with the growth of the individual.

Additional serial sections have been made of mature individuals, particularly for species with a strongly developed dorsal septum, in order to study the connection of the septum with the bottom of the ventral valve.

For the ontogenetic study in 5 species, *Kayserella lepida* (SCHNUR) excepted, there are nearly complete growth series, from the youngest postlarval stage (shells about 0.5 mm long) to the oldest.

In this series the strongest deviation from the standard mean is displayed by the youngest individuals, as well as by the oldest ones. Hence, the systematic part of this paper contains an exact description of the external morphology in the youngest specimens and a discussion of the changes taking place during the gerontic stage. Those features of the youngest individuals, which undergo changes during ontogeny, have been differentiated and discussed as fully as possible.

Individual variation has been studied in mature individuals of all the identified species. Measurements have been taken of both internal and external details. Those concerning external morphology were: length, width and thickness of shell, length of hinge-line, number of striae on the dorsal sulcus and ventral fold. The measured inner elements were mostly: length and width of the dorsal muscle area which was often markedly variable.

From these measurements it becomes evident that specimens of one species often differ markedly owing to the strong individual variation. Had the number of specimens been less abundant, their identification would probably have been fairly difficult.

GENERAL PART

REMARKS ON THE ONTOGENY OF THE STUDIED ORTHIDS

The five chief growth stages recognized in the ontogenetic series are based on the degree of differentiation in the internal and external shell features and on shell dimensions. An additional stage between the ephebic and the gerontic represents the period of termination of growth of the shell, but still without gerontic features. All stages, excepting the additional one, are comparable with the nepionic, neanic, ephebic and gerontic stages of Ch. E. Beecher. According to him, the ephebic stage is «...the period of complete normal growth, or the maximum of individual perfection. This corresponds to the adult, or mature organism...» (1892, p. 151).

In all species, shells approximately 0.4 to 1 mm long represent the nepionic stage; those from 1 to 3 mm long — the neanic stage; 3 to 7 mm long — the ephebic stage, and 12 to 14 mm long — the gerontic stage. Exceptions are *Schizophoria striatula* (Schlotheim) and *Skenidium polonicum*. In the former, distinguished by considerably greater shell dimensions, the successive growth stages show a greater range in length from approximately 0.45 to 2 mm in the nepionic stage; 2 to 6 mm — in the neanic; 6 to 20 mm — in the ephebic, to 20-30 mm — in the mature, and over 30 mm — in the gerontic stage. In *Skenidium polonicum*, on the other hand, owing to the small dimensions of the shell, the successive growth stages are represented by notably smaller ranges of shell length. Immature orthids of the nepionic stage are very similar in a few features; their shell is biconvex, always wider than long, with large pedicle foramen, encroaching on the delthyrium as well as on the notothyrium. The pedicle, which was probably thick, emerged through the pedicle foramen situated between both valves. The shell surface is smooth, with the exception of its distinctly plicated marginal parts. The hinge angles and the antero-lateral margins are rounded.

N. Spjeldnaes (1957 p. 49-50) mentions also that in the Orthacea the youthful shell has a high area, open delthyrium and notothyrium and that the pedicle was placed between the two valves. This type of development is noted in numerous species belonging to different genera, from Ordovician to Permian times. At this stage, the difference between species and genera is small, consisting mainly in details of ornamentation and in the outline of pedicle foramen.

The resemblance between young individuals of the here studied genera is undoubtedly very close. Nevertheless it must be admitted that even in the nepionic stage representatives of these forms display distinct differences in the following main features: 1) the number of primary radial costulae on both valves and the arrangement of the central striae forming the ventral fold and dorsal sulcus; 2) the shape and dimensions of the pedicle foramen; 3) the orientation of the two beaks; 4) the height of the ventral interarea; 5) the hinge-line length in proportion to the maximum shell width; 6) the outline of the shell, to a great extent resembling that in mature specimens of various genera.

Distinct differences, observable in the first postlarval stage of various brachiopods, have also been ascertained by E. A. Ivanova (1949, p. 260) through her study of the ontogeny of Carboniferous forms.

Ch. E. Beecher and J. M. Clarke (1889, p. 84) were of the opinion that during the nepionic stage even different groups of brachiopods are virtually identical in their shell outlines and in the convexity of their shell, in the development of the beaks and interareas. Hence, specimens at this stage would be only slightly differentiated and their identification difficult.

The nepionic-neanic and gerontic stages of the studied species are dissimilar when compared with mature specimens. The differences of the nepionic and neanic stages are due to the rapid development of all the external and internal features of shell. The differences of the old stage are due to the extensive and characteristic changes associated with an intensive gerontic process. Morphogeny is in fact almost completed during the two earliest ontogenetic stages. On the whole, changes take place with the shell length from 0.4 to 2 mm. Specimens about 2 mm long closely resemble individuals in later stages. In *Schizophoria striatula* the morphogeny is nearly complete when the length of the shell is about 5 mm, while in *Skenidium polonicum* — at about 1 mm.

Changes occurring during the nepionic stage are primarily those connected with the modification of the beak and ventral interarea, also the appearance of rudimentary radial sculpture on both valves.

The neanic stage is characterized by the differentiation of the internal details of the shell and of radial ornamentation. All these features are diagnostic for genera.

The ephebic stage is characterized by intensive growth of the shell, before the attainment of dimensions characteristic for mature specimens. The dimensions of all existing structural details increase in proportion with the growth of the shell. Radial ornamentation finally makes its characteristic appearance. Specific identification is easy during the ephebic stage. This stage is complete with the attainment of the individual's maturity. Intensive growth of shell dimensions and of the internal elements of structure also terminates.

The mature stage, a transition to the gerontic, is probably not of long duration. After the attainment of maturity, the growth of the dimensions of the shell nearly ceases and the gerontic stage slowly begins. The thickness (convexity) of the shell is gradually increased along its entire length and this is shown by the strong concentration of growth lines along the front and the antero-lateral margins. The thickness of the shell is always connected with individual age, increasing with it. Very frequently, however, a shell may display considerable thickness before attaining even the average dimensions of that particular species. In that case the gerontic features occur earlier than would be normal.

For the study of the early growth stages of the shell it is very necessary to have well preserved young specimens. This view agrees with the opinion of Ch. E. Beecher (1891*a*, p. 345) and J. A. Thomson (1927). It is of particular significance in respect to the nepionic stage. Very frequently, for want of adequate youthful specimens, observations are made in the umbonal regions of fully matured shells. The adult specimens, however, do not furnish material for a reliable study of incipient growth stages. Very often the results will not be very accurate and will not give a correct picture of the earliest stage of ontogeny.

In Devonian orthids, the changes occurring directly after the protegulum stage are rapid and often extensive. This is so especially in the case of the umbonal part. Features of greatest significance here are: the position of the beaks and ventral interarea; the shape and size of the pedicle foramen, and the large number of primary striae.

Species with a relatively low ventral interarea in the mature stage have both beaks nearly on the same level during the earliest stages of ontogeny. Therefore, changes taking place with the shell growth will not be extensive, as is the case for example in *Aulacella eifeliensis* and *Schizophoria striatula*. On the contrary, in species with a relatively high ventral interarea in the mature stage, as for example in *Phragmophora schnuri*, *Skenidium polonicum* and, to a lesser extent, in *Isorthis canalicula*, in the earliest postlarval stage the ventral beak is often strongly drawn aside, being in many cases almost perpendicular to the intervalve plane. The dorsal beak, on the other hand, is in a normal position, i. e. slightly raised above the hinge-line. With the growth of the shell, the relative length of the ventral beak increases, soon attaining the height and a similar position of the dorsal beak.

The length ratio of the ventral valve to that of the dorsal is always connected with the above features. On the whole, in species with both beaks on the same level, the two valves are of equal length and convexity. In the earliest ontogenetic stages of *Phragmophora schnuri* Cooper and *Skenidium polonicum*, the dorsal valve is larger than the ventral. This difference is soon compensated by accelerated growth of the ventral beaks. All the changes mentioned here occur in the nepionic stage and cannot be investigated in mature specimens.

During the earliest ontogenetic stage, the shape and dimensions of the pedicle foramen vary conspicuously in the species described. The foramen may be oval, as in *Phragmophora schnuri*, subcircular as in *Aulacella eifeliensis*, or more transversely elongate. The shape and dimensions of the pedicle foramen are connected with the height of the ventral interarea. Higher ventral interareas have larger and longitudinally more elongate pedicle foramina. On the other hand, lower ventral interareas have lower but somewhat broader pedicle foramina. Differences of appearance in the pedicle foramen are already discernible in the nepionic stage.

To sum up, the importance must be stressed again of studying the earliest stage of ontogeny on youthful specimens in order to make correct observations of modifications occurring directly after the protegulum stage.

PUNCTAE

Shells of all the species here described are punctate, with the exception of *Skenidium polonicum*. The punctae are small, rounded, usually regularly spaced on the umbonal and central parts of shell, while at the front they are present in the intercostal furrows and along both sides of the costulae. The summits of costulae are without punctae. They are seen even under weak magnification on the external and internal shell surface. In thin sections the punctae are readily recognizable owing to their dark brown colour being filled by iron oxides. They are tubular and penetrate the entire shell thickness almost perpendicularly to its surface. In some cases, however, they do not pierce more than one-third or even one-fourth of the shell thickness (from the external or occasionally from the internal surface of the valve). The tubules have a constant diameter throughout nearly all their length, sometimes expanding slightly near the exterior.

In all species the punctae bifurcate, occasionally even twice, mostly near exterior surface and only rarely deeper down. The branching punctae have been observed most frequently on cross- and longitudinal sections of *Phragmophora schnuri* Cooper and *Schizophoria striatula* (Schlotheim). The diameter of the tubulae of punctae increases considerably at the point of bifurcation, but the diameter of the branches is a little smaller than that of the bases.

Bifurcation of the punctae in Devonian Articulata (fig. 1) is of special interest. Hitherto it was known mainly among Inarticulata, having been observed among Articulata only in Siluro-Devonian terebratulids (P. E. CLOUD, 1942, p. 27). However in CLOUD's opinion the appearance of branching punctae is due to sections tangential to the shell surface intersecting the shell substance of costate shell at varying angles (H. M. MUIR-WOOD, 1955, p. 46). My observations confirm that bifurcation of the punctae in articulate genera is rare, but true and not accidental.

Comparing ordinary thin sections of the shell surface of all species shows the striking resemblance respecting the size, density and spacing of the punctae. Such a close similarity of punctae in different species is not rare. It has been noted by R. KOZŁOWSKI (1929, p. 33) in two very distinct species: *Dalmanella elongatuloides* KOZŁ. and *Dalmanella (Isorthis) szajnochai* KOZŁ. According to him, the diagnostic value of the punctae was thereby reduced.

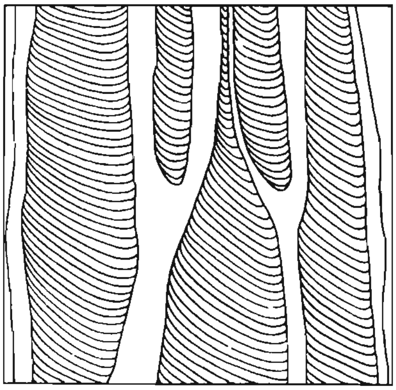


Fig. 1
Phragmophora schnuri COOPER
Bifurcating canaliculae of punctae (thin cross section of shell); × 150 approx.

Differences in punctation in the studied species are unimportant. They mostly concern the density of punctation, and much less the size of the punctae. The comparatively greatest density is observed in *Schizophoria striatula* (SCHLOTHEIM).

Size, outline and density of punctae vary even in a single valve. In the umbonal part the punctae are subcircular, very minute and on the whole uniformly spaced. Towards the centre of the valve their size increases only slightly, and there is no change in their spacing. In the antero-lateral portions of the valve, however, the punctae are twice or even three times the size of those in the umbonal part, and they are often of irregular outline.

The above changes are observable on a series of thin sections of shells of different dimensions, from the youngest to the oldest. They show that the size of punctae, their arrangement and spacing are connected with the individual age of specimen, i. e. with the thickness of the shell. The greater the shell thickness — particularly in the umbonal portion — the smaller the punctae, of regular outline and equal spacing. On the contrary, towards the front of the shell they are larger and mostly of irregular outline.

The density of the punctae on the same parts of the shell of the investigated species does not vary to any considerable extent in specimens of one species. Nevertheless, F. G. PERCIVAL (1916, p. 51-56), when investigating the punctation of two terebratuloid species from Great Britain, concluded that the density of punctae varies in conspecific individuals. Hence that author does not believe this feature to be of much specific value.

C. LEIDHOLD (1925), however, considers the size and density of punctae in Devonian orthoids of great systematic significance. He recognizes them as a constant feature independent of geographical distribution. In every individual he differentiated two types of punctae, with constant or varying diameter.

R. KOZŁOWSKI revised the opinion of LEIDHOLD and others concerning the diagnostic value of punctation. In this connection he investigated (1929, p. 33) nearly all the Podolian and many other, mostly Devonian, punctate species. As a result, he ascertained the lack of differences in the character of punctae on two valves of the same individual, but the presence of strong variations in the punctation of the different portions of the same valve (from the beak to the front.). Marked differences may occur in punctae of two congeneric species, this feature is naturally helpful in specific identification.

LEIDHOLD's opinion is opposed by A. KELUS (1939, p. 34). The latter compared the punctation of specimens of *Schizophoria striatula* (SCHLOTHEIM) collected from various central and west European localities. As a result, KELUS was led to the conclusion that this character is not constant and consequently has no great systematic significance, being reliable for the establishment of local varieties only. In support of his opinion, KELUS figured (p. 35, fig. 25a-e) the size and density of punctae in specimens of *Schizophoria striatula* collected from Ferques (France), Eifel (Germany), Skały (Holy Cross Mountains, Poland), and Pełcza (Volhynia, USSR). Differences of punctation, particularly between specimens from Ferques and Volhynia, as compared with those from the Holy Cross Mountains and from Eifel, are very distinct.

For the purpose of comparison the present writer has made thin sections of *Schizophoria striatula* from Skały and from Eifel. The density of punctae is the same in both cases. The size of punctae, however, is very different: in the Eifelian specimens they are three times as large as those from Skały; in their size and spacing they more resemble the punctae figured by LEIDHOLD (1925, p. 226, fig. 3) than those of KELUS (1939, p. 35, fig. d). According to KELUS the punctae of *Schizophoria striatula* from Eifel are three times smaller than those figured by LEIDHOLD. Both these writers, however, admit differences of size, larger punctae occurring along with small ones. A comparison of the Skały specimens with all those figured by KELUS (p. 35, fig. 25a-e) shows the spacing of punctae in the former almost identical with that in the Volhynian specimens, but they are nearly three times larger.

The punctae in *Schizophoria striatula* from Skały, figured by KELUS (fig. 25d), are particularly interesting. Certain discordances will be noted there in their arrangement and density, as compared with the writer's own observations. These discordances are figured in the microphotograph of the thin section of the topotype, made under the same magnification of $\times$ 47. The punctae figured by KELUS are of variable size, larger and of greater density than those in our specimens.

Supplementary thin sections have been made of *Aulacella eifeliensis* (VERNEUIL) from Skały and the Eifel Mountains. Differences of size and density of punctation are extremely small. Owing to the lack of adequate material, similar comparative studies could not be made in respect of the other species. CH. SCHUCHERT and G. A. COOPER considered that: «Among the orthoids punctation is of great generic value...» (1932, p. 42). According to CLOUD (1942, p. 27), the density of punctation appeared to be a valid specific criterion in some groups, while size and spacing of punctae were of little or no significance.

The conclusion to be drawn here is that problems of the systematic significance of punctation still require further work to be done, in particular detailed comparisons of numerous specimens belonging to many species and collected from different localities.

SEPTUM AND SEPTAL RIDGES

Among the group of the orthids studied, three species have a well developed high dorsal septum: *Skenidium polonicum* GÜRICH, *Kayserella lepida* (SCHNUR) and *Phragmophora schnuri* COOPER. In these species the septum reaches the inner surface of the ventral valve by its highest point. In *Phragmophora schnuri*, at the point of contact with the ventral valve, there occurs a depression bordered by a ridge. In old specimens this depression is particularly deep and distinct.

The presence of the septum gives a characteristic appearance to the shell: centrally the ventral valve is strongly folded, while laterally it descends. This is very distinct in *Skenidium polonicum* and in *Kayserella lepida*. In profile the shell is usually plani-convex or slightly dorsi-convex, sometimes being even subtriangular in outline (fig. 2).

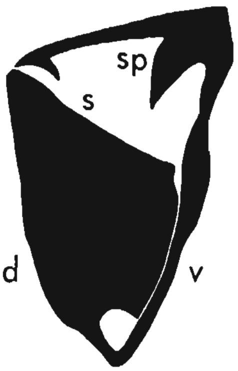


Fig. 2
Skenidium polonicum GÜRICH
Longitudinal section of both valves (dorsal septum plane); × 12.5
s septum, *sp* spondylium, *v* ventral valve, *d* dorsal valve.

The septum appears early in ontogeny, nearly at the same time as the other details of internal structure. It may thus be regarded as a nepionic feature. In an immature individual of *Phragmophora schnuri* COOPER, barely 2 mm long, the septum is already quite distinct, relatively high and subtriangular, i. e. approaching the characteristic shape.

In punctate species the septum is without punctae. It is made of a fibrous substance, similar to that in the brachiophores, the cardinal process or ventral teeth.

In the cross section of an adult shell, the beginning of the septum is seen near the cardinal process, in the form of a rod, expanding a little distally. It is of dark colour, composed of fibres oriented nearly perpendicularly to the shell surface, and differs from the shell substance. The septum is obviously connected with the external shell layer secreted by the borders of the mantle. The septal length and thickness increase together with the general growth of the shell. The fibres of the shell substance are initially arranged parallelly and later obliquely to the septal rod (fig. 3, 4).

In species with a dorsal septum, the ventral valve is without septal ridge.

Aulacella eifeliensis (VERNEUIL), *Schizophoria striatula* (SCHLOTHEIM) and *Isorthis canalicula* (SCHNUR) have the dorsal ridge typical of all orthids, medially dividing the adductors. It is developed as a low, broad axial thickening, originating in front of the cardinal process. With this dorsal ridge is always associated the ventral one, also low and broad, originating somewhat away from the apical cavity and attaining its maximum height at the front of the ventral muscle area.

The septal ridge develops late in ontogeny when all the details of internal structure have been completely differen-


Fig. 3
Phragmophora schnuri COOPER
Cross section of mature dorsal septum; × 36 approx.

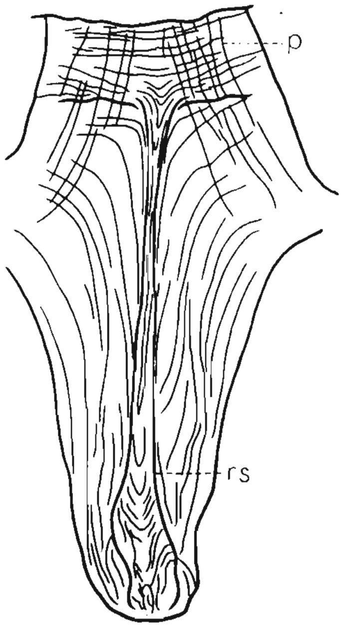


Fig. 4
Phragmophora schnuri COOPER
Cross section of dorsal septum; × 20 approx.
p canaliculae, *rs* septal rod.

tiated. The incipient ridge is observable as a slight elevation in valves of shells 4 to 5 mm long. Its thickness and distinctness are connected with individual maturity and increase especially in old shells when all the other internal elements grow thicker too. While the septum is of recognized taxonomic value, the septal ridge is hardly ever so (Schuchert & Cooper, 1932).

The septal ridges show punctation in species with punctate shells. They are intimately connected with the inner shell layer. In cross section of the shell figured (fig. 5) they are indicated by ridge-like elevations of the shell substance. The superimposed layers are oriented almost parallelly to the outer shell surface, some resemble short lenses squeezed in between two lines of coalescing shell layers.

Fig. 5
Isorthis canalicula (Schnur)
Cross section of ventral septal ridge in mature punctate specimen; × 47.

RADIAL ORNAMENTATION

Radial ornamentation of the studied forms constitutes one of the most important diagnostic features occurring in the early nepionic stage. In the available material it has been observed on the youngest specimen of *Phragmophora schnuri* Cooper, about 0.38 mm long, expressed as a distinct plication of the anterior margins of the shell, over a length of about 0.2 mm. It is possible, however, that the initial striae are present even in younger specimens.

M. A. Bolkhowitinova and P. N. Markov (1928, p. 273) observed radial striae on one specimen of *Enteletoides* Stuck, 0.2 mm long (from the Upper Carboniferous of the Urals). Its umbonal portion was still poorly differentiated, being occupied by a large open pedicle foramen. Those writers supposed that radial ornamentation appeared immediately following the protegulum stage, i. e. at the time when not only the pedicle emerged out of the foramen, but also when the distal portion of the visceral sack was discernible within the posterior part of the shell. Hence, there is a great probability that in Devonian orthids, similarly as in the above mentioned Upper Carboniferous form, incipient ornamentation appears immediately following the protegulum stage.

Data provided by the writer's studies and obtained from the literature indicate that radial ornamentation, being a feature of the early nepionic stage, is a major characteristic of the Orthoidea and Dalmanelloidea.

Incipient radial ornamentation has been observed by Beecher and Clarke (1889) on both valves of a young specimen of *Orthis elegantula* Dalman, 0.5 mm long and 0.75 mm wide. Those authors believed that a specimen with that length represents the earliest nepionic stage of growth.

E. R. Cumings (1903) also recognized radial ornamentation in *Platystrophia* as a nepionic character. He observed 9 ventral and 8 dorsal plications on a shell 0.66 mm long. The apical part of the specimen studied by him was covered solely with delicate concentric lines.

According to Beecher (1892), the appearance of radial ornamentation in the second stage of ontogeny is a prevailing rule. In general, the nepionic shells of all groups are nearly smooth, marked only by fine concentric growth lines. «Sometimes, however, a few radiating striae or other ornaments may appear over the nepionic portion, but this is not the prevailing rule» (1892, p. 150). The above mentioned specimen of *Orthis elegantula* DALMAN (*fide* BEECHER & CZARKE, 1889) may be an illustration of the presence of striae already before the nepionic stage.

E. A. IVANOVA (1949, p. 260) has not observed radial ornamentation during the second stage of ontogeny in some Carboniferous brachiopods: *Enteletes lamarcki* FISCHER, *Meekella eximia* EICHWALD, and others. The nepionic shells of the studied brachiopods were entirely smooth, without any traces of radial ornamentation.

Secondary costulae or striae in Devonian orthids appear at various stages of growth, a regular scheme being seemingly strictly followed. Radial ornamentation may be recognized not only as a feature of the earliest postlarval stage, but also as one showing the longest differentiation. The process is rather slow and gradual, continuing essentially over three successive stages of ontogeny. In the ephebic stage, the ornamentation attains the appearance characteristic of the respective species.

In forms with radial plications it is the other way about. BEECHER and CLARKE (1889, p. 94) established that in the latter case nearly all of the folds appear together, e. g. in *Rhynchonella indianensis* HALL and *Rhynchonella acinus* HALL. BEECHER (1892, p. 151) added that «...in many species with radiate plications or striae, a few radii appear in early nealogic growth, and are added to until the full number is present». They are comparable with *Skenidium polonicum*. In this species 12 to 14 folds appear. With growth their number increases to about 22. New folds are added on the lateral slopes of both valves, as in the two forms of *Rhynchonella* mentioned. Moreover, one central ventral fold and two dorsal folds are differentiated.

On the whole, some important changes respecting radial ornamentation of orthids occur during ontogeny. Although they are associated with the numerical increase of radial costulae, nevertheless the bilateral ramification of these costulae very often has some bearing on the nature of the ornamentation. Ornamentation of the nepionic-neanic shells with simple costulae or striae, compared against that of the adult, shows considerable differences. They are most conspicuous in *Phragmophora schnuri* and *Isorthis canalicula*, and somewhat less so in *Aulacella eifeliensis*. In the adult stage, these species have a distinctly fasciculate type of ornamentation, which is very characteristic and similar. The least differences are noted in *Skenidium polonicum* in which a strong simple plication is followed throughout ontogeny. The only exception is in the dichotomy of the central folds. Some slight differences are also encountered in *Schizophoria striatula*. Here the radial striae are so minute and numerous that dichotomy is not a decisive factor in the final character of the ornamentation.

During the earliest stages of growth, the primary costulae or folds, as in the case of *Skenidium polonicum*, are uniformly indicated in all species by plications of the marginal shell portions. Differences are observed in their numbers only and in the arrangement of the central costulae on both valves. With further growth, quite distinct simple costulae appear, arranged over the entire shell surface, with the exception of the umbonal portion. This occurrence is seen at the end of the nepionic stage. At this stage the writer has noted the special peculiarity of *Skenidium* due to the persistance of the folds. In *Schizophoria* this does not appear to be so marked owing to the greater number (about 14) of striae which are very much smaller than in the other forms.

With growth, new secondary costulae appear in the following way, as has been observed by BEECHER and CLARKE (1889): 1) addition on the lateral slopes of both valves, 2) intercalation between two primary striae or costulae already present, 3) general dichotomy and very rare intercalation.

According to the above authors, new striae or costulae may appear by means of all three, two or one of the mentioned ways.

In studied forms all the three modes occur with sequence as given above. The two first, i. e. that of addition and intercalation of costulae or striae between two primary, are noted in young specimens, about 2 mm long, in the nepionic and at the beginning of the neanic stages. Dichotomy occurs in older specimens at least 3 mm long, during the later nepionic stage. It is most frequent in the ephebic stage. At first we observe unilateral dichotomy. On the ventral valve dichotomy of the existing costulae is always external, while on the dorsal valve it is internal. Consequently it produces a bisymmetrical ramification.

When the radial ornamentation is complete (during the ephebic stage), subsequent changes will be unimportant. With the growth of shell the number of costulae or striae will increase, but very slightly, without affecting the general character of the ornamentation.

During the gerontic stage, particularly when advanced, shells often lose the ornamentation characteristic of their respective species. Moreover the ridges of costulae on the umbonal part become effaced. There are also certain differences in the height of the costulae. This is observable in extremely old individuals of *Schizophoria striatula* and *Aulacella eifeliensis*. The ridges of striae and costulae become rounded and seemingly lower. Often, owing to the concentration of growth lines which are slightly raised above the backs of the costulae, the margins appear imbricate, for example in *Aulacella eifeliensis*.

INDEX FEATURES IN STUDIED FORMS

In connection with studies of ontogeny and individual variation, the taxonomic significance of the displayed features becomes an important problem. It is a difficult one and up till now great arbitrariness has been tolerated with respect to the recognition of diagnostic features in the establishment of systematic units. In many cases, even the specific separation within one genus is not based on the same features. Thus one species is established on the evidence of one feature only, mostly pertaining to external morphology, i. e. to some difference of shell outline, height of interarea or degree of development of both beaks, whilst the separation of another species is based on several features of external or internal structure. Gürich, for example, separated a number of new species in the Devonian orthids from the Holy Cross Mountains, among others that of *Orthis (Rhipidomella) subtetragona*. He writes: «Die Art steht *Orthis Eifeliensis*, mit welcher sie zusammen vorkommt, sehr nahe, ist aber durch den sehr bestimmt subquadratischen Umriss von dieser leicht zu unterscheiden, die stets mehr gerundet ist» (1896, p. 240-241). Obviously, this simple feature is quite insufficient for the separation of a new distinct species. A standpoint of that kind causes difficulties in the identification of individual specimens, and the majority of species thus established must subsequently pass to synonymy.

Individual variations must be taken into consideration in the description of new species. This is possible only when great numbers of conspecific specimens are available at the same stage of growth. When the material is meagre, differences between almost every one of the available specimens appear quite striking suggesting a reasonable separation of a new species. The diagnostic value of these differences, however, deteriorates very much when the material is sufficiently abundant. As is evidenced by the copious material, described by the present writer, the species display very strong individual variation covering the greater part of both external and internal features.

The recognition of the ontogenetic stage of the investigated specimens is of great importance in specific descriptions. Investigations of ontogeny have shown considerable differences between individuals at various growth stages. The two final stages, the mature and the gerontic, are those most frequently described. They differ to a great extent, particularly so when the gerontic process is far advanced. The valves of old specimens generally grow more convex and thicker and have incurved beaks with partly effaced ornamentation; on the shell surface the ridges of striae are often much lower and more rounded. All these features would be sufficient for the separation of new species, if the individual age of the studied specimens were not taken into consideration. A. N. Sokolskaia (1949) advocated a similar viewpoint on growth changes in Carboniferous *Chonetes*. To illustrate this view, that author wrote that in one of her papers on Carboniferous spirifers and productids of the Moscow basin, she had separated several new species and varieties. Subsequently, however, on the evidence of her later investigations she was unable to retain their systematic position, as they proved to be merely gerontic representatives of previously known species.

As has been mentioned, every described species from Poland is represented by numerous specimens at various growth stages. The weak point of this material is its specific paucity, three or at least two species of one genus would be desirable. This makes difficult a precise determination of the specific features. Nevertheless, when analyzing the variations of the features of external and internal morphology during ontogeny, it is possible to distinguish certain features from those within individual variation and which are at the same time not related to growth stages. These features are useful specific indices. They are: 1) outline of shell, 2) width to length of shell ratio, 3) length of hinge-line, 4) number and arrangement of ventral and dorsal central striae, 5) number of incipient primary radial striae on surface of young shells.

Even small specimens display a characteristic outline, resembling to a great extent adult ones. This is stressed by the distinct cardinal angles, the length of the hinge-line and the constancy of the width to length of shell ratio. Changes of outline, observed in the ontogeny of orthids, are unimportant, and not of the rank noted in Carboniferous *Chonetes* (Sokolskaia, 1949, p. 270), productids or other brachiopods. In the orthids they consist mainly in that the antero-lateral angles are more distinct with the growth of shell, whereby the outline takes its final appearance common in the given form.

The width to length of shell ratio is constant throughout the growth stages, the shell being wider than long which is characteristic of all species. With the progress of individual age, the width of shell increases in proportion to its general growth.

The ratio of the length of the hinge-line to the maximum width of the shell is also constant. The hinge-line, throughout all the stages of ontogeny, is shorter than the greatest shell width. The length of the hinge-line increases slowly, proportionally to the general increase of shell size. This feature may be recognized as specifically diagnostic. Sokolskaia (1949, p. 270), however, does not accept this feature as diagnostic for species, not only in the case of *Chonetes*, but also of other brachiopods, owing to changes in growth stages. That author's studies on the *Chonetes* show that during early ontogeny their hinge-line is slightly shorter than the maximum shell width, being equal in adult specimens. During the gerontic stage, the ratio of the length of hinge-line to the width of shell approaches that in the earliest postlarval stage, due to the slow growth of shell length. It might be noted here that there is little probability of the shell length increasing, even slowly, during the gerontic stage. Recent studies have shown this process as completely terminated by the beginning of the gerontic stage. On the other hand, we may observe then an increase of the thickness of shell and of all its internal details of structure.

All the above mentioned features may be considered as diagnostic for the species here described.

The next feature, that of the number of central striae on both valves, is particularly important being very helpful in the specific identification of young individuals. A simple central stria on the ventral valve, for example in *Phragmophora schnuri*, *Isorthis canalicula* or *Skenidium polonicum*, is an incipient ventral fold. The two central striae on the dorsal valve of these species are the incipient sulcus depression, which is so characteristic in these forms. This feature has apparently not only a diagnostic value for species, but also for genera. It occurs in some species of *Isorthis*, such as *Isorthis szajnochai* Kozłowski. Similarly, two central striae are observable on the ventral valve, and one on the dorsal valve of species belonging to genus *Aulacella*. These central striae are very conspicuous and readily discernible throughout all the ontogenetic stages.

In what concerns the number of incipient primary costulae on the surface of both valves, it has been ascertained to be constant within conspecific forms. Probably, this may be a constant feature not only specifically but also generically. The inadequacy of comparative material available to the writer has, however, been an obstacle in confirming it.

SYSTEMATIC PART

Suborder **ORTHOIDEA** Schuchert & Cooper, 1931

Family SKENIDIIDAE Kozłowski, 1929

Genus **SKENIDIUM** Hall, 1860

Skenidium insigne Hall from the Lower Devonian of North America (Lower Helderbergian) is the type species of the genus *Skenidium* established by J. Hall in 1860. Its characteristic features are: small dimensions of shell which display a sub-semipyramidal outline, high trigonal ventral interarea and a similarly high trigonal delthyrium, presence of spondylium, shell surface marked by strong radial plications.

The genus *Skenidium* has since 1882 been identified with the genus *Mystrophora* Kayser, the latter generic name being now regarded as a synonym of the former.

In 1916 H. S. Williams and C. L. Breger expressed the opinion that these two genera ought to be separated on differences in shell structure. According to Hall and Clarke, the shell of *Skenidium pyramidale* Hall — a Gotlandian-Niagarian form from North America — is impunctate. *Skenidium levisii* (Davidson) from the Gotlandian of Europe (England, Scotland, Isle of Gotland, Podolia), as pointed out by Kozłowski (1929), likewise has a fibrous shell substance without punctae. *Mystrophora areola* Quenstedt is punctate as previously stated by E. Kayser (1871, p. 614). Kozłowski (1929, p. 46) suggested that a diagnostic generic significance might be attributed to the punctae: «...on est d'accord pour attribuer à leur présence ou à leur absence l'importance d'un caractère générique».

In 1931 Schuchert and Cooper separated the new genus *Skenidioides*, up to that time identified with *Skenidium*. *Skenidioides billingsi* Schuchert & Cooper from the Ordovician of North America is a species characteristic of *Skenidioides*. This new genus was separated on certain structural differences. In *Skenidioides* there are no distinct hinge plates so characteristic of *Skenidium*, the dorsal interarea is fully developed and distinct and the dorsal septum originates in front of the ridge-like cardinal process. There are differences in radial ornamentation and in the convexity of the ventral valve. *Skenidium* has about 16 strong single plications. In *Skenidioides*, on the contrary, there are numerous (about 40) fine plications bifurcating on the slopes. The ventral valve of *Skenidium* is arched along the midline, being thus seemingly pyramidal. In the other internal characters these two genera show close similarities.

According to Schuchert and Cooper, *Skenidioides* is characteristic of Ordovician-Silurian beds of North America and Europe, while *Skenidium* occurs in Devonian beds of North America and Europe (Poland).

