MORPHOLOGICAL OBSERVATIONS ON KOZLOWSKIELLINA (SPIRIFERIDA)

BY

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ABSTRACT

The genus *Kozlowskiellina* Boucot, 1957, which comprises about nine species, has a stratigraphic range from Wenlock (Middle Silurian) up to the Upper Emsian (Lower Devonian). In this paper, several characters are described: the micro-ornamentation, the internal characters of the pedicle valve, and the interior of the brachial valve. With respect to these three characters, there is a great diversity within the genus, especially in the pedicle valve, some of the species having dental plates and others lacking these structures. In addition to the description of the micro-ornamentation, a functional interpretation of some features of this ornamentation is given. Because of the diversity, it seems impossible to describe the genus with one chosen type species. Therefore, a historic interpretation is given that represents the essence of the genus. A genus is a group of species which are historically closely related; a description of a genus is the description of the morphological history of that genus. Consequently, an attempt has been made in this paper to define the historic relationship between the different species within the historic group of the genus *Kozlowskiellina*.

INTRODUCTION

In 1957, A. Boucot introduced the subfamily Kozlowskiellinae within the family Delthyridae Waagen, 1883. In this subfamily he made two genera: *Kozlowskiella* and *Hedeina*. In the genus *Kozlowskiella* he distinguished two subgenera, namely *Kozlowskiella (Kozlowskiella)* and *Kozlowskiella (Megakozlowskiella)*, with the type-species *K.(K.)strawi* Boucot, 1957 and *K.(M.)perlamellosa* (Hall, 1857). Boucot gives the following diagnoses:

"Kozlowskiellinae: Spiriferaceans possessing concentric growth lamellae terminating peripherally in frills. The surface of the shell has radial fine ornamentation, consisting of raised lines that terminate peripherally over the edge of each growth lamella as a fringe of minute spines.

Kozlowskiella: Kozlowskiellinins possessing a median septum in the pedicle valve, and a bifid cardinal process in the brachial valve.

Subgenus *K. (Kozlowskiella)*: Members of the genus *Kozlowskiella* which do not reach much more than 1 cm. in the greatest dimensions and have relatively flat brachial valves.

Subgenus *K. (Megakozlowskiella)*: Members of the genus *Kozlowskiella* which reach maximum dimensions of well over 1 cm. and up to 4–5 cm., and have strongly convex brachial valves.

Hedeina: Kozlowskiellinins lacking a median septum in the pedicle valve and having a simple, striate cardinal process."

In 1958 Boucot proposed the name *Kozlowskiellina* to replace the preoccupied name *Kozlowskiella*. Consequently, the subfamily is then called Kozlowskiellininae

and the subgenera *Kozlowskiellina (Kozlowskiellina)* and *Kozlowskiellina (Megakozlowskiellina)*.

Pitrat, 1965, not making the subgeneric distinction, gives the following diagnoses.

For the subfamily Kozlowskiellininae Boucot, 1957: "Lateral slopes with few, very strong plications; micro-ornament consisting of strong growth lamellae which tend to bend outward and become frilly at their anterior margins, and capillae which become fimbriate at edges of frills; interior of pedicle valve with well-developed dental plates, and generally median septum; brachial valve interior with short crural plates."

For the genus *Kozlowskiellina*: "Pedicle valve with well-developed median septum; brachial valve with deeply striate, bilobed cardinal process."

For the genus *Hedeina*: "Pedicle valve without median septum; brachial valve with simple, striate cardinal process; otherwise like *Kozlowskiellina*."

Amsden, 1968 p. 73 states that the distinction within the genus *Kozlowskiellina* into the two subgenera *K. (Kozlowskiellina)* and *K. (Megakozlowskiellina)* is a useful taxonomic distinction. Within the scope of this publication, however, I shall not make the subgeneric distinction.

The following species can be assigned to the genus *Kozlowskiellina*:

K. strawi Boucot, 1957 – Wenlock limestone, Britain.
K. vaningeni (Thomas, 1926) – St. Clair limestone – Clarita formation (Wenlock), U.S.A.
K. deltidialis (Hedström, 1923) – Halla limestone (Wenlock), Gotland.
K. velata Amsden, 1958 – Haragan (Helderberg), Okla., U.S.A.

K. perlamellosa (Hall, 1857) – New Scotland (Helderberg), New York, U.S.A.

K. cyrtinoides (Dunbar, 1920) – Upper Rockhouse (U. Silurian) – Birdsong Shale (Gedinnian), Tenn., U.S.A.

K. hesione (Billings, 1863) – Square Lake limestone (Helderberg), Maine, U.S.A.

K. raricosta (Conrad, 1842) – Early Deerpark (Lower Siegenian), Nevada – Onondaga (Upper Emsian) Williamsville, N.Y. – Emsian of Nevada (Johnson, Boucot, Murphy 1967), U.S.A.

K. new species Amsden & Ventress, 1963 – Frisco (Siegenian), Okla., U.S.A.

In this paper I shall describe some characters that I think are important for the taxonomy but are not yet known in full detail. Successively, I shall describe the micro-ornamentation, the interior of the pedicle valve, and the interior of the brachial valve.

MORPHOLOGICAL DESCRIPTION

MICRO-ORNAMENTATION

Kozlowskiellina strawi Boucot, 1957
(Plate I, Figs. 1/2, 3/4)

The micro-ornamentation consists of prominent growth lamellae and very fine radial lines called capillae (Williams & Rowell, 1965, p. H141). Besides the distinct growth lines (i.e. the anterior margin of each growth lamella), minor growth lines are also present on the growth lamellae. (See also description of *K. velata*). On the intersections of these minor growth lines and the capillae, small nodules have formed (text-figure 1). Usually, the radial capillae on the successive growth lamellae are situated in direct lines. In all specimens we found that the capillae in very young growth stages are thinner and closer to one another than the ones in adult stages.

Starting from the assumption that there may be a relation between the radial capillae and the position of the sensitive setae, the size differences mentioned above might be explained by the growth of the setae. Because of the smallness of *K. strawi*, the capillae near the commissure of adult specimens of this species are still smaller than the capillae near the commissure of, for instance, *K. vaningeni* and *K. velata*. The lateral parts of the ventral cardinal area also show growth lamellae and capillae. (For an explanation see the description of *K. velata*).

Kozlowskiellina vaningeni (Thomas, 1926)
(Plate II, Figs. 5/6, 7/8, 9/10)

The micro-ornamentation of *K. vaningeni* is very similar to that of *K. strawi*: Radial capillae, growth lamellae with minor growth lines giving rise at the intersections with the capillae to small nodules (Plate II, Fig. 9/10). In some cases the minor growth lines become more prominent than the radial capillae. The growth lamellae are flat and lie superimposed on each other. The capillae on the surface of the shell correspond with radial furrows in the inner surface of the valve (text-figure 1). These furrows, which are formed at the growing edge of the valve, were filled secondarily more posteriorly, towards the umbo. (For a functional interpretation, see the description of *K. velata*). The minor growth lines indicate the absence of minute spines terminating peripherally over the edge of the growth lamellae.

As in *K. vaningeni*, the lateral parts of the ventral cardinal area show growth lamellae and radial capillae. (For this point we refer to the description of *K. velata*, which is better preserved).

Kozlowskiellina deltidialis (Hedström, 1923)
(Plate II, Figs. 1/2, 3/4)

In principle, the micro-ornamentation of *K. deltidialis* is just the same as that of *K. vaningeni:* flat-lying growth lamellae, radial capillae mostly in even lines, and minor growth lines with a nodular aspect on the growth lamellae. The ventral cardinal area shows, as in *K. strawi* and *K. vaningeni*, very distinct growth lamellae on the lateral parts, having the same micro-ornamentation as that on the valves themselves.

Kozlowskiellina velata Amsden, 1958
(Plate III, Figs. 5/6, 7/8. Plate V, Figs. 1, 3, 5)

The micro-ornamentation consists of concentric growth lines and radial capillae. The growth lamellae sometimes lie upon each other as in *K. vaningeni* and *K. deltidialis*, but beetling growth lamellae also occur. Where this is the case, the growth lamellae are not flat but concave. This concavity is the most striking on the crests of the radial plications (Plate II, Fig. 5/6).

At the anterior margins of the valve the capillae on the outside correspond with furrows on the inside (Plate V, Fig. 1). New capillae have been formed by intercalation. On the growth lamellae there occur minor growth lines which are in fact fine concentric ridges, obviously formed by the curling up of the mantle edge at the end of each minor growth stage (Plate III, Fig. 5/6; Plate V, Fig. 5; text-figure 1).
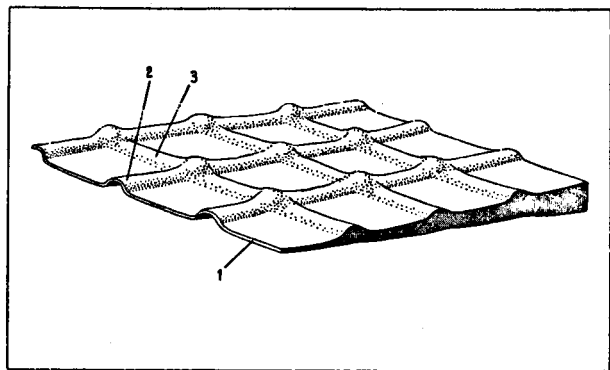

Fig. 1. Diagram showing the micro-ornament elements. Radial capillae and minor growth ridges. On the intersections of the minor growth ridges and the radial capillae, small nodules have formed.
1 = anterior margin of valve
2 = radial capillae corresponding with an internal furrow
3 = minor growth ridge

The minor growth lines show that spines did not occur.

From longitudinal sections it is evident that the growth lamellae of the two valves did not touch each other along the commissure in any of the growth stages (Plate V, Fig. 3). In many cases the two valves touch each other along two concentric ridges lying inside the actual anterior margins of the valves. This intramarginal ridge is formed during the growth of the growth lamella in front of it (text-figure 2).
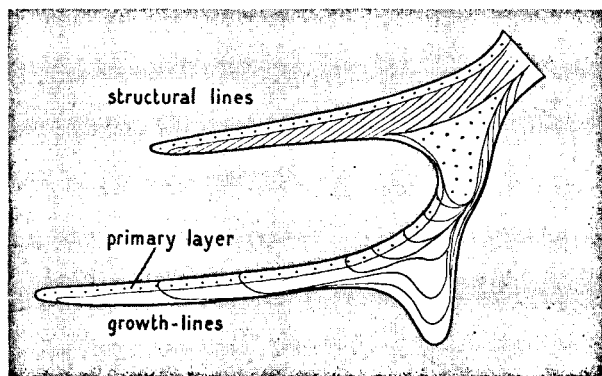

Fig. 2. Diagram showing the relation between the growth lamellae and the intramarginal ridge. The upper part of the diagram indicates the structural lines with the primary layer, the direction of the fibres in the secondary layer, and the fine-fibrous aspect of the intramarginal ridge (stippled). The lower part of the diagram gives the growth lines indicating that the intramarginal ridge formed during the radial growth of the adjacent growth lamella.

If it is accepted that the interior furrows in the valves at the growing margins of the valves served as the sites at which the setae were formerly situated, the functional margins of the valves with the sensitive setae would then have been situated anterior to the commissure proper (i.e. the touching intramarginal ridges). If the intramarginal ridges become more prominent, it is easy to see that the separation between the two sensitive margins of the mantle would become greater so that it would become more difficult for the setae to control the aperture between the two valves. As a result, at a certain stage the mantle would retract as far as the intramarginal ridge and the rows of setae of both valves would approach each other more closely again.

The intramarginal ridge is composed of very fine fibres formed by cells lying in a concentric outer epithelial zone of accelerated celldivision. The intramarginal ridge is more prominent under the crests of the radial costae than under the intercostal spaces (text-figure 3).

The combination of the greater concavity and the more prominent intramarginal ridge under the radial costae of both valves provides the parallelism of, and the equal distance between the two functional growth lamellae of both valves, which form, as it were, a pair of protruding lips at the anterior margin of the shell.
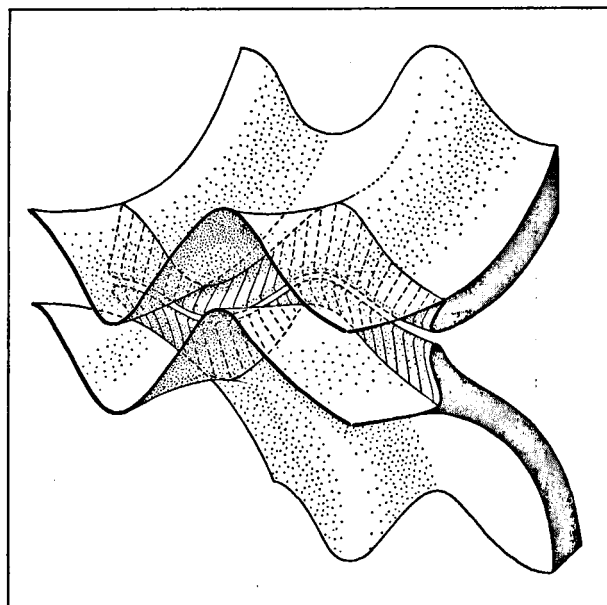

Fig. 3. Diagram showing the commissure and two opposite growth lamellae.
The actual commissure is situated at the level of the two contiguous intramarginal ridges. Note that underneath the crests of the costae the intramarginal ridge is more prominent. Note also that the growth lamellae are parallel and form a pair of extended lips.

There is a difference between young and older growth lamellae (text-figure 4). At the beginning of the formation of a new growth lamella, just after the retraction of the mantle, the two valves touch each

other along the growth lamellae. Furrows are formed in the inner surface of the valves to provide room for the protruding setae, the setal follicles lying behind the commissure. As the growth lamella extends further forward, the setal follicles will move forward too. It is possible that the intramarginal ridges are formed to give space to the follicles probably then lying anterior to the intramarginal ridges. Some sections show evidence for the presence of notches in the intramarginal ridges in an even line with the inner furrows in the growth lamellae, possibly serving to permit the protruding mantle canals to pass the intramarginal ridges. After the retraction of the mantle, the intramarginal ridge becomes the posterior part of the next growth lamella.
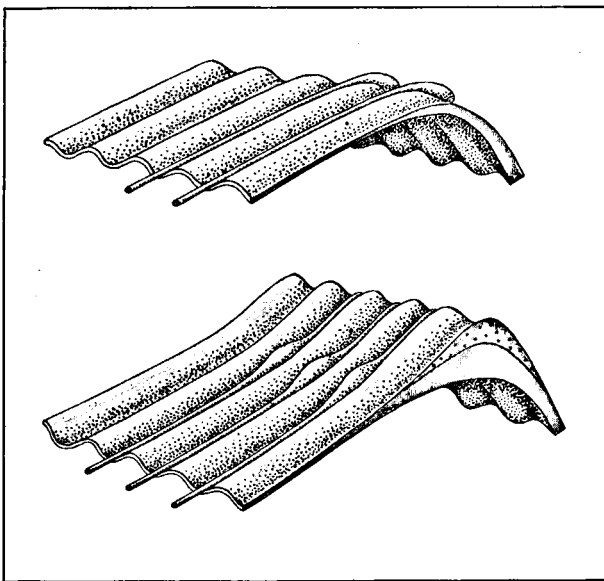
Fig. 4. Reconstruction of the supposed position of the setal follicles in relation to the radial capillae and the intramarginal ridge.
Above: young growth lamella
Below: older growth lamella with intramarginal ridge

An interesting feature is the presence of growth lamellae and capillae on the lateral parts of the cardinal areas, already mentioned for *K. strawi*, *K. vaningeni*, and *K. deltidialis*, but better preserved in *K. velata* (Plate III, Fig. 7/8). The presence of the capillae, which I think could be related to the setal arrangement along the commissure, gives some problems that can appropriately be discussed here.