Skenidium polonicum Gürich, 1896

(pl. I, fig. 1-9; text-pl. I, II; text-fig. 6-8)

1896. *Skenidium polonicum* n. sp.; G. Gürich, Das Palaeozoicum..., p. 237, pl. 10, fig. 3a-b, 14a-b.
1909. *Skenidium polonicum* Gürich; D. Sobolev, Srednij devon..., p. 457.

The described species from the Middle Devonian of the Holy Cross Mountains is apparently transitional between *Skenidium* Hall and *Skenidioides* Schuchert & Cooper, displaying features common to both these genera. In the outline, the lesser convexity of the ventral valve and smaller height of the ventral interarea, it resembles the latter of the two, while in details of internal morphology and in character of radial ornamentation it is nearer to *Skenidium*.

Skenidium polonicum Gürich has narrow hinge plates; the brachiophore plates constitute a distinct though low cruralium. The dorsal interarea is low, radial ornamentation here consists of more plications than in species of *Skenidium*. These plications are generally single as in *Skenidium* and bifurcation is rare.

The present writer has referred this species to *Skenidium* Hall in the belief that all the features mentioned here are of diagnostic value.

Material. — 150 complete shells with both valves of various growth stages, with predominance of mature individuals; 20 ventral and 10 dorsal valves, mostly in fragments.

Dimensions of 4 specimens *(in mm)*:

	1	*2*	*3*	*4*
Length	1.0	2.1	3.1	5.0
Width	1.6	2.9	4.6	5.6
Thickness	0.5	1.3	1.5	1.4

Description. — *External morphology* (pl. I, fig. 6 *f-j*). Shell small, plani-convex, transversally elongated, always wider than long; hinge-line straight, shorter than maximum shel-width, but with length moderately variable; hinge angles well marked, mostly straight; lateral margins either parallel or somewhat divergent anteriorly; anterior margin in most cases unisulcate.

Ventral valve strongly arched, highest at the beak, slopes depressed; a low ventral keel sometimes present, in most cases disappearing anteriorly; interarea high, usually attaining half the length of the hinge-line, with surface slightly concave, horizontally striated; delthyrium high, trigonal, open, about twice as high as wide.

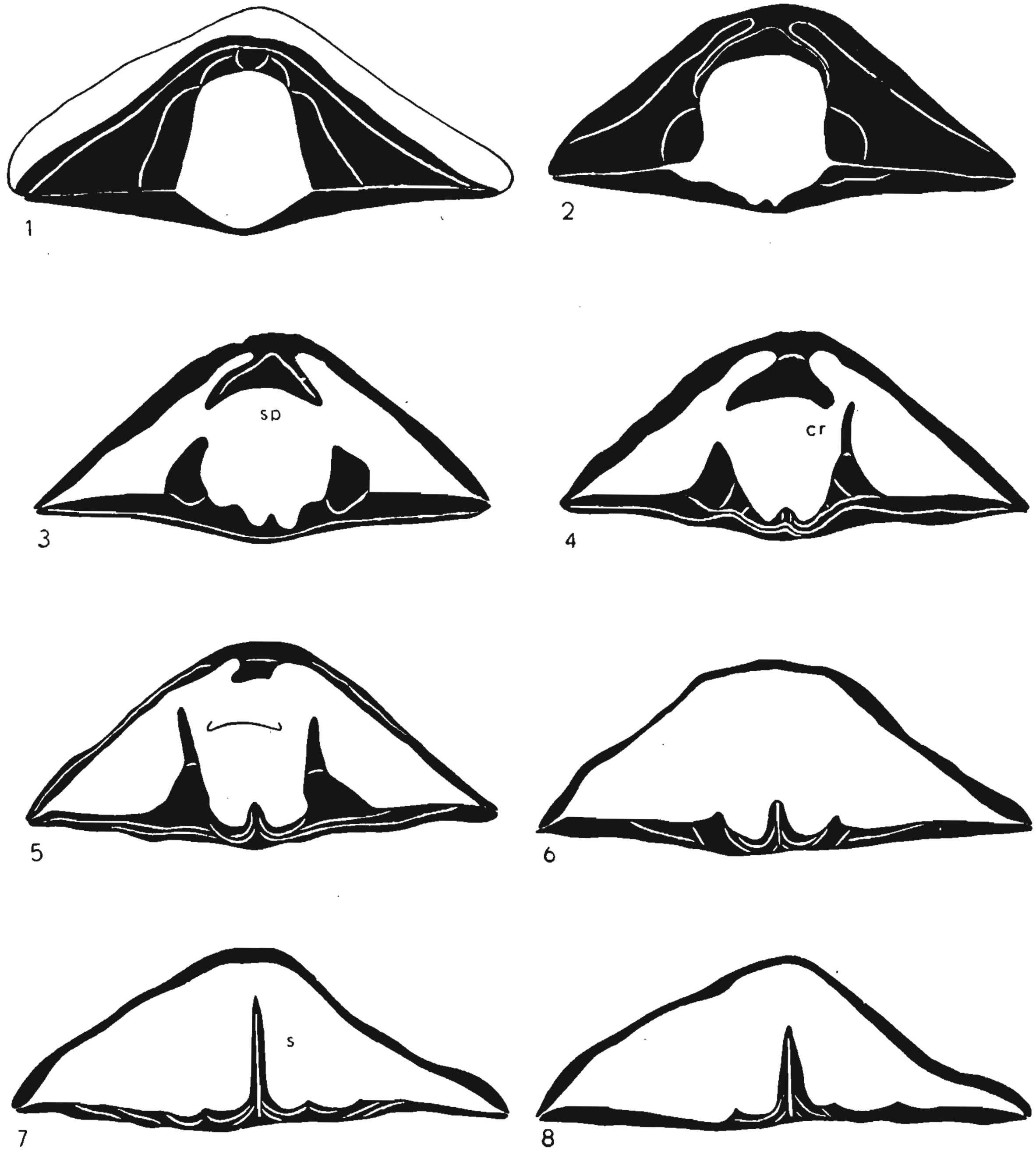
Dorsal valve flat or very slightly convex in the umbonal portion, anteriorly depressed; sulcus broad and shallow; interarea low, reduced, usually placed to the ventral interarea at an angle below 90°; notothyrium low, broad, trigonal, with cardinal process discernible centrally.

Ornamentation consisting of high single radial plications, with rounded ridges; furrows deep, narrower than the plications which are distinct on the internal surface; growth lines usually irregularly spaced, crowded anteriorly (pl. I, fig. 6 *f-g*).

Shell substance fibrous, impunctate.

Internal morphology (pl. I, fig. 7, 8; text-pl. I). Ventral valve teeth well developed, somewhat narrowing distally, unsupported by dental plates; spondylium present, varying in length,

TEXT-PLATE I



Skenidium polonicum GÜRICH

Series of eight thin cross sections showing structure of distal portions in a mature individual: *cr* cruralium, *sp* spondylium, *s* septum; × 20.

often half the length of delthyrium, in apical part spondylium fused with valve bottom, anteriorly supported by the low, stout septal ridge, which sometimes extends to midlength of shell; anterior margin of spondylium rectilinear or rounded; muscle scars not apparent.

Dorsal valve with cardinal process short, simple, shaped like a low ridge often expanding to the front; median septum usually thin, very high, reaching to bottom of ventral valve, highest and widest at about midlength of shell (near the anterior margin of cruralium), terminating not far from the front margin where it gradually tapers off (pl. I, fig. 8); brachiophores long, slender, somewhat laterally directed; dental sockets distinct, deep; between each brachiophore and the median septum is a low, distinct cruralium; crural plates as a rule rounded anteriorly, with lateral margins arching outwards; muscle scars readily discernible, impressed on both sides of cruralium; anterior adductors large, rounded, situated at the front of the cruralium, on both sides of septum; posterior adductors usually smaller and not always distinctly delimited from the anterior.

Variability. — Individual variability strong, as suggested by observations and measurements of 125 mature specimens, covering: maximum width, length and thickness of shell, length of hinge-line, height of ventral interarea, number of ventral and dorsal plications.

Width of shell is variable. The width index (width/length ratio) changes from 1.1 to 1.5:

Width index	Number of specimens	Per cent
1.1	12	9.6
1.2	35	28.0
1.3	45	36.0
1.4	25	20.0
1.5	8	6.4

Width index of the majority of specimens is at 1.3, with average shell length of 3.1 mm and average shell width of 4.1 mm. Graphically this variation is represented as a gently arched, unimodal, moderately regular curve.

Thickness of shell is also of a variable character. The thickness index (thickness/length of shell ratio) ranges from 0.4 to 0.7, as is shown by the following table:

Thickness index	Number of specimens	Per cent
0.4	2	1.6
0.5	38	30.4
0.6	75	60.0
0.7	10	8.0

In a graph the variability of the thickness index is represented by a greatly elevated curve.

The length of the hinge-line is apparently a very variable feature, as are the thickness and the width of the shell. Measurements of 125 mature specimens, however, show the small extent of that variability. The hinge-line length index (hinge-line length/shell width ratio) varies from 0.8 to 1.0. Most specimens (76), i. e. 56 per cent out of the total measured, are grouped at the 0.9 index. Only 16 per cent (20 specimens) are grouped at the 0.8 index, and 28 per cent (35 specimens) — at the 1.0 index. The unimodal variation curve of this feature very closely resembles that of the index of thickness variation.

The ratio of the hinge-line length to the shell length is likewise slightly variable. The length index of the hinge-line ranges from 0.9 to 1.1, half the specimens being grouped at the 1.0 index.

The external appearance of the hinge angles is very varied. They may be straight, the lateral shell margins being parallel or nearly parallel to one another. Obtuse hinge angles are very common, with anteriorly divergent lateral margins. The hinge angles may extend into small but distinct ears, frequently incised underneath. These ears are not always bilaterally uniformly developed, irregularity of shape being displayed in most cases. One ear may be more developed than the other, or may be absent.

The length of the hinge-line greatly depends on the development or absence of hinge ears. When the ears are well developed, the length of the hinge-line is in most cases nearly equal to the maximum width of shell, occasionally even greater. In the absence of ears the hinge-line is very frequently shorter than the maximum shell width.

The height of the ventral interarea is not subject to strong variations, as has been proved by measurements of 117 mature specimens. The measurements include: 1) height of ventral interarea/length of hinge-line ratio, and 2) height of ventral interarea/thickness of shell ratio. In the first case the height index of the ventral interarea ranges from 0.3 to 0.4, with the majority of specimens grouped at 0.3.

In the other case, the height index of the ventral interarea oscillates from 0.3 to 0.5, with the majority of measured specimens (69 per cent) grouped at 0.4. The 0.3 index is fairly frequent too, as 30 specimens (26 per cent) assemble round it. The 0.5 index, however, represents 5 per cent of the total measured specimens. The variation curve of this feature is strongly but regularly elevated.

The number of radial plications on the surface of both valves is not constant. Their number, as counted in 125 specimens, mostly vary from 18 to 27 on each valve; the first and last number is, however, very rare. When the plications are less numerous, they are apparently slightly thicker and somewhat enlarging to antero-lateral margins.

In internal structure the spondylium, ventral and dorsal septa are very variable.

Investigations concerning the variability of length of spondylium and height of dorsal septum are difficult owing to the fragmentary state of preservation. Their structure was delicate and they have been more or less fractured. Very few specimens have spondylium and septum completely preserved.

On the whole, the length of spondylium is approximately one-half that of the delthyrium. Often specimens of equal size display differences in length of spondylium. It may either attain or even exceed half the length of delthyrium, or extend to the hinge-line. If so, the length of spondylium is virtually equal to that of the delthyrium.

Variations in the width of spondylium are also observable. The width of spondylium depends on that of the delthyrium. These variations are, however, extremely small. The anterior margin of spondylium is also variable. It may be either straight, or more or less rounded.

The septum supporting the spondylium is not always well discernible. It is most conspicuous in old individuals in which, with the cessation of the growth of shell, elements of internal structure — hence the septum too — thicken considerably.

The dorsal septum is very high even in young specimens, above 1 mm long. It is extremely thin, hence damaged in most cases. It touches the bottom of the ventral valve with its highest free end. Length and height of the dorsal septum are very variable. It reaches beyond the midlength of the dorsal valve, but may even terminate at the anterior margin or at a small distance from it.

Variations in the shape and size of the dorsal muscle area are rather small. On the whole, the anterior adductors are distinctly delimited from the posterior. They are both semicircular. The ridges surrounding the muscle area are low, not very distinct, without lateral incisions. The anterior adductors are generally larger than the posterior scars, but sometimes they are of even size. Asymmetry may also be observed in the shape of muscle impressions on both sides of the cruralium (fig. 6).

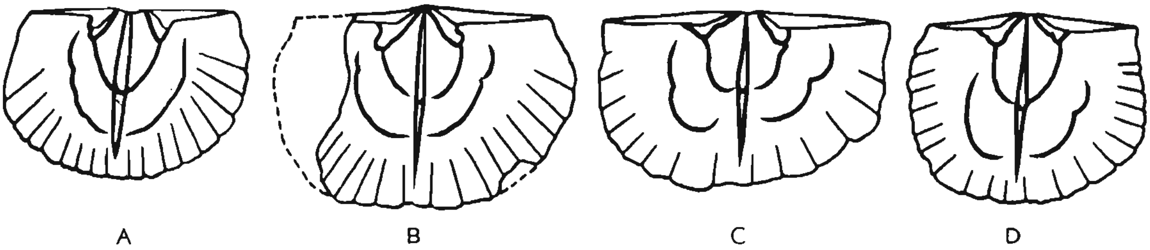


Fig. 6

Skenidium polonicum GÜRICH

A-D four interiors of the dorsal valves, showing variations of muscle area, inside view; × 9 approx.

Ontogeny (pl. I, fig. 1-6; text-pl. II; text-fig. 7). — Very young individuals are absent, the smallest single valve being 0.5 mm long. The ontogenic series starts with specimens 0.88 mm long and 1.25 mm wide. The most numerous specimens are those with length ranging from 2.5 to 4 mm. The successive growth stages are as follows:

1) length 0.5 to 0.88 mm — shell surface with concentric lines, incipient radial plications at a distance of about 0.2 mm from the apex, elongating together with growth of shell, pedicle foramen large, subcircular;

2) 0.9 to 1.25 mm — secondary plications appear on lateral slopes of shell and in the middle of both valves, ventral beak situated below the hinge-line;

3) 1.25 to 2.5 mm — ventral beak projecting above the hinge-line, pedicle foramen trigonal;

4) 2.5 to 4 mm — increased shell dimensions, concentric growth lines grouped along the antero-lateral margins;

5) up from 4 mm — commencement of slow gerontic process.

Mature shells are minute: their length is about 5 mm. The differentiation of the external and internal features of shell is very rapid. Specimens, about 1 mm long, already closely resemble the adult. The long persistance of the protegulum on both valves is characteristic of this species. Even old individuals display a vestigial protegulum as narrow ridges around the apex of both beaks.

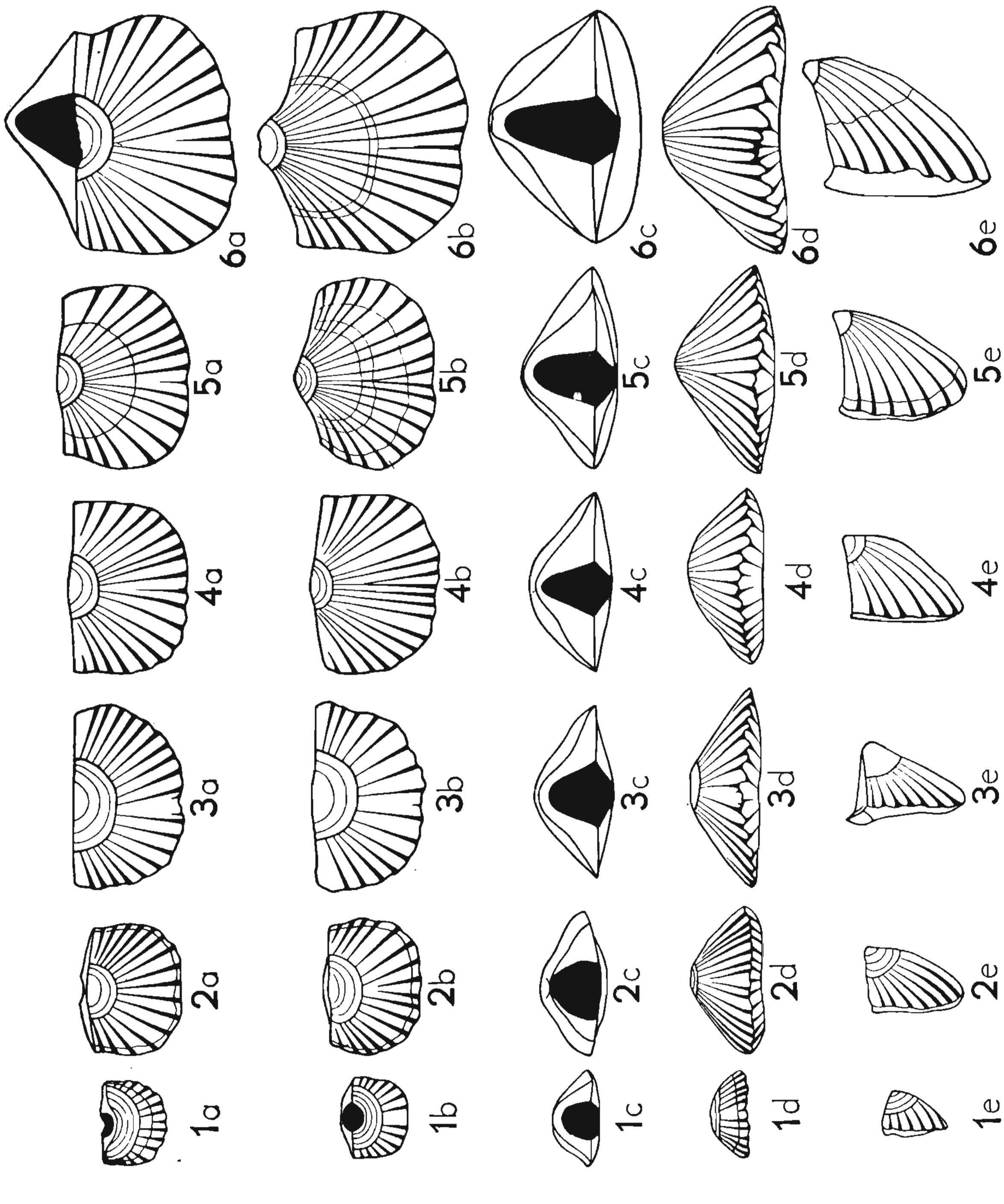
Description of the smallest specimen (text-fig. 7)

Only one ventral valve is available, with dimensions: length 0.5 mm, width 0.7 mm.

Valve strongly and uniformly convex; antero-lateral margins rounded; interarea high, delimited from valve by edges not readily discernible; pedicle foramen distally well rounded, equally wide along its length; 11 peripheral radial plications with low and gently rounded ridges, about twice as wide as the furrows; the plicated antero-lateral portion of shell slightly raised, separated from the smooth distal portion of valve by a narrow and shallow concentric furrow.

Smooth umbonal portion is the equivalent of the protegulum occupying four-fifths of the entire valve length, and represents the nepionic stage; protegulum transversely elon-

TEXT-PLATE II



Skenidium polonicum GÜRICH

Series of six successive growth stages, from five aspects: *a* dorsal, *b* ventral, *c* hinge-line, *d* anterior margin, *e* lateral; × 11 approx.

gated, its surface covered by fine growth lines, densely and uniformly arranged. Protegulum persisting long in gradually older specimens; in adult specimens expressed as a narrow and secondarily thickened string on the apex of beak.

Smallest complete shells are 0.8 mm long and 1.25 mm wide, differing considerably in comparison with the above described ventral valve (text-pl. II, fig. 1 *a-e*). The shell outline is now definitely fixed as a transversely elongated rectangle; hinge-line and hinge angles nearly straight; lateral margins nearly parallel. Ventral interarea markedly higher, in appearance resembling the interarea of a 0.5 mm valve. Pedicle foramen large, overlapping the dorsal valve. Dorsal beak poorly discernible. Protegulum distinct, occupying half the length of each of the two valves. On the dorsal valve it is slightly convex, centrally divided by a small and faint depression, often continuing anteriorly. Medially, in the dorsal hinge line, a semicircular

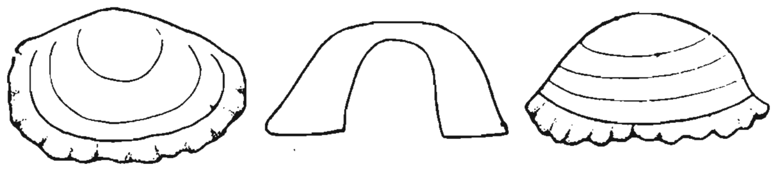


Fig. 7
Skenidium polonicum GÜRICH
Youngest specimen from ontogenetic series shown in pl. II; × 40 approx.
A ventral view, *B* hinge-line view, *C* anterior margin view.

incision occurs involving the umbonal portion of protegulum. Exterior of both protegula marked by distinct and relatively numerous concentric lines. Radial folds now differentiated, 14 on each valve.

Generally, juvenile shells strongly resemble the mature owing to the presence of the following constant characters: 1) shell outline always strongly transversely elongated; 2) protegulum with appearance varying during ontogeny; 3) ventral interarea high; 4) greatest convexity of ventral valve always at its umbonal portion; 5) ventral and dorsal plications simple, the central ones excepted.

The following are features which frequently change considerably during ontogeny: 1) ventral and dorsal umbonal portions; 2) shape of pedicle foramen-delthyrium; 3) convexity of valves; 4) outline of anterior margin; 5) radial ornamentation.

Changing features in ontogeny

Ventral and dorsal umbonal portions (text-pl. II, fig. 1*e*-6*e*). During ontogeny the position of the ventral beak undergoes change. In lateral view of shell (from 0.5 mm to about 1 mm long) it is perpendicular to the lateral margins at about the level of the hinge-line. Gradually, as a result of the growth of the beak, it is raised. Initially it slightly projects above the hinge-line. Subsequently, the beak becomes more conspicuous and protrudes further above the hinge-line.

In the dorsal valve of youngest individuals (up to 1 mm in length), at mid-hinge-line, a deep semicircular incision is noted. It corresponds to the notothyrium and constitutes approximately one-third of the delthyrial height. It is surrounded by the dorsal protegulum, occupying one-half of the complete shell length. The protegulum is smooth, covered by delicate concentric growth lines only. In connection with the growth of the umbonal portion of the valve, the depth of the notothyrial incision is gradually reduced. In specimens with length over 1 mm the incision is very slight and disappears completely at about 1.25 mm length of shell. The dorsal hinge-line straightens out. In mature individuals, the side of the incision is occupied by a convex elevation, initially gentle, which is an equivalent of the poorly differentiated dorsal beak, with apex hardly distinguishable. The hinge-line is not straight, but centrally arched and depressed towards both lateral sides.

Pedicle foramen — delthyrium (text-pl. II, fig. 1*c*-6*c*; text-fig. 7*B*). In a valve 0.5 mm long the pedicle opening is large, well rounded at the apex, uniformly broad along its length (fig. 6*B*). The successive changes are gradual. Specimens 0.88 mm long still retain approximately the same shape of the foramen. In specimens 1.25 mm long the delthyrial margins are somewhat curved outward, while the foramen itself slightly narrows apically. With shell length of 2 mm the foramen is distinctly trigonal with its apical portion gently rounded. This is observable also in the subsequent stages of ontogeny. The base of the triangle is broad, nearly one-third of the length of the hinge-line. In older individuals the width is somewhat reduced, e. g. with length of shell at 3 mm the base of the triangle is equal to about one-fourth of the length of the hinge-line. Further changes consist in growth of the triangle height along with the growth of the ventral beak and interarea.

Convexity of valves (text-pl. II, fig. 1*e*-6*e*). A ventral valve, 0.5 mm long, is comparatively strongly but uniformly arched along its length and width. The formation of the central keel is connected with growth of shell, the valve gradually takes on a pyramidal outline, strongly arched along midline, laterally conspicuously depressed. With the growth of shell the convexity of the dorsal valve decreases in its umbonal portion. The gentle convexity of this valve noted in youngest individuals is stronger distally. As individual age advances, the valve becomes more flat along its complete length. Only a narrow strip retains the convex outline, encircling the apical portion of the valve and representing the obsolete protegulum.

Anterior margin of juvenile specimens is rounded and smooth. Upon the appearance of the ventral keel and the dorsal sulcus it is slightly arched towards the ventral valve. Sometimes this margin is undulatory, sometimes the elevation is trigonal (text-pl. II, fig. 1*d*-6*d*).

Radial ornamentation (text-pl. II, fig. 1*a,b*-6*a,b*; text-fig. 8). In specimens 0.5 mm long incipient radial plications are already present, extremely delicate at the antero-lateral portions of shell. The plicated portion is slightly raised and thus distinctly delimited from the remaining smooth surface of shell. On the ventral valve there are 11 plications; one of these, centrally placed, is the incipient keel. On the dorsal valve there are 12 plications, six on each side of the central sulcus.

On specimens about 1 mm long, the plications are readily discernible, much longer and narrower, with rounded ridges, expanding to the front. The wide furrows correspond to the thickness of plications. The number of the latter increases to 13 on the ventral valve and to 14 on the dorsal. Secondary plications appear by addition to each lateral slope of both valves. The central ventral plication divides dichotomously in its turn.

With the length of shell about 1.5 mm, a plication bifurcating like the central ventral one appears in the middle of the dorsal sulcus. Dichotomy of the central plication of both valves does not occur more than 2 or 3 times in the course of the whole growth of shell. The number of plications on both valves is not identical, but there may be as many as 27. Together with the increase of shell dimensions, new, secondary plications appear by addition on the side slopes of valves. Dichotomy of plications, the central excepted, is extremely rare. Dichotomy occurring on one valve finds its equivalent dichotomy at a corresponding place on the other valve. Radial ornamentation of the form here considered differs generally from that in other orthids since the plications of the former are always simple. Dichotomy (central plications excepted) is sporadic not only on the surface of one shell, but in all specimens of this species.

Gerontic stage

Shells of mature individuals do not attain considerable dimensions. Usually, gerontic characters make their appearance as early as shells from 5 to 6 mm long. Many instances have

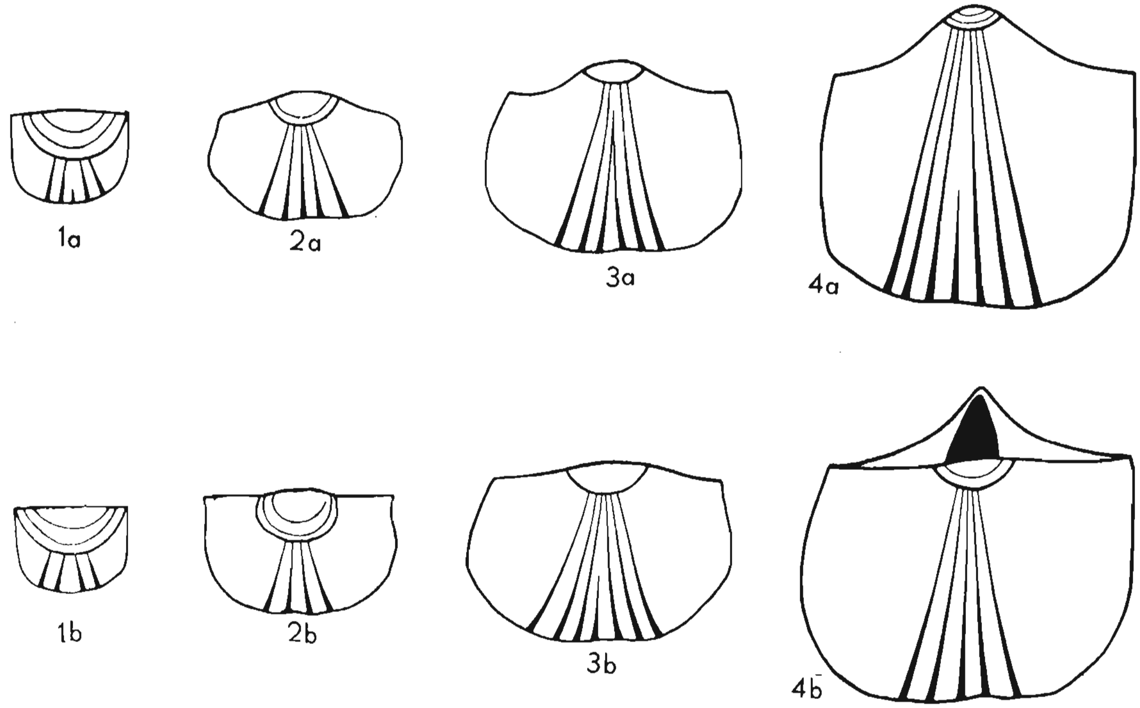


Fig. 8

Skenidium polonicum GÜRICH

1-4 four specimens in various growth stages, showing differentiation of plications in ventral fold (*a*) and in dorsal sulcus (*b*); × 10.

been noted of gerontic features present in specimens 3 mm long. In the first place the growth of shell dimensions stops, as well as that of the length of the ventral beak. An obsolete protegulum, as a narrow, thickened strip, persists at the apex of the ventral beak. The concentric growth lines along the antero-lateral margins have an imbricate arrangement. The ventral interarea is high, striated by distinct horizontal growth lines. In individuals in the gerontic stage, the dorsal protegulum very often becomes effaced, a semicircular depression only remaining.

Remarks. — *Skenidium polonicum* was first described by GÜRICH (1896, p. 237, pl. 10, fig. 3*a-b*, 14*a-b*). This new species was established on two single valves (ventral and dorsal) collected from Middle Devonian beds of Śniadka in the Holy Cross Mountains. The following features characteristic of *S. polonicum* are particulary noteworthy: small shell dimensions (length 5 mm, width 7 mm); pyramidal shape of ventral valve; high ventral interarea and high dorsal septum. No mention was made by Gürich of the spondylium, hence it is presumed that in his specimen it was missing.

On comparing Gürich's specimens with those here considered, their great resemblance seems very striking. It is expressed in similarities of shell dimensions, height of ventral interarea and internal structure (presence of cruralium and high dorsal septum). There is also a close similarity of radial ornamentation. In Gürich's description it is mentioned that his species have 16 thick costae, which do not divide; this is confirmed by his fig. 14a in pl. 10. This number of costae does not, however, seem constant, as is shown in his fig. 3a (pl. 10), giving an outside view of the ventral valve with more than 20 striae.

On specimens from Skały in the Holy Cross Mountains the number of plications ranges from 18 to 27. In most cases they are simple, and dichotomy has not been noted since it is of extremely rare occurrence.

Gürich does not give any information concerning the microstructure of *S. polonicum*. He only states that: «Die Schale ist anscheinend sehr fein perforiert», whence we may suppose that Gürich did not investigate the microstructure of shell by means of thin sections, since actually it is impunctate.

The resemblance between the above forms is so close that this writer has referred the Skały specimens to Gürich's species — *Skenidium polonicum*.

When comparing the above species with other forms of genus *Skenidium*, say with *S. insigne* Hall and *S. independense* Stainbrook, the occurrence is noted of many similar characters. The similarities are foremost those of internal structure, while the differences are mainly expressed in the smaller height of ventral interarea and the greater number of radial plications in *S. polonicum*. In this species the shell also displays a much stronger transversal elongation.

Suborder **DALMANELLOIDEA** Moore, 1952

Family DALMANELLIDAE Schuchert & Le Vene, 1929, emend. Bancroft, 1945

Genus **AULACELLA** Schuchert & Cooper, 1931

The type species is *Orthis eifeliensis* (Verneuil, 1850) from Middle Devonian beds of Germany and Poland (Holy Cross Mountains). As a rule referred to the family of Rhipidomellidae Oehlert, it was separated in 1931 by Schuchert and Cooper under the generic name of *Aulacella* Schuchert & Cooper. In the opinion of those authors, this genus displays external and internal similarities with such representatives of the family of Rhipidomellidae as *Rhipidomella* Oehlert and *Thiemella* Williams, as well as with forms of the family Dalmanellidae. On close similarities of the ventral muscle area and of dorsal cardinals, the systematic position of *Aulacella* is near *Dalmanella* Hall & Clarke and *Cariniferella* Schuchert & Cooper.

Aulacella resembles *Rhipidomella*: 1) in arrangement of the ventral adductors surrounded by diductors, the diductors in *Aulacella*, however, are less flabellate; 2) in external appearance of cardinals; they are strong and stout in relation to the small size of shell. According to Schuchert and Cooper, some resemblances may be noted also between *Aulacella* and *Thiemella*. The differences concern the cardinals and the central ridge dividing the ventral muscle area. In *Thiemella*, contrary to *Aulacella*, the cardinals are extremely delicate; the central ridge, extending from the front of the adductors beyond the centre of valve, is always direct and unforked (in *Aulacella* it may be considerably forked near the anterior margin of the diductors). This so-called «forked septum» was formerly believed to be of some diagnostic value for *Dalmanella* (*vide* SCHUCHERT & COOPER, 1932, p. 136).

The separation of the genus *Aulacella* on evidence supplied by *Orthis eifeliensis* VERNEUIL seems to be reasonably justified.

Aulacella eifeliensis (VERNEUIL, 1850)

(pl. I, fig. 10-15; pl. II; pl. III, fig. 9-10; pl. XII, fig. 1-2; text-pl. III; text-fig. 9, 10)

1850. *Orthis eifeliensis* n. sp.; M. de VERNEUIL, Note sur les fossiles..., p. 161.
1853. *Orthis eifeliensis* VERNEUIL; J. SCHNUR, Zusammenstellung..., p. 213, pl. 37, fig. 6a-c; p. 242, pl. 45, fig. 8.
1869. *Orthis eifeliensis* VERNEUIL; L. ZEUSCHNER, Geognostische Beschreibung..., p. 268.
1871. *Orthis eifeliensis* VERNEUIL; E. KAYSER, Die Brachiopoden..., p. 606, pl. 13, fig. 3a-b.
1895. *Orthis eifeliensis* VERNEUIL; E. HOLZAPFEL, Das obere Mitteldevon..., p. 295.
1896. *Orthis* (*Rhipidomella* OEHL.) *eifeliensis* VERNEUIL; G. GÜRICH, Das Palaeozoicum..., p. 241.
1896. *Orthis* (*Rhipidomella?* OEHL.) *subtetragona* n. sp.; G. GÜRICH, *ibid.*, p. 239, pl. 10, fig. 7a-e.
1896. *Orthis* (*Rhipidomella* OEHL.) *eifeliensis* var. *crassa* n. var.; G. GÜRICH, *ibid.*, p. 241.
1904. *Orthis* (*Rhipidomella* OEHL.) *eifeliensis* VERNEUIL; D. SOBOLEV, Devonskija..., **p. 66.**
1904. *Orthis eifeliensis* var. *crassa* GÜRICH; D. SOBOLEV, *ibid.*, p. 67, pl. 8, fig. 14-15.
1908. *Orthis (Rhipidomella) eifeliensis* VERNEUIL; F. R. C. REED, The devonian faunas..., p. 81, pl. 13, fig. 25, 26-a.
1908. *Orthis eifeliensis* VERNEUIL; K. TORLEY, Die Fauna..., p. 32, pl. 7, fig. 3-6.
1914. *Dalmanella eifeliensis* VERNEUIL; H. QUIRING, Zusammenstellung..., p. 121.
1932. *Aulacella eifeliensis* (VERNEUIL); CH. SCHUCHERT & G. A. COOPER, Brachiopod genera..., 122, pl. 19, fig. 7-8, 10-11, 13.