Closer examination reveals that both lateral parts of the cardinal area carrying the growth lamellae and the capillae do not lie in the same plane as the interarea proper, the anterior margin of the real interarea being the hinge line, whereas the anterior margin of both lateral parts are not in an even line with the hinge line but are in fact parts of the normal commissure. Upon opening of the shell, the lateral parts of the ventral cardinal area and those of the dorsal cardinal area would become separated by the normal com-

missural aperture. As a consequence, water could intrude into the mantle cavity not only from the anterior but also from the posterior side. Is seems logical that setae would also be present along the posterior commissural aperture, which could explain the presence of the micro-ornamentation on the lateral parts of the cardinal areas. It would also be logical that the mantle could also retract along the cardinal margins of these parts, just as it can along the anterior commissure. Consequently, free growth lamellae could be formed on these lateral parts (text-figure 5).
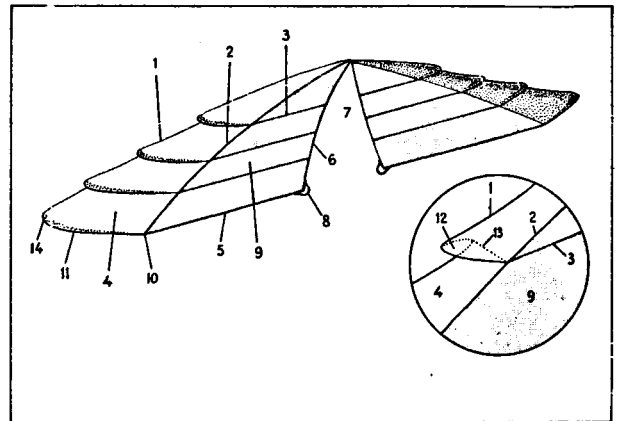

Fig. 5. Diagram of ventral cardinal area of *Kozlowskiellina*.

1	= beak ridge	9	= ventral interarea
2	= interareal side	10	= hinge extremity
3	= growth line	11	= cardinal margin
4	= ventral palintrope	12	= growth lamella
5	= hinge line	13	= limit of mantle retraction, giving rise to the growth lamella
6	= delthyrial side		
7	= delthyrium		
8	= hinge tooth (hinge point)	14	= cardinal extremity

Difficulties arise with respect to the nomenclature of these planes in the cardinal area, and some widely used terms require discussion.

A cardinal area (i.e. area Cloud 1942, p. 8) is the posterior sector of an articulate valve exclusive of delthyrium or notothyrium (Williams & Rowell, 1965, p. H141). In this respect we must distinguish between two types of cardinal area: The interarea and the palintrope. An interarea is a posterior sector of shell with a growing edge at the hinge line (Williams & Rowell, 1965, p. H146). A palintrope is a posterior sector of shell with a growing edge not coinciding with the hinge line.

Rudwick distinguishes strophic and non-strophic shells, the former with a hinge line, the latter without a hinge line. The interarea consequently occurs in strophic shells, whereas the palintrope will occur in non-strophic shells.

My definition is broader than is usually stated. Williams and Rowell (1965, p. H149) define the palintrope as the posterior sector in non-strophic shells. Because of the fact that a hinge line can only occur in strophic shells (by definition), the interarea can only

be present in strophic shells. Westbroek (1967, p. 66) points out that "the distinction between the strophic and non-strophic shells is by no means so clear-cut as Rudwick suggests". He shows that in some Rhynchonellids a non-strophic condition with palintrope is present, whereas in other species he finds interareas with strophic growing conditions. It is possible, according to Westbroek (1967), that in non-strophic shells a dorsal palintrope can also exist. Therefore, I think that the term 'nick points', i.e. the points at which the dorsal growing edge terminates (Rudwick, 1959, p. 20), should be used only in those cases in which the dorsal valve indeed grows hemiperipherally. Furthermore, the term nick line should be restricted to shells with hemiperipheral dorsal growth.

The essential difference between interarea and palintrope is that the former grows along the hinge line where the two mantle lobes are fused (Williams, 1956) whereas the palintropes are formed by growth along a line (cardinal margin Williams & Rowell, 1965, p. H141) that is not the hinge line and is in fact nothing more than the posterior part of the commissure between the cardinal extremities (Williams & Rowell, 1965, p. H141). The mantle lobes underneath the growing edges of the palintrope are not fused. The formation of the palintrope is not essentially different from the growth of the rest of the valve (excluding the interareas).

Applying these considerations on the cardinal area of *K. velata*, we can say that the median part of this cardinal area grows along the hinge line and that this part is therefore a true interarea, whereas the lateral part of the cardinal area is formed by growth along the cardinal margin and must be called palintrope. The cardinal margin is separated from the rest of the commissure by the cardinal extremities. The palintrope is separated from the flanks of the valve by the beak ridges (Williams & Rowell, 1965, p. H140).

The lines separating the interareas from the palintrope could be called interareal sides. The lines between the delthyrium and the interarea could be called delthyrial sides.

Kozlowskiellina perlamellosa (Hall, 1857)
(Plate VII, Fig. 4/5; Plate VIII, Fig. 7)

The entire surface of the valves is provided with prominent growth lamellae. Short growth lamellae are present near the umbo, whereas longer growth lamellae occur in the adult stages and become overhanging at the same time. In all specimens the overhanging growth lamellae have a crenated anterior margin, probably due to demolition of the very thin anterior parts of the growth lamellae. The growth lamellae carry radial capillae formed by corrugation of the growth lamellae (Plate VIII, Fig. 7). Near the umbo, where the growth lamellae lie superimposed on each other, the capillae of the successive growth lamellae form an even line. As soon as the growth lamellae become beetling, this radial feature is lost.

No indication for marginal spines was found.

The inner furrows in the valve corresponding with the outer capillae, extend rather far posteriorly before they are filled by secondary material. I have no data about intramarginal ridges as in *K. velata*.

Since the mantle retracts beyond the zone of the inner furrows, it is likely that the setal arrangement can undergo slight modifications, so that in the next growth lamella the capillae will have a somewhat different position.

The capillae of the two valves lack the congruence shown by the costae. The congruence of the costae is explained by the interaction of the commissural growth of both valves, the deflexions of the commissure giving rise of costae and opposite intercostal spaces. The capillae, assumed to be influenced by the setal arrangement in each individual valve are independent of any commissural interaction and are consequently not congruent in the valves.

Kozlowskiellina cyrtinoides (Dunbar, 1920)
Kozlowskiellina hesione (Billings, 1863)
Kozlowskiellina raricosta (Conrad, 1842)
(Plate XI, Fig. 7/8; Plate XII, Fig. 1)
Kozlowskiellina new species Amsden & Ventress, 1963
(Plate XII, Fig. 5/6)

The micro-ornamentation of these species is of the same type as that in *K. perlamellosa*.

Transverse sections of the growth lamellae of *K. raricosta* (Plate XII, Fig. 1) show that the undulations in the growth lamellae become deeper near the anteriormost margin of the growth lamellae. This means that the formation of interior furrows did not start immediately after the retraction of the mantle on the next growth lamella but that the undulations became more and more prominent during the anterior growth of the growth lamella. Moreover, the curvature of the growth lamella changes during its growth. At the beginning of the formation of a new growth lamella, the valves grow obliquely to one another. The growth lamellae become more and more parallel to each other. The setae would be depressed if no undulations were formed in the growth lamellae, but the furrows provided room for the protruding setae.

INTERIOR OF THE PEDICLE VALVE

Kozlowskiellina strawi Boucot, 1957
(Plate I, Figs. 5, 6)

Dental plates are present in all growth stages with a very clear mediotest * (text-figure 6).

The three apical cavities have not been filled by secondary material. A prominent median septum is present, although without a mediotest. The septum formed between the muscles, but the generative zone of the epithelial fold enveloping the septum was probably broad, so that no mediotest formed.

* The mediotest is a very thin layer, probably of prismatic calcite, lying within plate-like structures like dental plates and median septa. It was probably formed in a very sharp and narrow epithelial fold (Krans, 1965, p. 104).
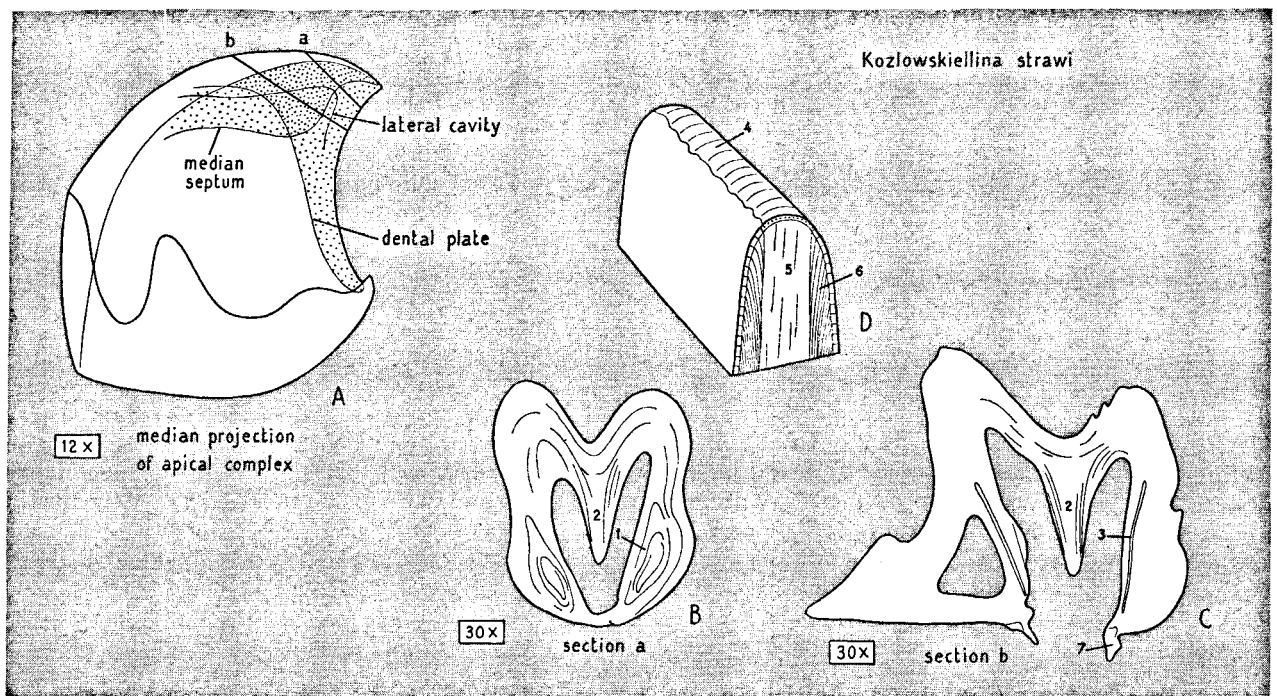
Fig. 6. *Kozlowskiellina strawi* Boucot, 1957
Ventral apical complex. Section a = acetate peel 6861A, 1; section b = acetate peel 6861A, 2. Wenlock ls. (nodular beds), West Side Wren's West Hill, N of Dudley, England.

1 = dental plate	4 = generative zone of epithelium enve-	6 = fine fibres
2 = median septum	loping the median septum	7 = deltidial plate
3 = mediotest	5 = coarse fibres secreted by generative zone	

I think that the septum of *K. strawi* differs from the septum that was formed in *K. velata, K. perlamellosa, K. raricosta,* and *K. hesione,* where all the septa have a mediotest. (Westbroek, 1967, p. 31, describes the same 'elementary difference' between the septa of *Kransia parallelepipeda* and *Sphaerirhynchia wilsoni).*

Kozlowskiellina vaningeni (Thomas, 1926)
(Plate III, Figs. 1, 2, 3, 4)

Sections of a juvenile specimen show short dental plates. They touch the bottom of the valve close to the umbo. In the dental plates a clear mediotest is to be seen. The dental plates touch the floor of the valve between the two costae bordering the sulcus (text-figure 7).

Young specimens invariably show the very thin dental plates. However, in adult specimens we find a very peculiar internal structure. Some of the adult specimens of *K. vaningeni* had almost no secondary thickening of the valve. In these valves we found rather thin and short dental plates with a clear mediotest (Plate III, Fig. 1).

In other specimens a very substantial filling of the apical cavities by secondary shell material had taken place. But curiously enough, in these cases we found no dental plates. The internal structure reveals very clearly that only dental ridges occurred before the

filling up started (Plate III, Fig. 2; text-figure 8). This raises the question of whether we are dealing with two distinct species or with only one species. The first possibility is not confirmed by the outer shape, which is identical in both forms. On the basis of present knowledge, it would be logical to regard these forms as to belong to a single species. Then the occurrences of two forms within this species must be explained. Within the scope of the following descriptions of *K. velata, K. perlamellosa,* and *K. cyrtinoides,* it is certainly a very interesting fact that this old species (Wenlock) shows a reduction of the dental plates. It is conceivable that some forms in the population already had reduction of the dental plates and that almost no dental plates occurred in these forms, or that the dental plates were present in all specimens but disappeared by resorption before the secondary filling up of the apical cavities. In my opinion, one thing is clear: this species ushered in a new evolutionary trend, which is clearly expressed in the younger species.

In the plane of symmetry a roof-like inward elevation is formed, its flanks lined with myotest * (Plate III,

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* The myotest is a shell layer formed at the sites of muscle attachment (Krans, 1967, p. 94–98). In the peels it has a somewhat cloudy appearance and a prismatic structure. After the muscle has shifted forward the myotest is covered by secondary shell material of fibrous structure.
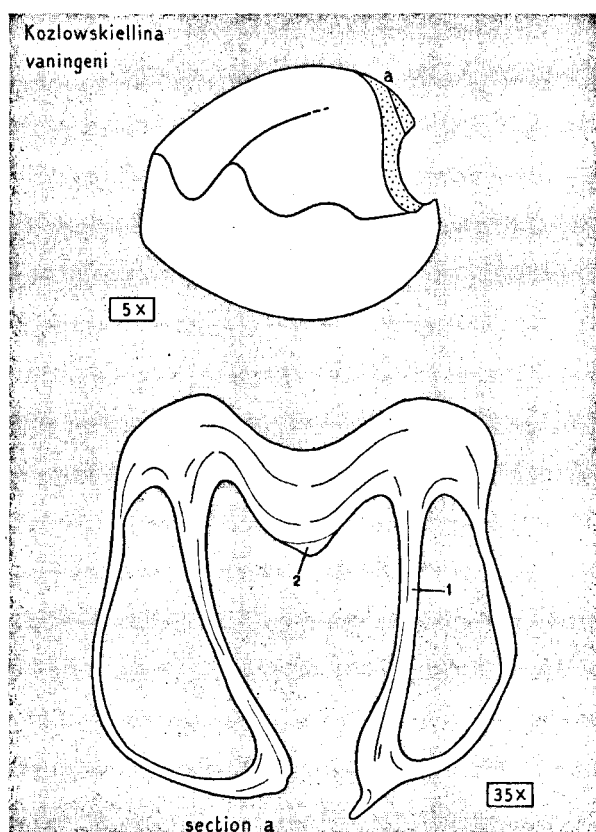
Fig. 7. *Kozlowskiellina vaningeni* (Thomas, 1926), young specimen.
Outline of dental plate in median projection and transverse section of pedicle valve. St. Clair Limestones (top beds), Cason Mine, 3 mi N of Batesville, Arkansas.
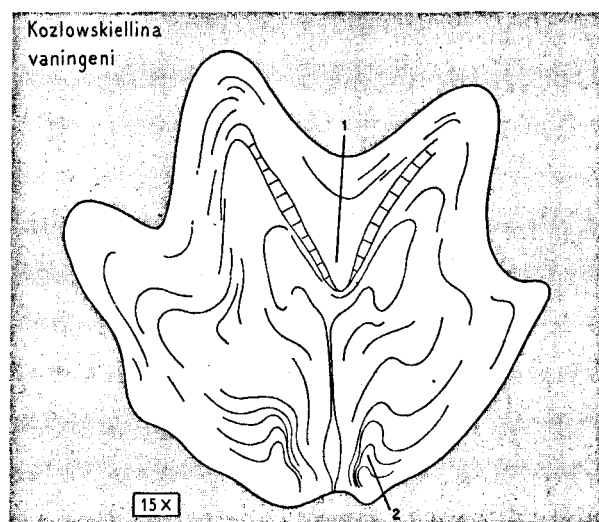Section a = acetate peel 6855a, 1.
1 = dental plate
2 = median ridge

Fig. 8. *Kozlowskiellina vaningeni* (Thomas, 1926), adult specimen.
Transverse section of pedicle valve. St. Clair Limestone (top beds), Cason Mine, 3 mi N of Batesville, Arkansas.
Acetate peel 6854a, 3.
1 = median ridge, lined with myotest
2 = dental ridge

Fig. 1). This ridge could be confused with a median septum. However, it never acquires the form of a real plate, and moreover it definitely has no mediotest in it. We prefer to apply to this structure the term median ridge.

Kozlowskiellina deltidialis (Hedström, 1923)

The interior of *K. deltidialis* is not known. Too few specimens were available to justify sectioning.

Kozlowskiellina velata Amsden, 1958
(Plate IV, Figs. 1/2, 3/4, 7; Plate V, Figs 2, 4; Plate VI, Figs. 1, 2, 3, 4, 5, 6; Plate VII, Fig. 1)

The apical cavity is filled with secondary material (Plate IV, Figs, 1/2, 3/4). Two dental ridges project forward; their inner faces are flat. They are fused to the floor of the valve by the filling up of the lateral parts of the apical cavity forming broad, vague ridges underneath the dental ridges. Besides the median

septum, two furrows for muscle attachment are present. The medially facing surfaces of the lateral fillings are determined by the muscles descending into the two 'muscle-furrows'.

Plate IV, Fig. 3/4 shows an advanced stage of the secondary filling of the apical cavity. On the lateral fillings, gonad impressions are present. The muscle field on both sides of the septum is differentiated. A paired muscle area, probably of the accessory diductor muscles, is elevated above the rest of the muscle field, forming two paired pits on both sides of the septum. Posterior to these pits the median septum is covered by secondary shell material forming the pedicle bed. This could indicate that the only function of the septum was to separate the paired muscles. Besides the two diductor pits the muscle field shows two somewhat elevated beds, probably the attachment areas of the ventral adjustor muscles (pedicle muscles).

In front of this area the attachment areas of the principal diductor muscles and of the adductors can be observed. The anterior curvature of the two ridges connecting the dental ridges with the floor of the valve is determined by the bypassing ventral adjustor muscles.

Serial sections of a juvenile specimen reveal that the very young stages lack dental plates (Plate V, Figs. 2, 3). Even very close to the umbo we find dental ridges (Plate IV, Fig. 7). In the sections it is rather difficult to locate just where the dental ridges are situated. However, Plate V, Fig. 3 shows that the dental ridges are very short and become fused to the floor of the valve by ventrally directed outgrowths of the dental ridges.
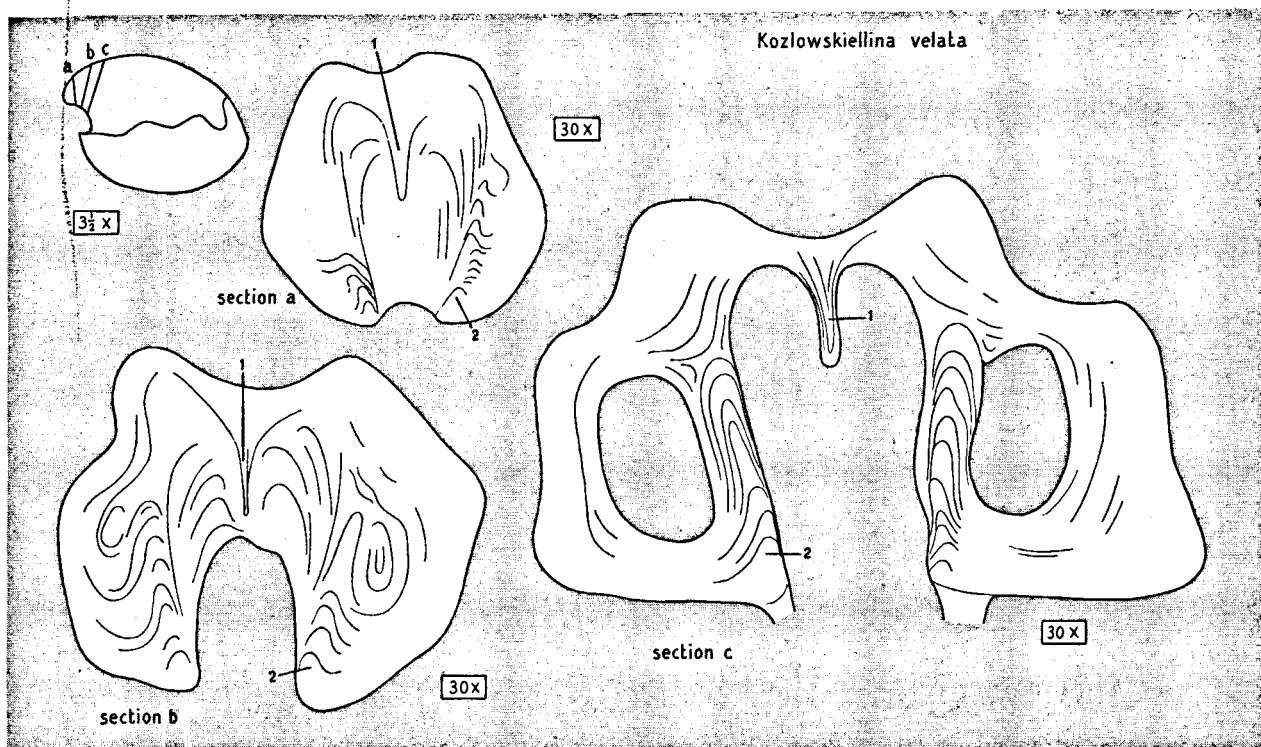
Fig. 9. *Kozlowskiellina velata* Amsden, 1958
Transverse sections of the pedicle valve. Haragan, Vines Dome, Sect. M1-J. Murray Co., Oklahoma. Section a = acetate peel 6856a, 1; section b = acetate peel 6856a, 3; section c = acetate peel 6856b.
1 = median septum   2 = dental ridge

In Plate VI, Fig. 1 the connecting ridges fusing the dental ridges to the floor of the valve become very prominent and form true short plates. Nevertheless, it is obvious that these plate-like structures are not homologous with the dental plates in *K. strawi* and *K. vaningeni*. This is made clear by a section of another specimen, where we see a different growth structure also resulting in a plate-like structure (text-figure 9). The dental ridges meet two secondary outgrowths of the floor of the valve. In a section more to the front of the same specimen we see that the formation of this plate-like structure is different again at this place. The growth of this apical structure was therefore rather irregular (text-figure 10).

Another interesting feature is the presence in the dental ridges of a very thin layer of clear prismatic calcite resembling the mediotest (Plate VI, Fig. 3). However, this layer is not formed in the middle of the dental ridges but only on the inner sides. Posteriorly, towards the umbo, this layer is covered by secondary shell material but appears at the surface where the inner faces of the dental ridges become flat (Plate VII, Fig. 1). In my opinion, it is conceivable that these inner surfaces of the dental ridges functioned as attachment areas for another pair of pedicle muscles, giving rise to the formation of a very thin myotest.

The median septum starts to grow as a roof-like

elevation of fibrous material comparable to the median ridge in *K. vaningeni* and covered by myotest. However, the growth continues with the formation of a
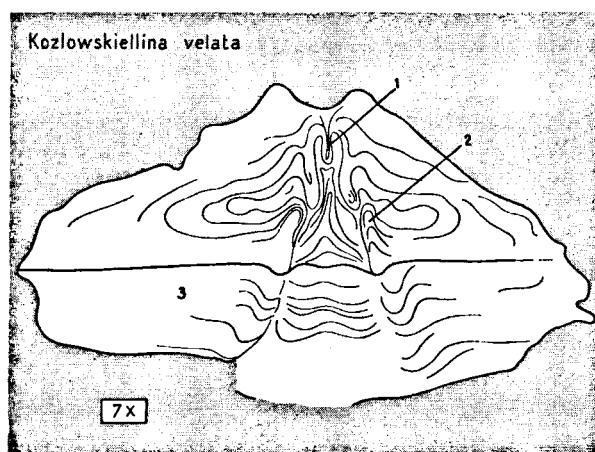
Fig. 10. *Kozlowskiellina velata* Amsden, 1958
Transverse section of pedicle valve. Haragan, SE of White Mound, Murray Co., TWA 6/19/56. Same section as the one of Amsden, 1958, text-figure 32, p. 122. Note the irregular connection of the dental ridges with the floor of the valve.

1 = median septum
2 = dental ridge
3 = section in the cardinal area

true plate between the paired muscles, which are attached to the flanks of the primary median ridge. The growing edge of the septum becomes sharper and narrower, and a mediotest is formed. The lower parts of the flanks of the median septum also served as an attachment area for the muscles, as shown by the myotest (Plate VI, Figs. 4, 5).
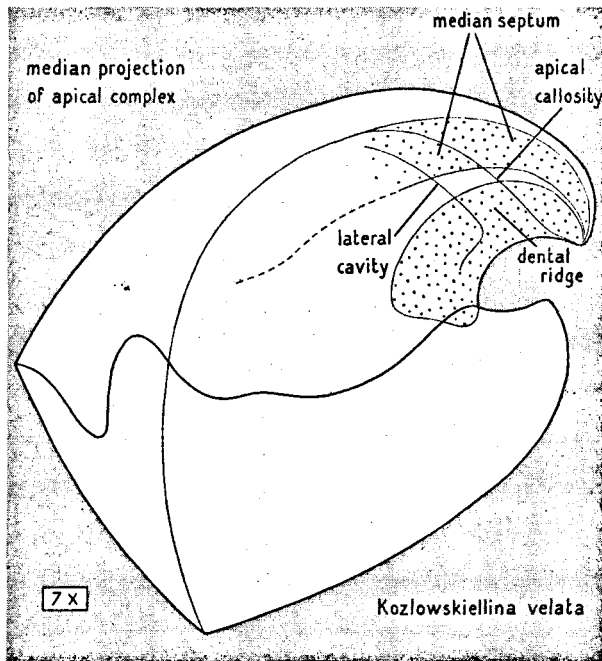
Fig. 11. *Kozlowskiellina velata* Amsden, 1958
Median projection of ventral apical complex.

Kozlowskiellina perlamellosa (Hall, 1857)
(Plate VII, Fig. 6/7; Plate VIII, Figs. 1/2, 3/4, 5/6, 8; Plate IX, Figs. 1, 2, 3, 4)

The interior of the pedicle valve of *K. perlamellosa* is in principle the same as in *K. velata*. Free-hanging dental ridges are seen only in the posterior part of the valve fused with the floor of the valve. The lateral parts of the apical cavity contain less secondary shell material than in *K. velata* (Plate VII, Fig. 6/7). The median septum separates the two symmetrical muscle fields.

The two teeth are directed medially. During the anterior growth, resorption of the teeth at their apical faces must have taken place. Underneath the teeth the dental ridges are curved, forming a rather substantial groove which provides room for the inner side of the dental socket of the brachial valve. This is shown very clearly in Plate VII, Figs. 6/7 and Plate VIII, Figs. 1/2, 3/4, 5/6, where it can be seen that the inner sides of the dental sockets just fit into the furrows underneath the teeth. It is also clear that the articulation takes place at the hinge line, and that during the opening of the valve the teeth and sockets are separated from each other. It seems quite

evident that the function of the teeth and sockets is not articulation but rather to prevent a sidewards movement of both valves (Plate VIII, Figs. 1/2, 3/4, 5/6; text-figure 14).

Text-figure 12 shows a series of sections of *K. perlamellosa*. There are no dental plates, the apical cavity is plugged to a certain extent, and the median septum is very prominent. The latter becomes a true plate in the sections as soon as the myotest crops out (text-figure 12 f). The dental ridges are connected to the floor of the valve by an exaggerated swelling of the first intercostal spaces. The dental ridges converge towards the floor of the valve (the first sections were cut more or less obliquely with respect to the direction of convergence and therefore show an aberrant picture). The V-shaped cavity formed by this convergence and having the form of a spondylium was not a muscle attachment area (no myotest is present) but probably served as a bed for the pedicle (Plate VIII, Fig, 8; Plate IX, Figs. 1, 2, 3, 4).

In the dental ridges a kind of mediotest is present. A closer look, however, shows that this layer is not situated in the middle of the dental ridges but at their median faces. More posteriorly this layer is covered by secondary material. This layer seems to me to be homologous to the one shown in *K. velata*. A problem presented by these sections, however, is that this probable myotest crops out only with a very small surface (Plate IX, Fig. 1). This might be explained by the fact that the pedicle probably became rudimentary, since the pedicle chamber is almost completely filled by secondary material; consequently, the pedicle muscles, which attached at the median flanks of the dental ridges, would become smaller and less important too.

As already mentioned, there is a groove in the dental ridges providing room for the inner sides of the dental sockets. The sections reveal that this groove is formed not only by the shape of the enveloping epithelial fold but also by resorption. It is easily seen in the sections that the growth lines in the delthyrial ridges are cut off, whereas originally these growth-lines would have been circular as the relicts of the former teeth (Plate IX, Fig. 3). These sections also show that the inner socket ridge of the brachial valve fits into this groove in the dental ridge (text-figure 14).

This sub-delthyrial groove is not found in the first sections near the umbo (Plate IX, Fig. 4). We must assume that only in later growth stages did a ventrolateral growth vector of the inner socket ridges cause the latter to touch the inner faces of the dental ridges. Good articulation required a groove.

A prominent median septum is present (Plate IX, Fig. 4). The median ridge, as its lower part, becomes less important. A mediotest is present in the median septum. Near the umbo the septum is covered by secondary shell material. A median projection of the apical structures made after the serial sections shows the plate-like extension of the median septum, the dental ridges, and the secondary secretions connecting the dental ridges with the floor of the valve (text-figure 15).
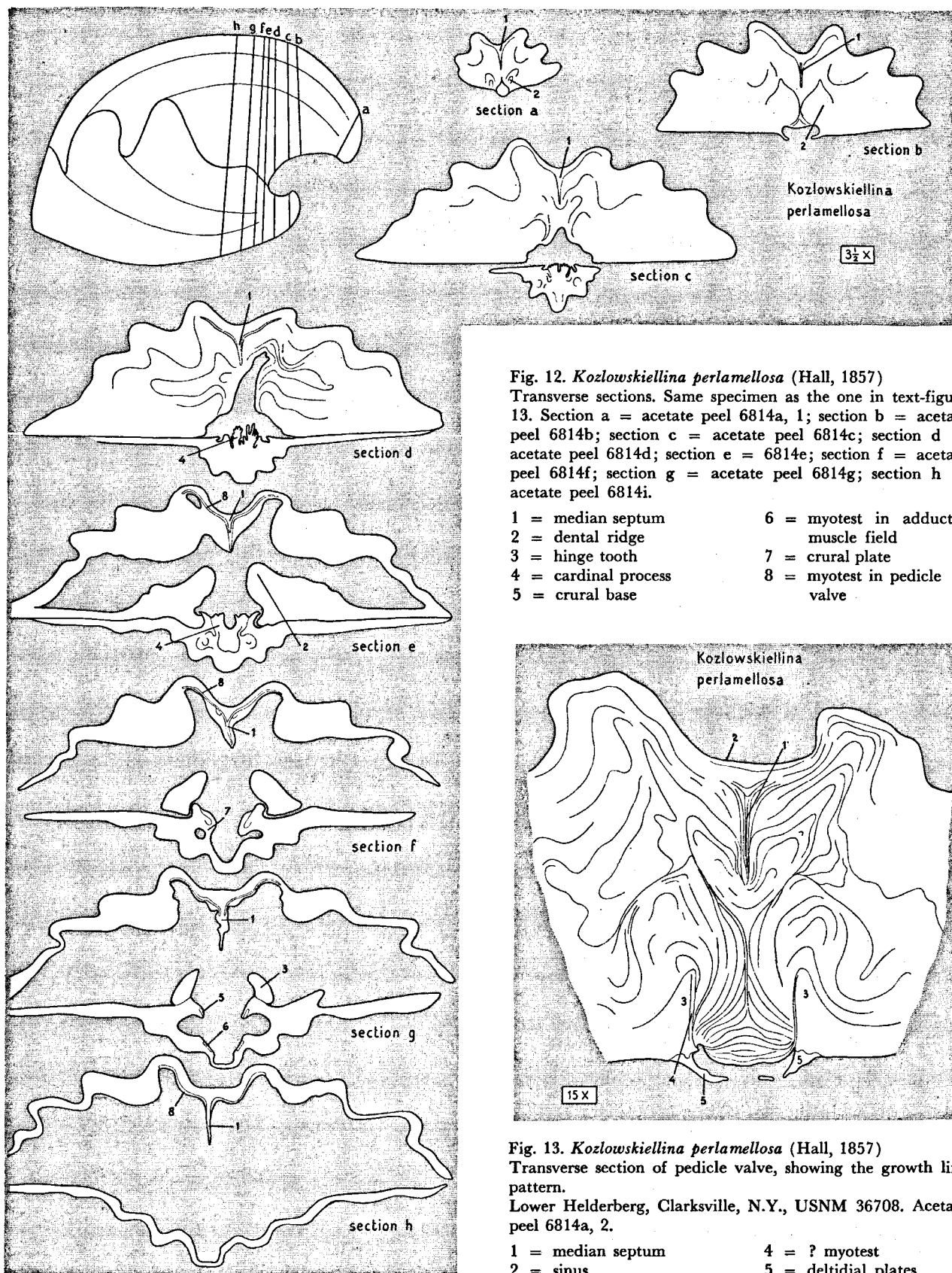
Fig. 12.