Material. — 8,000 shells (with both valves), 0.5 mm to 15 mm long, adult specimens (7 to 14 mm long) predominate; 420 ventral and 380 dorsal valves, the majority of the latter rather small, 2 to 5 mm long. All this material is well preserved.

Dimensions of 5 specimens of different growth stages *(in mm)*:

	1	*2*	*3*	*4*	*5*
Length	2.0	3.4	8.5	11.7	15.0
Width	2.3	4.3	9.0	12.3	16.0
Thickness	1.2	2.0	4.3	6.0	9.6

Description. — *External morphology*. Shell small, almost equally biconvex, subquadrate, usually wider than long; greatest convexity near the hinge-line; hinge-line straight and considerably less than greatest width of shell which occurs near the middle; hinge angles and antero-lateral margins rounded; anterior margin uniplicate.

Ventral valve (pl. III, fig. 9 *b*, 10) somewhat larger than the dorsal, most convex in umbonal portion; antero-central portions near margins somewhat depressed; beak small, strongly incurved; interarea low, curved beneath beak; trigonal delthyrium open; median fold low, usually indistinct at beak.

Dorsal valve (pl. III, fig. 9*a*) about as convex as the ventral, but more equally along its length; interarea very low, gently curved; beak small, slightly projecting; notothyrium low, broad, nearly filled by cardinal process; a shallow sulcus present, sometimes barely distinguishable.

Exterior of both valves marked by numerous radiating costulae distinctly rounded; in the central and anterior portions they are slightly fasciculate and increase by division; furrows flat, occasionally much larger than the costulae. On summits of the costulae may be circular tubules, most numerous near front margin; in the umbonal portion oval. They occur at the intersection of radial costulae with concentric growth lines, the latter are somewhat raised above the ridges of costulae in mature specimens, particularly so in old individuals.

Concentric growth lines, numerous and conspicuous on adult shells, are densely arranged along the antero-lateral margins of old specimens (pl. II, fig. 11 *d*, 12 *d*).

The shell is distinctly and minutely punctate. The circular punctae are readily discernible on the outer and inner shell surfaces. Their arrangement on the shell is nearly regular (pl. XII, fig. 2).

Internal morphology (pl. I, fig. 10-15). Ventral valve with large teeth strongly upcurved; dental plates thick, merging anteriorly with a low ridge bordering the muscle area; shape of muscle area varying, sometimes reaching beyond the midlength of valve and medially separated by a moderate septal ridge of varying length; this ridge present but not always distinct, terminating at the anterior of muscle area or extending distally (towards the apical cavity); adductors small, generally distinct, bordered by delicate ridges; these scars are elongate, narrowing at both distal ends to a spindle-like shape, with maximum width at middle of median ridge or in its distal portion; diductors large, strongly variable, occupying nearly the entire muscle area. Scars of the pedicle ligaments distinct, in the apical portion of valve preserved as a very strong, transversely striated triangular platform; scars of gonads not always preserved, sometimes occupying the major part of the internal surface of valve on both sides of the muscle area; pallial sulcus hardly discernible, often one or two pairs extending from the front of the muscle area, bifurcating anteriorly (pl. I, fig. 11).

Dorsal valve (pl. II, fig. 13-15). Cardinal process well developed, stout, undivided; brachiophores short, stout, divergent; brachiophore plates stout, sockets deep, narrow; in old shells fulcral plates distinct; muscle area mostly subquadrate, small, seldom reaching middle of valve; anterior adductors as a rule distinctly separated from the posterior, a forked median ridge present, with slightly flattened summit, expanding and rising at a small distance from the cardinal process and terminating near the front margin; scars of gonads and adductors not preserved.

Variability. — Individual variability is strong and covers nearly all features of external and internal morphology.

Relatively extensive variation in the width of shell is displayed by mature individuals, 9 to 14 mm long, as has been investigated in over thirteen hundred specimens. The width index, i. e. width/length of shell ratio, ranges from 0.9 to 1.3. Detailed numerical data are as follows:

Width index	Number of specimens	Per cent
0.9	14	1.1
1.0	387	29.3
1.1	827	62.6
1.2	83	6.3
1.3	9	0.7

The above variation diagrammatically expressed is an unimodal curve.

Similar variations are observed among young individuals whose dimensions range as follows: length 2.3—5.5 mm, width 3.7—6.5 mm, thickness 1.4—2.8 mm. 200 suitable specimens have been measured, nevertheless in comparison with the adults the differences are rather small. The following numerical data have been obtained:

Width index	Number of specimens	Per cent
1.0	2	1.0
1.1	59	29.5
1.2	122	61.0
1.3	17	8.5

In specimens with dimensions given above, individual variability is slightly smaller, ranging from 1.0 to 1.3. Width index in the majority of specimens is at 1.2, i. e. 0.1 higher than that shown by mature specimens where it is 1.1. In graphs the variability of this feature is expressed as an unimodal curve similar to that in mature specimens. Particularly strong variability of the thickness of shell is characteristic for adult individuals, as has been shown by measuring 1,510 specimens. Index of thickness, i. e. thickness/width of shell ratio, shows a wide range from 0.3 to 0.9 as given below:

Thickness index	Number of specimens	Per cent
0.3	6	0.4
0.4	147	0.7
0.5	748	49.5
0.6	546	36.2
0.7	56	3.7
0.8	4	0.3
0.9	3	0.2

The majority of specimens are grouped at the 0.5 index. The variation curve of this feature is unimodal but asymmetrical.

In opposition to mature individuals, the thickness of young specimens with length from 2.3 to 5.5 mm is more constant. Here the thickness index, as measured in 200 specimens, ranges from 0.4 to 0.5 only. Shells with 0.4 index are dominant, constituting 53 per cent (106 individuals) of the total. The remaining 94 specimens, i. e. 47 per cent of the total, are grouped at the 0.5 index.

Five principal types of shell outline, each one represented by numerous specimens, may be differentiated. They are: 1) subcircular, length of shell almost equal to shell width, hinge angles rounded and faintly conspicuous, lateral margins slightly divergent anteriorly; 2) subquadrate, length of shell equal to shell width, hinge and antero-lateral angles moderately distinct, lateral margins nearly parallel; 3) longitudinally rectangular, shell slightly longer than wide, hinge and antero-lateral angles distinct, lateral margins almost parallel or slightly divergent anteriorly; 4) distinctly pentagonal, maximum shell width approximately at the level of hinge angles and decreasing anteriorly, hinge and antero-lateral angles obtuse; 5) transversally rectangular, shell occasionally wider than long, hinge and antero-lateral angles obtuse or forming right angle, lateral margins slightly divergent outwards or nearly parallel.

Maximum shell width is usually nearer the middle, rarely slightly anterior, or at the level of the hinge-line.

In adult specimens there occur many transitions from an almost straight anterior margin to strongly sinuous (pl. II, fig. 5*d*-10*d*). The presence of a dorsal sulcus or ventral fold does not have much bearing on the shape and distinctness of the sulcus of the anterior margin. The fold and the sulcus are generally indistinct. Anterior margin may be: 1) wide and low but gently sinuous, not always distinctly, sometimes barely indicated; 2) narrow, arcuately sinuous, of varying width, occasionally only half that mentioned above; 3) with narrow, subtrigonal sulcus.

The cardinal process and the muscle area (ventral particularly) are internal elements showing moderately strong individual variation.

The cardinal process (fig. 9) in young individuals, 2-3 mm long, usually has a constant appearance in the form of a short stout ridge. In mature individuals it is more or less trigonal. Distally it narrows to the width of the dorsal apical cavity, anteriorly it widens out. The varying

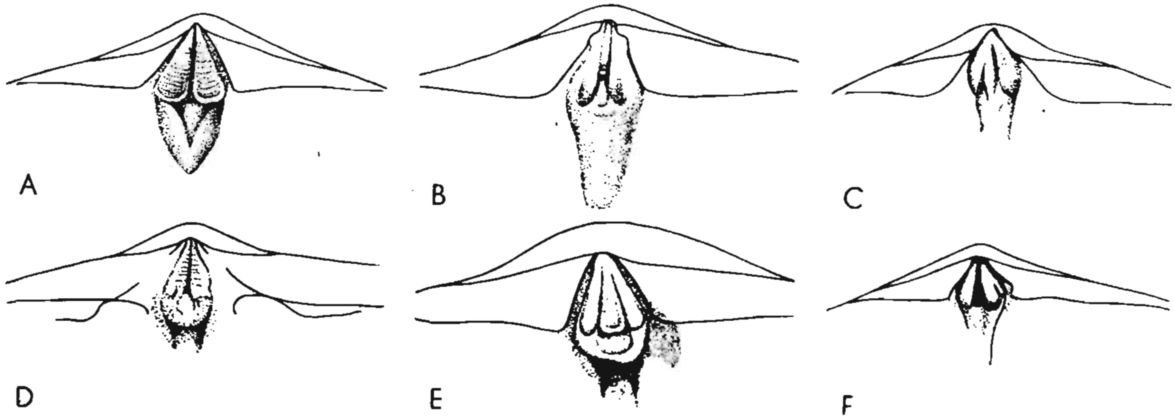


Fig. 9
Aulacella eifeliensis (VERNEUIL)
A-F variations of cardinal process in mature specimens; × 20.

appearance of the cardinal process results from: 1) its various width, in most cases suited to the width of the notothyrium; 2) its variable length; 3) varying development of the distal surface of the cardinal process, with superficial incisions giving a bi- or trifid appearance to the cardinal process which is actually single; 4) frequent distinct asymmetry in the shape of the cardinal process; 5) development of the myophore portion of the cardinal process.

The length of the ventral muscle area varies in relation to length of the ventral valve. It is either one-half that of the entire length of valve, less than that, or in excess of it. On the other hand, the relation of its width to the width of the ventral valve is almost constant, always less than half the shell width. The width of the muscle area itself is fairly variable, varying from 3 to 5 mm, in most cases 4 mm. The muscle area, particularly distinct in mature and old individuals, has a strongly variable shape, from regularly longitudinally oval to conspicuously flabellate (pl. I, fig. 10-15). On the whole, two principal types of the size of the muscle area may be differentiated: 1) more or less oval, 2) more or less flabellate.

Numerous gradual transitions are observable. The muscle area is separated from the remainder of shell surface by thick distinct ridges. These may be without any lateral incisions, or be more or less undulate. Asymmetry in shape of muscle area is frequent. Its general appearance and particular dimensions may differ on both sides of the septal ridge. The ridge surrounding the muscle area may, on one side, be more arcuate or straight, or more or less distinctly undulate.

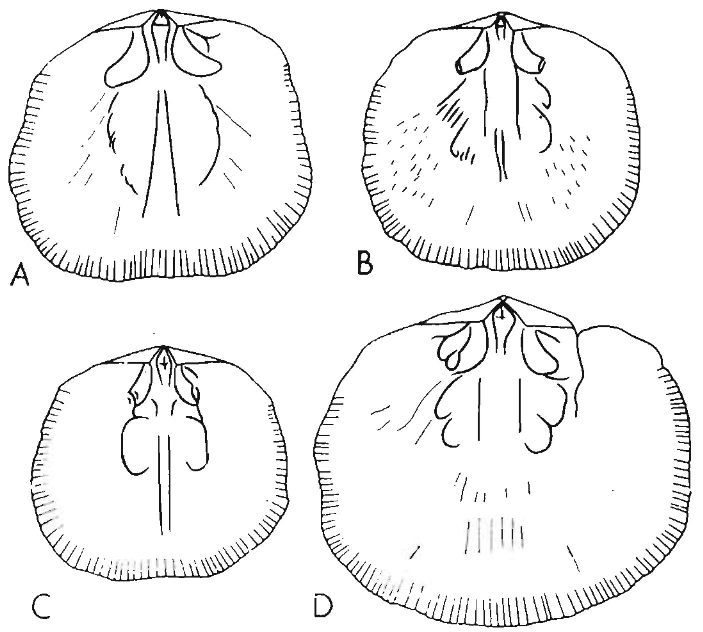


Fig. 10

Aulacella eifeliensis (VERNEUIL)

A-D four interiors of the mature dorsal valves, showing variations of muscle area; × 3.5.

The thickness of these ridges is associated with individual age of specimens. In old specimens they are very thick. In young specimens, about 4 mm long, they are thin.

Dorsal muscle area (pl. II, fig. 13-14; text-fig. 10) is less distinct than the ventral. Often muscle scars are slightly impressed, even in mature individuals. On the whole, the muscle area may be subquadrate, without important oscillations. A certain variability, however, does occur primarily in the size ratio of the posterior adductors to that of the anterior. The posterior adductors may be smaller than the anterior (in most cases), or they may be larger, or finally of equal size to the anterior adductors. In a large number of valves the anterior adductors are not clearly separated from the posterior on one side of the septal ridge or on both.

Ontogeny (pl. II, fig. 1-12; text-pl. III). — The youngest individual is 0.46 mm long. Every ontogenetic stage, the first one excepted (3 specimens), is represented by numerous specimens in the material investigated. Mature and old individuals are, however, the most abundant.

The successive growth stages, distinguished in the sequence of the development of internal and external features, are:

1) length 0.46 to 1 mm — radial costulae incipient, gradually developing into distinct, long costulae; pedicle foramen round, small;

2) 1 to 3 mm — secondary costulae present on lateral slopes of valves; internal elements such as ventral teeth, cardinal process and brachiophores present; dorsal sulcus incipient;

3) 3 to 7 mm — radial ornamentation differentiated owing to dichotomy of primary costae; ventral valve from its midlength somewhat curved towards the dorsal;

4) 8 to 12 mm — slow increase of shell dimensions, few new radial costulae appear; growth lines gradually more distinct at the front of shell;

5) 12 to 15 mm — shell thickness increases, strong concentration of growth lines along the antero-lateral margins.

Shell, about 0.5 mm in length, is exteriorly very similar to *Isorthis canalicula* (SCHNUR). The differentiation of *Aulacella eifeliensis* in its external and internal features is very rapid. Specimens 1 mm long being already very much like mature individuals. The main difference between young individuals of *Aulacella eifeliensis* and those of *Isorthis canalicula* consists in the number of central costulae on both valves. In *Aulacella* two central ventral costulae are present and one in *Isorthis*. On the other hand, there is one central dorsal costula in *Aulacella eifeliensis*, and two — in *Isorthis*.

Description of the smallest specimen

Dimensions: length 0.46 mm, width 0.53 mm.

Shell wider than long, in section equally ventri-biconvex; ventral valve more convex, a little above the hinge-line, the dorsal slightly below the hinge-line (towards the middle); outline subquadrate; hinge-line straight, shorter than maximum width of shell which occurs near the centre; both beaks slightly incurved, the ventral more so; ventral interarea low, rather indistinct, the dorsal slightly indicated; pedicle foramen round, encroaching on the delthyrium and notothyrium; hinge angles and antero-lateral margins rounded, anterior margin straight; incipient radial ornamentation expressed as plicated marginal shell portion.

Features changing during ontogeny are few; the chief are: 1) shape of pedicle foramen in connection with differentiation of the delthyrium and notothyrium and with growth or both beaks; 2) convexity of valves; 3) cardinal process; 4) radial ornamentation; 5) anteriof margin; 6) size and shape of ventral muscle area.

The following are constant features, not subject to any major variation: 1) subquadrate outline of shell; 2) width/length ratio; 3) ventral beak always larger than the dorsal; height of both beaks only occasionally equal; 4) straight hinge-line, always shorter than maximum shell width; 5) presence of one dorsal central costula and of two ventral costulae.

The last of the characters mentioned is very important, facilitating the identification of young individuals of this species.

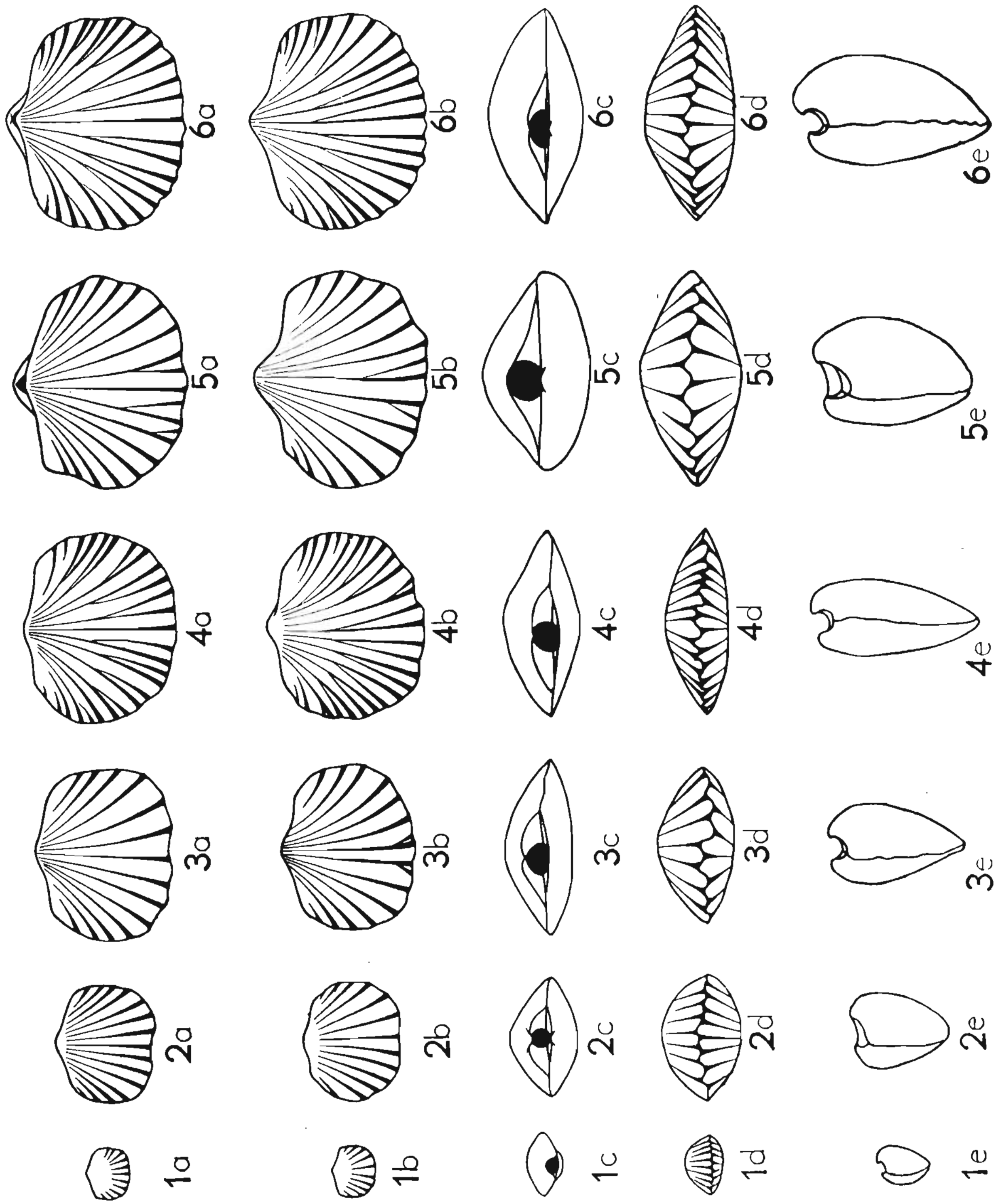
Changing features in ontogeny

Pedicle foramen-delthyrium (text-pl. III, fig. 1*c*-6*c*). In the young stage (length about 1 mm), when the shell is strongly ventri-biconvex, the pedicle foramen is round, relatively small, though encroaching on the delthyrium and notothyrium. Its size is closely connected with the height of the ventral interarea. With general growth of shell, in specimens up to 2.5 mm long, the foramen is initially suboval, remaining broadly rounded beneath the beaks. When the notothyrium is differentiated, the foramen is confined to the ventral valve only. Gradually, in specimens with length up of 3 mm, it becomes slightly subtrigonal, narrowing beneath the ventral apex with the lateral margins slightly curved outwards. With further growth of shell the delthyrium becomes decidedly trigonal. It is low, basally broad and always open.

Convexity of valves (pl. II, fig. 1*c*-12*c*; text-pl. III, fig. 1*e*-6*e*). In young specimens, about 1.5 mm long, the shell is strongly and uniformly ventri-biconvex. Gradually but slowly it becomes biconvex. On the whole, the shell remains biconvex throughout the life of the individual. Dorsi-biconvex shells are very rare. The maximum convexity of the shell occurs at about the level of the hinge-line, sometimes beneath it. In connection with changes in convexity of the shell, we may, in the first place, note the reduced ventral convexity. Its lateral view may change too. Initially, the strongest convexity is in the umbonal portion of the valve; subsequently, in older individuals, at the level of the hinge-line. Starting from the midlength, towards the front, the ventral valve slowly flattens out, sometimes quite extensively; in some cases it is medially incurved dorsally. In older individuals, owing to the considerable increase in thickness, the ventral valve again becomes almost uniformly arched throughout its length.

During growth the convexity of the dorsal valve does not change very much, only increasing gradually together with the growth of shell. The dorsal sulcus has no influence on the convexity of this valve. It starts as a narrow and distinct furrow at a distance of 0.5 to 1 mm from the apex. Anteriorly it flattens out, sometimes disappearing altogether.

TEXT-PLATE III



Aulacella eifeliensis (VERNEUIL)

Series of six successive growth stages, from five aspects: *a* dorsal, *b* ventral, *c* hinge-line, *d* anterior margin, *e* lateral; × 10 approx.

Similar changes of convexity of shell were noted by BOLKHOWITINOVA (1928, p. 275) in *Rhipidomella* aff. *cora* D'ORBIGNY. Namely, young specimens of this form were nearly uniformly convex. In specimens about 0.7 mm long the convexity of the ventral valve is reduced (1928, pl. 8, fig. 4), whereas mature individuals may again become almost biconvex or dorsi-biconvex.

To sum up, the strongest convexity is observed in the neanic-ephebic stage. In adult and gerontic stages the shell convexity approaches that of young individuals (nepionic stage).

The *cardinal process*, with length of shell approximately 2-3 mm, has the appearance of a low and distinct ridge, uniformly thick over its entire length. It runs throughout the length of the notothyrial cavity, its height increasing slowly. At first, it attains half the depth of the notothyrial cavity, and gradually reaches the level of the dorsal interarea. With length of shell at about 3 mm, the cardinal process rises above the surface of the interarea. Its anterior end projects up, the posterior portion being considerably lower. In some specimens the entire upper surface of the cardinal process is raised above the interarea.

The cardinal process becomes thicker with the growth of shell, particularly basally. It fills in one-third and never more than two-thirds of the notothyrial width. Starting from the length of shell at about 4-5 mm, it gradually becomes trigonal, distally greatly narrowed, widening out anteriorly. Its anterior margin is generally rounded. In older individuals, with length of shell 6-7 mm, it is already distinctly trigonal. In adult specimens it often displays asymmetry. It is not always trigonal, being sometimes irregularly developed.

The cardinal process remains single throughout its ontogeny. In adult specimens it is apparently bi- or trifid owing to the presence of surficial incisions. They occur as shallow furrows when the length of shell exceeds 3 mm. These furrows, particularly in mature and old individuals, strongly influence the outer appearance of the cardinal process, which is sometimes very variable.

Radial ornamentation (text-pl. III, fig. 1*a*,*b*-6*a*,*b*). Shells, about 0.5 mm in length, have their marginal portions plicated. There are ten ventral plications, two of which are central, and eleven dorsal plications with one central in the sulcus which is formed, with length of shell about 1 mm.

The first secondary costae appear on the lateral slopes of both valves, 1 to 3 on each slope. Specimens, about 1.2 mm long, have 12 to 16 ventral costulae, 12 or 14 being most frequent. On the dorsal valve there occur from 13 to 17, but the latter number is very rare.

Additional secondary costulae appear by dichotomy on shells about 2 mm long. On the ventral valve we may note almost simultaneous dichotomy from the outer sides of two central costulae, on the dorsal valve — from the inner sides of the central. The remaining primary costulae on both valves successively divide dichotomously.

Specimens 2 mm long usually bear from 16 to 18 ventral costulae, and 17 to 19 dorsal. With length of shell at about 3 mm there are usually 26 ventral costulae and 25 dorsal. On specimens 8.5 mm long their number has increased to 48-50 on the ventral and to 47-49 on the dorsal valve. Finally, on specimens 12 mm long there are 54-56 ventral costulae and 50-52 dorsal ones. Further additional costulae do not, as a rule, appear; if so, only very seldom, on the lateral slopes of shells. On the whole, there is no intercalation; if so, it is very rare.

In most cases, the central dorsal costula remains undivided throughout ontogeny. Only sometimes, with length of shell at 9 mm, it divides at the anterior margin, in a similar way to the two central ventral costulae. Dichotomy on the inner sides of these costulae is very rare. The furrow separating these central costulae is fairly deep and conspicuous and of almost uniform width over its entire length.

Radial costulae in adult individuals are not all of the same height. Both primary and secondary costulae, formed during the early stages of ontogeny, differ in height from those in later stages. These differences are gradually effaced, but not before the gerontic stage when ornamentation is fairly uniform.

Radial ornamentations, present on the outer shell surface, are reflected on the inner surface in specimens 1.5 to 2.5 mm long.

Radial microstriae and concentric microlines are observable over very small portions of the shell only. They are like extremely fine threads discernible only under very strong magnification.

Microstriae, in most cases one only, extend along the middle furrows. Sometimes there are 2 to 4. When present, they are arranged over the lateral sides of the normal radial costulae. Concentric microlines run zigzag over the entire width of shell, both along the sides and ridges of radial costulae, and of furrows. They are aggregated fairly regularly between two concentric growth lines and number about 12 to 14 on 1 mm of shell surface. Naturally, this number varies but this is difficult to ascertain since the microlines have been preserved only over very small portions of the shell. A VANDERCAMMEN (1954) believes them to be important individual age markers. Similar, so-called «concentric microcostules» have been observed by him in Frasnian spirifers.

Gerontic stage (pl. II, fig. 10-12)

The number of individuals belonging to the advanced gerontic stage is small, barely 40 out of a total of 8,000 specimens. They are of various size, from 6 to 15 mm long. The main features of this stage are as follows: 1) strong convexity of both valves, the lateral view of shell is subglobose; 2) very dense arrangement of concentric growth lines along the antero-lateral commissures; that portion of shell is up to 5 mm in thickness, with length of shell at 14.5 mm and its general thickness up to 11 mm; the valve here attains a thickness of 2 mm; 3) almost complete obliteration (through effacement) of radial ornamentation on the slopes and umbonal portions of the shell; sometimes there are vestiges of radial ornamentation as fine radial lines; 4) sometimes, owing to strong convexity of shell in its anterior central portion, the dorsal sulcus disappears almost completely; it is, however, always discernible on the umbonal portion; 5) thickening of both beaks, strongly incurved; 6) all internal elements thick as a result of the superposition of new layers; the presence of fulcral plates is a distinctly gerontic feature.

Remarks. — GÜRICH (1896) and SOBOLEV (1904, 1909) have given fairly accurate descriptions of *Orthis (Rhipidomella) eifeliensis* VERNEUIL from the Devonian of the Holy Cross Mountains. Among specimens of this species, two new additional varieties were separated by GÜRICH on the evidence of what are now regarded as unimportant differences. One of them, collected in abundance from the «brachiopod shale» beds at Skały in the Holy Cross Mountains he called *Orthis (Rhipidomella) subtetragona*. This species is characterized by a semiquadrate outline. All its other features agree with those of *Aulacella eifeliensis* (VERNEUIL), as has been confirmed by GÜRICH (1896, p. 240). The outline of *Orthis (Rhipidomella) eifeliensis* var. *crassa* GÜRICH coincides with that of *Aulacella eifeliensis* (VERNEUIL), only the sulcus is more distinct, and the radial costulae apparently more delicate. Unfortunately, this variety was not figured by GÜRICH. In spite of the abundance of material GÜRICH did not take into consideration the strong individual variability of this species.

SOBOLEV (1904, p. 66) described *Orthis subtetragona* GÜRICH from the section of Grzegorzowice-Skały. He reported its close resemblance to *Aulacella eifeliensis* stating that the recognition of *Orthis subtetragona* GÜRICH was difficult. SOBOLEV moreover added that the separation of a new form cannot be based on one feature only, particularly on the shell outline which is subject to strong variations. *Orthis eifeliensis* var. *crassa* — GÜRICH's new variety — was however accepted by SOBOLEV. Illustrations of this variety (1904, pl. 8, fig. 14-15) show no differences from *Aulacella eifeliensis* (VERNEUIL). Thus both forms: *Orthis (Rhipidomella) subtetragona* GÜRICH and *O. (Rhipidomella) eifeliensis* var. *crassa* GÜRICH are referable to the same species — *Aulacella eifeliensis* (VERNEUIL).

In 1909 SOBOLEV placed *O. (Rhipidomella) eifeliensis* VERNEUIL and *O. (Rhipidomella) subtetragona* GÜRICH in the genus *Dalmanella* on the similar development of the dental plates merging anteriorly with ridges bordering the muscle area, scars of gonads and arrangement of pallial sinuses.

Specimens of *Aulacella eifeliensis* from the Holy Cross Mountains are identical with those from the Eifel Mountains in Germany, as has been ascertained by investigation of comparative material.

M. A. STAINBROOK (1945) described *Aulacella infera* (CALVIN) (p. 15-16, pl. 1, fig. 19-28) from the Devonian beds of North America in Iowa. This species displays a few internal and external similarities with *A. eifeliensis* from Poland, namely in the shell outline, character of ornamentation, absence of distinct ventral fold and dorsal sulcus, and a little in shape of the muscle area in both valves.

Aulacella eifeliensis is very common in the upper *Calceola* and crinoidal beds of the Eifel Mountains in Germany, the *Calceola* beds in Belgium, Middle Devonian in Spain and in Poland.

Family MYSTROPHORIDAE SCHUCHERT & COOPER, 1931

Genus **KAYSERELLA** HALL & CLARKE, 1892

This genus is poorly differentiated both numerically and specifically. So far only two spe cies, of scanty occurrence, are known. They are: *Kayserella lepida* (SCHNUR, 1853) from the crinoidal beds of Germany and Poland, and *Kayserella americana* (COOPER, 1955) from the Marcellus formation of North America, which is an equivalent of the Middle Devonian beds of Europe.

In 1853, SCHNUR described *Orthis lepida*, a new species from the limestone beds of Pelm and Gerolstein (p. 218, pl. 45, fig. 9a-b). His diagnosis of this species was succinct and restricted to external morphology only.

In 1871 (p. 617) KAYSER identified three species described in 1853 by SCHNUR, namely: *Orthis testudinaria* (p. 212, pl. 37, fig. 3), *O. plicatella* (pl. 38, fig. 4) and *O. lepida* (p. 218, pl. 45, fig. 9a-b), differring from the two former. He united them under the name of *Streptorhynchus? lepidus*.

In 1892, HALL and CLARKE established the new genus *Kayserella* for *Streptorhynchus? lepidus*.

In 1955, COOPER pointed out the lack of resemblance between *O. lepida* SCHNUR, *O. testudinaria* SCHNUR and *O. plicatella* SCHNUR, but stressed the connection between *O. lepida* and *Mystrophora*, in the presence of a high dorsal septum, a bifid cardinal process and, most important, a cruralium. According to COOPER, small differences between these forms are seen in the outline of shells and in the lack of a short dorsal septum in the first form. On SCHNUR's types of *O. lepida*, COOPER based his detailed diagnosis of *Kayserella lepida* (SCHNUR) on the external and internal morphology of this form (1955, p. 47). *Mystrophora* is very similar to *Kayserella* in internal structure and in the punctation of the shell. The assignment of *K. lepida* (SCHNUR) to the family of Mystrophoridae SCHUCHERT & COOPER thus seems reasonable.

Kayserella is rather rare. Shells of *K. lepida* (SCHNUR) found in Poland are also very scanty. Hence no studies could be made of the individual variability and ontogeny of this species. The youngest specimens, 2.5 mm long, are already completely differentiated internally and externally. They, therefore, closely resemble adult specimens, 5 mm long. Old individuals, even in the beginning of the gerontic stage, are lacking. Hence it is difficult to determine in adult individuals of greatest dimensions (5 mm long) whether the growth process has terminated or not.

Kayserella lepida (SCHNUR, 1853)

(pl. III, fig. 1-8; pl. XI, fig. 1; text-fig. 11)

1853. *Orthis lepida* n. sp.; J. SCHNUR, Zusammenstellung..., p. 218, pl. 45, fig. 9a-b.
1871. *Streptorhynchus? lepidus* KAYSER; E. KAYSER, Die Brachiopoden..., p. 6r8.
1892. *Kayserella lepida* SCHNUR; J. HALL & J. M. CLARKE, An introduction..., p. 259.
1896. *Skenidium fallax* GÜRICH; G. GÜRICH, Das Palaeozoicum..., p. 236, pl. 10, fig. 9.
1955. *Kayserella lepida* SCHNUR; G. A. COOPER, New genera..., p. 46, pl. 11-b.
1896. [non] *Kayserella lepida* SCHNUR; G. GÜRICH, Das Palaeozoicum..., p. 234, pl. 10, fig. 4.
1904. [non] *Kayserella lepida* SCHNUR; D. SOBOLEV, Devonskija..., p. 61, pl. 8, fig. 5, 5a, 6, 7, 7a, 8, 8a.
1909. [non] *Kayserella lepida* SCHNUR; D. SOBOLEV, Srednij devon..., p. 453.