Fig. 12. *Kozlowskiellina perlamellosa* (Hall, 1857)
Transverse sections. Same specimen as the one in text-figure
13. Section a = acetate peel 6814a, 1; section b = acetate
peel 6814b; section c = acetate peel 6814c; section d =
acetate peel 6814d; section e = 6814e; section f = acetate
peel 6814f; section g = acetate peel 6814g; section h =
acetate peel 6814i.

1 = median septum		6 =	myotest in adductor
2 = dental ridge			muscle field
3 = hinge tooth		7 =	crural plate
4 = cardinal process		8 =	myotest in pedicle
5 = crural base			valve
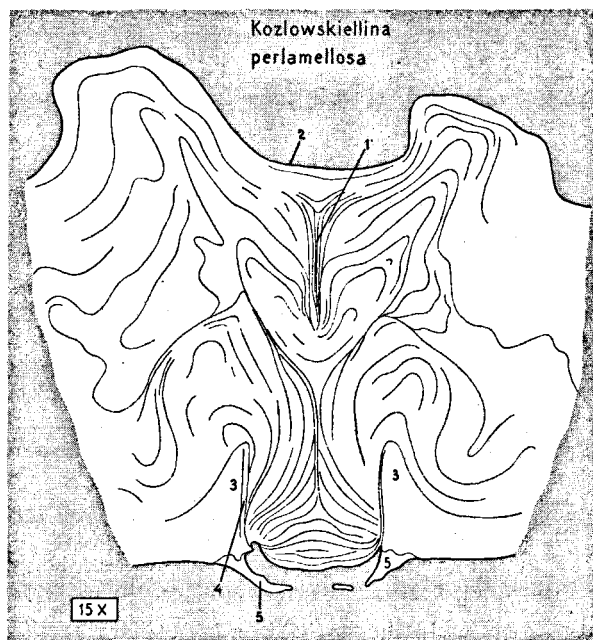
Fig. 13. *Kozlowskiellina perlamellosa* (Hall, 1857)
Transverse section of pedicle valve, showing the growth line
pattern.
Lower Helderberg, Clarksville, N.Y., USNM 36708. Acetate
peel 6814a, 2.

1 = median septum	4 =	? myotest
2 = sinus	5 =	deltidial plates
3 = dental ridges		
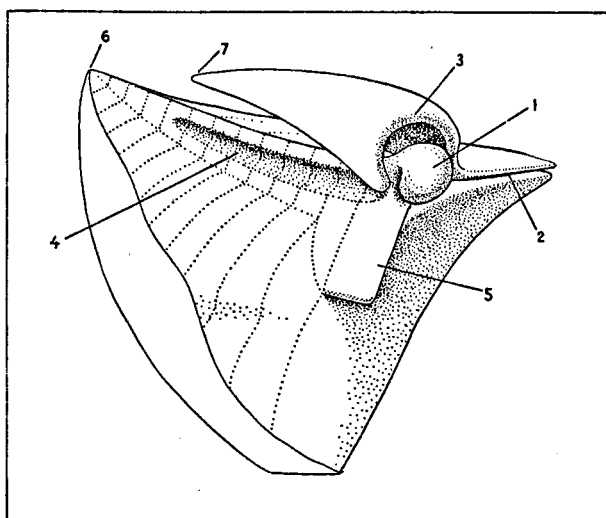
Fig. 14. Diagram showing the articulation of *Kozlowskiellina perlamellosa* (Hall, 1857). Drawn in exaggerated open position. Note that actual articulation takes place along the hinge line, the hinge tooth within the socket preventing a left-right movement. The delthyrial groove gives room to the inner socket wall.

1	= hinge tooth	5	= dental ridge
2	= hinge line	6	= ventral apex
3	= dental socket	7	= dorsal apex
4	= delthyrial groove		
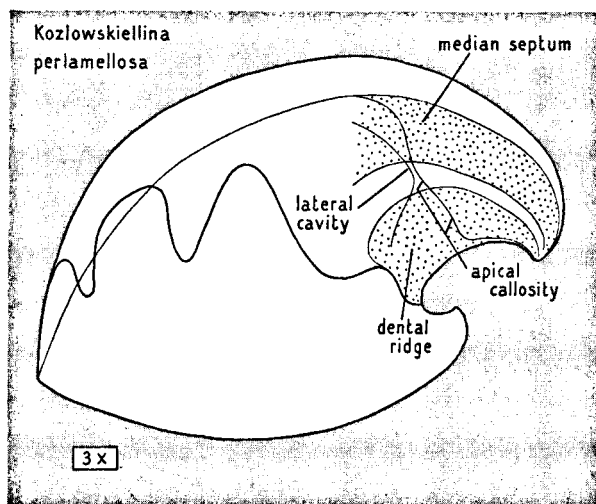
Fig. 15. *Kozlowskiellina perlamellosa* (Hall, 1857) Median projection of ventral apical complex.

Kozlowskiellina cyrtinoides (Dunbar, 1920)
(Plate X, Figs. 3/4, 5/6; Plate XI, Fig. 1/2)

No dental plates. The dental ridges converge towards the stout median septum and fuse with this septum by secondary outgrowths. In this way a spondylium-like structure is formed. The presence of the septum in this 'spondylium' could indicate that the spondylial bed functioned as muscle attachment. The lateral cavities

are open (Plate X, Fig. 3/4; Plate XI, Figs. 1, 2). In Plate X, Fig. 5/6 the probable attachment area (pits) for the accessory diductors are elevated above the floor of the valve, as in *K. velata,* and are situated at the same level as the rest of the 'spondylium'. Because of the silicification of this material, no instructive sections are available.

Kozlowskiellina hesione (Billings, 1863)
(Plate XI, Figs. 5, 6)

No dental plates. Dental ridges are present covered by secondary material. These dental ridges diverge towards the floor of the valve (Plate XI, Fig. 5, text-figure 16). The structure of the dental ridges and the plugging of the apical cavities are comparable to the situation in *K. velata.*
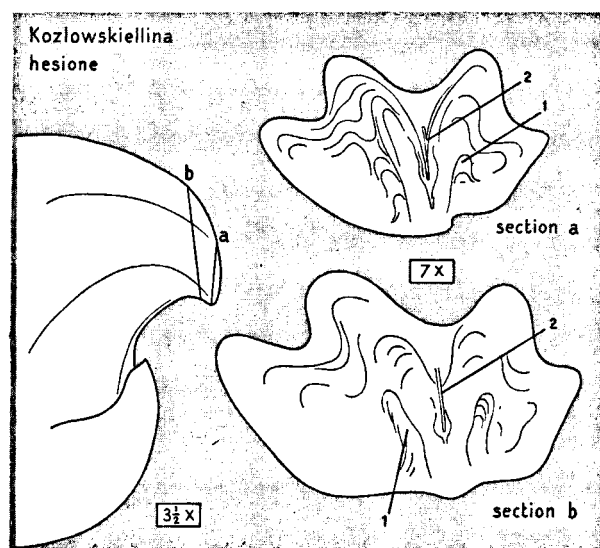
Fig. 16. *Kozlowskiellina hesione* (Billings, 1863) Transverse sections of pedicle valve. Helderberg, Square Lake Is., Square Lake, Aroostook Co., Maine. Section a = acetate peel 6819,1; section b = acetate peel 6819,2.

1 = dental ridge
2 = median septum

Prominent median septum with a distinct median ridge as its base. In the median ridge no mediotest is present. The formation of the mediotest starts at the point where the septum becomes sharp and narrow (Plate XI, Fig. 6).

Kozlowskiellina raricosta (Conrad, 1842)
(Plate XII, Fig. 2)

No dental plates. Converging dental ridges with the probable myotest on their flanks for the adjustor attachment. This myotest crops out at a certain distance from the umbo. The pedicle seems to be still functional, as judged from the open pedicle chamber.
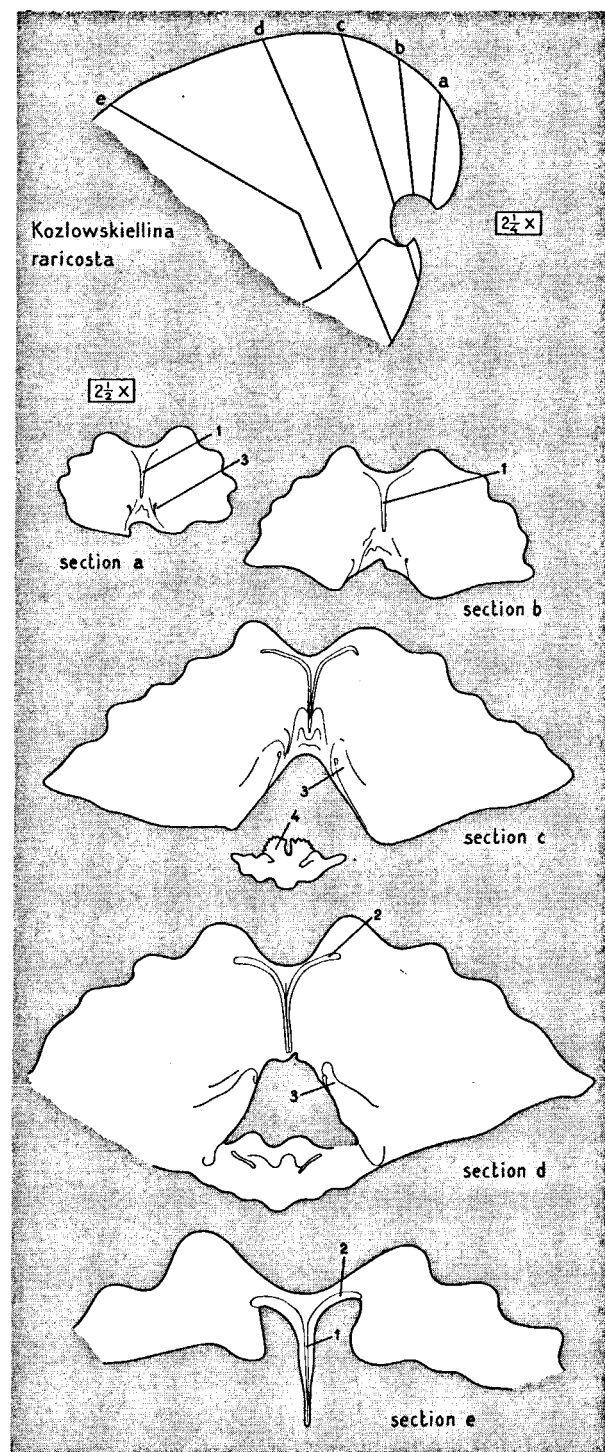
Fig. 17. *Kozlowskiellina raricosta* (Conrad, 1842)
Transverse sections. Devonian, Onondaga, Williamsville, Erie
Co., N.Y. Section a = acetate peel 6816b; section b =
acetate peel 6816c; section c = acetate peel 6816e; section
d = acetate peel 6816g; section e = acetate peel 6816j.

1 =	median septum	3 =	dental ridge
2 =	myotest	4 =	cardinal process

Very prominent median septum with mediotest (the
median ridge underneath the septum is obsolete).
Thick myotest in the floor of the valve partially lining
the sides of the median septum (text-figure 17).

INTERIOR OF THE BRACHIAL VALVE

Kozlowskiellina strawi (Boucot, 1957)

The apical structure of the brachial valve of this
species is only known from sections (text-figure 18).
Crural plates are present, as well as shallow small
lateral cavities.
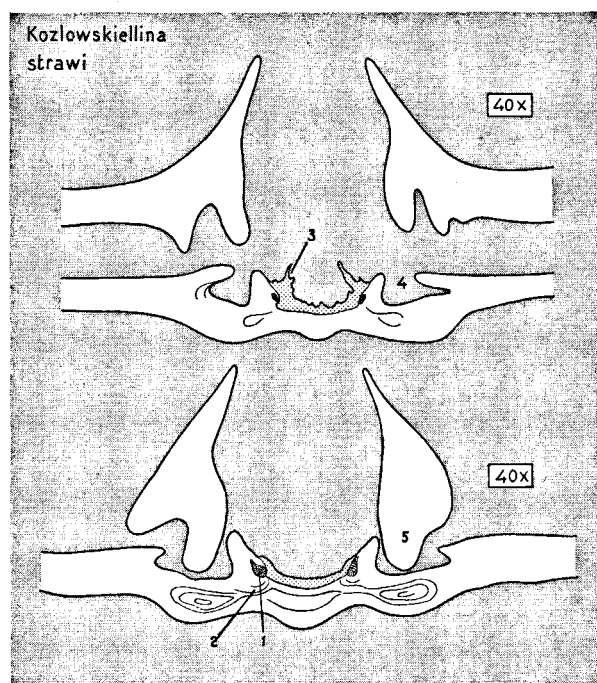
Fig. 18. *Kozlowskiellina strawi* Boucot, 1957
Transverse sections, showing brachial valve. Wenlock ls. (no-
dular beds), West Side Wren's West Hill, N of Dudley, Eng-
land. Acetate peel 6861a,4 and 6861b.

1 =	crural base	4 =	dental socket
2 =	crural plate	5 =	hinge tooth
3 =	cardinal process		

The diductor muscles were attached on the floor of
the central cavity, which has an irregular surface, and
also at two outgrowths on the inner sides of the
brachiophores, which carry some highly irregular la-
mellae forming a very obsolete cardinal process. The
crural bases are very small.

Kozlowskiellina vaningeni (Thomas, 1926)
(Plate III, Figs. 3, 4)

Only known from sections (text-figures 19 and 20).
Crural plates are present; they consist of the inner
socket ridges, the connection between the inner socket
ridges and the crural bases (i.e. outer hinge plate), the
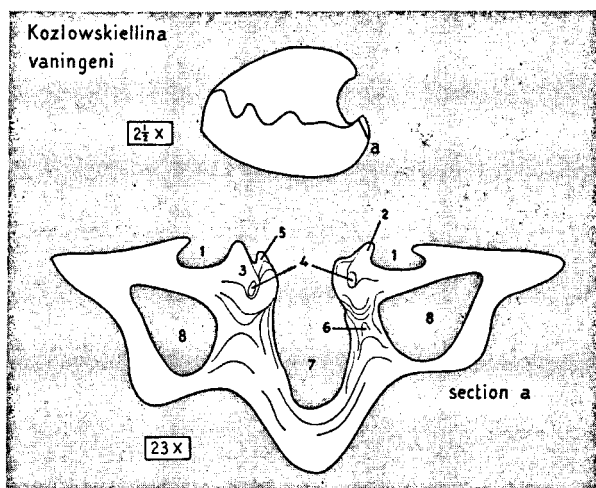
Fig. 19. *Kozlowskiellina vaningeni* (Thomas, 1926)
Transverse section of brachial valve. St. Clair Limestone (top
beds), Cason Mine, 3 mi N of Batesville, Arkansas. Acetate
peel 6858,1.