Material. — 40 complete shells with both valves, 1 dorsal and 1 ventral valve. All the specimens have small dimensions and mostly represent mature individuals with length of shell from 2.5 to 5 mm. There are no old individuals. All the material is well preserved.

Dimensions of 4 specimens *(in mm)*:

	1	*2*	*3*	*4*
Length	2.8	3.5	4.5	5.0
Width	3.6	4.7	5.7	7.3
Thickness	1.6	2.0	2.0	2.2
Length of hinge-line	3.2	4.3	5.0	6.5

Description. — *External morphology*. Shell nearly plani-convex, wider than long; outline semioval or semicircular; hinge-line straight and long, but shorter than maximum shell width; hinge angles in most cases slightly obtuse; antero-lateral margins well rounded, anterior margin sometimes gently sinuous.

Ventral valve (pl. III, fig. 6g-h, fig. 8). In lateral view gently arched, with maximum convexity in the umbonal portion; beak large, gently incurved; interarea high, slightly concave; delthyrium large, trigonal; a keel-like elevation present, not always readily discernible, often disappears anteriorly; both slopes of valve strongly flattened.

Dorsal valve (pl. III, fig. 6*f*). Umbo weakly convex, beak short, slightly incurved; valve nearly flat, gently convex in the umbonal portion, the front centrally depressed owing to the faint mesial sulcus.

Ornamentation (pl. III, fig. 6*f-h*, fig. 8). Radial costulae numerous, minute but fairly distinct, with rounded ridges; furrows narrow and not very deep. Fasciculate arrangement of striae as in *Phragmophora* and *Isorthis*. In these fascicles primary striae always more distinct and higher than the secondary. Arrangement of primary costae on the youthful portions of both valves agrees with that in *Isorthis*, i. e. apical portions of shell are smooth, the costae originate at a distance of about 0.3 to 0.4 mm from both apices. On the ventral valve 9 primary costae, the central one constituting the incipient fold, the remaining 8 costae arranged on its two sides. Two secondary costae bifurcate on each side of the central at about 0.5 to 0.6 mm from the apex, the next two at about 0.7 mm from the apex.

Distance from apex *(in mm)*	Number of costae	
	ventral valve	dorsal valve
1.0	20	21
2.4	25	26
2.8	31	30
3.0	40	40
3.6	42	42
3.8	46	46
4.2	52	54

On the dorsal valve there are 8 primary costae, 4 on each side of the sulcus. The sulcus deep, of nearly uniform width throughout its length, gradually delimited by secondary costae which increase twice by intercalation and a third time by dichotomy.

New secondary costae appear first by addition on the both slopes only, and on the remaining shell surface by dichotomy of the already existing costae. Primary costae divide several times symmetrically throughout shell growth. On ventral valves secondary costae bifurcate first on the outer and later on the inner sides of primary costae. On dorsal valves it is the other way about. Dichotomy of secondary costae often occurs too, but mostly once only.

The costae increase proportionately with the growth of shell. The numbers of costae at various distances from the ventral and dorsal apex are given above.

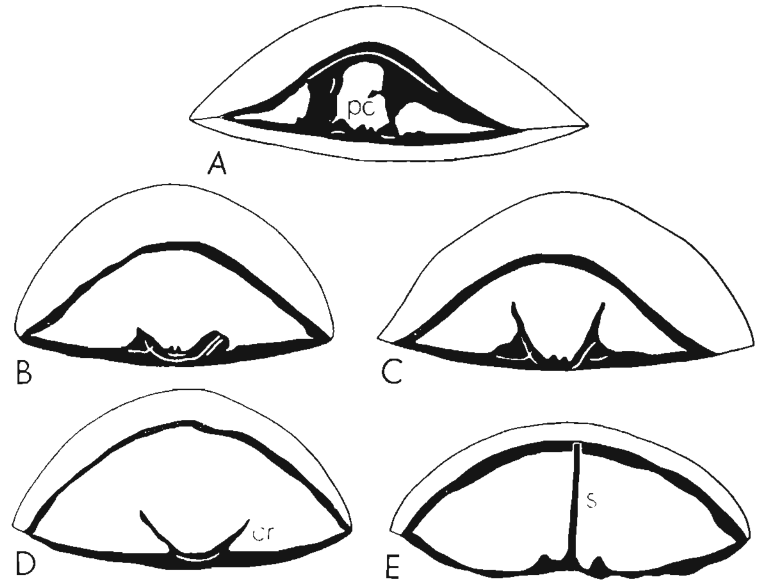


Fig. 11

Kayserella lepida (SCHNUR)

A-E series of five thin cross sections, showing internal structure of mature individual; × 10

cr cruralium, *pc* cardinal process, *s* dorsal septum.

Variation in the number of costae on both valves is small. Concentric growth lines are rarely discernible. If so, they are delicate and never more than two.

The shell is punctate. The punctae are mostly round, minute and abundant. Owing to the scarcity of specimens, only few thin sections have been made. Fig. 1 in pl. XI illustrates punctae on the anterior margin of valve. They have also been noted in transverse thin sections. The shell of *Kayserella lepida* is thin, and generally impregnated with iron oxides which often fill every depression. This has led to incorrect interpretations of the punctae.

Internal morphology (text-fig. 11). Ventral valve. Teeth relatively large, dental plates short, muscle area mostly confined to the apical cavity, not conspicuous; scars of diductors and of the slightly broader adductors faint.

Dorsal valve (pl. III, fig. 7). Notothyrium broad, cardinal process bifid, projects into notothyrium, myophore portion indistinct; sockets deep; brachiophores well developed, strongly divergent, anteriorly narrowing, supported by crural plates constituting the cruralium; cruralium long, extending beyond the midlength of valve, subtrigonal, septum thin, high, trigonal in lateral view, arising below the cardinal process, highest at midlength of valve, terminating nearly at the anterior margin where its height is greatly reduced; adductor scars not known. Cooper (1955, p. 47) supposed that in *Kayserella americana* Cooper the adductors were attached to the septum. It is, however, possible that in *K. americana* Cooper and in *K. lepida* they were attached to the cruralium. Unfortunately, this could not be proved owing to lack of detached dorsal valves of *K. lepida*.

Remarks. — External resemblance of our species from Middle Devonian beds of Poland to *Kayserella lepida* (Schnur) from the crinoidal beds of Germany (Eifel, Gerolstein) shows that it belongs to the same species. This is confirmed by data from the literature as well as by comparison with the original specimens of *Streptorhynchus? lepidus* from Kayser's collection in Berlin. The Polish and German specimens of this species are identical in dimensions, outline, character of ornamentation and of the umbonal portions. They differ in the length of cruralium. In the Polish specimens it is long, extending beyond the midlength of the dorsal valve, while in the German specimens it is markedly shorter, not even attaining the midlength of valve. This is also shown in Cooper's pl. 11-B, fig. 22-23 (1955), probably figuring one of Schnur's original specimens. On the strong individual variability of most of the internal and external features of all the studied orthids, it may be inferred that the length of the cruralium in *Kayserella lepida* (Schnur) also varies considerably. The above difference is, therefore, probably referable to individual variability. Unfortunately, lack of specimens has hindered investigation of the internal morphology of the Polish and German specimens.

In 1896, from the marly beds of Śniadka, Gürich described and figured (p. 236, pl. 10, fig. 9) *Skenidium fallax* Gürich, showing the close similarity of this species with *Kayserella:* «Dem Habitus nach stehen dieselben den vorher genannten Arten von *Kayserella* sehr nahe». Also the interior of the dorsal valve of *S. fallax* is identical to that of *K. lepida*. A similar form was described by Sobolev (1904, p. 63-64; 1909, p. 455) once as *S. fallax* Gürich and again as *S. areola* Quenstedt, unfortunately, without figures.

Specimens of *K. lepida* Schnur from Poland slightly differ from those of *K. americana* Cooper, the latter is more rounded, radial costae slightly coarser and ventral keel more distinct.

Kayserella lepida occurs within the crinoidal Middle Devonian beds of Germany (Eifel, Gerolstein) and of Poland (Holy Cross Mountains).

Family ONNIELLIDAE Öpik, 1933

Genus **PHRAGMOPHORA** Cooper, 1955

Phragmophora is represented by one species only, described from the crinoidal Middle Devonian beds of Germany (Eifel Mountains, Gerolstein) and from the Givetian of the Holy Cross Mountains in Poland.

This form is interesting owing to the presence of a covered delthyrium which is an uncommon feature in Devonian orthids. Since 1892 (Hall & Clarke, p. 259) to 1955 (Cooper, p. 46) this species has been erroneously recorded as *Kayserella lepida* (Schnur).

The systematic position of this form was a difficult question.

Kayser in 1871 described it as *Streptorhynchus? lepidus* Schnur on the presence of a ventral «pseudodeltidium».

Kozłowski (1929, p. 38) has questioned the placing of «*Kayserella lepida*» (recte *Phragmophora schnuri*) in the Strophomenacea. He proved the shells of all Strophomenacea to be impunctate, whereas those of «*Kayserella lepida*» are punctate as in the punctate orthids.

According to Schuchert and Cooper (1932, p. 132, pl. 16, fig. 7, 8, 10). «*Kayserella*» is near *Dalmanella* mainly in the punctation of the shell. On the clearly orthoid cardinal process and punctate shell those authors firmly exclude *Kayserella* from *Streptorhynchus*. These two features are sufficient to place *Kayserella* in the Dalamanellacea. Because the genetic relations are imperfectly known, Schuchert and Cooper have provisionally placed *Kayserella lepida* in the family Mystrophoridae Schuchert & Cooper.

Finally, in 1955, Cooper (p. 50, pl. 12-b, fig. 12-26; pl. 14-a, fig. 1-7) revised the systematic position of *K. lepida* (Schnur). The examination of Schnur's specimens has shown that the interpretation of this species was erroneous. The name of *K. lepida* (Schnur) ought to be applied to quite a different form described by Schnur (1853, p. 218, pl. 45, fig. 9). In the first place *K. lepida* has an open delthyrium and small dimensions of shell whose length in most cases does not exceed 5.5 mm. Cooper introduces new names, both generic and specific for the species revised by him, describing it under the name of *Phragmophora schnuri* Cooper. At the same time, on external resemblances, he included *Phragmophora* into the family Onniellidae Öpik. In *Phragmophora* the brachiophores are supported by shell thickenings and the cardinal process fills the notothyrial cavity. Those features, in Cooper's opinion, link *Phragmophora* with the Onniellidae rather than with the Mystrophoridae. Of the principal features in which *Phragmophora* differs from *Mystrophora* and *Kayserella*, Cooper stresses only one, i. e. the presence in the last two genera of a distinct cruralium.

The systematic position of *Phragmophora schnuri* Cooper apparently remains an open question. The features mentioned by Cooper as linking *Ph. schnuri* with the family Onniellidae Öpik are not sufficiently diagnostic. *Phragmophora* is a characteristic form, far removed from the known Devonian orthids. The establishment of a separate family for it were perhaps desirable.

Phragmophora schnuri Cooper, 1955

(pl. IV-VI; pl. XII, fig. 3; text-pl. IV, V; text-fig. 12-19)

1853. *Orthis testudinaria* SCHNUR; J. SCHNUR, Zusammenstellung..., p. 212, pl. 37, fig. 3a-c; p. 242, pl. 38, fig. 4a-c = Orthis plicatella Schnur.
1871. *Streptorhynchus lepidus* KAYSER; E. KAYSER, Die Brachiopoden..., p. 617, pl. 14, fig. 2.
1885. *Streptorhynchus lepidus* MAURER; F. MAURER, Die Fauna..., p. 138, pl. 5, fig. 10.

1892. *Kayserella lepida* HALL & CLARKE; J. HALL & J. M. CLARKE, An introduction .., p. 259.
1896. *Kayserella lepida* GÜRICH; G. GÜRICH, Das Palaeozoicum..., p. 234, pl. 10, fig. 4.
1904. *Kayserella lepida* SCHNUR; D. SOBOLEV, Devonskija..., p. 61, pl. 8, fig. 5-8.
1909. *Kayserella lepida* SCHNUR; D. SOBOLEV, Srednij devon..., p. 453-454.
1914. *Kayserella lepida* SCHNUR; H. QUIRING, Zusammenstellung..., p. 125.
1922. *Streptorhynchus? lepidus* SCHNUR; W. PAECKELMANN, Die mitteldevonische Massenkalk..., p. 65.
1932. *Kayserella lepida* (SCHNUR); CH. SCHUCHERT & G. A. COOPER, Brachiopod genera..., p. 132, pl. 16, fig. 7, 8, 10.
1955. *Phragmophora schnuri* n. sp.; G. A. COOPER, New genera..., p. 52, pl. 12-b, fig. 12-26; pl. 14-a, fig. 1-7.

Material. — 180 shells with both valves, of various individual age; 200 ventral and 200 dorsal valves of different dimensions. All specimens well preserved.

Dimensions of 4 specimens of different growth stages *(in mm)*:

	1	*2*	*3*	*4*
Length	2.8	7.7	11.3	15.2
Width	3.7	8.5	13.0	15.3
Thickness	1.7	3.8	5.8	7.6

Description. — *External morphology* (pl. IV, fig. 12-14). Shell slightly wider than long, outline sub-semiquadrate or semicircular, ventri-biconvex, maximum convexity slightly below the hinge-line towards the centre of shell; hinge-line straight, shorter than greatest width of shell; hinge angles distinct, very obtuse; lateral margins rounded, anterior margin straight, occasionally gently sinuous.

Ventral valve (pl. IV, fig. 13*b*) more convex than the dorsal; umbo small, distinct, raised, beak gently incurved; interarea trigonal, high, gently curved below the apex, placed at a very obtuse angle to the dorsal interarea; delthyrium trigonal, large, with basal width equal to one-third of the entire length of the interarea, covered by deltidium (pl. IV, fig. 13*a*); a distinct fold extending over the middle of valve.

Dorsal valve (pl. IV, fig. 13*a*) less convex than the ventral; umbo small, beak very slightly incurved; interarea long, low, at a sharp angle to the ventral interarea; notothyrium trigonal, filled by the cardinal process, on both sides partly covered by raised chilidial plates; sulcus flat, expanding anteriorly.

Ornamentation (pl. IV, fig. 13-14) consisting of fasciculate costae; costae and furrows distinct, concentric growth lines moderately numerous and conspicuous in the umbonal portion, anteriorly occasionally dense along the antero-lateral margins. Punctae small, subcircular, uniformly spaced (pl. XII, fig. 3).

Internal morphology. Ventral valve (pl. V, fig. 12, 13; text-fig. 12). Delthyrial cavity moderately deep; teeth small, dental plates short, stout; muscle area small, occupying the whole delthyrial cavity, with variable outline, delimited by distinct ridge; adductors and the much wider diductors readily discernible; of the vascular sinuses the anterior pair has been preserved, stretching from the anterior margin of the muscle area and forked anteriorly; impressions of gonads occasionally very distinct; on mature and gerontic ventral valves a strong median depression often present, corresponding to the dorsal septum whose highest point touches the bottom of the ventral valve.

Dorsal valve (pl. VI; text-fig. 12). Cardinal process large, bifid, each lobe often superficially subdivided into 2 or 3 secondary lobes; septum strongly developed, of variable shape and length, usually attaining two-thirds of the full length of shell; brachiophores well developed, short, narrow, strongly divergent, supported by shell thickenings; in gerontic individuals fulcral plates clearly distinguishable (pl. VI, fig. 9); muscle area large, of varying shape stretching to midlength of valve. Serial sections (fig. 12) from a mature individual illustrate the internal structure.

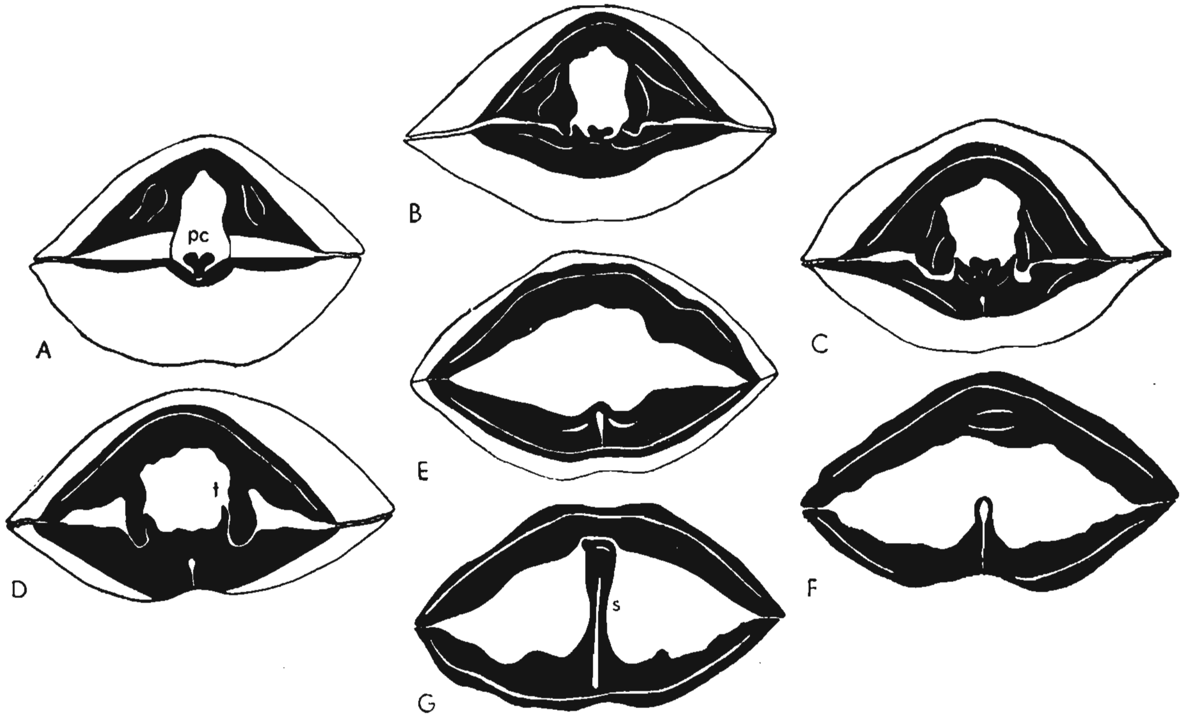


Fig. 12

Phragmophora schnuri COOPER

A-G series of seven thin cross sections, showing internal structure of mature specimen, × 9 approx.

pc cardinal process, *s* septum, *t* teeth.

Variability. — Shells of this species on the whole display uniform outline, but their individual external and internal details are subject to strong variation.

The shell outline shows relatively small variability, being quadrate or semiquadrate in all individuals. This has been proved by measurements of 88 adult shells. The width index (width/length) ranging from 0.9 to 1.2 shows that two specimens are grouped at the 0.9 index, 13 specimens at the 1.0, 57 at the 1.1 and, finally, 16 specimens at the 1.2 index. This suggests that variability of the studied feature is not particularly characteristic. In view of the fairly large number of measured individuals (88) the oscillation from 0.9 to 1.2 appears very moderate.

Thickness and width of shell are not strongly variable. The thickness index (thickness/width) as measured in 88 mature individuals, ranges from 0.4 to 0.7. The majority of specimens seem to have a thickness index of 0.5. The length of the hinge-line is subject to stronger variations. (Indexes-on tables, p. 42).

This feature, however, as the preceding one, is not very characteristic. The curve of its variation is regular, with low summit.

The appearance of the ventral interarea does not vary to any great extent. Though certain differences of height occur, the oscillations are unimportant.

Thickness index	Number of specimens	Per cent
0.4	10	11.2
0.5	46	52.3
0.6	30	34.2
0.7	2	2.3

Length index of hinge-line	Number of specimens	Per cent
1.0	16	12.0
1.1	39	29.3
1.2	43	32.4
1.3	25	18.8
1.4	8	6.0
1.5	2	1.5

The strongest variability is seen in the deltidium, particularly that of adult individuals 8 to 12 mm long. In the first place we observe a lack of uniformity in the development of this element. As is partly illustrated in fig. 13, the deltidium in the mature stage may be complete

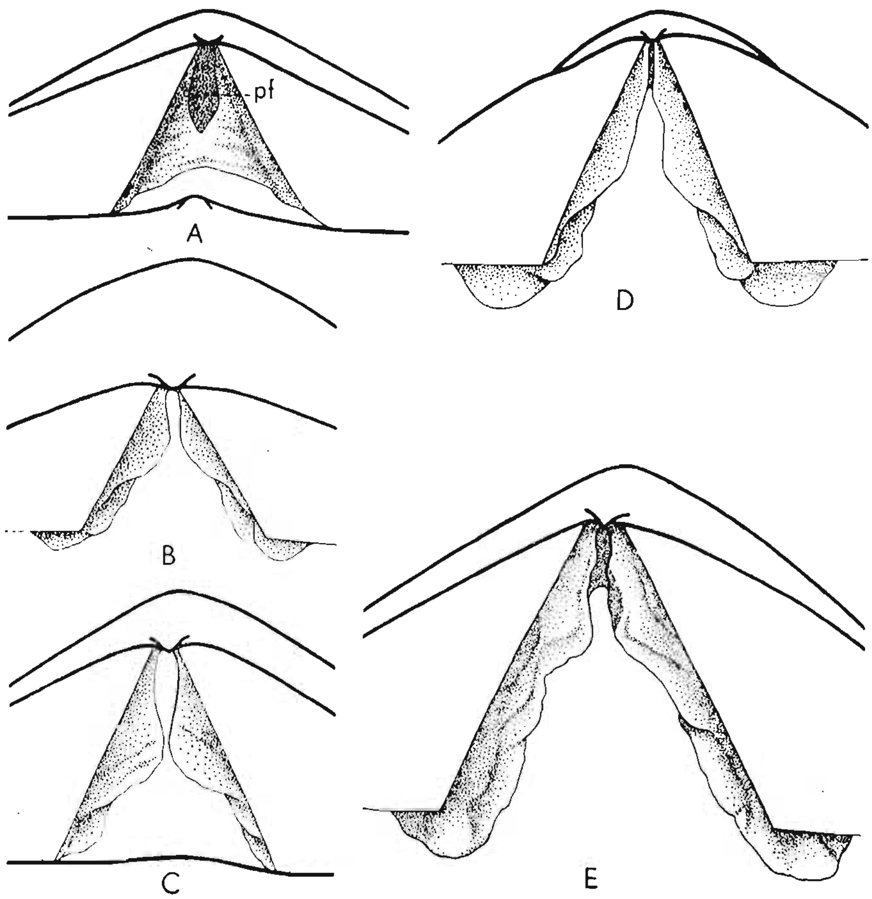


Fig. 13
Phragmophora schnuri COOPER
A-E series of old specimens, showing different development of deltidium; ×20 approx.
pf pedicle foramen.

or nearly complete. Very often only the deltidial plates are present, fused to the shell substance at the apex.

The length of the deltidial plates and of the deltidium also varies in specimens of the same individual age. The plates arise at various points along the length of the delthyrial margins, sometimes even at the base of the ventral interarea, and extend to the apical angle where they often fuse. This is particularly distinct in young individuals, 2 to 6 mm long (fig. 14, 15).

The convexity of the deltidium varies too, from flat to strongly convex. A certain relation exists between the convexity of the deltidium and the height of the ventral interarea. The

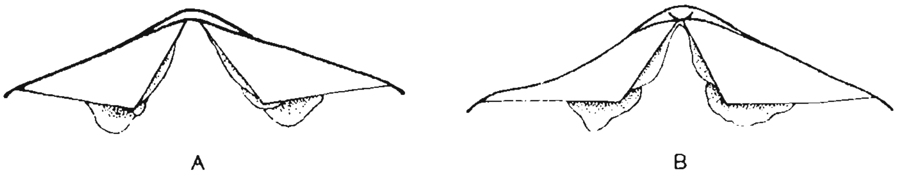


Fig. 14

Phragmophora schnuri COOPER

A-B two young specimens with different appearance of deltidial plates; × 15 approx.

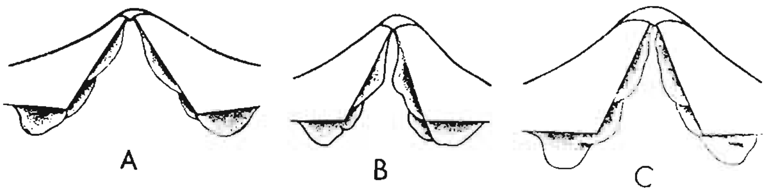


Fig. 15

Phragmophora schnuri COOPER

A-C three young specimens, showing different development of deltidial plates; × 10 approx.

deltidium is more flattened when the interarea is lower, being more strongly convex in the case of a high interarea. The base of the deltidium is also variable. It may be distinctly arched and be either regular or irregular.

Width and length of the dorsal chilidial plates vary too. The chilidial plates extend over different distances of both notothyrial margins. They begin from the base of the dorsal interarea, just above it, or not before midlength of both notothyrial margins. Frequently they join below the dorsal apex. Chilidial plates are mostly in the shape of lists, often uniformly narrowing at both their distal ends. Sometimes they are trigonal, narrowing below the apex and expanding at the anterior margin which constitutes the base of the triangle. The chilidium is often asymmetrical. One chilidial plate may be broader or narrower, longer or shorter than the other.

Among the internal features subject to strong variation, the cardinal process, the dorsal septum and the outline of the dorsal muscle area are the most noteworthy. The ventral muscle area, commonly confined to the apical cavity, does not display any important variations either of dimensions or outline.

The cardinal process (fig. 16) varies particularly with regard to its outline and dimensions. Normally, the bifid cardinal process fills the notothyrium, adjusting to a suitably trigonal shape. Specimens occur, however, with the cardinal process distally narrow and strongly elongated, its broadest portion already projecting beyond the notothyrial cavity. In some cases the cardinal process seems to be simple, since the central furrow is superficial. One to three delicate additional incisions are often noted on the surface of each lateral part of the

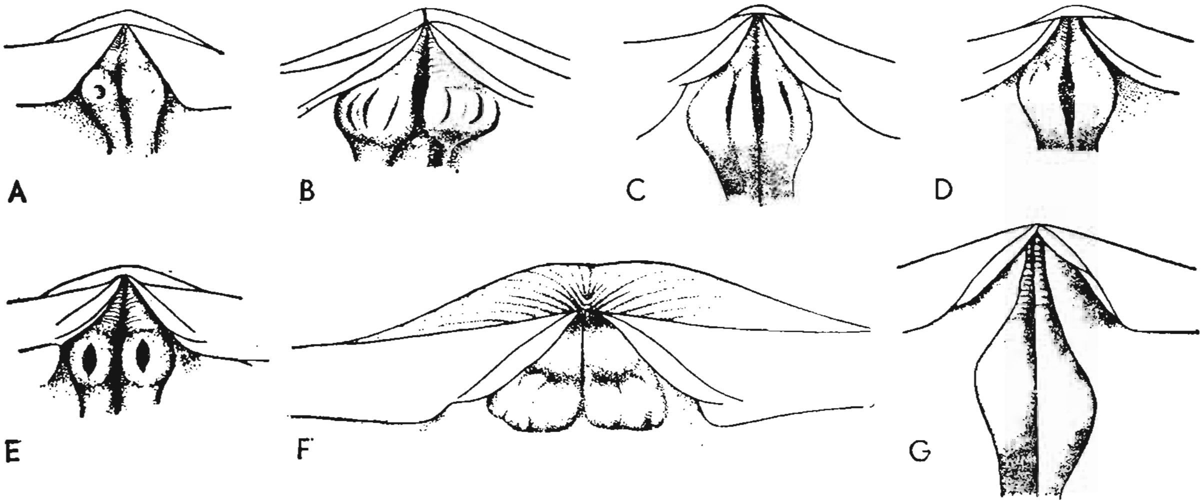


Fig. 16
Phragmophora schnuri COOPER
A-G variations of cardinal process in mature specimens; × 30 approx.

cardinal process. Their number is not usually the same on the two parts of the cardinal process. Their presence enhances the differences of the outer appearance of the cardinal process. Asymmetry sometimes also occurs.

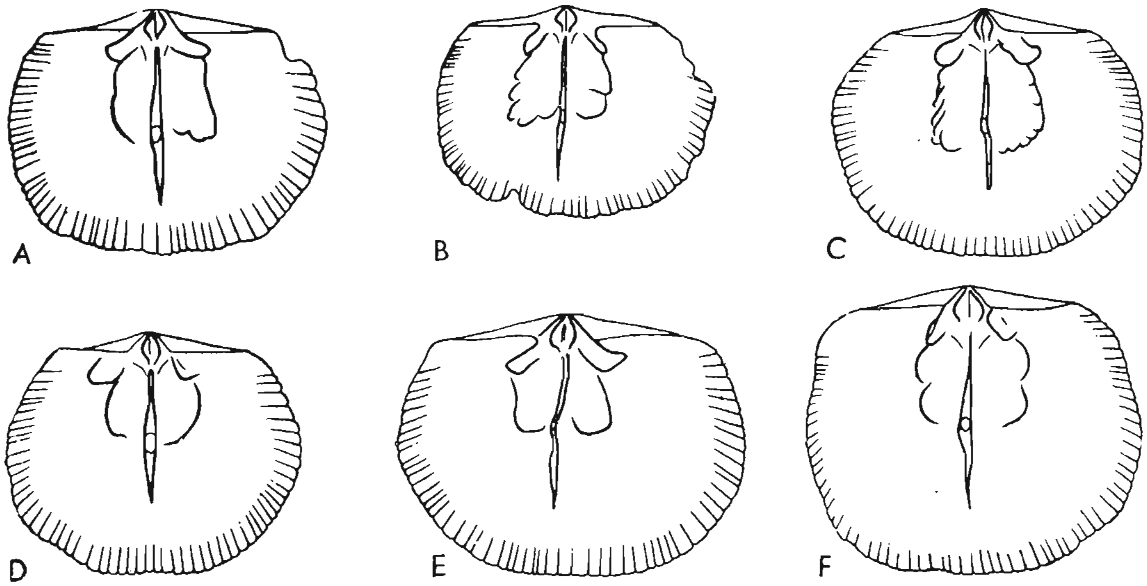


Fig. 17
Phragmophora schnuri COOPER
A-F six mature dorsal valves, showing variations of muscle area; × 4.

The variability of the dorsal septum (pl. VI, fig. 1-7) is mainly the result of differences of length, height and thickness. The septum may extend over the entire length of the dorsal valve and terminate 3 to 5 mm from the anterior margin, or it may not attain much more than the midlength of the dorsal valve.

The septal height is strictly connected with septal length: on the whole, the longer the septum — the less its height, and *vice versa*. The septum is subtrigonal, with the apex generally placed at the midlength of the shell. In numerous specimens, however, it is either below or above midlength. Both septal ends may be narrow. Often, however, the anterior end is distinctly rounded, sometimes semicircular. Two types of septum may be differentiated: 1) one is long, distinctly trigonal, with the two ends fairly uniformly narrowing; 2) the other type is short, with anterior end more or less semicircularly rounded. Each of the two types is represented by an almost even number of specimens.

The dorsal muscle area (fig. 17) is strongly irregular and of variable size. The width is subject to particularly strong variations. Measurements made of 130 dorsal valves show the width index (length/width of muscle area) to range from 0.8 to 1.4.

Width index of muscle area	Number of specimens	Per cent
0.8	1	0.8
0.9	1	0.8
1.0	16	12.4
1.1	39	30.0
1.2	54	41.5
1.3	15	11.5
1.4	4	3.0

The group at the 1.2 index is most numerous, the average width of the muscle area here is 3.4 mm. The variation diagram shows a regular distinctly unimodal curve.

The length of the muscle area is moderately variable.

Length index of muscle area	Number of specimens	Per cent
1.0	1	0.8
1.1	26	20.0
1.2	92	70.7
1.3	11	8.5

Specimens with length index at 1.2 predominate. On the whole, the length of the muscle area only slightly exceeds a half of the full length of the dorsal valve (length index of muscle area = length/width ratio of muscle area). The variation curve of this feature is regular and pointed.

The muscle area, particularly conspicuous in mature individuals, and especially in the old, is delimited from the remaining shell surface by a distinct regular or irregular ridge. This ridge may be without incisions or it may bear 1 to 3 incisions on the lateral sides. In most cases, when the area is flabellate, the adductors are separated from the diductors by fairly distinct transverse thickenings.

An examination has shown that individual variability is strong and involves all external and internal characters. It can, however, be ascertained only on adequately numerous material of the same individual age. From the lack of it, difficulties may be encountered in specific identification.

Ontogeny (pl. IV, fig. 1-11; text-pl. IV, V; text-fig. 18, 19). — The series representing successive post-embryonic stages of growth, although containing few young specimens, was complete enough for the determination of the principal ontogenetic changes. The most numerous specimens are from 7 to 12 mm long, the next from 2 to 5 mm long. There are only very few young individuals up to 1 mm long, but these are excellently preserved.

On the observed sequence of the appearance and differentiation of such internal and external structural details as the ventral umbo, deltidium, radial ornamentation, muscle area, dorsal septum etc., all the material has been separated into the following growth stages:

1) length 0.38 to 1 mm — with incipient primary radial costulae, first expressed as distinct plication on antero-lateral margins, subsequently as delicate costulae covering the entire shell surface, the umbonal portions excepted;

2) 1 to 3 mm — first secondary costulae appear on the slopes of both valves by addition, as well as by bilateral dichotomy of the central costula on the ventral valve, also by intercalation in the dorsal sulcus; ventral umbo increases markedly, deltidial plates appear first as thickenings of delthyrial margins, later as trigonal plates;

3) 3 to 7 mm — deltidial plates gradually fuse together into a convex deltidium, radial ornamentation assumes its final, distinctly fasciculate character;

4) 7 to 12 mm — the fully mature stage, shell length only increases slowly;

5) 12 to 15 mm — the gerontic stage, shell, valves and internal details grow thicker.

Description of the smallest specimen (fig. 18)

Length 0.38 mm, width 0.40 mm; shell strongly ventri-biconvex; maximum thickness and width just about the middle; hinge angles distinctly rounded; lateral margins nearly parallel; antero-lateral angles well rounded, anterior margin straight or slightly rounded. Incipient radial ornamentation present as plicated marginal portions.