1 = dental socket
2 = inner socket wall
3 = outer hinge plate
4 = crural base

5 = outgrowths of outer
    hinge plate forming
    the cardinal process
6 = crural plate
7 = central cavity
8 = lateral cavity

crural bases themselves, and the secondary connections
of the crural bases with the floor of the valve (text-
figure 19). Amsden's peel 3, shown in text-figure 20,
has been cut perpendicular to the plane of separation.
Here we see, situated on the delthyrial faces of the
outer hinge plates, two lamellated outgrowths consti-
tuting the two lobes of a very small bilobed cardinal
process.
The lamellae of the cardinal process are rather low and
directed towards the median plane.
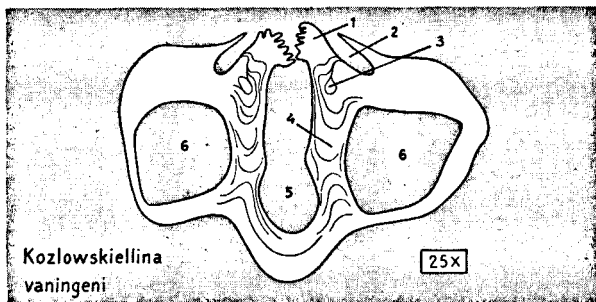
Fig. 20. *Kozlowskiellina vaningeni* (Thomas, 1926)
Transverse section of brachial valve. St. Clair Limestone (top
beds), Cason Mine, 3 mi N of Batesville, Arkansas. Peel from
Amsden collection, no. 3.

1 = cardinal process
2 = dental socket
3 = crural base

4 = crural plate
5 = central cavity
6 = lateral cavity

Kozlowskiellina velata Amsden, 1958
(Plate IV, Fig. 5/6; Plate VII, Figs. 2, 3)

The crural plates are short and the lateral cavities are
shallow. The crural bases are not situated underneath
the inner socket ridges but closer to the median plane.
Consequently, the outer hinge plates are more promi-
nent than in *K. vaningeni*. A very thin myotest is pre-
sent on the medially directed faces of the outer hinge
plates. They probably served for the attachment of the
dorsal adjustor muscles (Plate VII, Fig. 3).
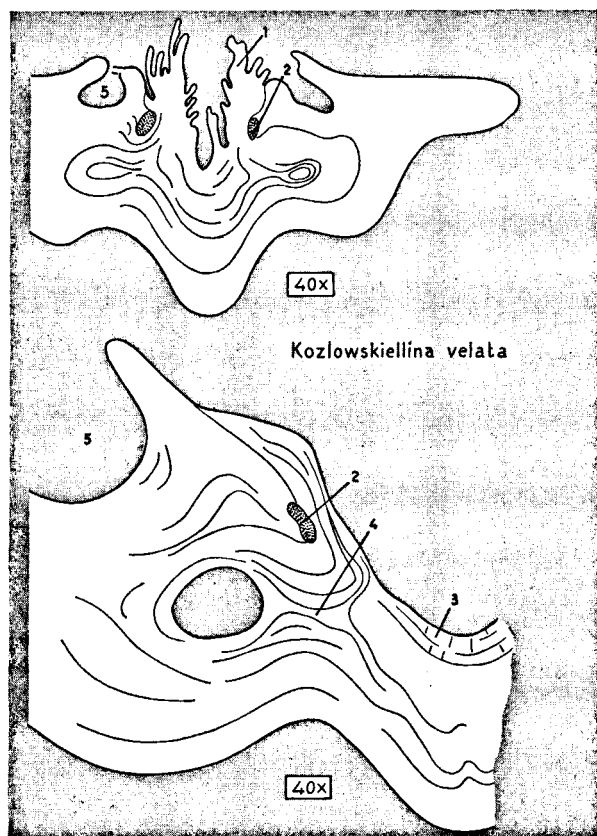
Fig. 21. *Kozlowskiellina velata* Amsden, 1958
Transverse sections of brachial valve. Haragan, Buckhorn
Ranch, SW ¼, SE ¼, Murray Co., Oklahoma. Acetate peels
6853b,3 and 6853c,1.

1 = cardinal process
2 = crural base
3 = myotest

4 = crural plate
5 = dental socket

The central cavity is plugged, and this has some
consequences for the situation of the cardinal process.
The two lobes of the cardinal process developed on
two outgrowths of the outer hinge plates. At the same
time, the apical callosity of the central cavity rises,
so that the lamellae of the cardinal process lie on both
the outgrowths and the floor of the central cavity.
The cardinal process becomes much more prominent
in *K. velata* than in *K. strawi* and *K. vaningeni*. In
Plate IV, Fig. 5/6, one lobe of the cardinal process

can be seen clearly. Note also the attachment area for the dorsal adjustor muscles, the crural bases, the shallow lateral cavities, the plugged central cavity, and the dorsal myophragme.

Kozlowskiellina perlamellosa (Hall, 1857)
(Plate VIII, Figs. 1/2, 3/4, 5/6, 8; Plate IX, Figs. 1, 2; Plate X, Figs. 1, 2)

Crural plates are present. Underneath the crural bases they resemble ridges more than true plates (Plate VIII, Fig. 1/2), because the lateral cavities are plugged with secondary material. Plate VIII, Fig. 3/4 shows the prominent crura and, near the socket area, the formation of the crural plates by the incorporation of the crura into the socket complex. The projecting crura point directly towards the umbo of the brachial valve, and as a result no resorption at the posterior faces of the crural bases was necessary during the anterior growth of the crura. Plate VIII, Figs. 1/2, 8 and Plate IX, Fig. 1 show the bilobed character of the cardinal process.

The outer hinge plates connecting the crural bases with the inner socket ridges are well developed.

Sections of *K. perlamellosa* (Plate VIII, Fig. 8; Plate IX, Figs. 1, 2; Plate X, Fig. 1; text-figure 22) show that the crural plates are short. The depth of the lateral cavities is reduced by secondary filling. The secondary outgrowths around the crural bases have angular shapes and are directed towards the median plane, giving the platform for the cardinal process a V-shape. The lamellae of the cardinal process not formed until the platform had been established (Plate X, Fig. 2); this growth starts on both sides of the platform. Later on, lamellae are also formed in the central part of the platform (Plate VIII, Fig. 8). Below the platform a shallow cavity may be present. These sections also show that on the anterior part of the platform rather thick lamellae are formed. In later growth stages they become divided into several lamellae and as a result there are more lamellae on the posterior part of the platform than on the anterior part.

Kozlowskiellina cyrtinoides (Dunbar, 1920)
(Plate XI, Fig. 3/4)

Crural plates are present. Outer hinge plates prominent. Very distinct bilobed cardinal process.

Kozlowskiellina hesione (Billings, 1863)

The interior of the brachial valve is not known.

Kozlowskiellina raricosta (Conrad, 1842)
(Plate XII, Figs. 3, 4)

Crural plates rather obscure. All cavities plugged. Since the crural bases are situated rather close to the median plane, discrete outer hinge plates formed; these become sub-horizontal.
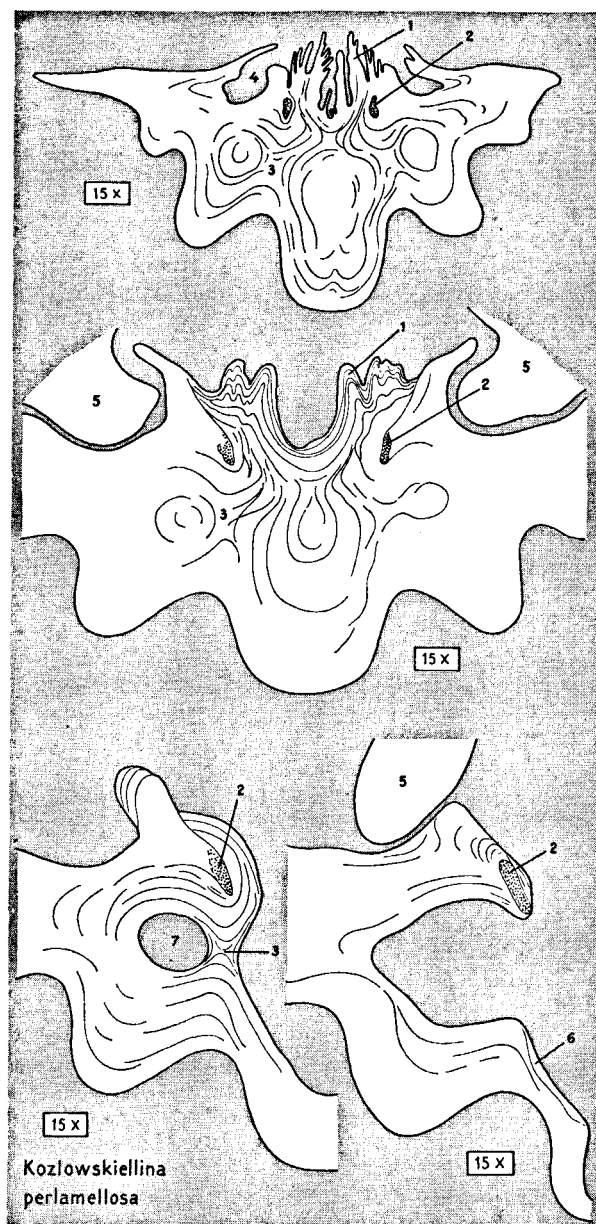
Fig. 22. *Kozlowskiellina perlamellosa* (Hall, 1857) Transverse sections of brachial valve. Lower Helderberg, Clarksville, N.Y., USNM 36708. Acetate peels: 6841c,2; 6814e; 6814f; 6814g.

1 = cardinal process	5 = hinge tooth
2 = crural base	6 = myotest in adductor field
3 = crural plate	7 = lateral cavity
4 = dental socket	

A true platform for the cardinal process has been formed by the medially directed outgrowths around the crural bases (text-figure 23).

The cardinal process is high and bilobed. Near the umbo, the lamellae of the cardinal process formed when the platform was still concave or flat. More anteriorly, the secondary secretion of shell material continued in the central sector until the platform thus formed reached a level higher than the one of the dorsal cardinal area. Only then were the lamellae formed. This growth pattern seems to be the same as that in *K. cyrtinoides*.

Fig. 23. *Kozlowskiellina raricosta* (Conrad, 1842)
Transverse section of brachial valve. Devonian, Onondaga, Williamsville, Erie Co., N.Y. Acetate peels 6816e; 6816f; 6816g.

1 = dental socket
2 = crural base
3 = outer hinge plate
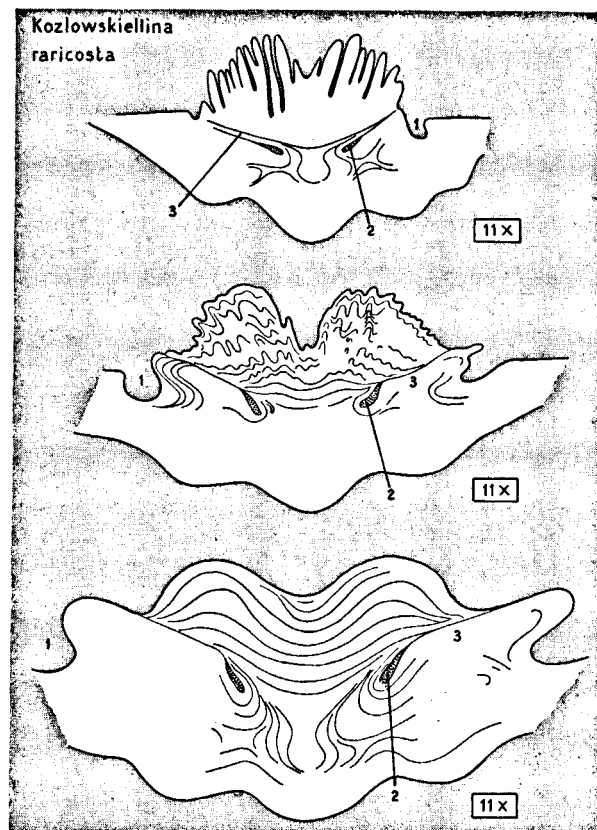
PHYLOGENY OF THE GENUS KOZLOWSKIELLINA

Besides the morphological features, stratigraphic data must also be taken into account. We have seen the following Wenlock-species: *K. strawi, K. deltidialis, K. vaningeni.*

Investigated Gedinnian Kozlowskiellinins: *K. velata, K. perlamellosa, K. cyrtinoides, K. hesione.*

Siegenian: *K.* new species Amsden & Ventress, 1963.

Siegenian and Lower Emsian: *K. raricosta.*

K. strawi and *K. deltidialis* are European forms, whereas all the other species occur in North America. The Silurian forms are smaller than the Devonian ones; their ventral cardinal area is more or less procline, whereas the ventral cardinal area of the Devonian forms is apsacline. The brachial valve of the Silurian forms is relatively flat in contrast with the rather convex brachial valve of the Devonian forms. For these reasons, Boucot (1957) and Amsden (1968) divided the genus in two subgenera, the Silurian forms being placed in *K. (Kozlowskiellina)* and the Devonian forms in the subgenus *K. (Megakozlowskiellina).*

For the phylogenetical consideration, four characters will be taken into account: the micro-ornamentation,

the dental plates and ridges, the ventral median septum, and the apical structure in the brachial valve.

Concerning the micro-ornamentation:

All investigated species have a micro-ornamentation consisting of growth lamellae and radial capillae.

In *K. strawi, K. vaningeni,* and *K. deltidialis* we found well-limited capillae lying in the rather flat surface of the growth lamellae. The minor growth lines together with the capillae gave rise to well-defined nodules at the surface of the growth lamellae. The growth lamellae themselves are mostly flat and lie superimposed on each other.

In *K. velata, K. perlamellosa, K. cyrtinoides, K. hesione,* and *K.* new species Amsden & Ventress, the growth lamellae become free and beetling. They become concave on the crests of the costae. The capillae are more and more formed by the undulation of the growth lamellae, and consequently the inner furrows are less well delimited. This feature becomes very evident in *K. raricosta,* where the undulations are broad. The minor growth lines have no influence on the capillae.

Taking into account the stratigraphic occurrence of the species, we may say that the micro-ornamentation shows a tendency to overhanging growth lamellae and

to undulation of the growth lamellae in the radial sense instead of the well-defined capillae of the Silurian species.

Concerning the dental plates:

In *K. strawi* dental plates with a distinct mediotest were present. In *K. vaningeni* the young specimens invariably have dental plates, whereas the adult specimens show a tendency to the reduction of the dental plates. In that case dental ridges formed and the apical cavity became substantially filled by secondary secretion.

In *K. velata* no dental plates are present. The dental ridges are covered by secondary material irregularly connecting the dental ridges with the floor of the valve.

In *K. perlamellosa,* too, we found dental ridges without the presence of dental plates. These ridges approach each other. This converging feature is seen very clearly in *K. cyrtinoides,* where even a spondylium-like structure has been formed.

In *K. raricosta* we also find converging dental ridges, whereas in *K. hesione* these ridges diverge towards the floor of the valve.

Therefore, the evolutionary tendency in the dental plate structure is the reduction of the diverging dental plates of *K. strawi* over the intermediate species *K. vaningeni* towards the formation of dental ridges which become converging in most species but not in *K. hesione.*

Concerning the median septum:

In *K. strawi* a prominent median septum is present. However, no mediotest is to be seen. The septum is broad and to a considerable extent covered with myotest.