The following features are characteristic of young individuals and subject to gradual change during ontogeny: 1) ventral beak in the youngest individuals strongly turned aside

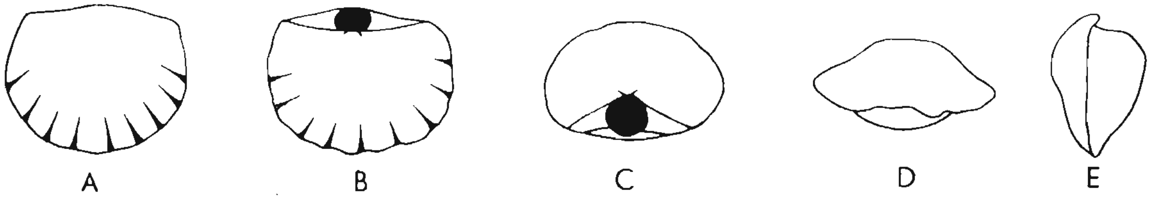


Fig. 18

Phragmophora schnuri COOPER

Youngest specimen, from 5 aspects; × 40 approx.

A dorsal, *B* ventral, *C* hinge-line, *D* anterior margin, *E* lateral.

at an angle of 120° to the intervalvular plane; 2) pedicle foramen elongate, oval; 3) deltidium; 4) irregularity of deltidium; 5) radial ornamentation; 6) maximum convexity of shell at centre; 7) length of both valves, especially of the ventral.

There are also constant features facilitating the identification of specimens with small dimensions: 1) ventri-biconvex shell with depressed slopes; 2) width of shell greater than shell length; 3) straight hinge-line, shorter than maximum shell length, hinge angles distinct; 4) high ventral interarea; 5) presence of incipient ventral central costulae (ventral fold) and of the corresponding dorsal central furrow (sulcus).

Changing features in ontogeny

Ventral and dorsal umbonal portions (pl. IV, fig. 1*c*-11*c*; text-pl. IV, fig. 1*e*-5*e*). During growth the appearance and position of the ventral umbo gradually changes. In specimens 0.38 mm long, umbo is faintly indicated, placed below the hinge-line, turning aside at an angle of 120° to the intervalvular plane. The dorsal umbo with gently incurved apex is larger, conspicuous and in a normal position, i. e. projecting above the hinge-line. With shell growth the ventral umbo is larger and more distinct. In specimens 0.76 mm long the beak is at the same level with the hinge-line, at length of 1.27 mm it protrudes above the hinge-line, and finally, in specimens over 1.60 mm long it is higher than the dorsal umbo and slightly incurved. With further shell growth, the dimensions of the ventral umbo only are increased.

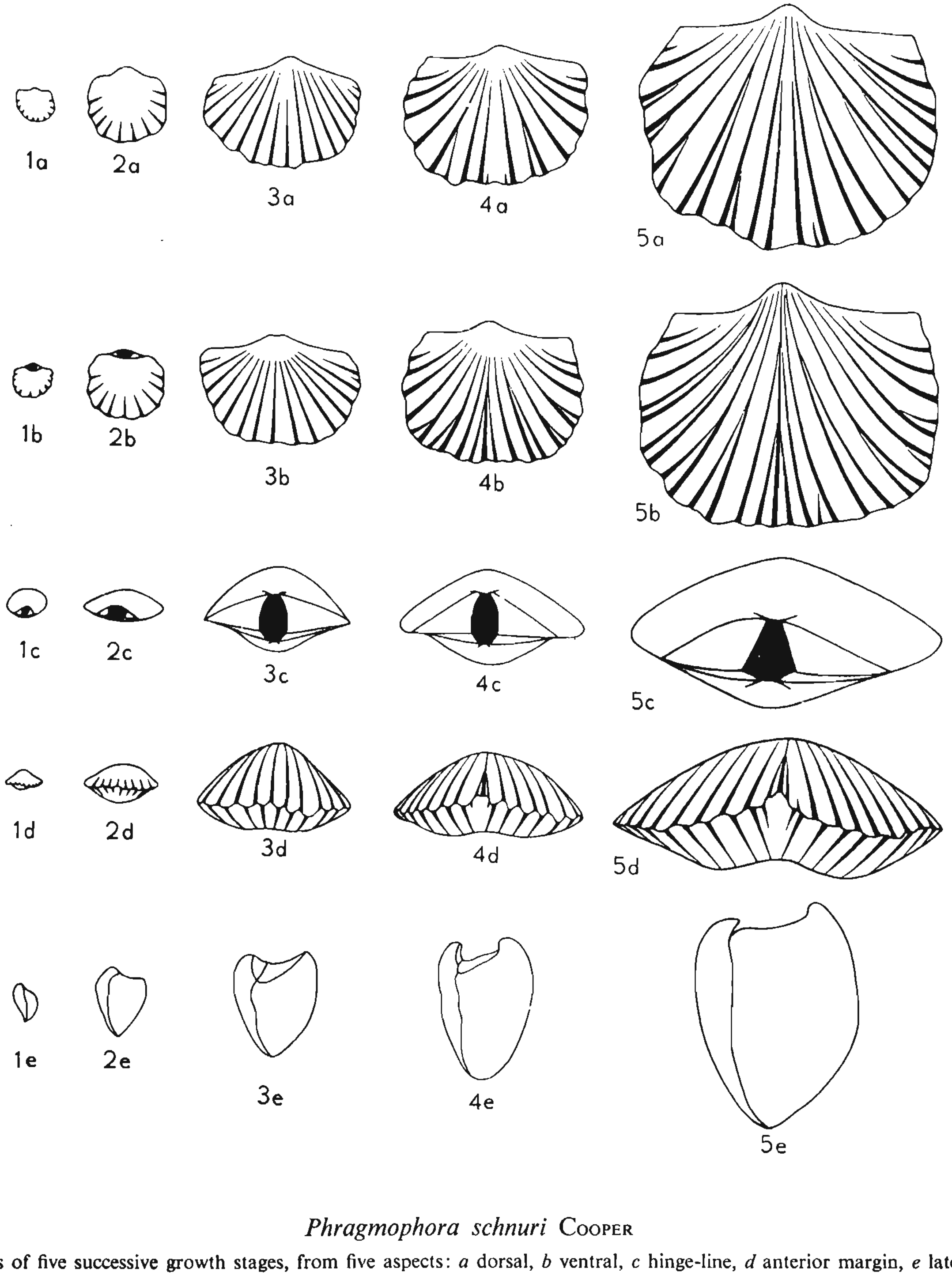
The appearance and position of the ventral interarea is closely correlated with the above changes. In youngest individuals the interarea is comparatively high, though poorly developed. It is straight and strongly turned aside. With older individuals it grows gradually, approaching the dorsal interarea. The flat surface of the interarea also passes to one gently concave throughout its height. In individuals approaching maturity the interarea is distinctly concave below the ventral apex.

Pedicle foramen-delthyrium (text-pl. IV, fig. 1*c*-5*c*; text-fig. 18*c*). A markedly large pedicle foramen is noted in the younger ontogenic stages. In specimens about 0.5 mm long it is large, oval, encroaching on both the future ventral delthyrium and the dorsal notothyrium. During growth of shell, with length at 1.5 mm, the dorsal notothyrium slowly passes into a broad, low triangle. Subsequently it is almost completely filled by the cardinal process. By then the pedicle foramen is confined to the ventral valve only, which already has a clearly indicated trigonal delthyrium. This is gradually more and more delimited by the growing deltidial plates. With the growth of plates the pedicle foramen continues to expand, finally to migrate slowly towards the apex when the deltidial plates have coalesced into a single deltidium. It retains an elongate, oval or round shape. During a relatively long time it communicates with the apical cavity. At the beginning of the gerontic stage it usually becomes sealed up on the underside by a substance excreted by the shell. This suggests that the pedicle was functional for a rather long time, perhaps until maturity was reached. In older individuals the apical portion of the delthyrial cavity is completely filled by secretion of calcium carbonate. Only a superficial elongate trace of the pedicle foramen persists and even this may become entirely effaced. Cooper (1955, pl. 14, fig. 7a) figures a specimen of *Phragmophora schnuri* Cooper displaying a fully developed single deltidium, without vestiges of the pedicle foramen. The present writer has not, however, found any such specimens in her material.

Deltidium (pl. IV, fig. 1*e*-11*e*; text-fig. 19). In *Phragmophora schnuri* Cooper, as in the *Telotremata*, the deltidial plates appear late in ontogeny and may therefore be regarded as a neanic character.

During earliest growth stages the delthyrium is entirely open. The incipient deltidial plates are known in specimens about 2 mm long, having nearly completely developed their external and internal details, the radial ornamentation excepted. Deltidial plates are expressed as thickenings of the delthyrial margins. In specimens about 2.1 mm long they take on the appearance of narrow plates with free edges rised obliquely outwards. At shell length between 2.3 and 2.7 mm, the plates fairly quickly become subtrigonal and occasionally spindle-like. The length of these deltidial plates is variable. In shells about 5.6 mm long they are distinctly trigonal; when the shell length is about 8 mm, the anterior ends of the plates grow more rapidly, gradually approach each other and join below the pedicle foramen. Subsequently their free la-

TEXTE-PLATE IV



Phragmophora schnuri Cooper

Series of five successive growth stages, from five aspects: *a* dorsal, *b* ventral, *c* hinge-line, *d* anterior margin, *e* lateral; × 12 approx.

teral margins fuse together too, over a gradually increasing length. Initially a central suture marks distinct traces of that fusion. In the final stage a single deltidium is present, with out vestiges of the central suture or even of the pedicle foramen.

Irregularity in development of deltidium (pl. V, fig. 1-9; text-fig. 13). The above is a description of the gradual development of a normal, typical deltidium, ascertained on several series of specimens, from the youngest to the oldest. It is noteworthy that a similar process, though more rapid since it is reduced to one growth stage only, may occasionally be observed in mature individuals from 8 to 14 mm long. There the deltidial plates pass from narrow lateral

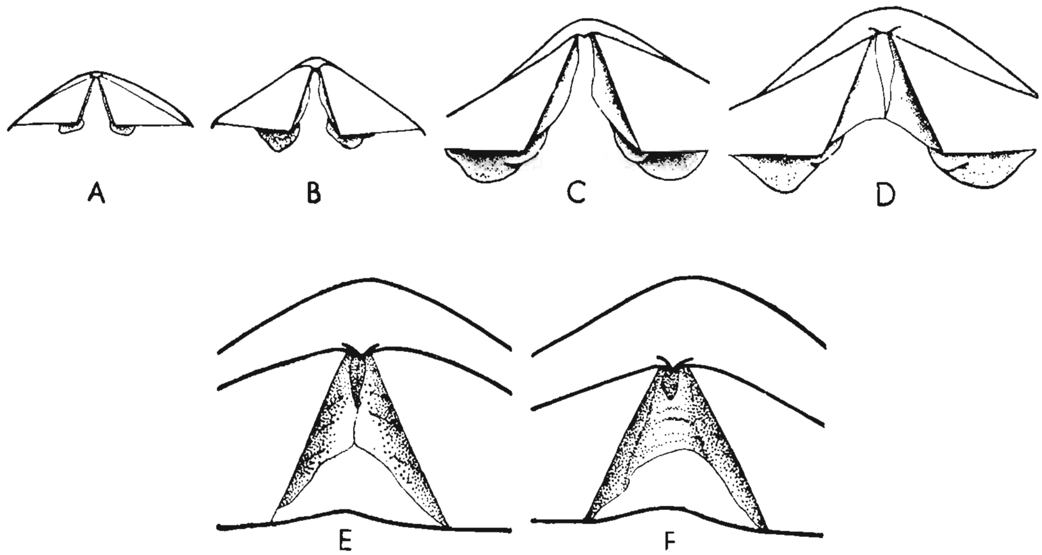


Fig. 19
Phragmophora schnuri COOPER
A-F development of deltidium during ontogeny; × 10 approx.

laminae into a single deltidium. This is not an isolated occurrence. Similar observations have been made by COOPER (1955) on mature individuals of *Phragmophora schnuri* COOPER from the Middle Devonian beds of Germany. That author ascertained several successive growth stages which, however, commence with an open delthyrium. Detached deltidial plates, merging into one uniform deltidium, were subsequently ascertained by him.

On the contrary, the collection of mature individuals from the Holy Cross Mountains does not contain any specimen with a completely open delthyrium. Many, however, bear traces of broken off deltidial plates. The examination of fairly copious material has led to the conclusion that more or less developed deltidial plates are present in every ontogenic stage, beginning with the neanic. They may occur during the gerontic stage too. Hence their presence and degree of development are not closely connected with the age of the individual. The deltidium, however, is always connected with maturity, both when it is gradually differentiated during ontogeny, or during the mature stage only.

The normal deltidium developed during shell growth differs sometimes from that developed during the mature stage. These differences are particularly striking in the gerontic stage. In the first case, the deltidium is usually a regular plate which gradually and slowly thickens. Owing to this, the deltidial opening for a long time communicates with the delthyrial cavity. In the second case, along with a fully developed deltidium we may frequently observe its in-complete development. In the gerontic stage there are, in most cases, two separate deltidial plates only, whose thick and free lateral margins do not fuse together. Their undersides, however, thicken quickly and usually coalesce. On the upper surface the margins are not fused and retain the distinct outline of the earlier deltidial foramen. Such fusion of deltidial plates occurs along various points of their length. Occasionally it takes place just under the apex. In this connection the deltidial foramen soon ceases to communicate with the delthyrial cavity (fig. 13).

The deltidial plates, as is shown in microscopic sections, grow obliquely to the ventral interarea. Their substance is fibrous. The punctae have not been observed. In their origin and appearance the deltidial plates in *Phragmophora schnuri* closely resemble the deltidial plates of Telotremata. This similarity is also stressed by COOPER (1955, p. 51). He writes that they bear more resemblance to BUCH's deltidium than to the pseudodeltidium of BRONN. Moreover he adds that the lateral plates in *Phr. schnuri* differ from the plates in other orthids in that they coalesce at an angle with the ventral interarea. On these differences he suggests for them the term: notodeltidial plates (notodeltidium for the fused plates).

Radial ornamentation (text-pl. IV, fig. 1*a*, *b*- 5*a*, *b*, text-pl. V). The first incipient radial costae, in shells 0.38 mm long, are merely fine plications of the antero-lateral commissures. The ridges of plications are gently and uniformly rounded, the width equal to that of the furrows. The plications originate at about 0.2 mm from both apices. Their number and arrangement are constant, being characteristic of this particular species (fig. 18).

On the ventral valve there are 9 plications: a central one which is the incipient ventral fold (maximum elevation of valve) and 4 on each side. On the dorsal valve there are 10 plications, five on each side of the central furrow which constitutes the incipient flat sulcus. With the growth of shell the plications become more distinct, longer, and take on the appearance of costae.

The first secondary costae appear on the lateral slopes of valves in specimens 1 mm long; on the ventral valve they are six, 3 on each side; on the dorsal valve they are four, 2 on each side. Very soon 2 more costae appear by intercalation in the central dorsal furrow.

The dichotomy (initially in the central costae only) is observable in specimens over 1.5 mm long. On the ventral valve dichotomy occurs on either side of the central costa and on the outer sides of the other primary costae. On the dorsal valve dichotomy is noted on the inner sides of primary costae. Moreover, another pair of secondary costae is added by intercalation in the central furrow. The repeated addition of 2 costae check the progress of its expansion due to age. As a rule, there are 22 costae on each valve in specimens about 2.5 mm long. During further growth of shell additional costae are formed mostly by dichotomy. The increase of costae by addition of 4—6 new costae is occasionally observable on the side slopes of both valves. Specimens about 10 mm long bear approximately 50 costae on each valve.

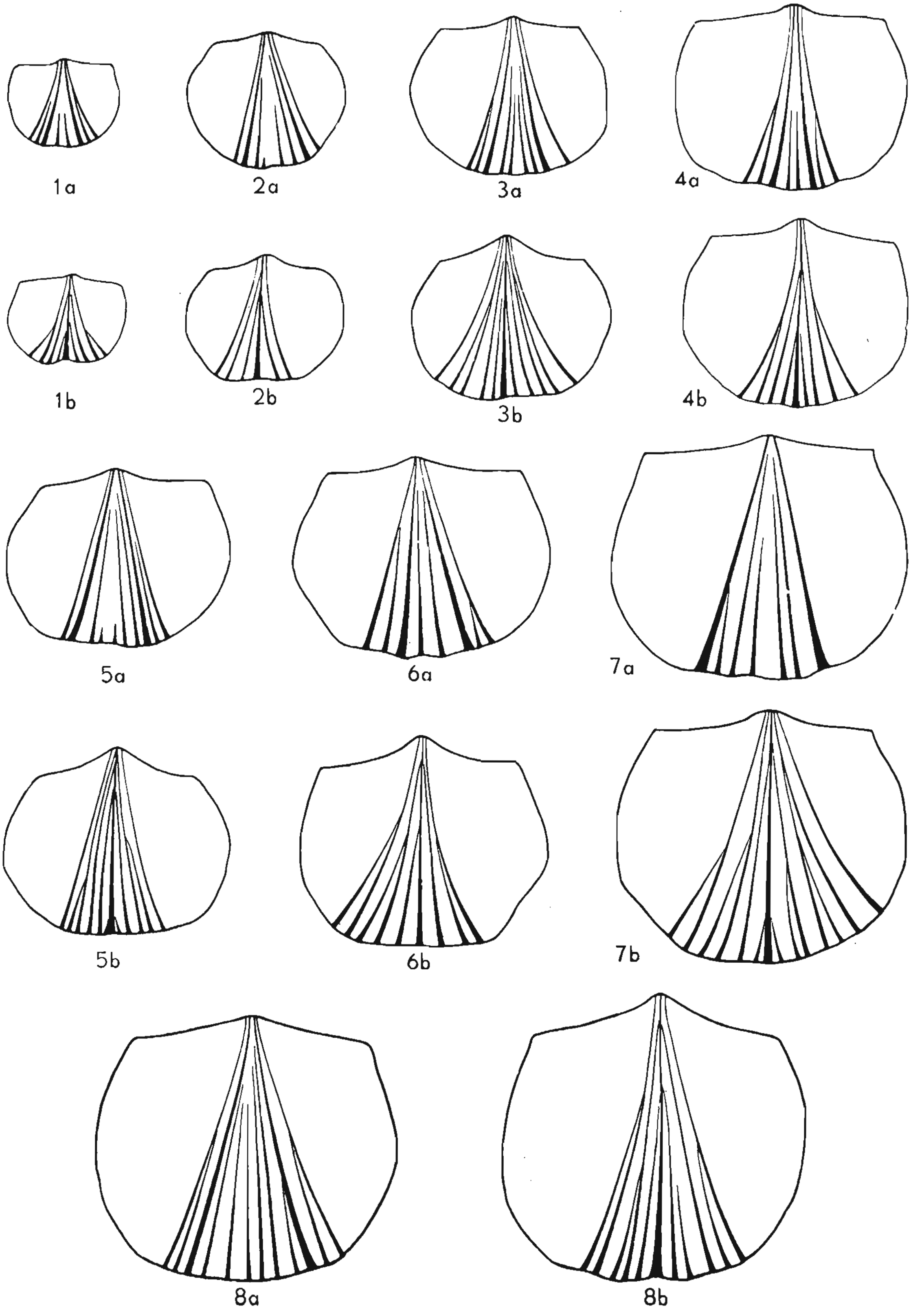
The gradual appearance of new costae occurs with notable regularity.

The ornamentation of mature individuals is characteristic. The radial costae are arranged in fascicules in which we may distinguish the higher, most conspicuous primary costae, and the secondary lower ones. All costal ridges are gently rounded. The shallow furrows are broader than the costae which make the latter all the more readily discernible. A central costa, with secondary ones on its sides, is distinguishable in the centre of the ventral valve. It constitutes the

Phragmophora schnuri COOPER

Eight different growth stages showing differentiation of costae: *a* in dorsal sulcus, *b* on ventral fold; × 5.

TEXT-PLATE V



highest keel-like ventral elevation. A furrow, almost uniformly broad throughout its length, occurs on the dorsal valve, in the flat sulcus gradually expanding anteriorly. The increase of costae both in the ventral fold and the dorsal sulcus does not follow a constant pattern. Hence their number may be greater in specimens of smaller dimensions than in larger ones. Thus their number cannot always be correlated with dimensions and the individual age of the shells. Text-pl. V illustrates the differentiation of costae on the ventral fold and the dorsal sulcus.

Gerontic stage

Among specimens collected by the writer extremely senile individuals are lacking. Many specimens, however, represent gradual gerontic stages. Their external features are as follows: 1) foremost, constantly increasing concentration of growth lines along the antero-lateral commissures; 2) thickened interarea, particularly the ventral, where distinct horizontal growth lines are readily discernible, uniformly arranged over the whole height of the interarea, or sometimes crowded at its base; 3) thickness of deltidium or of deltidial plates; the former is covered by distinct horizontal lines, while the deltidial foramen migrates towards the apex and may subsequently become completely sealed up; 4) gradual effacement of ornamentation in the umbonal portions.

All the internal structural details gradually thicken. Fulcral plates lacking in the ephebic stage are now formed. In the mature stage they are very rudimentary or even altogether absent and are never fully developed before the gerontic stage. These fulcral plates are distinctly gerontic characters and hence without diagnostic value. A. Öpik (1933, p. 16) noted the presence of fulcral plates in *Onniella navis* (Öpik) also a representative of the family Onniellidae. He stressed the fact that they were lacking in some individuals of that species. They are always absent in juvenile specimens, being markedly strong in old ones. Öpik was also of the opinion that this character could not be regarded as constant. He writes: «Die Fulcralplatten scheinen ausserdem eine polyphyletisch entstandene Einrichtung des Dalmanellenschlosses zu sein». Fulcral plates also occur in old individuals of *Aulacella eifeliensis* and *Isorthis canalicula*. Their distinctness depends on the progress of the gerontic process and on the intensity of the associated excretion of calcium carbonate.

The dorsal septum is likewise unusually strong, although it dilates gradually along with the individuals growth. The septum is high in every stage of ontogeny, touching the bottom of the ventral valve with its highest end. In younger specimens a faint corresponding trace is observable on the ventral valve. It is not until the beginning of the gerontic stage that the ventral ridge becomes more readily distinguishable. With the continued growth of shell in thickness, the strongly swollen distal end of septum may penetrate deep into the bottom of the opposite valve. A deep corresponding depression, rimmed by a thick and distinct ridge, occurs. The above seems interesting and the writer believes it to be very rare among brachiopods, since no references to it are to be encountered in literature.

Most probably, a septum so strongly developed as well as its contact with the ventral valve served to re-inforce the shell, particularly during the gerontic stage.

Remarks. — *Phragmophora schnuri* Cooper is one of the characteristic though not numerically abundant form within the Givetian beds of the Holy Cross Mountains. Detached specimens were found there by Gürich (1896) and by Sobolev (1904, 1909), and described by those authors under the name of *Kayserella lepida* (Schnur). The specific description and figures given by GÜRICH (pl. 10a-c, pl. 13) and by SOBOLEV (pl. 8, fig. 5, 5-a, 6, 7, 7-a, 8, 8-a) perfectly agree with *Phr. schnuri* of COOPER.

Comparative studies on specimens from Germany (Eifel, Gerolstein) and Poland have proved the close identity, external and internal, of these forms. The German material also contained KAYSER's original specimens, described by him in 1871 from the crinoidal beds of Eifel under the name? *Streptorhynchus lepidus* (pl. 14, fig. 2). Upon comparison with the Polish specimens, the differences proved to be unimportant and without diagnostic value. The German specimens are with a slightly lower ventral interarea, and a somewhat smaller ventral beak. Owing to the strong individual variability of *Phr. schnuri* COOPER, these differences are within the limits of individual variation. P. N. WENJUKOFF (1886) also mentions *Streptorhynchus? lepidus* (SCHNUR) among the Devonian fauna described by him from North and Central Russia. In his opinion, the external similarities with this species are very close. He noted, however, in the form he described the presence of an open delthyrium, not covered by any plates. The internal structure was not studied by that author. The figures of WENJUKOFF (pl. 2, fig. 4a-c) show that the form described by him differs greatly even externally from the true *Phr. schnuri* COOPER, being more like the true *Kayserella lepida*.

The occurrence of the above described species is confined to the Middle Devonian beds (Givetian) of Germany (Eifel, Gerolstein) and of Poland (Holy Cross Mountains).

Family SCHIZOPHORIIDAE SCHUCHERT & LE VENE, 1929

Genus **SCHIZOPHORIA** KING, 1850

The group of species (now with the generic name of *Schizophoria*) formerly known as the *Orthis resupinata* group, attracted considerable attention during the last century.

In 1850, W. KING introduced the generic name *Schizophoria*. In 1887, a brief diagnosis for this genus was given by OEHLERT in P. FISCHER's «Manuel de Conchyliologie» (p. 1287). His data concern external and internal morphology (shell outline and convexity, and mostly muscle scars on both valves, also pallial sinuses). He also figured *Orthis (Schizophoria) striatula* SCHLOTHEIM from Eifel in Germany (p. 1287, fig. 1055).

From a comparison of *Orthis? morganiana* DERBY (the type species of the genus *Orthotichia*) with *Orthis resupinata*, HALL and CLARKE (1892) proved a close external and internal resemblance between *Schizophoria* KING and *Orthotichia* HALL & CLARKE. They also believed that *Orthotichia* structurally formed a passage between *Schizophoria* and *Enteletes* FISCHER de WALDHEIM (p. 214).

In 1932, C. O. DUNBAR and G. E. CONDRA (p. 55) also stressed the great resemblance between *Schizophoria* and *Orthotichia*.

A detailed diagnosis of *Schizophoria* was given in 1932 by SCHUCHERT and COOPER (p. 143). Those authors wrote that «*Schizophoria* is a long-ranging genus and for this reason shows considerable variation in its internal anatomy». In their opinion, the ventral and dorsal muscle areas, dental plates and dorsal pallial sinuses were very variable.

Also according to SCHUCHERT and COOPER (1932) *Orthotichia* closely resembles *Schizophoria* externally and internally. The differences between these genera are not great. Like HALL and CLARKE, they supposed that «*Orthotichia* structurally forms the passage between *Schizophoria* and *Enteletes*...» (p. 145). According to SCHUCHERT and COOPER, there are certain external and even internal similarities between *Schizophoria* and *Hebertella* HALL

& CLARKE, for example, the ventral muscle area in *Schizophoria* is obcordate as in *Hebertella*. These genera differ mainly in the structure of the shell and the development of the cardinals.

Schizophoria is also comparable to *Pionodema* FOERSTE, but chiefly externally. It resembles *Isorthis* KOZŁOWSKI in the outline of the ventral muscle area, the brachiophores and in the presence of 3 pairs of dorsal pallial sinuses.

Schizophoria is characterized by a very strong variability of internal and external features. Comparisons, therefore, of species of this genus with many species of other genera frequently reveal close similarities in respect of a number of structural features.

Schizophoria striatula (SCHLOTHEIM, 1813)

(pl. VII-IX; pl. XI, fig. 3; text-pl. VI; text-fig. 20, 21)

1813. *Anomites Terebratulites striatulus* SCHLOTHEIM; E. F. SCHLOTHEIM, Miner. Taschenbuch, pl. 1, fig. 6.
1820. *Terebratulites striatulus* SCHLOTHEIM; E. F. SCHLOTHEIM, Die Petrefactenkunde... I, p. 254; II, p 67. pl. 15, fig. 4a-b.
1837. *Spirifer striatulus* PUSCH; G. G. PUSCH, Polens Palaeontologie, p. 28.
1842. *Spirifer striatulus* D'ARCHIAC & DE VERNEUIL; V. D'ARCHIAC & M. DE VERNEUIL, On the fossils..., p. 395, pl. 2.
1853. *Orthis striatula* D'ORBIGNY; J. SCHNUR, Zusammenstellung..., p. 215, pl. 38, fig. 1.
1853. *Orthis striatula* D'ORBIGNY; J. STEININGER, Geognostische Beschreibung..., p. 81.
1864/65. *Orthis striatula* SCHLOTHEIM; TH. DAVIDSON, A monograph..., p. 87, pl. 17, fig 4-7
1869. *Orthis striatula* SCHLOTHEIM; L. ZEUSCHNER, Geognostische Beschreibung..., p. 267.
1871. *Orthis striatula* SCHLOTHEIM; E. KAYSER, Die Brachiopoden..., p. 598.
1871. *Orthis excisa* SCHLOTHEIM; F. A. QUENSTEDT, Petrefactenkunde..., 561, pl. 55, fig. 138-145.
1880. *Orthis striatula* SCHLOTHEIM; G. D. ROMANOVSKIJ, Materiały..., p. 134, pl. 17, fig. 3a-b, 4a-b.
1886. *Orthis striatula* SCHLOTHEIM; P. N. WENJUKOFF, Fauna devonskoj sistemy...
1887. *Orthis striatula* SCHLOTHEIM; TH. TSCHERNYSCHEW, Die Fauna..., p. 104.
1891. *Orthis striatula* SCHLOTHEIM; F. J. WHITEAVES, The fossils..., p. 218.
1895. *Orthis striatula* SCHLOTHEIM; E. HOLZAPFEL, Das obere Mitteldevon..., p. 293.
1896. *Orthis striatula* (*Schizophoria* KING) SCHLOTHEIM; G. GÜRICH, Das Palaeozoicum..., p. 242.
1897. *Orthis striatula* SCHLOTHEIM; FR. SMYČKA, Devonsti Brachiopodi.... p. 16, pl. 2, fig. 17a-b.
1901. *Orthis striatula* SCHLOTHEIM; FR. DREVERMANN, Die Fauna..., p. 264-270.
1902. *Orthis striatula* SCHLOTHEIM; MC MAHON & HUDDLESTON, Fossils..., p. 53, pl. 2, fig. 6a-b, 7a-c.
1904. *Orthis striatula* SCHLOTHEIM; D. SOBOLEV, Devonskija..., p. 68, pl. 8, fig. 12, 13a-b.
1908. *Orthis (Schizophoria) striatula* SCHLOTHEIM; F. R. C. REED, The devonian faunas..., p. 79, pl. 13, fig. 19-24.
1909. *Schizophoria striatula* SCHLOTHEIM; D. SOBOLEV, Srednij devon..., p. 242.
1915. *Orthis striatula* SCHLOTHEIM; G. DAHMER, Die Fauna..., p. 238.
1922. *Orthis (Schizophoria) striatula* SCHLOTHEIM; W. PAECKELMANN, Die mitteldevonische Massenkalk..., p. 64.
1932. *Schizophoria striatula* (SCHLOTHEIM); CH. SCHUCHERT & G. A. COOPER, Brachiopod genera..., p. 143.
1952. *Schizophoria striatula* (SCHLOTHEIM); T. G. SARYČEVA & A. N. SOKOLSKAJA, Opredelitel..., p. 27, pl. 2, fig. 10.

Material. — 530 specimens of various individual ages, among them 460 shells with both valves, 37 ventral and 13 detached dorsal valves in fragments, 20 different fragments of shells or valves. This material represents all stages of ontogeny. Its state of preservation is not uniform, being rather unsatisfactory in young specimens, which are crushed or fractured, and thus not suitable for measuring. Older individuals are better preserved.

Dimensions of 5 specimens *(in mm)*:

	1	*2*	*3*	*4*	*5*
Length	2.0	4.3	14.3	32.0	40.0
Width	2.7	5.5	16.8	36.0	42.0
Thickness	1.5	2.3	8.2	25.5	28.0

Description. — *External morphology* (pl. VIII, fig. 3*a-d*). Shell dorsi-biconvex; maximum convexity near the hinge-line; outline subcircular to transversely elongated; hinge-line straight, shorter than maximum shell width; hinge angles rounded and slightly obtuse; lateral margins straight, nearly parallel or slightly divergent outward; anterior margin slightly to strongly uniplicate in mature individuals, usually rectimarginate in young.

Ventral valve (pl. VIII, fig. 3*b, c*) gently convex, posteriorly sometimes almost flat, anteriorly depressed; beak small; apex pointed, slightly incurved; interarea well developed, low, slightly curved, faintly striated horizontally; delthyrium trigonal, narrow, open; a broad and shallow sulcus present, continuing to the front from about midlength of valve.

Dorsal valve (pl. VIII, fig. 3*a, c*) more convex than ventral, strongly arched from beak to front; beak small, apex incurved; interarea about half as high as ventral, slightly curved; notothyrium trigonal, broad, low.

Ornamentation (pl. VII, fig. 13). Radial striae numerous, fine, distinct, with gently rounded ridges. On the summits of striae or somewhat laterally irregularly spaced tubules occur, being more abundant near front margins. Concentric growth lines abundant and fairly regular, spaced 1 to 3 mm in the umbonal portion. In mature specimens there are 3 to 6 of them over 1 mm of the anterior shell surface, and about 10 in senile specimens. Shell punctate, punctae minute and numerous (pl. XI, fig. 3).

Internal morphology. Ventral valve (pl. IX, fig. 4). Teeth small; dental plates short but thick, merging anteriorly with a low ridge bordering muscle area; muscle area distinct, of varying shape, mostly much shorter than one-half of valve length, divided by a distinct, low median ridge, extending only a short way posteriorly, but anteriorly to front margin; pallial sinuses occasionally preserved, central trunks mostly extending anteriorly from margin of muscle area; traces of gonads are not always distinct, sometimes occupy nearly the whole interior of the valve (pl. IX, fig. 4).

Dorsal valve (pl. VII, fig. 12). Cardinal process of variable shape; myophore portion thin, long, strongly crenulate transversally, occupying about two-thirds of length of the notothyrial cavity; anterior of cardinal process enlarged and keeled, occasionally bifid or trifid; dental cavities deep, brachiophores large, strongly divergent; muscle area broad, mostly flabellate, divided by a low median ridge; anterior adductors distinct; pallial sinuses readily discernible on fragmentary valves; 3 to 4 pairs extend from the front of the muscle area, nearly parallel to one another, bifurcating anteriorly; traces of gonads occasionally present.

Variability. — Exterior of specimens varies considerably, chiefly owing to variability of thickness and width indices (on measurements of 92 mature specimens).

The thickness index (thickness/width ratio) varies between 0.5 and 0.9.

Thickness index	Number of specimens	Per cent
0.5	3	3.3
0.6	29	31.5
0.7	42	45.6
0.8	15	16.3
0.9	3	3.3

The majority of the measured specimens are grouped at the 0.7 index (their average thickness — 18.8 mm, length — 26.5 mm). The thickness is not restricted to large individuals only. Very often shells are strongly convex even before attaining the average dimensions of the species. Thickness of shell is connected with the gerontic stage. The variability curve of that feature is distinct, unimodal and slightly asymmetrical.

The width index varies from 1.0 to 1.3.