K. vaningeni shows a median ridge lined with myotest. In young specimens this median ridge is still very obsolete. In adult forms the median ridge becomes more prominent. No real septum.

In *K. velata* a true median septum with mediotest is present, situated upon a low obsolete median ridge.

The same feature is to be found in *K. hesione.*

In *K. perlamellosa* and *K. raricosta* the septum becomes high and plate-like.

Phylogenetically, therefore, we see in the median septum a tendency to the formation of a median plate starting in *K. vaningeni* as a median ridge, and leading to the median ridge in *K. strawi,* whereas in *K. velata, K. perlamellosa, K. hesione,* and *K. raricosta* we find the formation of a true septum at the cost of the median ridge.

Concerning the apical structure in the brachial valve:

The crural bases in all investigated species are rod-shaped and lie somewhat medially from the dental sockets giving rise to the outer hinge plates. This is especially the case in *K. raricosta.* The crura point straight toward the umbo.

The cardinal process shows a more differentiated picture.

In *K. strawi* the floor of the apical cavity has an irregular surface. At the medially facing flanks of the brachiophores, there are some irregular lamellae. Therefore, both the floor of the cavity and the outgrowths of the brachiophores must have served for the attachment of the diductor muscles.

In *K. vaningeni* the floor of the apical cavity is smooth. On the brachiophoral outgrowths low lamellae have been secreted, thus forming the bilobed cardinal process which is not in direct contact with the floor of the valve.

In *K. velata* the lamellae on the brachiophoral outgrowths are much higher, and during growth the lamella formation extended into the furrow of the apical central cavity, so that this cavity too is provided with lamellae.

In *K. perlamellosa* the lamellae of both lobes of the cardinal process are more numerous than in *K. velata.* They also descend into the central cavity, so that, as in *K. velata,* the two lobes of the cardinal process become connected by the more deeply situated lamellae in the central cavity.

In *K. raricosta* the central cavity is plugged with secondary shell material, thus forming the median part of the platform for the cardinal process. In younger stages this platform is concave and lies at a lower level than the inner socket ridges; in older growth stages the platform rises above the socket level and forms a bilobed elevated platform for the cardinal process.

Phylogenetically, therefore, the cardinal process is formed as a few irregular lamellae at two brachiophoral outgrowths in *K. strawi,* in which the diductors are also still attached at the floor of the central cavity. Starting in *K. vaningeni,* the lamellae at the brachiophoral outgrowths become more important, giving rise
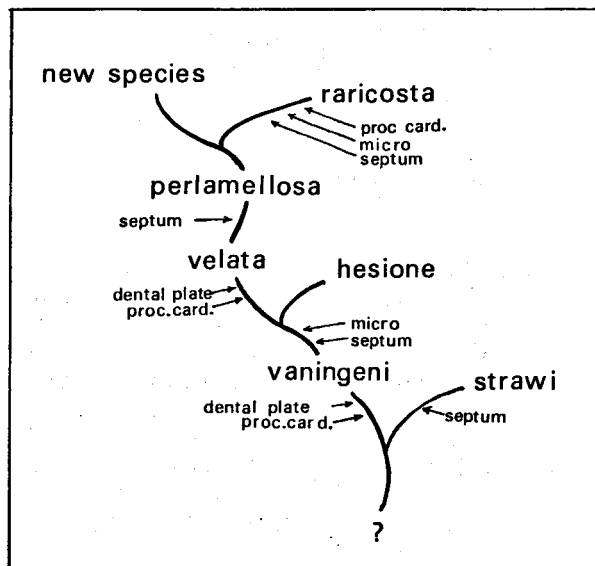

Fig. 24. Phylogeny of the genus *Kozlowskiellina.*

in *K. velata* to an elevated bilobed cardinal process that also occupies the central cavity. This is also the case in *K. perlamellosa*, where, as in *K. velata*, the platform for the cardinal process is concave. Finally, in *K. raricosta* the platform is initially concave but becomes convex and bilobed in older stages.

On the basis of these four characters, we constucted the phylogenetic diagram shown in text-figure 24. Due to

lack of information I cannot decide whether *K. deltidialis* should be placed near *K. strawi* or *K. vaningeni*.

I think that *K. cyrtinoides* comes very close to *K. perlamellosa*, as the new species of Amsden & Ventress probably also does. An interesting aspect of this scheme is the difference in the importance of the connecting lines in the diagram for the different characters; the points at which the various characters change are indicated in the diagram.

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PLATES

PLATE I

Figs. 1-6. *Kozlowskiellina strawi* Boucot, 1957
Wenlock ls. (nodular beds), W.-side Wren's Hill, N. of Dudley, England,
935920 (130 Kidderminestor).

1/2. Stereoscopic photograph of brachial valve; note the radial capillae and their
nodular aspect due to the minor growth lines, x 12.
3/4. Stereoscopic photograph of micro-ornament, x 25. Detail of photo 1/2.
5. Section of pedicle valve, x 40, acetate peel 6860. Note the dental plates and
the median septum. (Section of Amsden collection).
6. Detail of photo 5, x 100, acetate peel 6860. Left dental plate and median
septum. Note the mediotest in the dental plate.
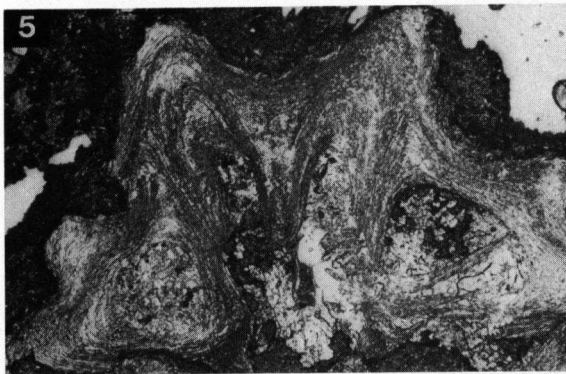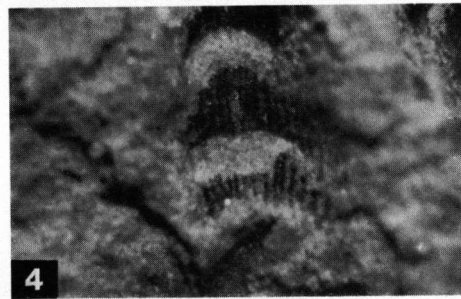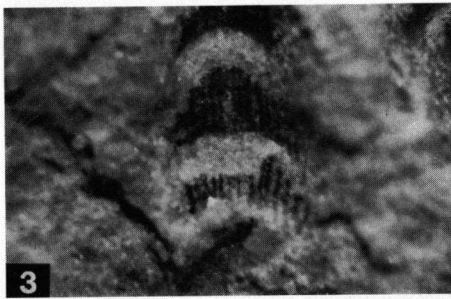
PLATE II

Figs. 1-6 *Kozlowskiellina deltidialis* (Hedström, 1923)
Halla Limestone (Reef limestone), Gandarve Säg, Parish of Dalhem, Gotland.
Boucot coll. 12781.

1/2. Stereoscopic photograph of pedicle valve, x 6.
3/4. Stereoscopic photograph of brachial valve, x 6. (Same specimen as Fig. 1/2).
5/6. Stereoscopic photograph; detail of micro-ornament, x 12.

Figs. 7-10. *Kozlowskiellina vaningeni* (Thomas, 1926)

7/8. Stereoscopic photograph, x 6. St. Clair formation, Cason Mine, 3 mi N of
Batesville, Arkansas; USNM 158070. (Same specimen as Amsden, 1968, Pl. 2,
Fig. 1a, c).
9/10. Stereoscopic photograph; detail of micro-ornament, x 12. St. Clair Lime-
stone, Searcy Mine, 7—9 mi N of Batesville, Arkansas; USNM 158076. (Same
specimen as Amsden, 1968, Pl. 2, Fig. 1s).
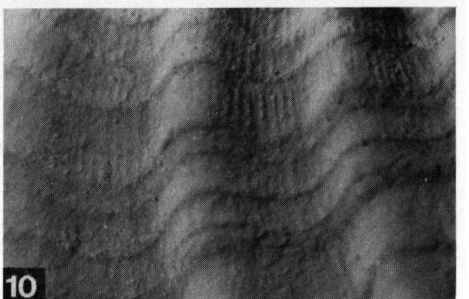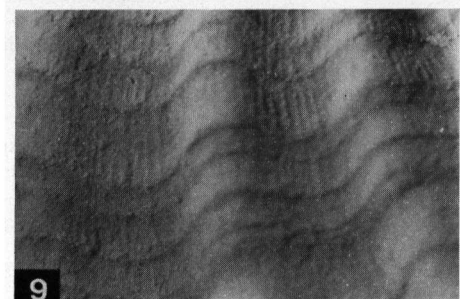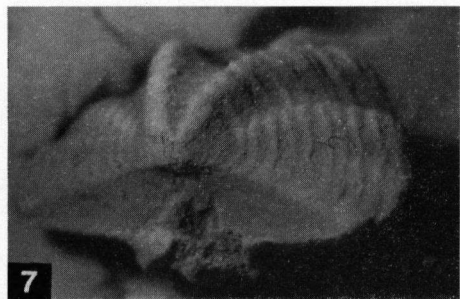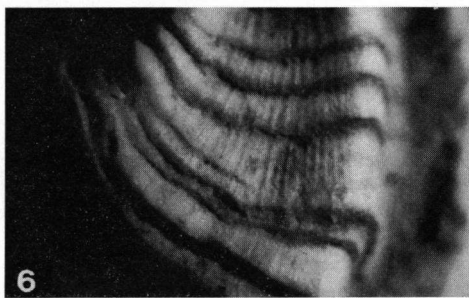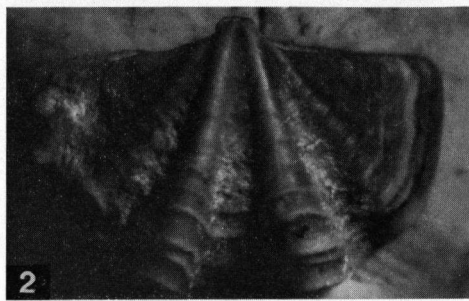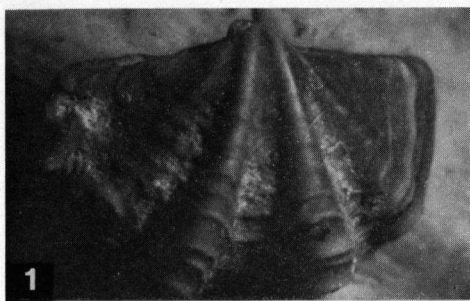
PLATE III

Figs. 1-4. *Kozlowskiellina vaningeni* (Thomas, 1926)
St. Clair Limestone (top beds), Cason Mine, 3 mi N of Batesville, Arkansas.

1. Transverse section of pedicle valve, x 25. Acetate peel no. 6865.
2. Transverse section of pedicle valve, detail of the two dental ridges, x 25. Acetate peel no. 6854b.
3. Transverse section of brachial valve, x 25. Acetate peel 6854b, 2. Note the crural plates and the crural bases. Same specimen as the one in Fig. 2.
4. Transverse section of brachial valve, x 25. Acetate peel 6858, 1. USNM 286 VI. Note the outgrowths on the outer hinge plates, giving rise to the cardinal process.

Figs. 5-8. *Kozlowskiellina velata* Amsden, 1958

5/6. Stereoscopic photograph of micro-ornament, x 12. Haragan-formation, Murray Co., 1000 ft. SE of White Mound, M2-N, OU-1046. (See Amsden, 1958, Pl. VIII, Fig. 5).
7/8. Stereoscopic photograph of ventral cardinal area, x 6. Haragan-formation near old Hunton townsite; OU-1053. Note the free-hanging growth lamellae on the palintrope and the corresponding growth lines on the interarea. (See Amsden, 1958, Pl. VIII, Fig. 3).
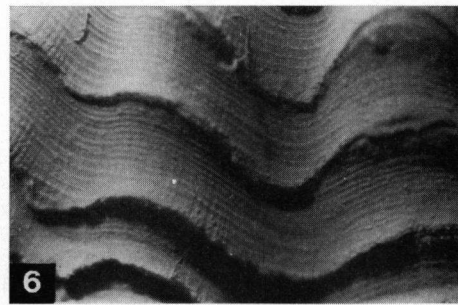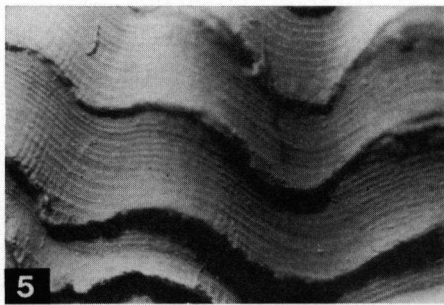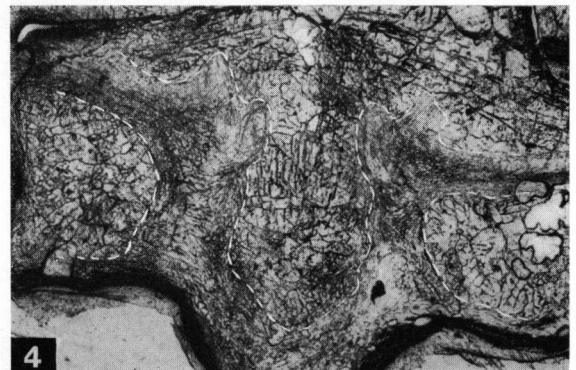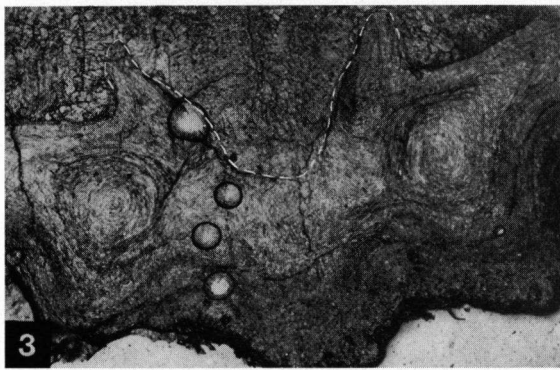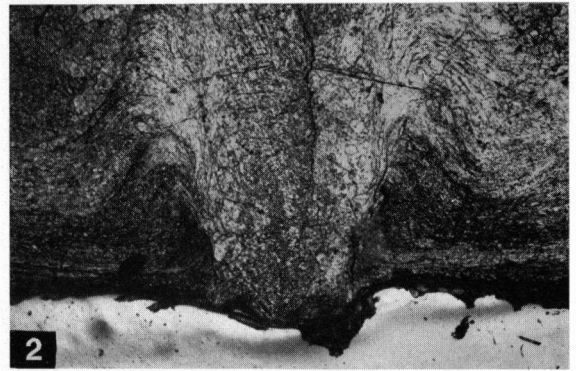
PLATE IV

Figs. 1-7. *Kozlowskiellina velata* Amsden, 1958

1/2. Stereoscopic photograph of pedicle interior, x 6. Haragan-formation on north side of Coal Creek, Pontotoc Co., Oklahoma. Coll. P9-K, OU-1054. (See Amsden, 1958, Pl. VIII, Fig. 12). Note the deeply impressed muscle field, also for the accessory diductors (cf. Fig. 3/4).

3/4. Stereoscopic photograph of pedicle interior, x 6. Haragan-formation, Vines Dome, Murray Co., Oklahoma. (Okl. Geol. Surv. 1047) Coll. M1-H. (See Amsden, 1958, Pl. VIII, Fig. 6). Note that the accessory diductor field has been elevated and that two clear pits have been formed.

5/6. Stereoscopic photograph of brachial interior, x 6. Haragan-formation, Coal Creek, Pontotoc Co., Oklahoma. Coll. P9-K (OU-1054). (See Amsden, 1958, Pl. VIII, Fig. 13). Note one conserved part of the bilobed cardinal process, the deep trough between the two lobes and the crural bases which point toward the dorsal umbo, also forming clear outer hinge plates. The outer hinge plates probably served as attachment area for the dorsal adjustor muscles.

7. Transverse section of pedicle valve, x 25. Acetate peel 6853a, 2. Haragan-formation, Buckhorn Ranch, SW ¼, SE ¼, Murray Co., Oklahoma. Note the median septum, the two dental ridges, and the very prominent deltidium.

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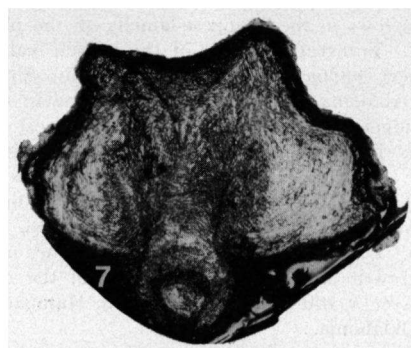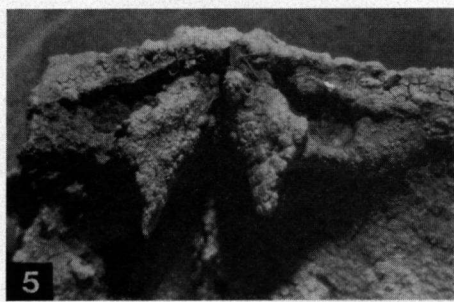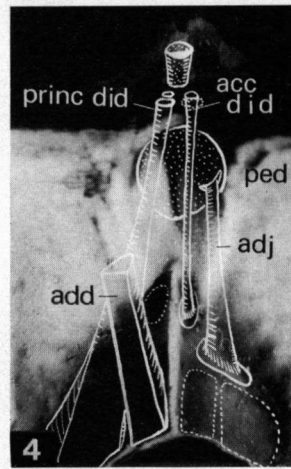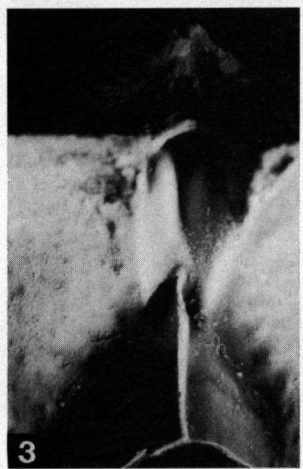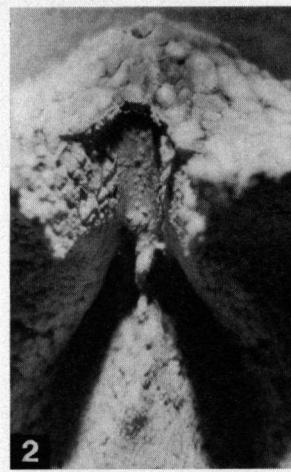
PLATE V

Figs. 1-5 *Kozlowskiellina velata* Amsden, 1958

1. Transverse section near the commissure, x 100. Acetate peel 6857c, 2. Haragan-formation, White Mound, Murray Co., Oklahoma. Sections of some free-hanging growth lamellae. The uppermost lamella is the oldest in this section and indicates the inner part of the shell. It is quite clear that the capillae correspond with furrows in the youngest lamella on the photograph.
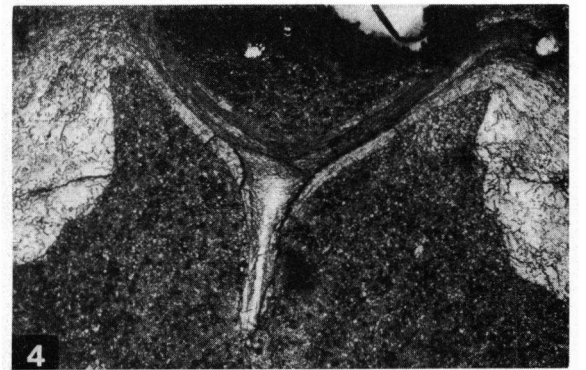
2. Transverse section of the pedicle valve of a young specimen, x 40. Acetate peel 6856a, 1. Haragan-formation, Vines Dome, Sec. M1-J., Murray Co., Oklahoma. Note the prominent median septum and the vaguely exposed dental ridges (the one on the right is the most clearly visible, see Fig. 3).

3. Detail of photo 2, showing the right dental ridge, x 100. Acetate peel 6856a, 1.

4. Longitudinal section cutting the crest of a costa at the commissure and showing the intramarginal ridge and the free-hanging growth lamellae, x 40. Acetate peel 6857a. Haragan-formation, White Mound, Murray Co., Oklahoma.

5. Longitudinal section (same as the one of photo 4) showing a free-hanging growth lamella and the section of the minor growth lines. Very clear primary layer, x 100. Acetate peel 6857a. Haragan-formation, White Mound, Murray Co., Oklahoma.
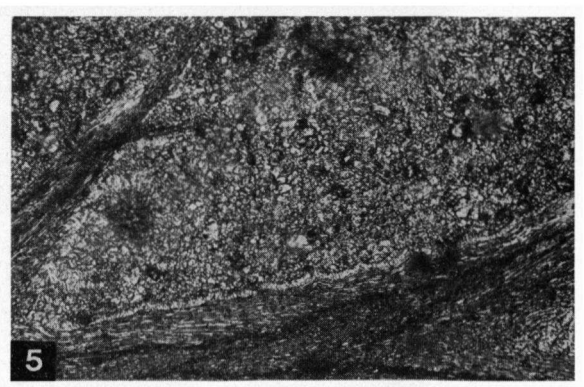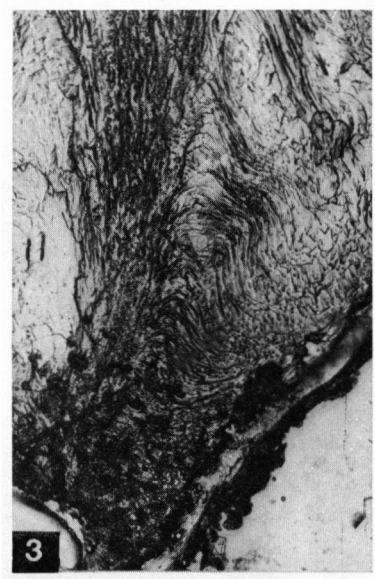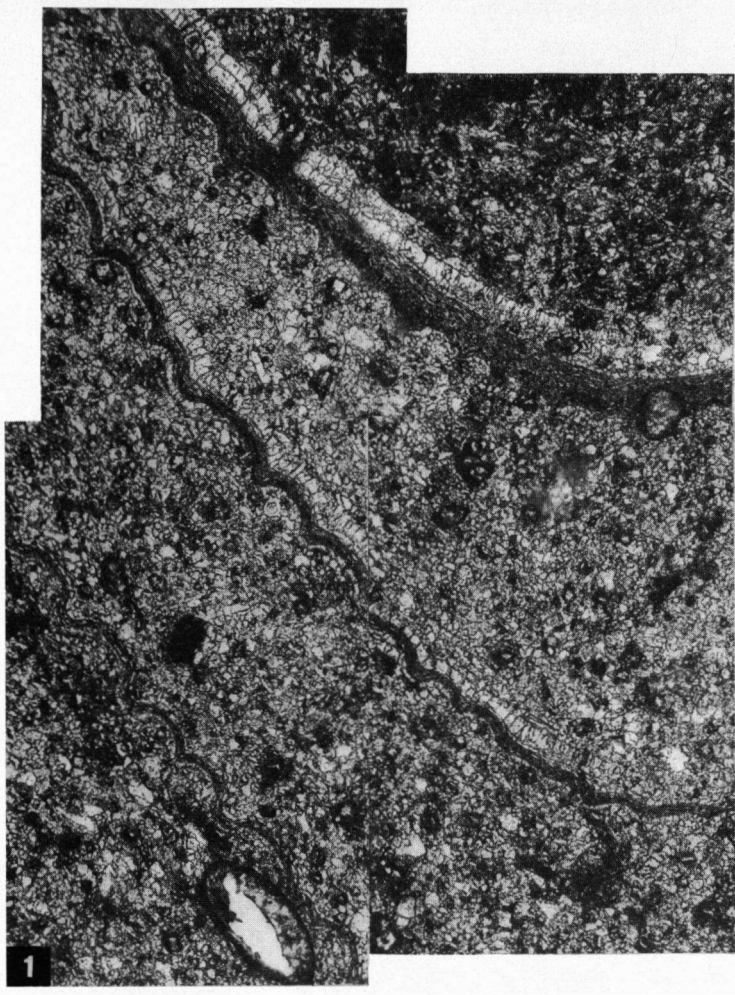
PLATE VI

1. Transverse section of pedicle valve of young specimen, x 40. Acetate peel 6856, b. (Same specimen as Plate V, Figs. 2, 3). Haragan-formation, Vines Dome, sect. M1-J, Murray Co., Oklahoma. Note the dental ridges, touching the floor of the valve and forming plate-like structures.

2. Transverse section of right delthyrial ridge and the fused deltidium, x 100. Acetate peel 6853b, 3. (Same specimen as Plate IV, Fig. 7). Haragan-formation, Buckhorn Ranch, SW ¼, SE ¼, Murray Co., Oklahoma. Note the growth lines in the delthyrial ridge, indicating resorption of a tooth in an earlier growth stage.

3. Transverse section of pedicle valve, showing dental ridges and deltidium, x 40. Acetate peel 6853b, 2. (Same specimen as the one of photo 2).

4. Transverse section of pedicle valve showing the prominent median septum, lined by a very clear myotest (see also Fig. 6), x 25. Acetate peel 6853b, 4. (Same specimen as Fig. 3).

5. Transverse section of pedicle valve, x 40. Acetate peel 6853b, 2. Median septum still embedded in secondary shell material. Same peel as the one of Fig. 3 and closer to the ventral umbo than in the section of Fig. 4. Note the myotest.

6. Detail of photo in Fig. 4, showing the base of the median septum with the very clear myotest, x 100. Acetate peel 6853b, 4.
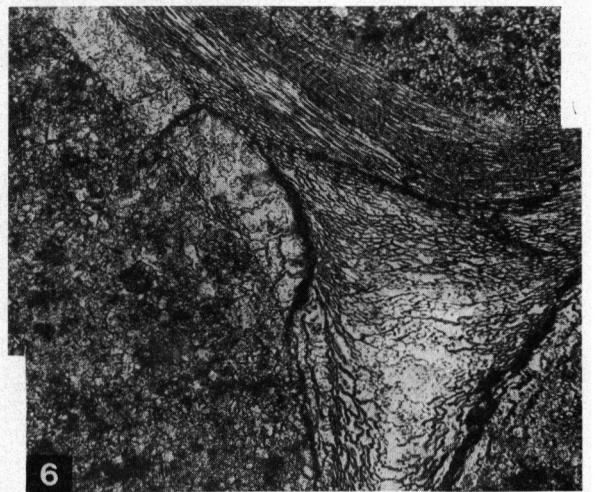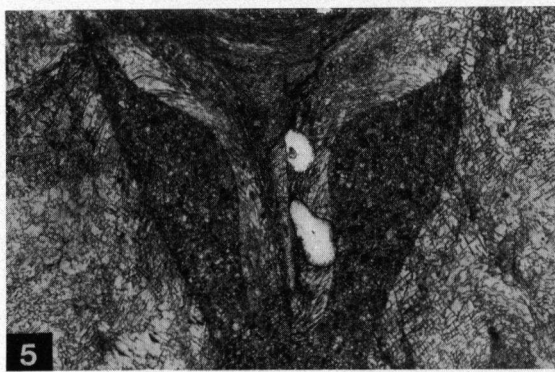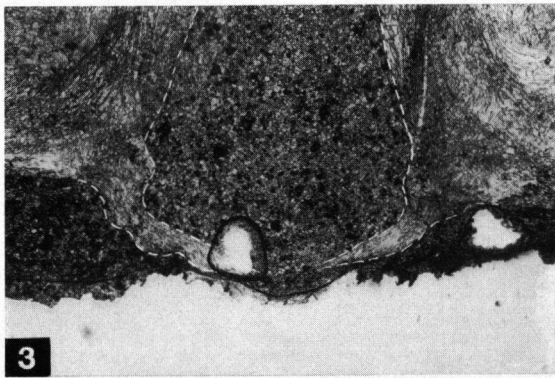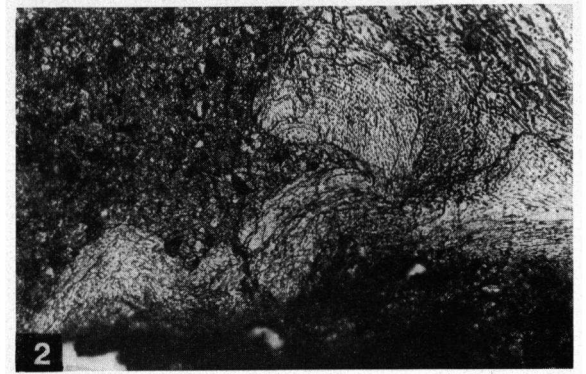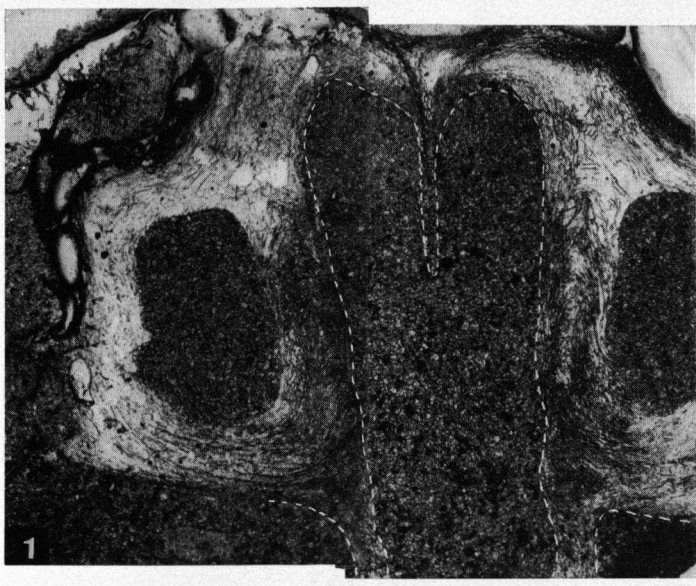
PLATE VII

Figs. 1-3 *Kozlowskiellina velata* Amsden, 1958

1. Transverse section of pedicle valve showing the left dental ridge with the possible myotest, x 40. Acetate peel 6853c, 1. (Same specimen as the one in Plate IV, Fig. 7, and Plate VI, Figs. 2-6).
2. Transverse section of brachial valve, x 40. Acetate peel 6853b, 3. (Same specimen as the one in Fig. 1).
3. Transverse section of ·brachial valve, x 25. Acetate peel 6853c, 1. (Same specimen as the one in Fig. 2. Note the left crural base).