Width index	Number of specimens	Per cent
1.0	17	18.5
1.1	52	56.6
1.2	21	22.8
1.3	2	2.1

The most typical specimens, with width index at 1.1, show an average length of 26.5 mm width of 28.4 mm. The width index is not dependent on the shell length. The same variations are observed in small as well as in large individuals.

Length of the hinge-line varies to a small degree. Its index (length of hinge-line/width of shell ratio) oscillates from 0.4 to 0.7.

Length index of hinge-line	Number of specimens	Per cent
0.4	5	5.4
0.5	29	31.5
0.6	50	54.4
0.7	8	8.7

The majority of specimens (54.4 per cent) are at the 0.6 index. The average length of the hinge-line is 16.8 mm.

To sum up, the most typical specimens have an average length of 26.5 mm, width 28.4 mm, thickness 18.8 mm, and length of hinge-line 16.8 mm.

The exterior is particularly variable in mature and gerontic individuals. Immature individuals, to 20 mm long, vary only a little. Their outline is the same, shell wider than long, well rounded hinge angles and antero-lateral margins. Measurements show that subquadrate shells occur with length equal to width. In lateral view of all young specimens, ventral valves (the youngest biconvex excepted) are «pseudoresupinate», while the dorsal valves are regularly convex.

Exterior and interior of mature and gerontic individuals are especially variable. Their shell outline varies from subquadrate through a rectangular to a pentagonal (pl. VIII, fig. 1*b*-5*b*). Three chief outline types may be distinguished: 1) quadrate, width only slightly exceeding length, often equal to it, nearly uniform along the parallel lateral margins; 2) transversely rectangular, width considerably exceeding length, but as in the former group — nearly uniform along the lateral subparallel margins; 3) pentagonal, on the whole wider than long, with maximum width nearer to the anterior margin, and with lateral margins occasionally strongly divergent outwards.

All these types are numerous. There are also transitional forms. The variations of outline of *Schizophoria striatula* have been cited in literature. This varying feature sometimes makes specific identification difficult, but characteristic radial ornamentation (uniform in smaller and larger specimens) serves to differentiate them immediately. McMahon (1902, p. 53) wrote that «...the character of the ornamentation becomes the principal factor for specific determination».

The contour of the anterior margin depends on the outline of shell. When this is quadrate, the anterior plication is narrow but strongly sulcate, while it is broad and flat with the rectangular or pentagonal outline. Transitional forms are also observable.

The length of the hinge-line is also connected with the shell outline. In quadrate or transversely rectangular specimens it is long, nearly equal to shell width; in pentagonal specimens it is markedly shorter.

Shell dimensions are not connected with individual age. Old specimens with numerous concentric lines, grouped anteriorly, vary in length from 27 to 40 mm. There are small shells which are old having grown in thickness, but not in length. Such specimens are very common.

Internally the shape of the muscle area and the cardinal process show considerable variation. The ventral muscle area varies from extremely elongated to flabellate. Three characte-

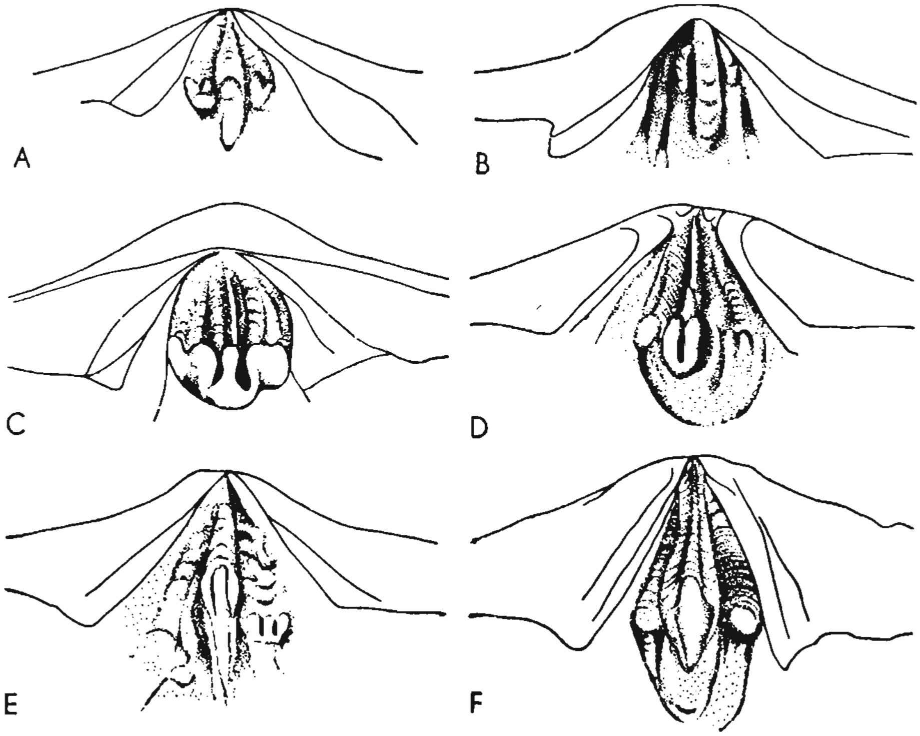


Fig. 20
Schizophoria striatula (SCHLOTHEIM)
A-F variations of cardinal process in mature individuals; × 15.

ristic shape types of ventral muscle area are seen: 1) subrectangular, ridge bordering the area without incision, rarely with a lateral one; 2) distinctly quadrate, ridges bordering the area without incisions, diductors not clearly separated from adductors; 3) flabellate, strongly incised (pl. IX, fig. 3-6).

The dorsal muscle area is usually less variable. It is flabellate with clearly separated anterior adductors. On only a few preserved dorsal valves it is seen that the anterior adductors are always trigonal, the posterior oval and elongated (pl. VII, fig. 12; pl. IX, fig. 1-2).

The shape, height and thickness of the cardinal process vary strongly. It may be single or bifid. The former is generally thin, long, somewhat expanded in front, slightly superficially incised. The bifid process has the anterior portion strongly enlarged, with additional superficial incisions on the side lobes. Text-fig. 20 illustrates the variation in the cardinal process.

Ontogeny (pl. VII, fig. 1-11; text-pl. VI; text-fig. 21). — A complete ontogenetic series is initiated with specimens 0.45 mm long and 0.60 mm wide. The youngest individuals are very scarce, while mature and old ones are fairly abundant.

Among all the species here considered, the maximum length, up to 40 mm, is attained by mature shells of *Schizophoria striatula* (Schlotheim). Their morphogeny is rather short. Specimens 5 mm long have internal details completely differentiated and their external morphology nearly complete. Five growth stages have been distinguished:

1) 0.45 to 2.0 mm — shell biconvex, wider than long, incipient radial ornamentation, development of internal details;

2) 2 to 5 mm — differentiation of ornamentation, shell ventri-biconvex, internal details fully developed;

3) 5 to 20 mm — shell «pseudoresupinate», from biconvex gradually passes to dorsi-biconvex, ornamentation characteristic of the species;

4) 20 to 30 mm — shell mature, further growth of length very slow;

5) 30 to 40 mm and above — growth of shell convexity, valve and internal details thicken.

There are few differences between specimens of the above stages, unlike other orthids in which the nepionic-neanic and gerontic stages were very dissimilar. In *Schizophoria striatula* the differences are mostly those of shell convexity, observable throughout the growth stages. The gerontic stage is clearly distinguished owing to increased thickening along the antero-lateral commissures.

Description of the smallest specimen (fig. 21)

Dimensions: length 0.45 mm, width 0.60 mm.

Shell wider than long, equally ventri-biconvex, arched from beak to front along midline, maximum convexity slightly anterior to hinge-line; hinge-line shorter than maximum shell width; hinge angles well rounded; both beaks nearly flush, the ventral thicker, slightly incurved, with apex discernible; the dorsal beak considerably thinner, projecting apex incurved; ventral interarea slightly concave, delimited from the remaining shell surface by faint ridges, the dorsal interarea not readily discernible; antero-lateral margins rounded, anterior margin rectimarginate; incipient radial ornamentation along antero-lateral commissures.

The following features characteristic of immature specimens vary during process of growth: 1) ventral and dorsal umbonal portions (degree of development, position and thickness of beaks), 2) shape of pedicle foramen-delthyrium, 3) convexity of valves, 4) outline of anterior margin in connection with the appearance of the ventral sulcus, 5) internal features — cardinal process, 6) dorsal and ventral muscle areas, 7) radial ornamentation.

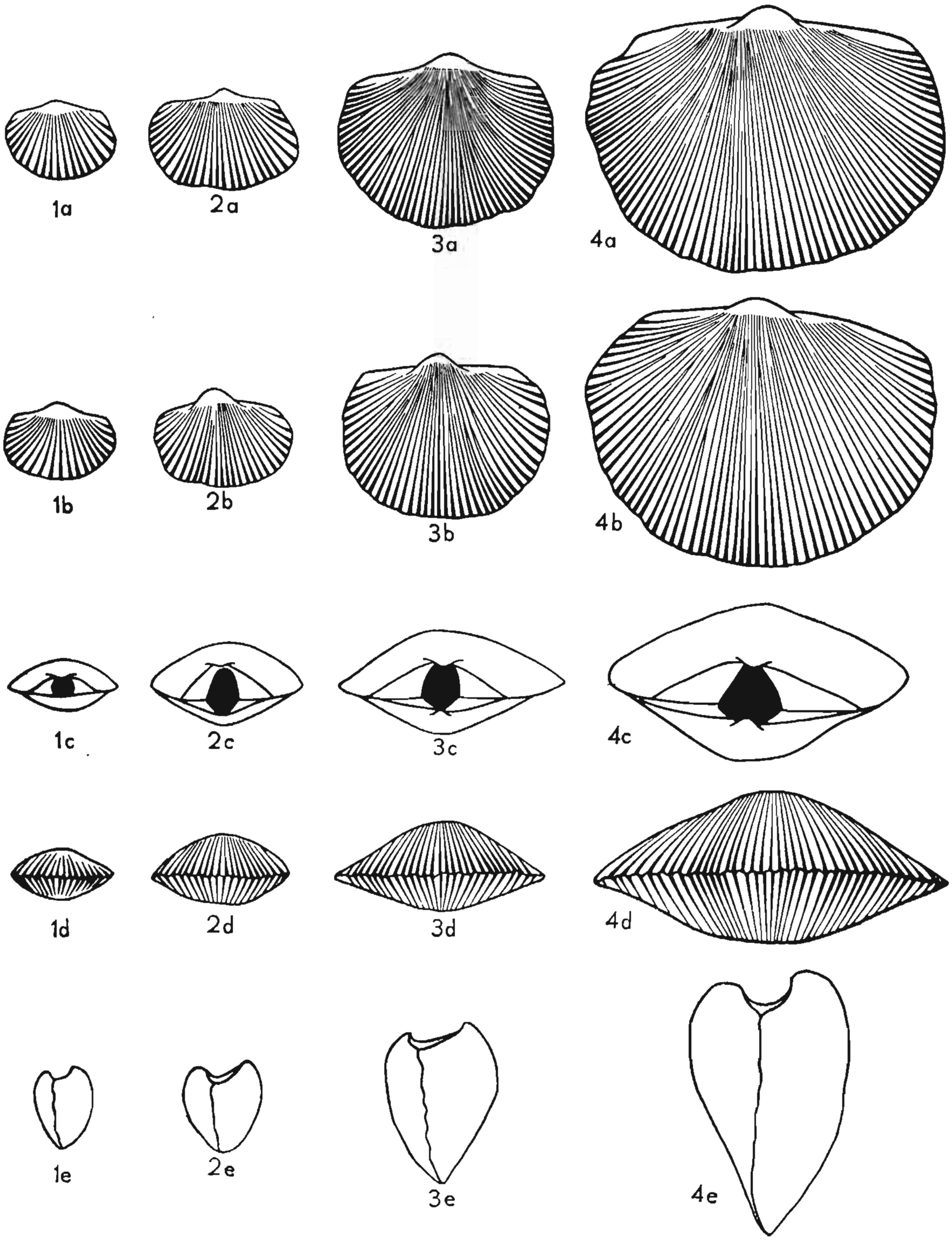
In addition to above variable features the following are constant: 1) shell transversely elongate, 2) width greater than length, 3) hinge-line always shorter than maximum shell width, 4) maximum shell thickness near middle, in extremely gerontic specimens — anteriorly.

Changing features in ontogeny

Ventral and dorsal umbonal portions (pl. VII, fig. 1*c*-11*c*; text-pl. VI, fig. 1*e*-4*e*). In the youngest specimens, about 0.45 mm long, the beaks are situated on the same level. The ventral is larger, without distinct apex; the dorsal thinner, with slightly incurved apex.

In older individuals, up to 3 mm long, the dorsal beak is higher than the ventral which has a more distinct apex. From approximately 4 mm in length the ventral beak is higher than the dorsal, thinner and incurved. The dorsal beak becomes more broad and thick, only slightly projecting above the hinge-line, somewhat incurved. The ventral beak continues to be higher than the dorsal, till growth ceases.

TEXT-PLATE VI



Schizophoria striatula (SCHLOTHEIM)

Series of four successive growth stages, from five aspects: *a* dorsal, *b* ventral, *c* hinge-line, *d* anterior margin, *e* lateral; × 10.

Pedicle foramen — delthyrium (text-fig. 21*C*; text-pl. VI, fig. 1*c*-4*c*). The pedicle foramen in the youngest specimens is round and large, encroaching on both the delthyrium and the notothyrium. With length of shell at 1.2 mm it becomes longitudinally oval and apically broadly rounded. Both its lateral margins are subparallel, sometimes curving outwards. In specimens about 1.5 mm long, the delthyrium gradually narrows beneath the ventral apex, while its lateral margins slightly diverge outwards. In individuals 3-4 mm long the delthyrium becomes distinctly trigonal.

All the successive modifications mentioned here in the shape of the delthyrium are closely associated with the progressive differentiation of the umbonal portions of shell.

Convexity of valves (pl. VII, fig. 1*c*-11*c*; pl. VIII, fig. 1*c*-5*c*; text-pl. VI, fig. 1*e*-4*e*). Variations of shell convexity are slow and gradual, more extensive in ventral valves, while the dorsal

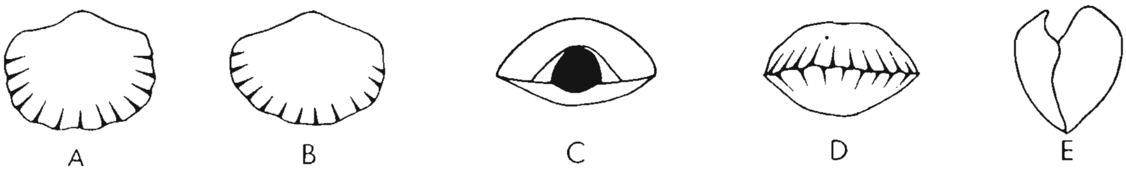


Fig. 21
Schizophoria striatula (SCHLOTHEIM)
Youngest specimen, from 5 aspects; × 35
A dorsal, *B* ventral, *C* hinge-line, *D* anterior margin, *E* lateral.

usually varies only slightly. Abundant specimens of different dimensions show the gradual passage of the biconvex shell through the ventri-biconvex to the dorsi-biconvex or even the plani-convex.

Shells 0.45 mm long are strongly and equally biconvex, their umbonal portions distinctly and gently rounded, the ventral particularly so. With length at 5 mm the convexity of shell changes to ventri-biconvex. With length at 8 mm the ventral valve tends to become moderately concave anteriorly and a flat ventral sulcus appears.

With growth, occasionally at about 30 mm long, the anterior of ventral valve becomes more concave. In lateral view the ventral valve is «pseudoresupinate», Shells of this growth stage are mostly strongly compressed, probably owing to their poor resistance against the pressure of overlying sediments. The described convexity variations are referable to those, defined by SCHUCHERT and COOPER (1932) as «pseudoresupination». It occurs in other species too and has been observed in *Aulacella eifeliensis*, where it is less extensive than in *Schizophoria striatula*.

During the gerontic stage, the ventral valve of *Schizophoria striatula* is slightly convex and shallow. The shell is gibbous, distinctly dorsi-biconvex or even plani-convex; convexity of the dorsal valve continues to be strongly and regularly arched from beak to front.

Anterior margin (pl. VII, fig. 1*d*-11*d*; pl. VIII, fig. 1*d*-5*d*). The anterior margin changes from rectimarginate to uniplicate. In juvenile biconvex or ventri-biconvex individuals it is rectimarginate and slightly rounded. At shell length of 8 mm the anterior margin becomes undulatory. This is associated with the gradual depression of the anterior portions and the origin of the ventral sulcus. With shell growth, the anterior margin gradually becomes more acutely uniplicate, very often with a lingual extension, particularly distinct in senile individuals.

Cardinal process. In young individuals 2 mm long it is like that of *Aulacella eifeliensis.* It is a simple, short, erect ridge uniformly thick. With growth its myophore portion elongates considerably, occupies nearly three-quarters of the notothyrial cavity length, and becomes thinner and strongly crenulated. The process projects slightly anteriorly and expands. In old specimens 2 to 3 elevations appear in the notothyrial cavity on each side of the cardinal process. Thus, anteriorly this process appears to be multifid. These small elevations are one-half the height of the process. In very old specimens they are thicker and together with the cardinal process fill all width of the notothyrial cavity.

Dorsal and ventral muscle areas. Changes during ontogeny are on the whole small, they involve the size of the muscle area.

The ventral area, with length of shell at about 5 mm, is mostly cordate, distally narrow and expanded anteriorly. The low bordering ridge is not incised. With the growth of the shell, the area becomes more or less flabellate. In most mature individuals it is distinctly flabellate with several lateral incisions, not always readily discernible. In some valves the ridge bordering the area is without incisions and the latter is quadrate.

In shells 5 mm long the dorsal muscle area is relatively large, distinct, bordered by a ridge without incisions. Anterior subtrigonal adductors are clearly delimited from the oval posterior ones which are elongated.

Traces of gonads are observable only in some mature specimens. They are less distinct on the dorsal valves, and if preserved, they occupy the distal portion of the valve only, on each side of the muscle area.

Traces of gonads are more distinct and frequent in pedicle valves. Often they occupy nearly the entire interior of the valves. When the gonads traces are larger, one central trunk only is observed at the end of the septal ridge. On the case of smaller gonads besides the central pallial trunk, two or three additional ones are present. They extend and become arboresceut anteriorly. Interior of valves may be also nearly smooth, i. e. only with indistinct traces of gonads (pl. IX, fig. 5).

Radial ornamentation on youngest specimens is not like that of old ones (text-pl. VI, fig. 1*a*,*b*-4*a*, *b*).

On a shell about 0.45 mm long it is expressed by plications of the admarginal parts. The plications which constitute the incipient primary costae, are abundant: there are 12 ventral, two of them central, while on the dorsal valve — 13, with one central.

At about 0.6 to 0.7 mm in length, delicate but distinct striae are seen over the entire shell surface, the umbonal portions excepted.

The first secondary striae appear by addition on the lateral slopes of both valves, from 2 to 6 on each valve, i. e. 1 to 3 on each side of the valve.

On specimens not much more than 1 mm long, the number of striae is rapidly doubled. One or even two secondary striae are introduced between each pair of the primary, the two central on the ventral valve excepted. Thus, specimens about 1.2 mm long have 25 striae on each valve.

Dichotomy of primary striae is observed at 2.5 to 3 mm shell length. Their number is then 36.

With shell length of 7 mm, intercalation is observable as well as dichotomy. The number of costae is 70 to 80, but there may be as many as 86 to 90 on specimens 10 mm long. The hinge angles area is frequently smooth.

Secondary striae most frequently appear between two concentric growth lines by dichotomy or by intercalation.

At the length of shell from 0.45 to 10 mm, and even more, the character of the striae changes. Differences consist in their size and distinctness. The primary striae are considerably wider, therefore more distinct, the secondary lower and finer. These variations in size are particularly observable on younger specimens owing to the rapid increase in the number of striae. With growth, differences are slight and ornamentation is more uniform.

In mature specimens the striae are about equal in size over most of the surface, except for the few secondary ones that are sparsely added. Greatest uniformity of ornamentation is displayed by old individuals. New striae do not appear and differences between those already present gradually disappear.

Gerontic stage

At the beginning of the gerontic stage the shell is thin, but gradually thickens. The concentric growth lines are crowded anteriorly along the antero-lateral commissures. Initially there are very few densely spaced growth lines. The thickness of shell is still small, not more than 1 mm. Gradually it increases to 5-10 mm. In the oldest specimens it attains 20 mm.

The junction line of the two valves is sometimes distinct on specimens in the beginning of the gerontic stage. Its distinctness is connected with thickness of the growth laminae. In old specimens the thickness of the valves may be about 3 mm, being nearly equal in the umbonal portion and at the anterior margin. Both umbo are convex and large, with the beaks incurved, the ventral one more so. On the whole, with the thickening of the shell, the beaks become more incurved and more closely placed, the anterior margin more uniplicate, and the concentric growth lines along the antero-lateral commissures very crowded.

Besides the above, radial ornamentation is posteriorly almost completely effaced. Medially and anteriorly the striae are about equal in size.

Remarks. — *Schizophoria striatula* (Schlotheim) is a well known, widely distributed form. In Poland this species was noted by Pusch in 1837, in his «Polens Palaeontologie» (p. 28). In 1869, Zeuschner cited *Orthis striatula* (p. 267) in his faunal list from the Holy Cross Mountains. Gürich described (1896, p. 242) the internal structure of *Schizophoria striatula* from Skały (Holy Cross Mountains).

In 1904, Sobolev described and figured (pl. 8, fig. 12, 13a-b) *Schizophoria striatula* also from Skały. In 1909, he also noted *Schizophoria* cf. *krotovi* (1909, pl. 5, fig. 17a-b) from the same locality, as well as *Sch. striatula.* He recognized the former species by its general resemblance to the typical *Sch. krotovi* Tschernyschew from the *Stringocephalus* horizon in the Urals. According to Sobolev, it differs from the latter form in its longer fold and sulcus. Sobolev added that the sulcus and fold in *Schizophoria* cf. *krotovi* are not always equally distinct. This difference is variable and not sufficient to establish a species. According to Sobolev, *Sch.* cf. *krotovi* from Skały may be a transitional form to the typical *Sch. striatula* (Schlotheim).

The present author's observations suggest that *Schizophoria* cf. *krotovi* from Skały is the true *Sch. striatula*, but represented by old individuals. Abundant material from Skały contains numerous old specimens with sulci of different length. It is worth noting that individual variation of this species, like that in other forms, is very great and covers both internal and external features.

Compared with Volhynian *Schizophoria striatula* var. *parvaepunctata* Kelus, both forms are superficially similar internally, even in the microstructure of the valves (size and distribution of punctae).

Specimens of *Schizophoria striatula* from Poland are identical with those from the Middle Devonian of Germany (Eifel), as has been confirmed by direct comparisons.

Schizophoria striatula (SCHLOTHEIM) occurs in the Devonian beds of Poland, Germany, France, Great Britain, Spain, U.S.S.R., Irak, Asia Minor, Turkistan, Western Siberia, North America and Australia.

Genus **ISORTHIS** KOZŁOWSKI, 1929

Dalmanella (Isorthis) szajnochai KOZŁOWSKI is a type species of the genus *Isorthis*, initially separated as a subgenus of *Dalmanella* HALL & CLARKE. The main features distinguishing *Isorthis* from *Dalmanella* are: shell biconvex in lateral view, differences in shape of dorsal and ventral muscle areas, brachiophores with fulcral plates.

KOZŁOWSKI (1929) believed that some Devonian orthids, including *Orthis canalicula* SCHNUR, were referable to the subgenus *Isorthis*.

In 1932, SCHUCHERT and COOPER established for the genus *Isorthis* within the family of Schizophoriidae SCHUCHERT (p. 149), the subfamily Isorthinae SCHUCHERT & COOPER.

Isorthis is near to *Schizophoria* in having similar brachiophores with fulcral plates, 3 pairs of dorsal pallial sinuses and a ventral muscle area with elongated and divergent diductors.

Isorthis resembles the Ordovician genus *Pionodema* FOERSTE (KOZŁOWSKI, 1929), in its biconvex shell, the position of the ventral muscle scars and size of cardinal process.

Isorthis includes a number of European and American forms. It appears during the Silurian and persists to the end of the Middle Devonian.

Isorthis canalicula (SCHNUR, 1853)

(pl. X; pl. XI, fig. 2; text-pl. VII, VIII; text-fig. 22,23)

1853. *Orthis canalicula* n. sp.; J. SCHNUR, Zusammenstellung..., p. 213, 243, pl. 45, fig. 6a-e (non pl. 37, fig. 5a-b).
1853. *Orthis ausavensis* STEININGER; J. STEININGER, Geognostische Beschreibung..., p. 80, pl. 8, fig. 1a-b.
1871. *Orthis canalicula* SCHNUR; E. KAYSER, Die Brachiopoden..., p. 607, pl. 13, fig. 4a-b.
1885. *Orthis canalicula* SCHNUR; F. MAURER, Die Fauna..., p. 136, pl. 5, fig. 5.
1896. *Orthis canalicula(?)* SCHNUR; G. GÜRICH, Das Palaeozoicum..., p. 242.
1904. *Orthis canalicula* SCHNUR; D. SOBOLEV, Devonskija..., p. 67, pl. 8, fig. 10, 10-a, 11, 11-a.
1909. *Dalmanella canalicula* SCHNUR; D. SOBOLEV, Srednij devon..., p. 461.
1914. *Dalmanella canalicula* SCHNUR; H. QUIRING, Zusammenstellung..., p. 121-122.
1932. *Isorthis canalicula* (SCHNUR); CH. SCHUCHERT & G. A. COOPER, Brachiopod genera..., p. 150, pl. 21, fig. 24

Material. — 185 specimens with both valves of various individual ages, 77 ventral valves, 74 dorsal valves of different dimensions. All well preserved.

Dimensions of 4 specimens of different growth stages *(in mm)*:

	1	*2*	*3*	*4*
Length	2.6	5.5	11.0	14.5
Width	3.3	7.7	14.9	15.7
Thickness	1.6	3.3	7.8	10.1

Description. — *External morphology* (pl. X, fig. 8*a-e*). Shell transversely elongate, subquadrate in outline, ventri-biconvex, maximum convexity at level of hinge-line or slightly below it; hinge-line straight, shorter than maximum width of shell; lateral margins mostly straight, anterior margin rounded, sulcate or acutely uniplicate; hinge angles and antero-lateral angles rounded.

Ventral valve (pl. X, fig. 8*b-c*) slightly larger and more convex than the dorsal; beak moderately convex, apex incurved; interarea low, trigonal, slightly concave; delthyrium small, trigonal, open, with length of base about 1.6 mm; fold distinct, originating at beak and extending to the front.

Dorsal valve (pl. X, fig. 8*a, c*) a little smaller and less convex than the ventral; beak small with apex slightly incurved; interarea low, straight, at an acute angle to the ventral interarea; trigonal notothyrium broad, low, filled by cardinal process; a narrow sulcus present, beginning at the apex and terminating at anterior margin.

Ornamentation (pl. X, fig. 12). Costulae numerous, distinctly fasciculate near the middle of shell, simple on slopes. Costulae strong, rounded, of the same width as furrows. Concentric

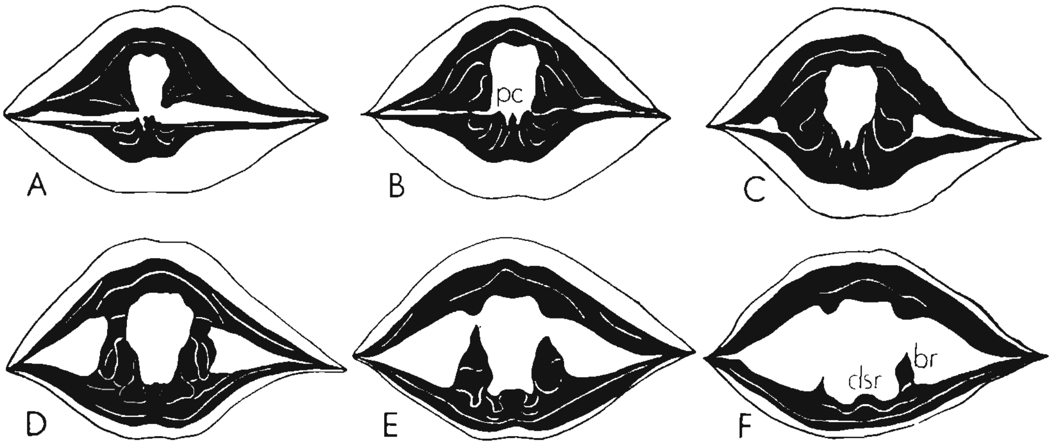


Fig. 22

Isorthis canalicula (SCHNUR)

A-F series of six thin cross sections, showing internal structure of mature specimen; × 5

pc cardinal process, *dsr* dorsal septal ridge, *br* brachiophores.

growth lines indistinct in umbonal portions of shell, more crowded along the antero-lateral commissures in mature and senile specimens. The shell is regularly and densely punctate (pl. XI, fig. 2).

Internal morphology (pl. X, fig. 9-11; text-fig. 22). Ventral valve. Delthyrial cavity deep, with a small apical plate, distinctly striated horizontally; teeth strong, nearly twice as wide as long, laterally and dorsally divergent; thick dental plates merging anteriorly with a low ridge bordering muscle area; brachiophore cavities distinct, deep; muscle area usually reaching centre of valve, medially divided by a longitudinal ridge, highest and thickest at about midlength and bifurcating towards the front; diductors distinctly separated from adductors; pallial sinuses and gonads slightly impressed.

Dorsal valve (pl. X, fig. 9-10). Cardinal process bifid, filling the notothyrium; septal ridge broad; brachiophores well developed, laterally divergent; dental cavities deep; muscle area large, subquadrate; anterior adductors separated from the posterior by transversal ridges, vertical to the septum; occasionally three trunks of pallial sinuses present, extending to the anterior margin, obliquely to the antero-lateral angles of shell, and to the lateral margin.

Variability (text-fig. 23). — The width index (width/length of shell ratio) very variable as opposed to the outline of shell. Data on the variability of this feature, obtained by measurements of 311 mature specimens are given below:

Width index	Number of specimens	Per cent
1.0	3	1.0
1.1	92	29.6
1.2	157	50.5
1.3	50	16.0
1.4	9	2.9

The majority of specimens are grouped here at the 1.2 index. Specimens with this index display an average width of 12.6 mm. The variation curve of this feature is regular and has a very high peak.

The thickness index measured on 130 mature individuals is more variable than the width index.

Thickness index	Number of specimens	Per cent
0.4	1	0.8
0.6	14	10.6
0.7	74	57.0
0.8	39	30.0
0.9	1	0.8
1.0	1	0.8

The length of the hinge-line, measured on 295 mature specimens, shows extensive variability.

Length index of hinge-line	Number of specimens	Per cent
0.4	4	1.3
0.5	16	5.3
0.6	60	20.3
0.7	150	50.8
0.8	58	20.0
0.9	4	1.3
1.0	3	1.0

Index of the majority of specimens is at 0.7, with average length of the hinge-line 9.1 mm.

The dorsal sulcus is generally as wide as the ventral fold.

Extensive oscillations are noted in the width of sulcus and fold 2 mm from either apex, and near the anterior margin. In the first case, the width changes from 0.2 to 0.6 mm, the most frequent being 0.4 mm.

At the anterior margin of the shell the width of the sulcus and fold are more variable. It oscillates between 2.2 and 4.2 mm and is not connected with the width or length of the shell.

The number of costulae in the dorsal sulcus and the ventral fold varies (counted on 80 mature individuals). In the dorsal sulcus their number varies from 6 to 12, most frequently 9

(31 per cent of the total of 80 specimens), in the ventral fold — from 7 to 13. Specimens with 10 costulae are the most numerous. Variation curves is unimodal and asymmetrical.

A certain degree of variability is observed in the cardinal process. It is mostly bifid, separated by a more or less distinct furrow. In some cases, however, the furrow is absent, the process being then simple. Symmetry of this process is very rare. Its strong irregularity is due to hypertrophy or atrophy of one of the lobes, unequal number of superficial incisions on either of the two lobes, or finally to the different thickness and length of the process.

Dorsal and ventral muscle areas are less variable than in other orthids. The outline of the ventral muscle area particularly varies slightly (fig. 23 *b*). There are some oscillations

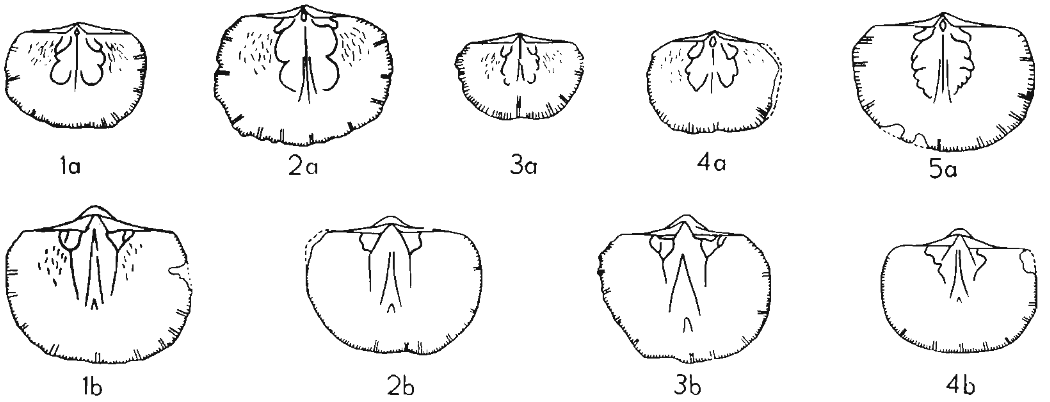


Fig. 23

Isorthis canalicula (SCHNUR)

1a-5a five mature dorsal valves, showing variations in muscle area, × 3; *1b-4b* four mature ventral valves, showing variations in muscle area and in ventral ridge, × 3 approx.

in the length and width of the ventral area. Septal ridge is of unequal length and thickness (width), and variable in its appearance.

The dorsal muscle area is subject to stronger variations than the ventral. In most cases it is semiquadrate in outline (text-fig. 23 *a*). Usually the adductors are distinctly separated, particularly so when the ridge bordering the muscle area is without incisions, but when this ridge is strongly incised, the adductors are indistinctly separated. The length and width of the muscle area and of individual muscle scars vary somewhat too.

Ontogeny (pl. X, fig. 1-8; text-pl. VII). — The ontogenetic series is almost complete. It begins with specimens 0.51 mm long. The following successive stages of ontogeny have been differentiated:

1) length 0.51 to 1 mm — incipient radial costulae, gradually passing to distinct, long ones; ventral beak strongly turned aside;

2) 1 to 3 mm — dichotomy of radial costulae, differentiation of delthyrium and notothyrium;

3) 3 to 7 mm — radial ornamentation complete, fasciculate;

4) 7 to 12 mm — further slow increase of shell length;

5) 12 to 14 mm — appearance of gerontic features.

Immature specimens, about 0.51 to 1 mm long, externally resemble *Phragmophora schnuri* COOPER and *Aulacella eifeliensis* (VERNEUIL). Similarities to the former are in the number of central radial costulae on the ventral and dorsal valves (one on the ventral and two on the dorsal), and in the position of the ventral beak. These forms differ in the height of the ventral interarea, length of the hinge-line and shell outline.

Aulacella eifeliensis (Verneuil) is near *Isorthis canalicula* in convexity of immature shells, position of ventral beak, lenght of hinge-line and height of ventral interarea, but differs in the number of central radial costulae on the ventral and dorsal valves (two ventral and one dorsal).

Constant features of young specimens 0.51 mm long of *Isorthis canalicula* (Schnur), observable in all stages of ontogeny, are: 1) hinge-line shorter than maximum width of shell, 2) shell wider than long, 3) low ventral interarea, 4) number of central costulae on both valves.

Description of the smallest specimen

Dimensions: length 0.51 mm, width 0.63 mm.

Shell markedly wider than long, subquadrate in outline; ventri-biconvex, maximum convexity a little below the hinge-line; hinge-line straight, slightly shorter than greatest width of shell; ventral interarea low, slightly concave under the apex; pedicle foramen small, semicircular; hinge angles nearly right angles or slightly obtuse, lateral margins and antero-lateral angles rounded, antero-lateral margins plicated; 9 incipient ventral costulae, of which one is central, 10 dorsal costulae, with two central.

An analysis of the structure of the shell suggests that many internal and external features are associated with growth and therefore are without taxonomic value. Only a few may be considered characteristic: 1) ventral and dorsal umbonal portions; 2) size of pedicle foramen-delthyrium; 3) reduction of convexity of valves; 4) outline of anterior margin; 5) radial ornamentation; 6) development of ventral fold and dorsal sulcus.

Specimens only slightly older, 1.5 mm long and 1.8 mm wide, do not resemble those described above. Their exterior is like that of mature individuals, which thus facilitates their identification. Shell remains gently and equally ventri-biconvex; both beaks incurved towards one another; the ventral interarea still low but strongly concave throughout its height, delthyrium becoming elongated; the lateral margins more parallel-sided or slightly divergent; radial costulae distinct, fold marked on the ventral valve and sulcus on the dorsal.

Changing features in ontogeny

Ventral and dorsal umbonal portions (pl. X, fig. 1*c*-8*c*; text-pl. VII, fig. 1*e*-4*e*). At 0.51 mm length of shell, the dorsal beak is moderately large and incurved. Conversely the ventral is markedly smaller than the dorsal, strongly turned aside nearly to the level of the hinge-line.

With the growth of the shell, the ventral beak gradually elongates; it attains the height of the dorsal beak, and later exceeds it. In specimens 1.5 mm long, ventral beak is slightly larger than the dorsal and similarly slightly incurved.

Specimens 2.5 mm long have ventral beak like that of mature individuals, large and projecting above the dorsal.

Similar changes are also observable in *Phragmophora schnuri* Cooper and in *Skenidium polonicum* Gürich (see above).

Pedicle foramen-delthyrium (pl. X, fig. 1*e*-8*e*; text-pl. VII, fig. 1*c*-4*c*). In the smallest specimen, 0.51 mm long, the pedicle foramen is moderately large and subcircular. Its width is equal to nearly one-third of the length of the hinge-line. In specimens 1.5 mm long it is confined to the ventral valve only, becoming distinctly trigonal, narrowing apically, with lateral margins gently diverging outwards and arching somewhat. In specimens 2 mm long it is similar, but its width is smaller. At 2.5 mm length and 3.2 mm width of shell the delthyrium is already trigonal. The height of delthyrium is closely connected with that of the ventral interarea, while its width is very variable even in specimens of the same individual age.

Convexity of valves (pl. X, fig. 1*c*-8*c*). Specimens about 1 mm long are gently and equally biconvex, highest in the umbonal portions in the vicinity of the hinge-line.

With the development of the ventral fold and of the dorsal sulcus, the shell gradually becomes ventri-biconvex. The ventral valve remains gently equally convex, with the fold more elevated above the remainder of the valve. The dorsal valve is highest at the level of the hinge-line, being a little depressed anteriorly. Its convexity increases in mature and senile specimens. In lateral view the shell is well rounded, but still ventri-biconvex, sometimes even biconvex. This characterizes not only *Isorthis canalicula*, but most likely the whole genus too. Comparisons of mature specimens of *Isorthis canalicula* (Schnur) with those of *Isorthis szajnochai* Kozłowski shows a similarity of shell convexity, but in the latter it tends to be stronger (Kozłowski, 1929, p. 78, fig. 18; pl. 2, fig. 33-37). Strong shell convexity is a feature common to a number of other species in *Isorthis* (Schuchert & Cooper, 1932, pl. 21, fig. 17-28, 30-33; pl. 23, fig. 15, 19).

Anterior margin (pl. X, fig. 1*d*-8*d*). In specimens 0.51 mm long the anterior margin already displays gentle plications, which grow stronger, as the ventral fold and dorsal sulcus become more distinct. With length of shell at 1.5 mm the plication is still rather indistinct. With length of shell at 2 mm the anterior margin is strongly uniplicate. This elevation is trigonal; its width always corresponds to that of the ventral fold and of the dorsal sulcus. With growth this uniplication becomes more distinct, but slowly diminishes in older individuals. In very old individuals the anterior margin is gently plicated as in young shells up to 1.5 mm long.

Radial ornamentation (text-pl. VII, fig. 1*a*,*b*-4*a*,*b*; text-pl. VIII). Its differentiation is slow, taking place with shell growth. With length of shell at 0.51 mm, nine primary pedicle costulae are present. The central one is the incipient fold. On the brachial valve there are ten costulae, of which the two central limit laterally the sulcus. All these costulae extend only to the midlength of the shell. They are faint.

With length of shell about 1 mm the costulae grow longer and more distinct, beginning 0.3 to 0.4 mm from either apex. When the shell is about 1.3 mm long, the first secondary costulae appear by addition on slopes of both valves, usually four on the ventral and two on the dorsal. The total number of ventral costulae is 13, that of the dorsal — 12.

At about 2 mm shell length, new costulae branch from the external sides of the primary pedicle costulae, and from internal sides ot the brachial ones.

In individuals 2.5 mm long branching is bilateral. There are 39 to 41 ventral costulae and 38 to 40 dorsal. The costulae become distinctly fasciculate, except the simple ones on the slopes of both valves. In every fascicle the primary costula is stouter and higher.

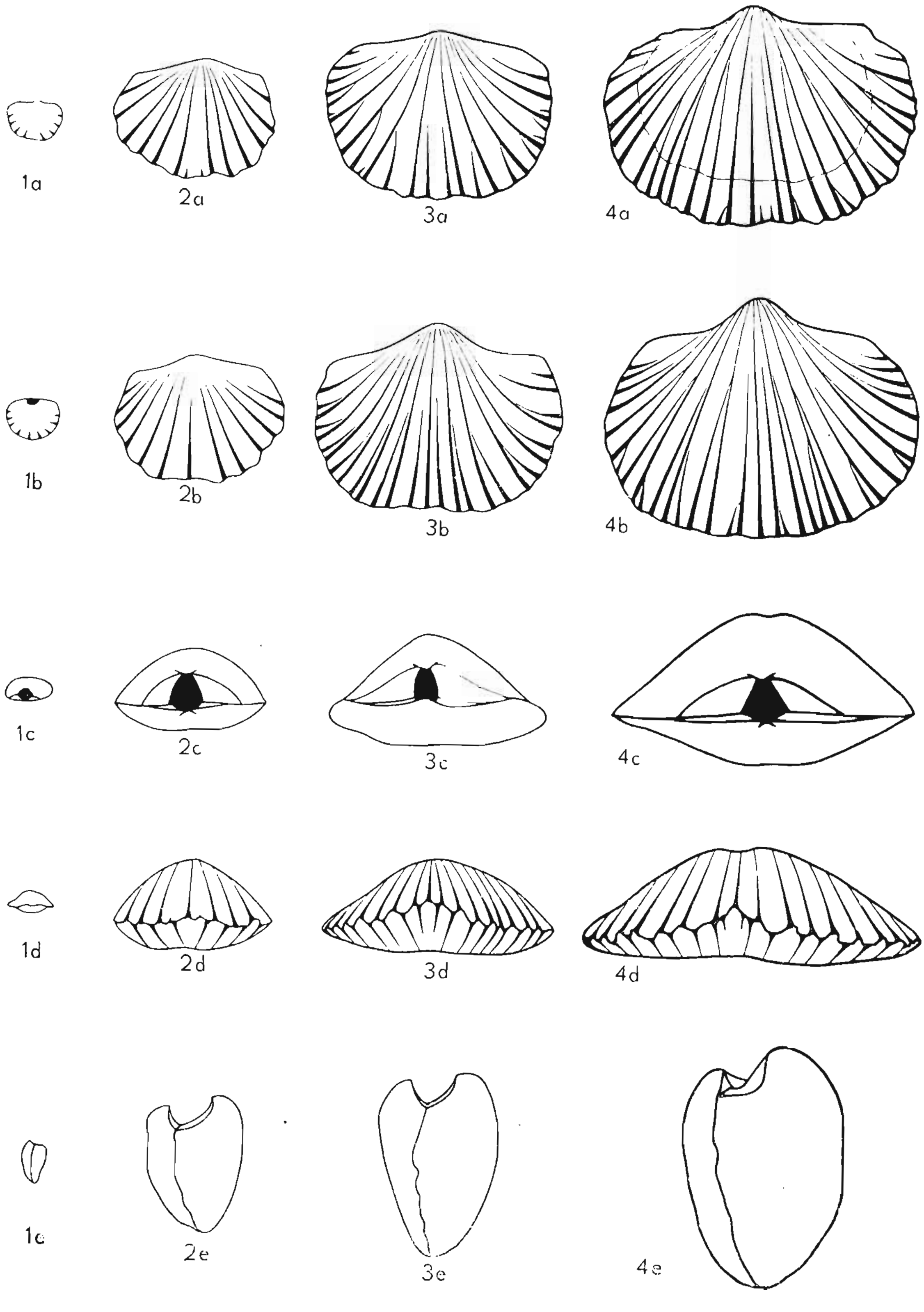
Specimens 5 mm long have 55—60 costulae on each valve.

The ventral fold and dorsal sulcus are important for the identification of specimens. Incipient fold and sulcus are already present at about 0.5 mm shell length. The fold and sulcus are always distinctly delimited from the remainder of the valves, the first is bordered laterally by sulci, the latter — by small folds. Costulae on the fold and in the sulcus are generally higher

Isorthis canalicula (Schnur)

Series of four successive growht stages, from five aspects: *a* dorsal, *b* ventral, *c* hinge-line, *d* anterior margin, *e* lateral; × 12.5.

TEXT-PLATE VII



than those of the slopes, averaging 8-10 at the anterior margin. Generally, on the fold there are 3-5 costulae on each side of the central one. Often, however, on one side appear 1 or 2 costulae, on the other — 4-5. Their number is increased by intercalation, sometimes by bifurcation. The central costula remains simple. In the sulcus the number is increased by gradual intercalation (text-pl. VIII).

Deep but short grooves about 1.5 mm long, bordered by high, rounded ridges, occur interiorly at the antero-lateral shell margins. They are deeper, longer and wider than the intercostal furrows. The number of grooves on each valve varies from 2 to 8. Often they are displaced asymmetrically along the margins, lying oppositely one to another and always corresponding to the primary external radial costulae. This does not seem to be accidental. Primary costulae are always higher and more rounded than the secondary, and this may have some influence on the depth of the grooves. It is very probable that they were filled with marginal pallial setae, since between them there are no traces of connections. The grooves are not restricted only to this form. For example, in some Strophomenids there are also deep ciliar grooves along the margins. They correspond to the major ribs of the external ornamentation. In *Eoplectodonta acuminata* (Holtedahl) they are not connected with the vascular system, similarly as in *Isorthis canalicula* (Schnur) (see Spjeldnaes, 1957, p. 31, pl. 3, fig. 9). The similar grooves are also observed in *Enteletoides žuravlinkae* Bolkhowitinova & Markov from the Upper Carboniferous beds of the Urals (see Bolkhowitinova & Markov, 1928, pl. 9, fig. 25, 26).

Gerontic stage

Senile specimens are fairly abundant with shell length from 11 to 14 mm. Some of them display features of a far advanced gerontic stage. Their growth lines are strongly crowded anteriorly and the front of the shell is greatly thickened, generally to one-third of the maximum shell thickness at the level of the hinge-line. The anterior margin is strongly and trigonally uniplicated, especially in younger specimens, becoming gently plicated, and sometimes slightly sinuous. The convexity of the shell is increased too, particularly that of the dorsal valve. Throughout its length the shell is equally ventri-biconvex, often even biconvex, as in youth. Both beaks are strongly incurved, and one-half of the delthyrium may be covered by the ventral beak.

The umbonal portions of the shell, particularly of the ventral valve, gradually become smooth, without ornamentation. The internal details of the shell become thicker and thicker owing to increased excretion of calcium carbonate.

Remarks. — Gürich (1896) and Sobolev (1904, 1909) described this species from the Middle Devonian of the Holy Cross Mountains.

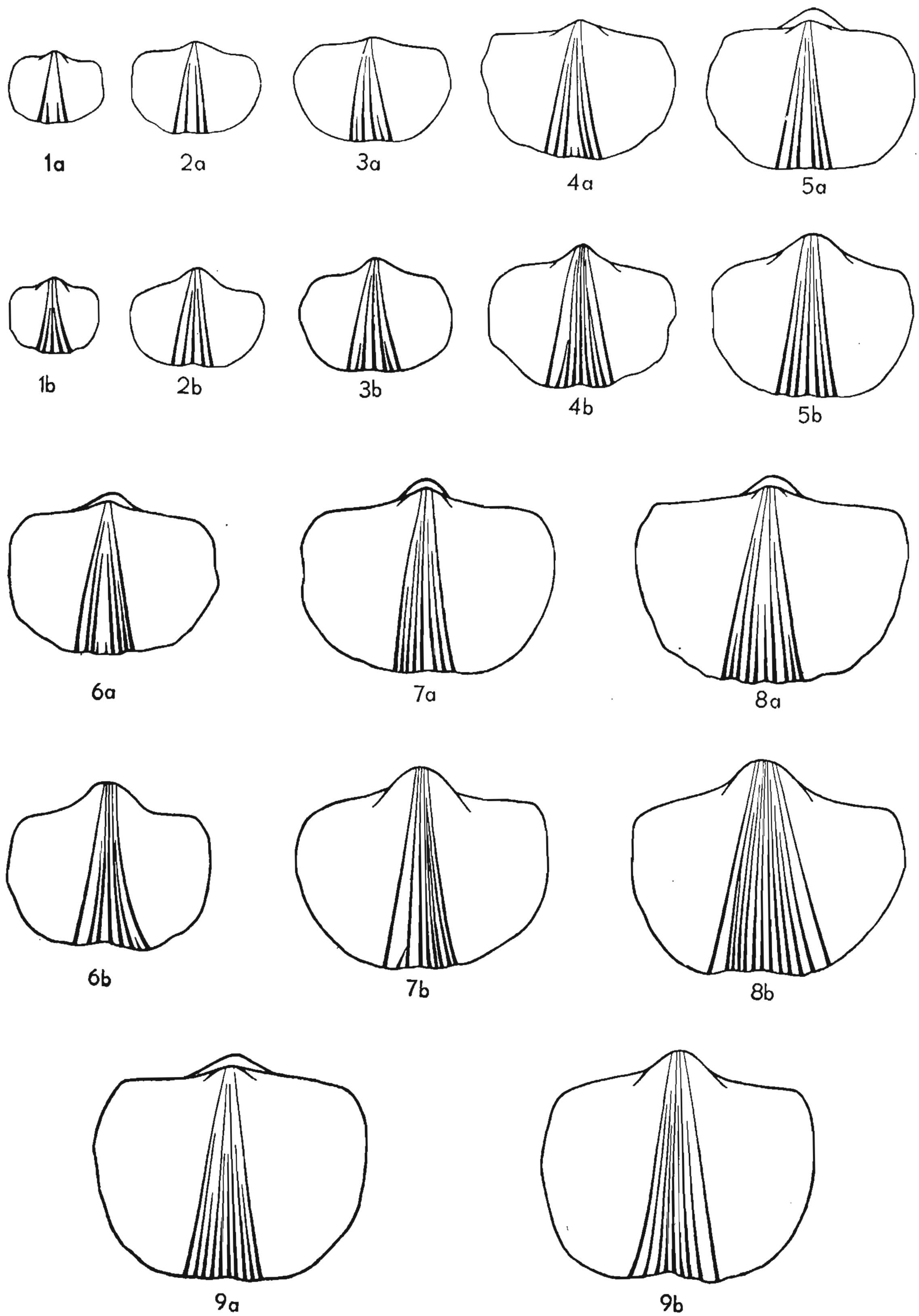
The direct comparison with *Isorthis canalicula* (Schnur) from the Middle Devonian of Germany (Gerolstein) showed their identity, so that it was difficult to distinguish them. There are some differences, such as a little stronger convexity of the Polish specimens and more distinct hinge angles, sometimes slightly auriculate and very little extended. These, however, are without taxonomic value.

In 1853, Schnur gave an exact description of the external appearance of *Orthis canalicula*. Schnur's specimens figured in pl. 45, fig. 6a-e, fully agree with the specimens from Skały;

Isorthis canalicula (Schnur)

Nine different growth stages showing differentiation of costae: *a* in dorsal sulcus, *b* on ventral fold; × 5.

TEXT-PLATE VIII



Orthis canalicula in fig. 5a of pl. 37 differs from the type specimen in lacking a distinct ventral fold and dorsal sulcus — so characteristic of *Isorthis canalicula*, and in the radial costulae not being fasciculate.

SCHNUR, as well as KAYSER, compared *Orthis canalicula* SCHNUR with *Orthis dumontiana* VERNEUIL (VERNEUIL, 1850, p. 181, pl. 4, fig. 7) from the Upper Devonian beds of Spain and Belgium. There is a small difference — the absence in the latter of a distinct separation of the ventral fold and dorsal sulcus from the remainder of the surface of the shell.

Isorthis canalicula (SCHNUR) from the Holy Cross Mountains also shows considerable internal resemblances to *Orthis canalicula* SCHNUR, figured by KAYSER (1871, pl. 13, fig. 4). In the latter, however, the dorsal anterior adductors are not readily separated from the posterior and the ridge bordering the muscle area is without lateral incisions.

STEININGER (1853, p. 80) described *Orthis ausavensis* STEININGER from the limestones of Gerolstein. This species, as he mentioned, had been earlier described by SCHNUR as *Orthis canalicula*. *Orthis ausavensis*, figured by STEININGER (pl. 8, fig. 1a-b), is the true *Orthis canalicula* and agrees with it in every detail.

Orthis tetragona ROEMER, figured by QUENSTEDT (1871, pl. 55, fig. 125), is very close to *Isorthis canalicula* (SCHNUR) in the outline of the shell, the appearance of the umbonal portions and particularly in the ornamentation. It is very probable that the former may be referable to *Isorthis canalicula*.

In 1885, MAURER mentioned *Orthis canalicula* in limestone beds in the vicinity of Giesen. Figures of his specimens closely resemble *Orthis canalicula*. *Orthis canalicula* var. *acuta*, new form of MAURER, has considerable external similarity to *Orthis canalicula*, but is slightly wider. This difference is variable and does not appear sufficient to establish even a new variety (subspecies).

From the Devonian fauna of the north-western region of Central Russia, *Orthis svinordi* was described by WENJUKOFF (1886). According to him, this species closely resembles *Orthis canalicula* and differs only in the ornamentation. In *Orthis svinordi* WENJUKOFF the radial costulae have more rounded summits, the dorsal sulcus and the ventral fold are slightly separated from the remaining surface of both valves. A comparison of *Orthis svinordi* (WENJUKOFF, 1886, pl. 2, fig. 11) shows that its external resemblance with *Orthis canalicula* is very slight.

Internally and externally *Isorthis canalicula* resembles the American *Cariniferella iovensis* STAINBROOK, but differs in having a more convex shell, a shallow dorsal sulcus and a less elevated ventral fold; also the dorsal muscle area is larger, extending far forward.

Isorthis canalicula (SCHNUR) is a very characteristic form of the Middle Devonian beds of Europe (Poland and Germany).

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PLATES

G. BIERNAT: MIDDLE DEVONIAN ORTHOIDEA OF THE HOLY CROSS MOUNTAINS AND THEIR ONTOGENY

PLATE 1

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Skenidium polonicum GÜRICH 16

Fig. 1-6. Series of specimens of various dimensions, ventral view; nat. size.
Fig. 1*a-e*. Smallest specimen of that series, from five aspects: *a* dorsal, *b* ventral, *c* lateral, *d* anterior margin, *e* hinge-line; × 6.
Fig. 6*a-e*. Largest specimen of that series, as above; nat. size.
Fig. 6*f-j*. Same; × 5.
Fig. 7. Ventral valve, inside view; × 6.
Fig. 8. Dorsal valve, inside view; × 6.
Fig. 9. Ventral ornamentation; × 8.5.

Aulacella eifeliensis (VERNEUIL) 26

Fig. 10-15. Six ventral valves showing variations in muscle area, inside view; × 5.

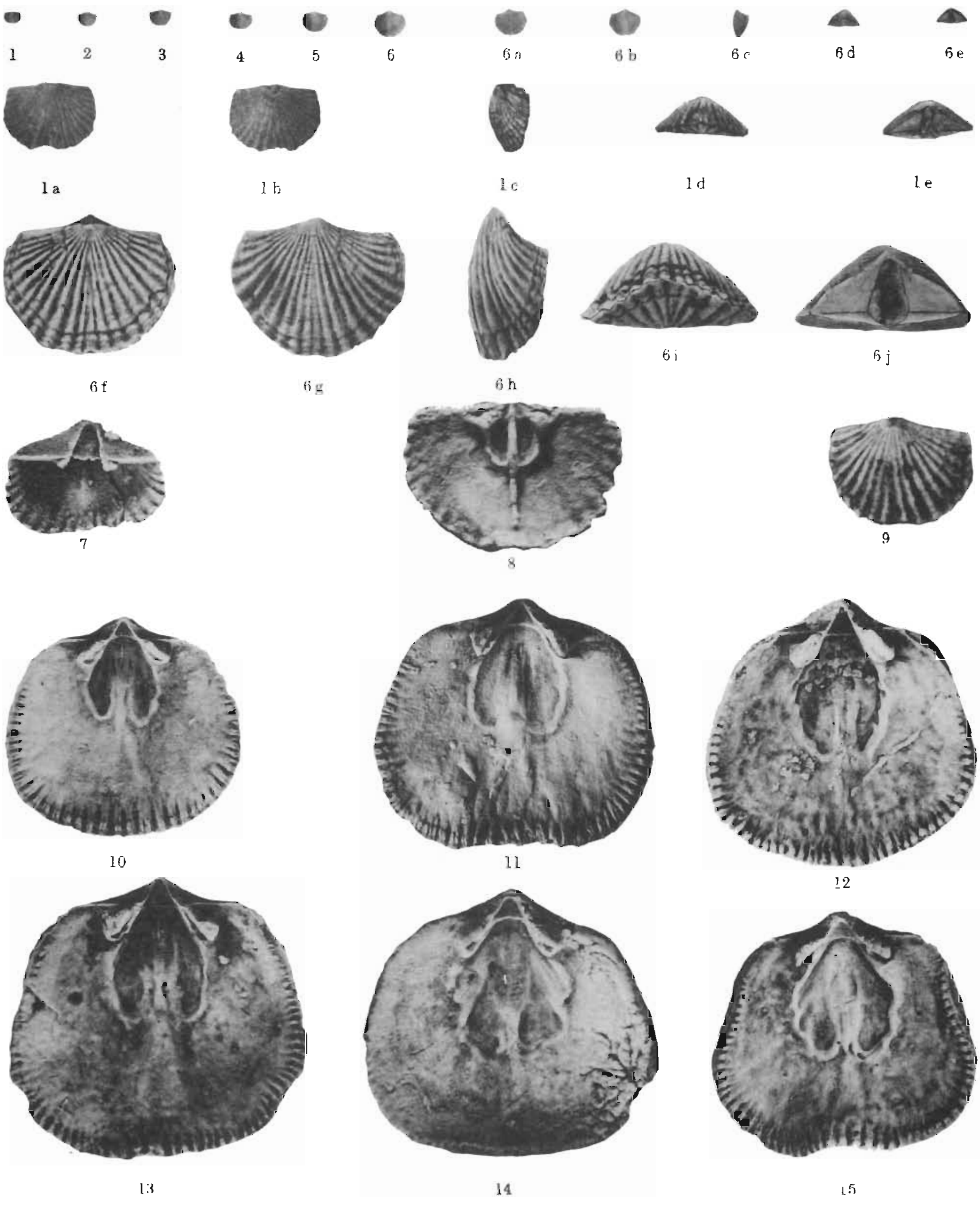

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PLATE II

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Aulacella eifeliensis (VERNEUIL) 26

(see also pl. I, fig. 10-15)

Fig. 1-12. Series of various growth stages, from five aspects: *a* dorsal, *b* ventral, *c* lateral, *d* anterior margin, *e* hinge-line; nat. size.
Fig. 1*f-j*. Smallest specimen of that series, from five aspects: *f* dorsal, *g* ventral, *h* lateral, *i* anterior margin, *j* hinge-line; × 6.5.
Fig. 13-14. Two dorsal valves, inside view; × 5.
Fig. 15. Dorsal valve, hinge-line; × 5.

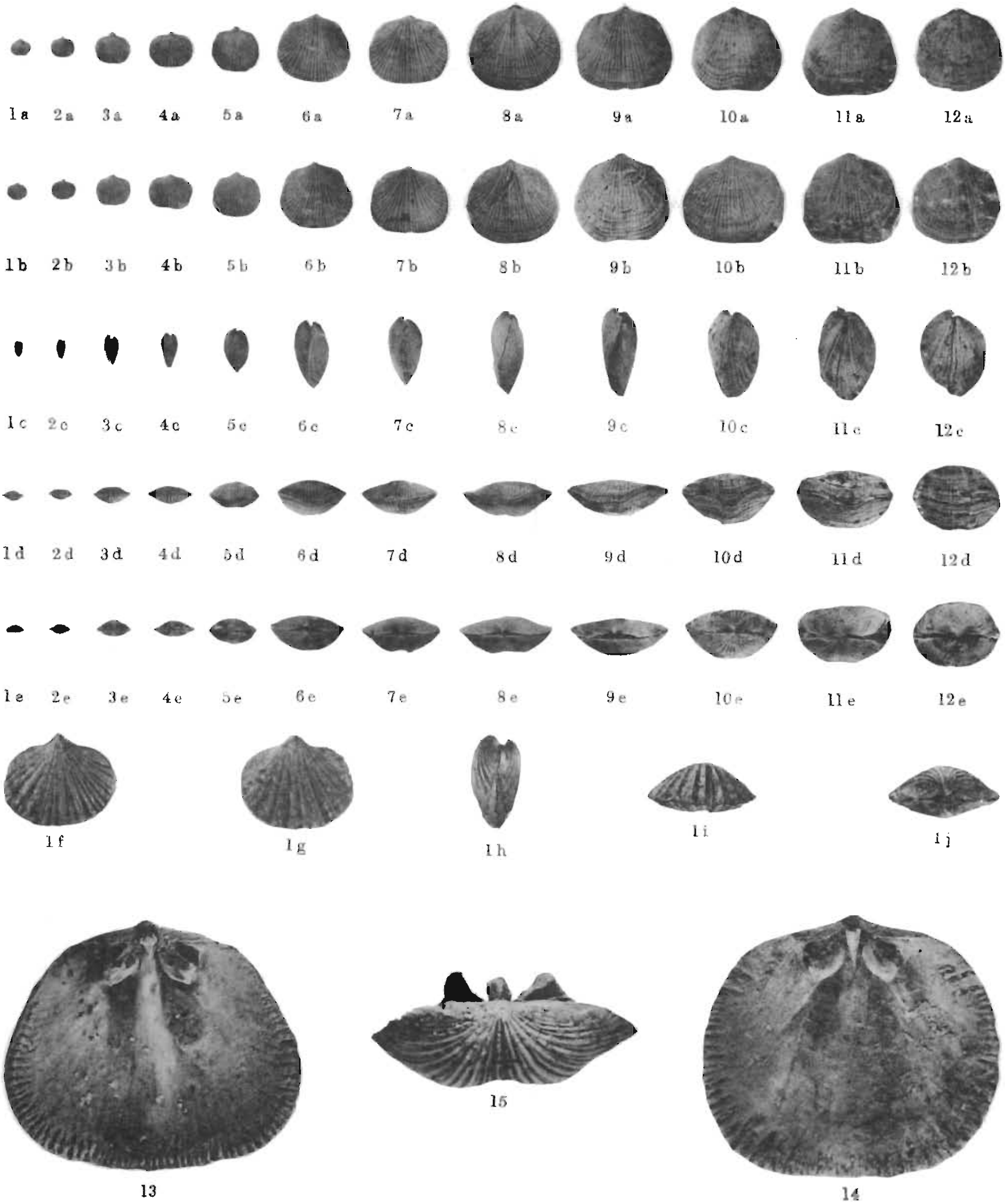

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PLATE III

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Kayserella lepida (Schnur) 36

Fig. 1-6. Series of six successive growth stages, ventral view; nat. size.
Fig. 1*a-e*. Smallest specimen of that series, from five aspects: *a* dorsal, *b* ventral, *c* lateral, *d* anterior margin, *e* hinge-line; × 6 approx.
Fig. 6*a-e*. Largest specimen of that series, as above; slightly magnified.
Fig. 6*f-j*. Mature specimen (fig. 6*a*), as above; × 6 approx.
Fig. 7. Dorsal valve, inside view; × 5.
Fig. 8. Ventral ornamentation of a mature specimen; × 8.

Aulacella eifeliensis (Verneuil) 26

Fig. 9. Mature specimen: *a* dorsal view, *b* ventral view; × 5.
Fig. 10. Ventral ornamentation of a mature specimen; × 8.

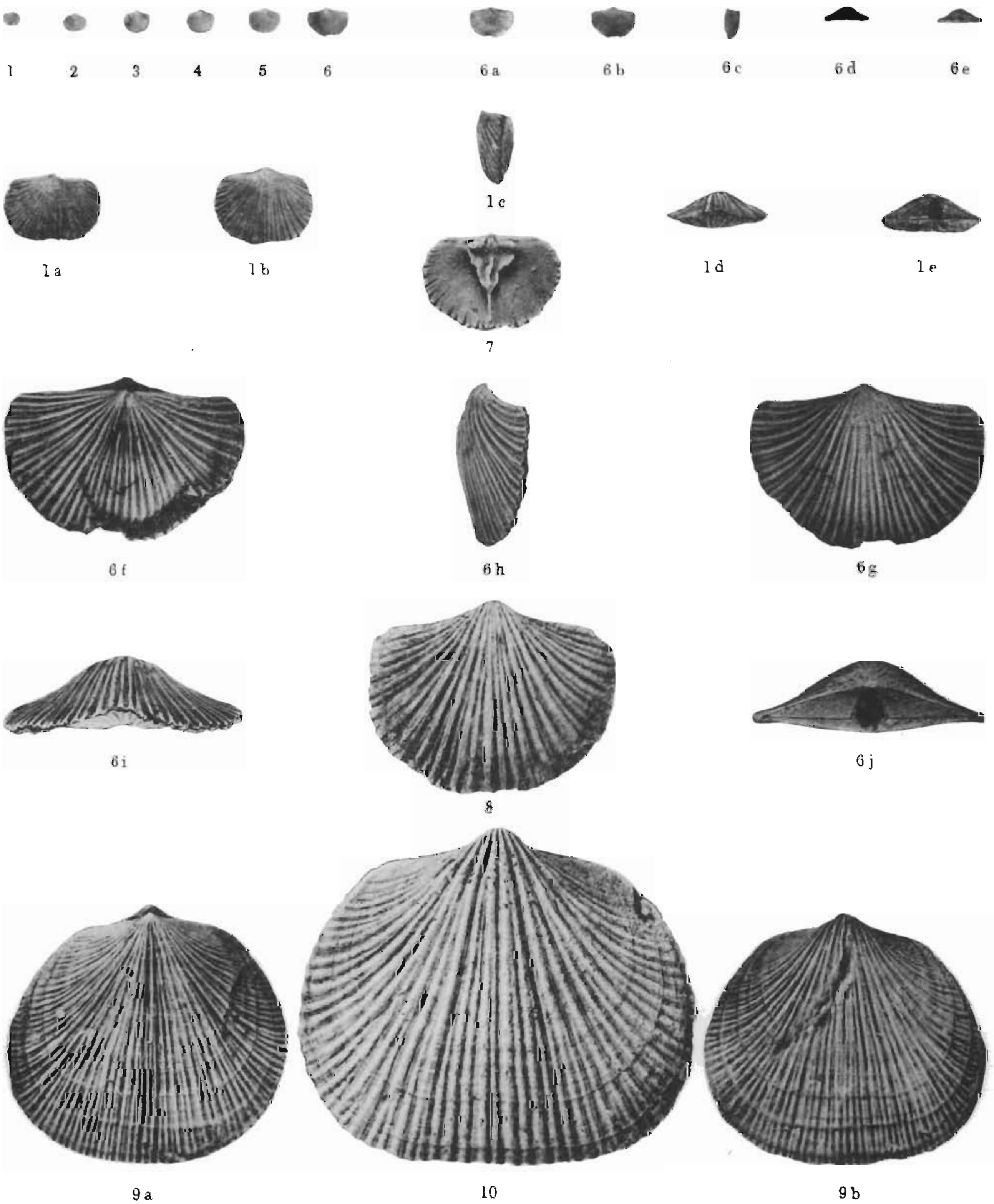

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PLATE IV

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Phragmophora schnuri COOPER 39

Fig. 1-11. Series of successive growth stages from five aspects: *a* dorsal, *b* ventral, *c* lateral, *d* anterior margin, *e* hinge-line; nat size.
Fig. 1*f-j*. Smallest specimen of that series, as above; × 6.4 approx.
Fig. 12. Mature specimen: *a* dorsal view, *b* ventral view; × 3.
Fig. 13. Mature specimen: *a* dorsal view, *b* ventral view; × 3.
Fig. 14. Ventral ornamentation; × 7.