Figs. 4-7 *Kozlowskiellina perlamellosa* (Hall, 1857)

4/5. Stereoscopic photograph of the micro-ornament, x 6. Helderberg, Clarksville, N.Y. 36708. Note the free-hanging growth lamellae and the very prominent radial capillae.
6/7. Stereoscopic photograph of pedicle interior, x 6. Helderberg (New Scotland), Road (Route 250), ½ mi W of Cow Pasture River, Vas. Note the dental ridges, the shape of the teeth and the groove in the inner faces of the dental ridges. On both sides of the septum we see deep muscle impressions. The two posterior pits being the attachment fields for the accessory diductors.
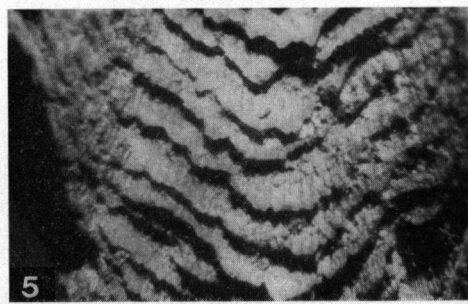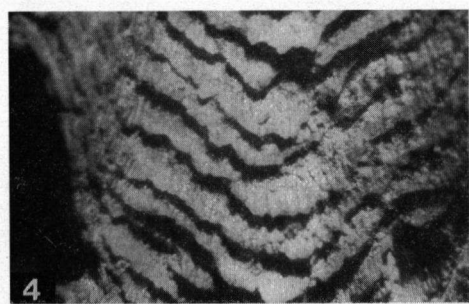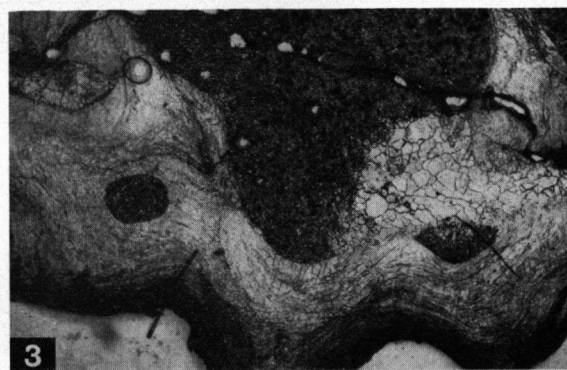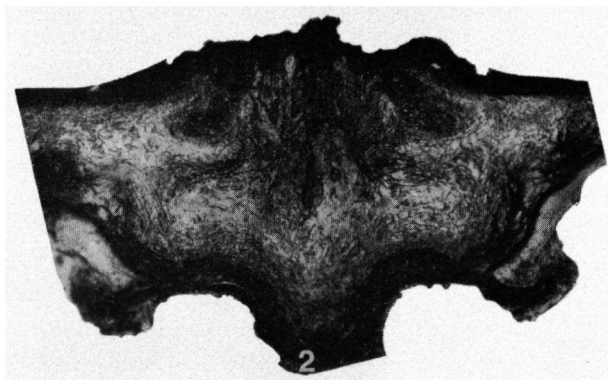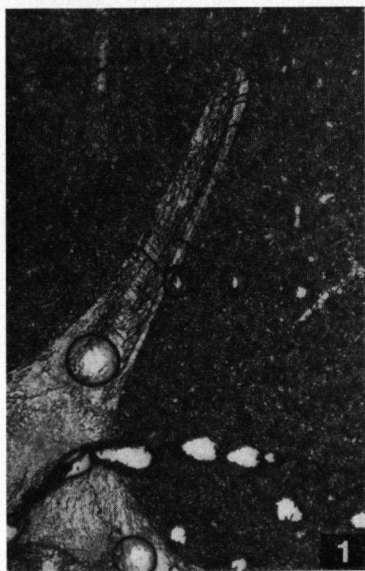
PLATE VIII

Figs. 1-8 *Kozlowskiellina perlamellosa* (Hall, 1857)

1/2. Stereoscopic photograph of the apical structure in a silicified specimen, x 6. Helderberg (New Scotland), Indian Ladder, Thatcher Park, 15 mi SW of Albany, N.Y. Note the dental ridges, the internal view on the deltidial plates, the so-called bilobed cardinal process lying in a deep central furrow, the crura, and the crural plates.

3/4. Stereoscopic photograph, x 6. (Same specimen as Fig. 1/2). Note the right crus pointing towards the dorsal umbo and the articulation. It is clear that the articulation does not take place at the tooth and the socket, but rather at the hinge line. The teeth and the sockets prevent the valves from moving in a left-right direction.

5/6. Stereoscopic photograph of the articulation, x 12. Right tooth and socket. (Same specimen as the one in Figs. 1/2 and 3/4).

7. Transverse section of a free-hanging growth lamella in the pedicle valve, showing the radial capillae, x 100. Acetate peel 6814d. Lower Helderberg, Clarksville N.Y. USNM 36708. Note that the outer surface of the valve underneath the growth lamella does not show the radial capillae, which means that these capillae were formed only at a later stage during the growth of a growth lamella.

8. Transverse section of pedicle and brachial valve, x 10. Acetate peel 6814d. (Same specimen as Fig. 7). Note the median septum, the dental ridges, the irregularly filled apical cavity, the crura and the crural plates, and the cardinal process.
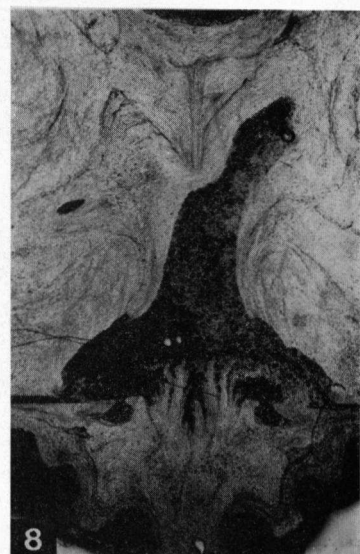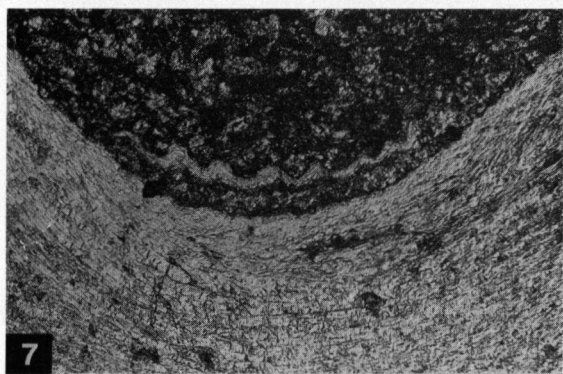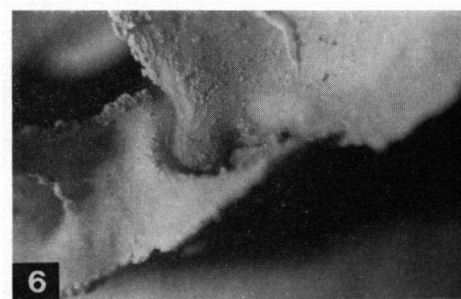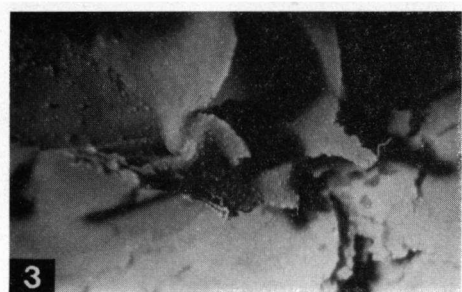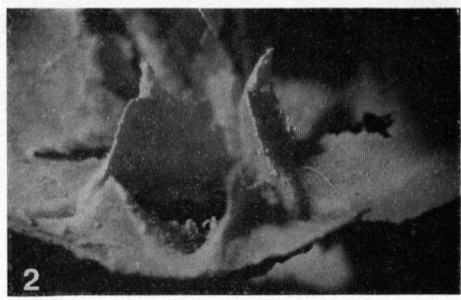
PLATE IX

Figs. 1-4 *Kozlowskiellina perlamellosa* (Hall, 1857)
Lower Helderberg, Clarksville N.Y., USNM 36708.

1. Transverse section, x 10. Acetate peel 6814e. Note the cardinal process.
2. Transverse section, x 10. Acetate peel 6814f. Note the crural plates.
3. Detail of Fig. 1, x 25. Note the resorption in the dental ridge, forming the furrow that gives room to the inner wall of the socket.
4. Transverse section of the pedicle valve, x 25. Acetate peel 6814a, 2. The dental ridges are very clearly visible and also the growth patterns in the secondary filling of the apical cavity.
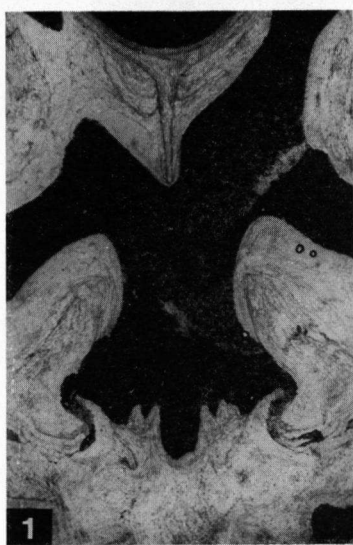
PLATE X

Figs. 1-2 *Kozlowskiellina perlamellosa* (Hall, 1857)
Lower Helderberg, Clarksville N.Y., USNM 36708.

1. Detail of Plate IX, Fig. 2 showing the left crural plate, x 25.
2. Detail of Plate IX, Fig. 1 showing the cardinal process, x 40.

Figs. 3-6 *Kozlowskiellina cyrtinoides* (Dunbar, 1920)

3/4. Stereoscopic photograph of pedicle interior, x 6. Birdsong shale, Fossil Point, 5 mi NE of Eva, Tenn. on Tennessee River at foot of Pilot Knob. Spondylium-like structure, with a part of the median septum still present as a septum in the spondylium. This could indicate that on both sides of the septum in the 'spondylium' two muscles were attached, probably the accessory diductors (cf. *K. velata*). The two dental ridges are partly broken but still visible.
5/6. Stereoscopic photograph of pedicle interior, x 6. Upper Rockhouse Shale, 5 1/3 mi SE of Savannah, Tenn., just W of bridge that crosses Holland Creek. Coll. Boucot & Undin, 1967. USNM 13604. Spondylium-like structure. It is clear that the accessory diductor fields are situated in two pits within the 'spondylium' (cf. *K. velata*). Note the dental ridges.
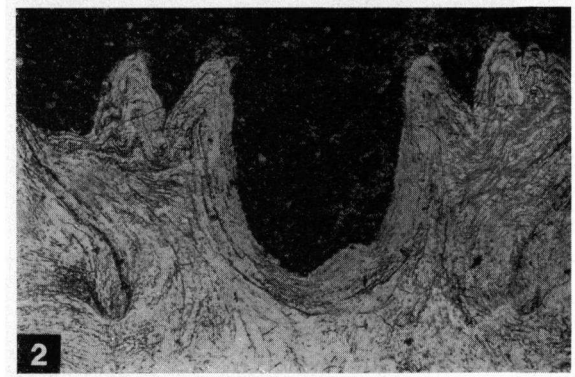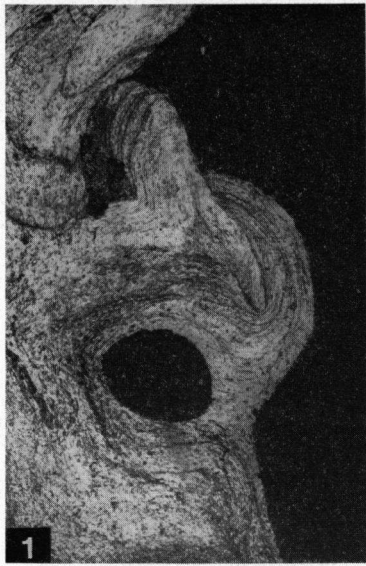
PLATE XI

Figs. 1-4 *Kozlowskiellina cyrtinoides* (Dunbar, 1920)
Upper Rockhouse shale, 5 1/3 mi SE of Savannah, Tenn., just W of bridge that crosses Holland Creek. Coll. Boucot & Undin, 1967. USNM 13604.

1/2. Stereoscopic photograph of pedicle interior showing 'spondylium' and median septum, x 6. (Same specimen as Plate X, Fig. 3/4).
3/4. Stereoscopic photograph of brachial interior, x 12. Note the cardinal process, which is of the same type as the one in *K. perlamellosa,* and the outer hinge plates.

Figs. 5-6 *Kozlowskiellina hesione* (Billings, 1863)
Helderberg, Square Lake Is., Square Lake, Aroostook Co., Maine, USNM 88354.

5. Transverse section of pedicle valve, x 10. Acetate peel 6819b. Note the median septum and the diverging dental ridges.
6. Transverse section of median septum, x 40. Acetate peel 6819a. Note the clear mediotest and the median ridge.

Figs. 7/8 *Kozlowskiellina raricosta* (Conrad, 1842)
Stereoscopic photograph of micro-ornament, x 12. Onondaga, Devonian. Williamsville, Erie Co., N.Y. Note the growth lamellae and the very broad radial capillae.
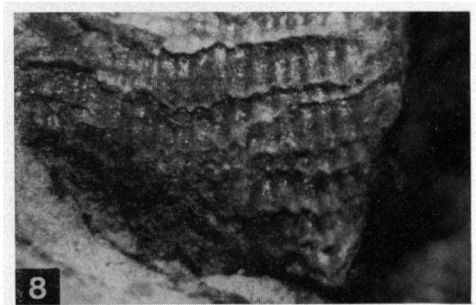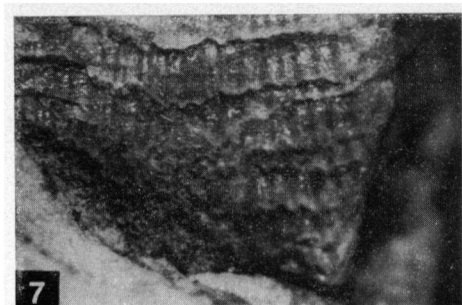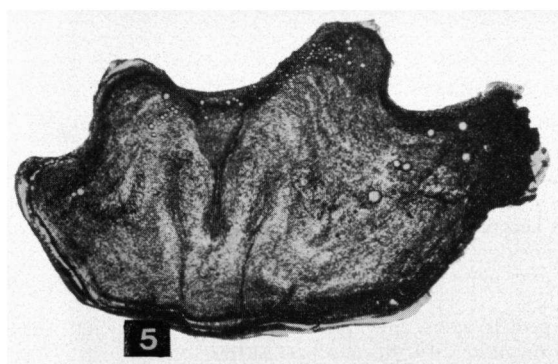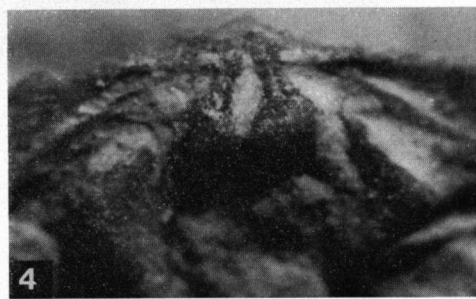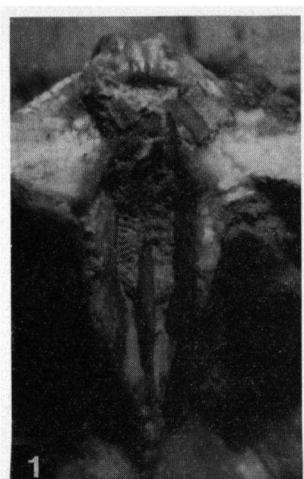
PLATE XII

Figs. 1-4 *Kozlowskiellina raricosta* (Conrad, 1842)
Onondaga, Devonian. Williamsville, Erie Co., N.Y. All same specimen.

1. Transverse section of some growth lamellae showing the radial capillae, which are formed by undulations of the growth lamellae, x 100. Acetate peel 6816h. Note that the undulations become more prominent from the inside to the outside, which means that when a new growth lamella formed, the undulations were very weak and became more and more prominent during the radial growth of the lamellae.
2. Transverse section of pedicle valve showing the position of the dental ridges, indicated by the probable myotest, x 10. Acetate peel 6816d.
3. Transverse section of brachial valve, showing the cardinal process, x 25. Acetate peel 6816f.
4. Transverse section of brachial valve, showing the convex platvorm for the cardinal process in a more anterior section than the one of Fig. 3. x 10. Acetate peel 6816g.

Fig. 5/6 *Kozlowskiellina* new species Amsden & Ventress, 1963
(Amsden & Ventress, 1963, p. 114, Pl. V, Fig. 1, 2.)

Stereoscopic photograph of the micro-ornament, x 12. Frisco — 60 above Bois d'Arc Creek (at Highway 99) Pontotoc Co. O.G.S. 3313. Note the nodular aspect of the radial capillae.

Fig. 6/7 *Kozlowskiellina* spec.

Stereoscopic photograph of pedicle interior (probably young specimen), x 6. Lower Devonian, between 80° & 81° N Lat and 70° W Long Cape Leidy.