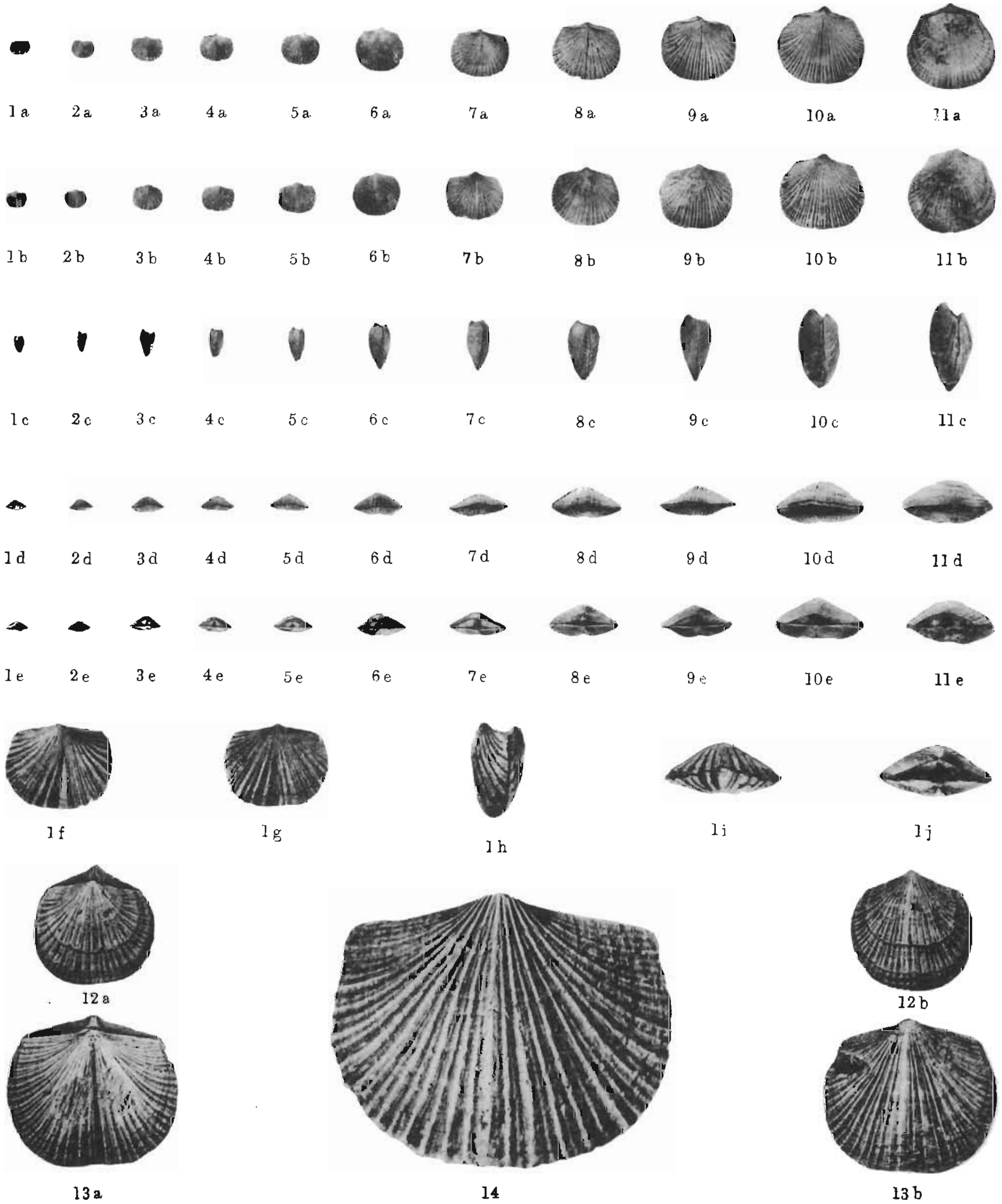

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PLATE V

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Phragmophora schnuri COOPER 39

Fig. 1-9. Series of mature specimens showing different development of deltidium; × 4.
Fig. 10-13. Four ventral valves in various growth stages, inside view; × 4.
Fig. 12, 13. Same, with conspicuous dorsal septum cavities.

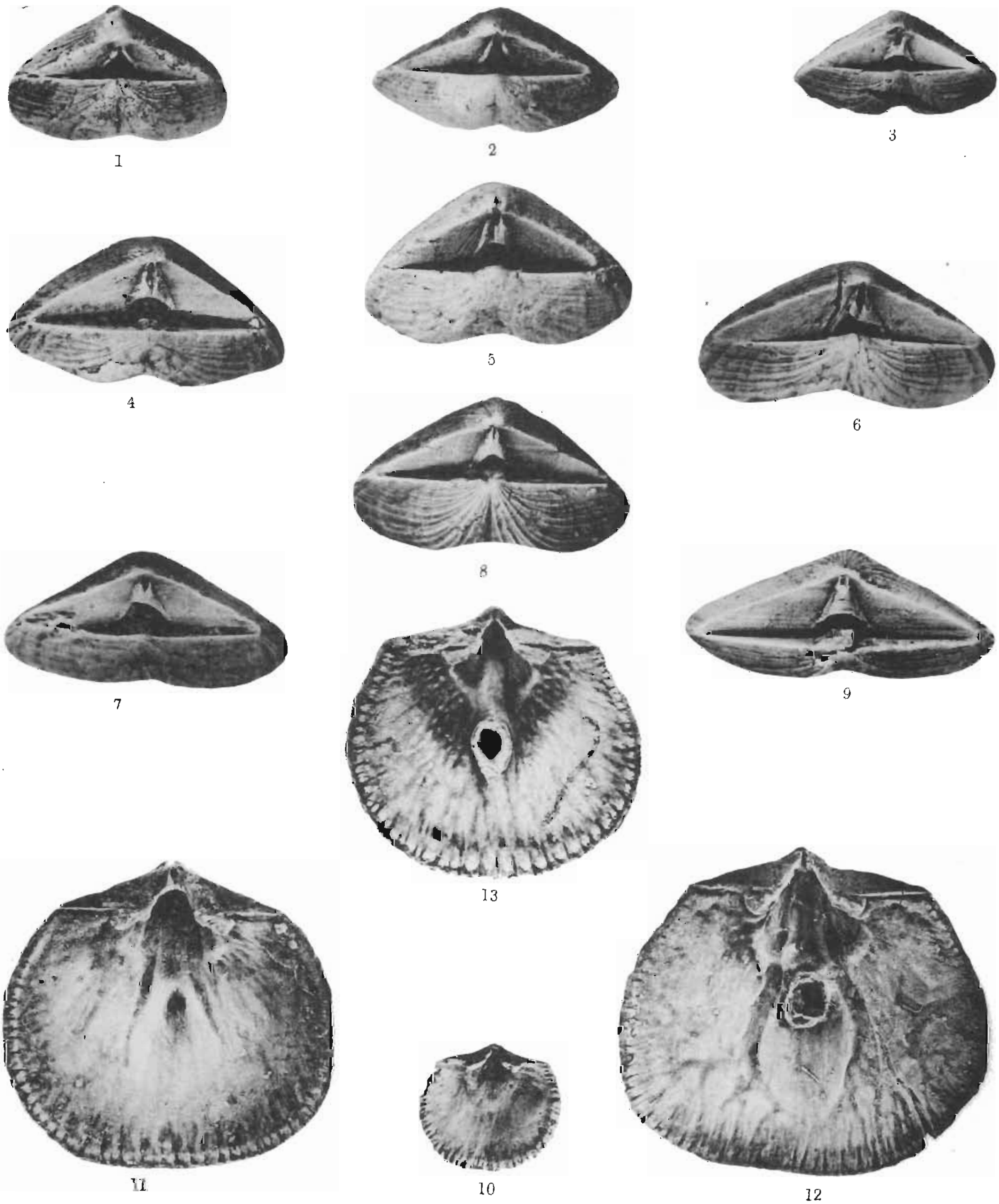

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PLATE VI

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Phragmophora schnuri Cooper 39

Fig. 1-7. Mature dorsal valves showing variations of septum, inside oblique view; × 4.
Fig. 8. Mature dorsal valve, hinge-line view; × 4.
Fig. 9-11. Three mature dorsal valves, inside view; × 4.


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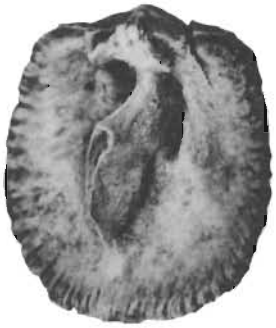
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PLATE VII

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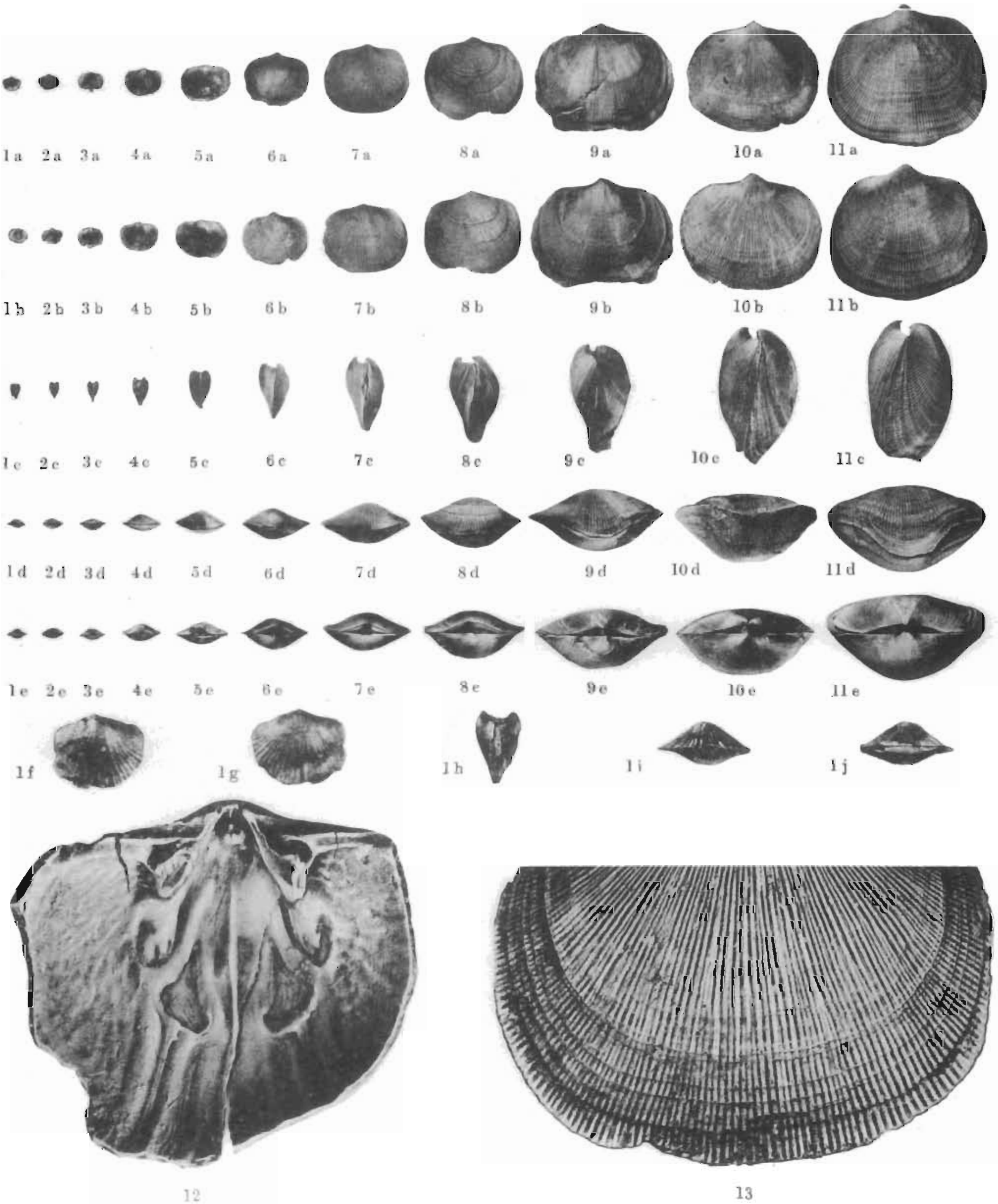
Schizophoria striatula (SCHLOTHEIM) 54

Fig. 1-11. Series of successive growth stages, from five aspects: *a* dorsal, *b* ventral, *c* lateral, *d* anterior margin, *e* hinge-line; nat. size.

Fig. 1*f-j*. Smallest specimen of that series (fig. 1), as above; × 6.5.

Fig. 12. Mature dorsal valve, inside view; × 3.5.

Fig. 13. Ventral ornamentation of juvenile specimen; × 6.



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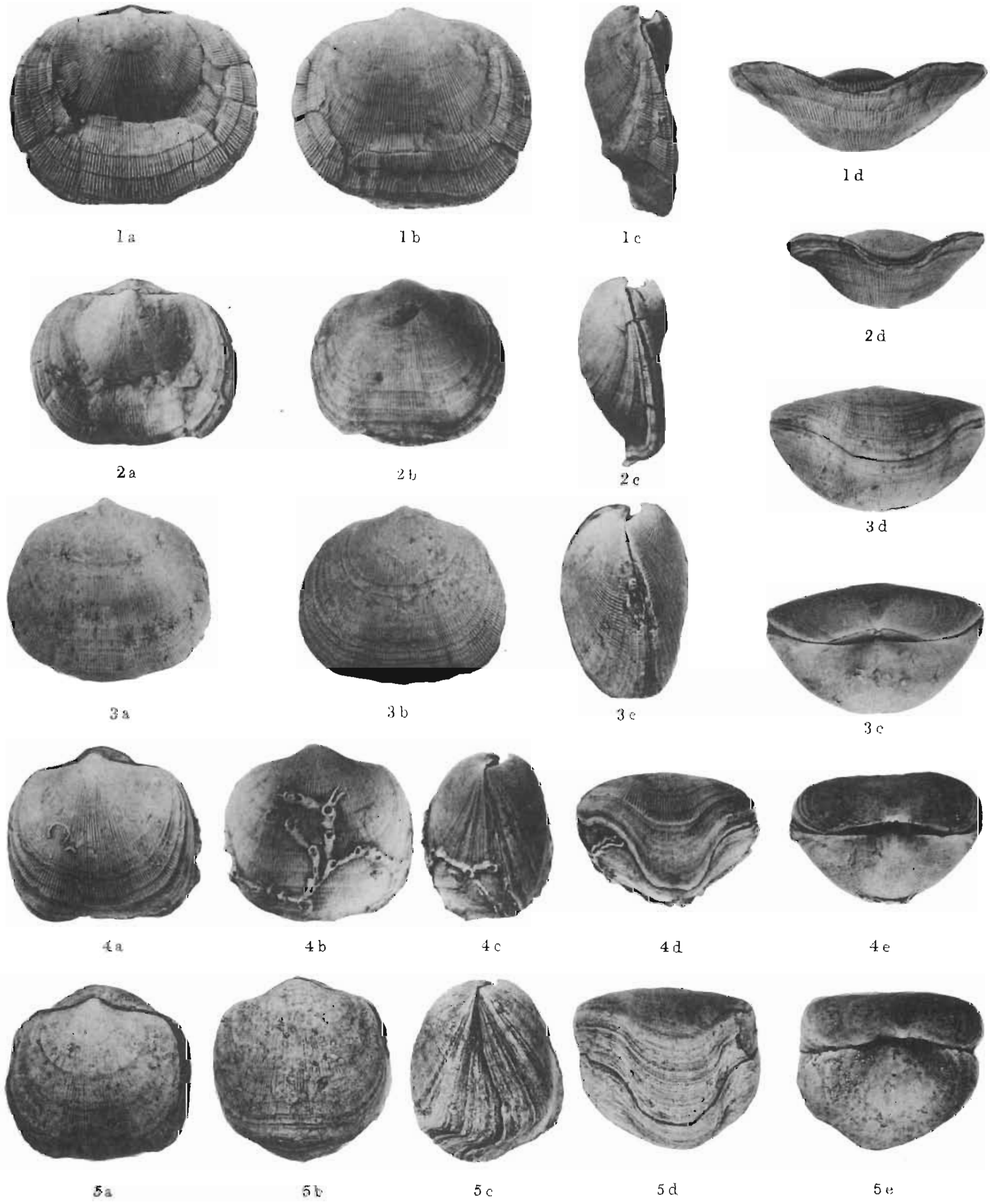
Schizophoria striatula (SCHLOTHEIM) 54

Fig. 1-5. Series of mature specimens of different thickness, from five aspects: *a* dorsal, *b* ventral, *c* lateral, *d* anterior margin, *e* hinge-line; nat. size.

Fig. 4*b*. Old specimen with *Aulopora* sp.

Fig. 5*a-b*. Markedly senile specimen.



G. BIERNAT: MIDDLE DEVONIAN ORTHOIDEA FROM THE HOLY CROSS MOUNTAINS AND THEIR ONTOGENY

G. BIERNAT: MIDDLE DEVONIAN ORTHOIDEA OF THE HOLY CROSS MOUNTAINS
AND THEIR ONTOGENY

PLATE IX

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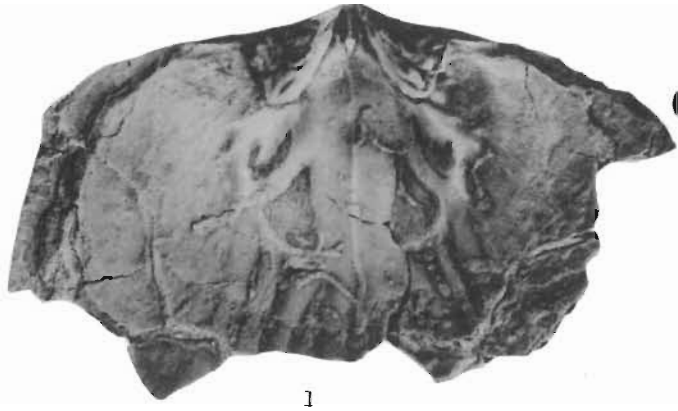
Schizophoria striatula (SCHLOTHEIM) 54

Fig. 1, 2. Two mature dorsal valves, inside view; × 3.
Fig. 3-6. Four ventral valves showing variations of muscle area, impressions of gonades and pallial sinuses: *3* young specimen, *4-6* old specimens, inside view; × 3.



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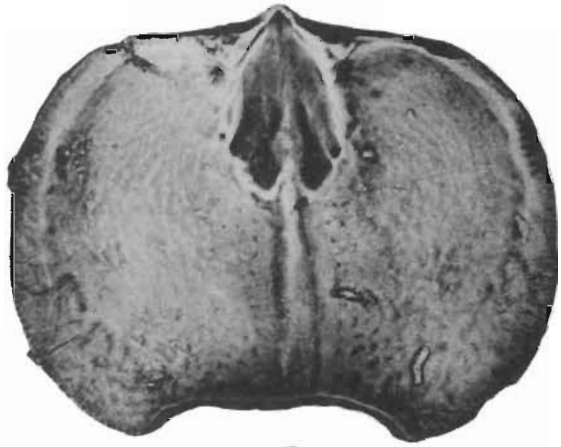

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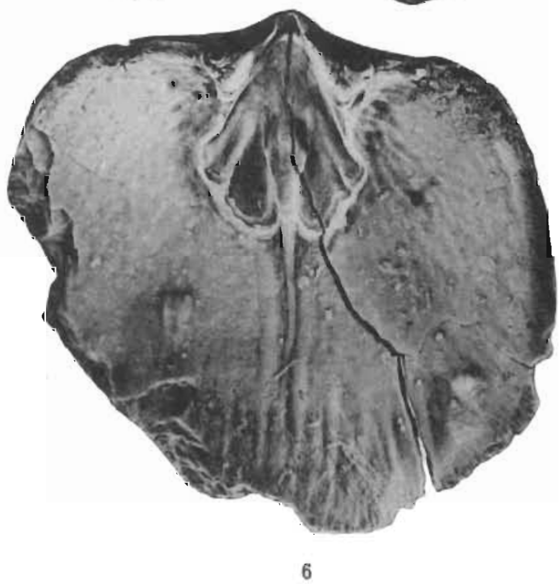

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G. BIERNAT: MIDDLE DEVONIAN ORTHOIDEA FROM THE HOLY CROSS MOUNTAINS AND THEIR ONTOGENY

G. BIERNAT: MIDDLE DEVONIAN ORTHOIDEA OF THE HOLY CROSS MOUNTAINS AND THEIR ONTOGENY

PLATE X

Page

Isorthis canalicula (SCHNUR) 63

Fig. 1-8. Series of successive growth stages, from five aspects: *a* dorsal, *b* ventral, *c* lateral, *d* anterior margin, *e* hinge-line; nat. size.

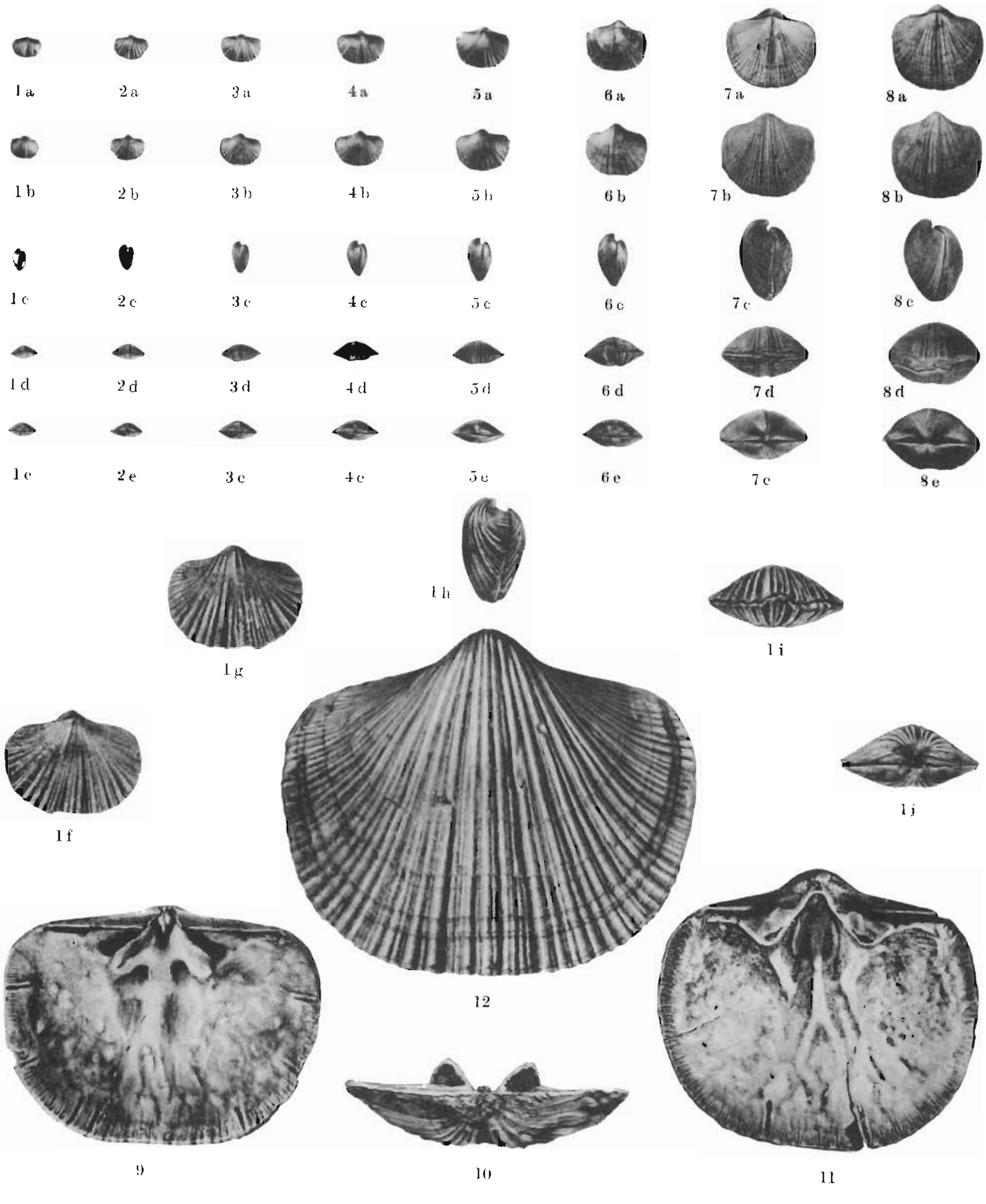
Fig. 1*f-j*. Smallest specimen of that series, as above; × 5.

Fig. 9. Dorsal valve, inside view; × 4.

Fig. 10. Dorsal valve, hinge-line view; × 4.

Fig. 11. Ventral valve, inside view; × 4.

Fig. 12. Ventral ornamentation in mature specimen; × 6.



G. Biernat: Middle Devonian Orthoidea from the Holy Cross Mountains and their ontogeny

G. BIERNAT: MIDDLE DEVONIAN ORTHOIDEA OF THE HOLY CROSS MOUNTAINS AND THEIR ONTOGENY

PLATE XI

Page

Kayserella lepida (SCHNUR) 36

Fig. 1. Ventral valve punctae in specimen 3 mm long.

Isorthis canalicula (SCHNUR) 63

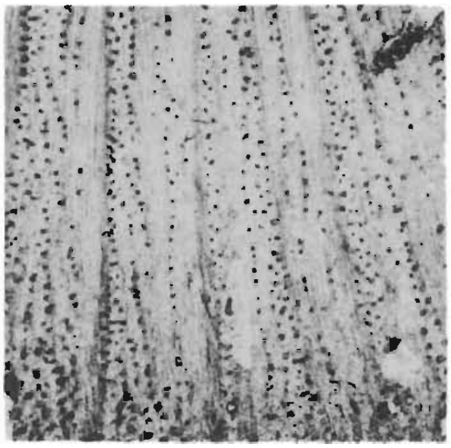
Fig. 2*a-b*. Ventral valve punctae in mature specimen: *a* in central portion of valve, *b* near anterior margin.
Fig. 2*c*. Ventral valve punctae in young specimen about 2 mm long.

Schizophoria striatula (SCHLOTHEIM) 54

Fig. 3. Ventral valve punctae in mature specimen: *a* in central portion of valve, *b* near anterior margin.

All specimens × 47 approx.

1



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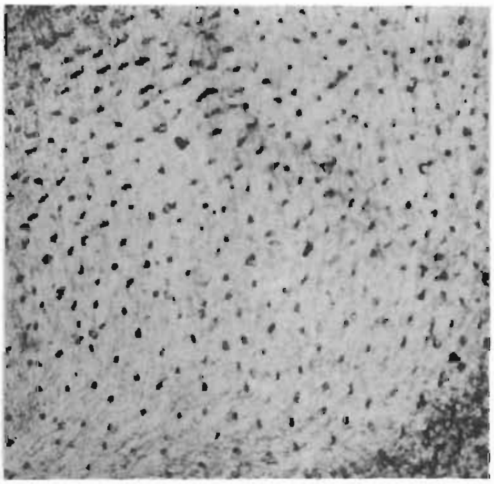

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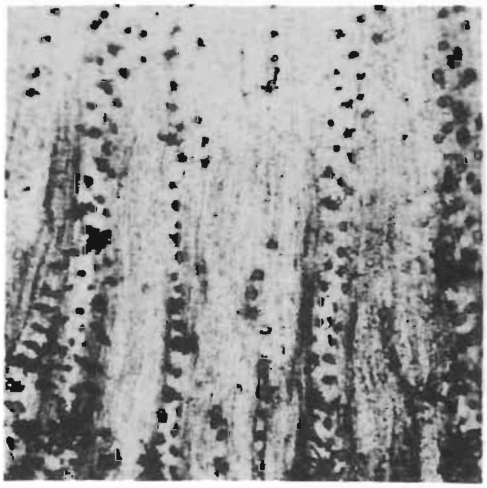

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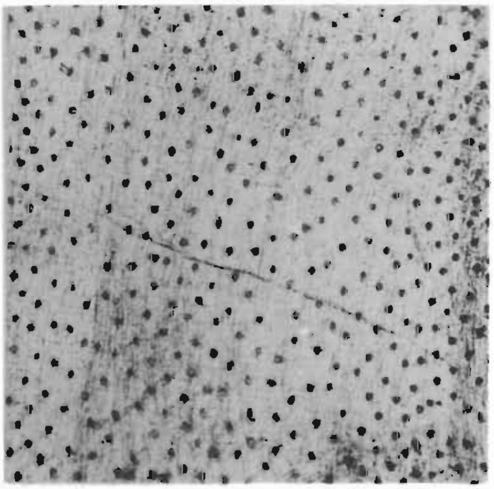

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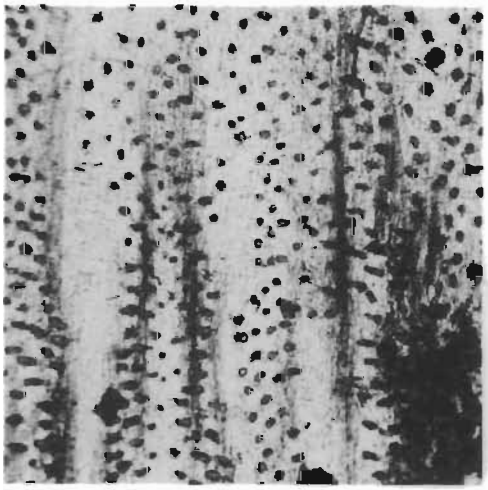

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PLATE XII

Page

Aulacella eifeliensis (VERNEUIL) 26

Eifel, Germany

Fig. 1. Ventral valve punctae in mature specimen: *a* towards the centre of valve, *b* near anterior margin.

Aulacella eifeliensis (VERNEUIL) 26

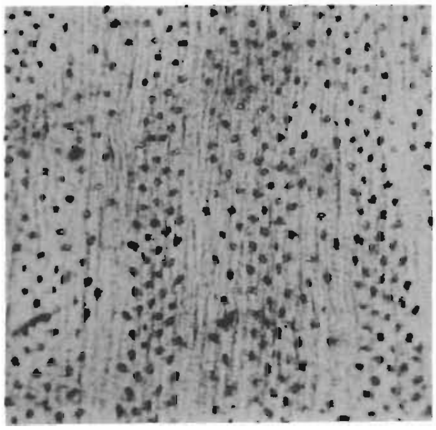
Holy Cross Mts., Poland

Fig. 2. Ventral valve punctae in mature specimen: *a* in centre of valve, *b* near anterior margin.

Phragmophora schnuri COOPER 39

Fig. 3. Ventral valve punctae in mature specimen: *a* near anterior margin, *b* in centre of valve.

All specimens × 47 approx.



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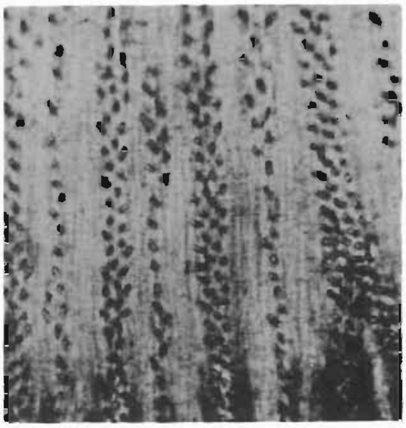

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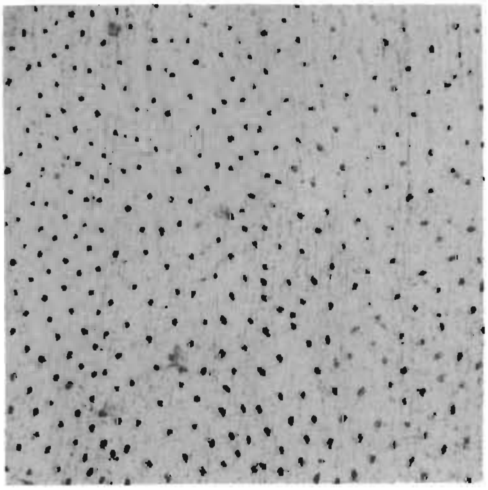
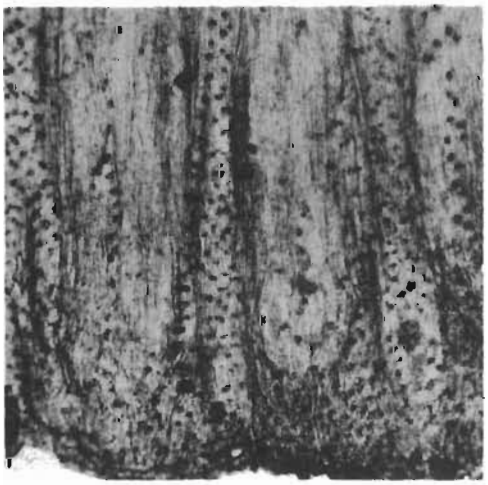


2 a

2 b



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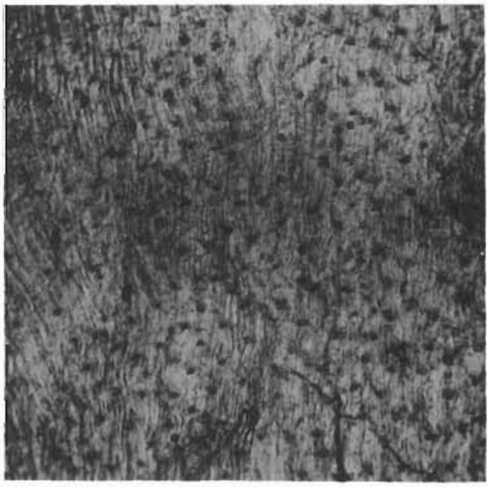

3 b

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ACHATS

Pour achat de „Palaeontologia Polonica" à l'étranger prière s'adresser à

Centrala Handlu Zagranicznego „Ars Polona"
Krakowskie Przedmieście 7, Warszawa, Pologne.