

ON THE BASAL STRUCTURE OF SIPHONODELLA COOPERI HASS, 1959 AND SIPHONODELLA LOBATA
(BRANSON & MEHL), 1934

BY

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ABSTRACT

Scanning Electron Microscope photographs of *Siphonodella cooperi* and *Siphonodella lobata* suggest that basal pits decrease in size after having reached a maximum. Analysis of biometric data and computed regression lines confirm this. The phenomenon is explained by postulating migration of the plane of separation between the conodont and the basal plate, downwards in the holoconodont.

INTRODUCTION

Until recently relatively little attention has been given to the basal openings of conodonts. Müller & Clark (1967) and Clark & Müller (1968) made a study of basal openings and a distinction between basal cavities and basal pits. At the moment it is generally accepted that the basal opening is an important feature in the description of form genera and form species, and their evolution. However, only a few studies give more detailed data about the basal opening of species and genera.

The present study aims to give a contribution to the knowledge of basal openings. As examples two species of *Siphonodella* have been chosen: *Siphonodella cooperi* and *Siphonodella lobata*. *S. cooperi* is regarded here as a typical representative of *Siphonodella*, whereas *S. lobata* is a species with a more *Polygnathus*-like keel and with an outer lateral lobe.

Klapper (1966) distinguished *Siphonodella* and *Polygnathus* on the morphology of the lower side of the platform. He stated (p. 15): "*Polygnathus* has a raised keel, interrupted only by the basal cavity" (= basal pit), while "... the keel of *Siphonodella* is either absent or represented by a thin groove for some distance posterior to the basal cavity" (= basal pit). The basal opening of *Siphonodella* is often indistinct, when studied with a normal binocular microscope.

Two lines of study have been used:

Firstly, photographs made with the Scanning Electron Microscope (Cambridge) have been studied. Photographs were taken on a Kodak Panatomic X (16 DIN/32 ASA) film mounted in an Exa camera with a Domiplan 2.8/50 lens. The specimens have been coated twice with gold. The best results were obtained with a 20kV electron beam; a lower voltage resulted in lower resolution, while a voltage above 20kV damaged the specimens.

Secondly, bivariate analysis based on measurements of some important characters of the basal structure has

been applied. Regression lines were obtained by using the technique of the reduced major axis (Imbrie, 1956). In some cases isometric regression lines gave the best fit ($y = ax + c$), in other cases an allometric regression line ($y = bx^a$) was preferable. Additionally the correlation coefficient r has been computed. The computations were carried out on the IBM 360-65 computer of the Centraal Rekeninstituut (C. R. I./Leiden.

Müller and Nogami (1971) prepared thin sections, which enabled them to count the number of lamellae forming the basal pit. This method could not be applied because the material was highly recrystallized.

In studying the basal opening, it became evident that the basal opening cannot be considered separately from the whole of the lower side of the platform, the basal structure. The lamellae forming the platform are often partly responsible for the form and size of the basal opening. Therefore not only the basal opening is discussed, but also the keel and the feature which has been described as the 'attachment area' or 'inverted basal cavity'. Since it is known that the lamellae of the basal plate "pass into the conodont with no readily apparent morphologic discontinuity or change" (Pierce & Langenheim, 1970, p. 3233), the attachment area must be considered as a scar, and the basal opening just as a part of it. It is therefore confusing to use the term 'attachment area' only for the area surrounding the basal pit with outcropping lamellae. The term 'inverted basal cavity' is also misleading, because an inverted cavity is completely different from the morphologically well defined basal cavity. Furthermore, species with an inverted basal cavity do not possess a basal cavity but a basal pit (Clark & Müller, 1968, p. 563), according to the original definitions of Müller & Clark (1967, p. 906). Therefore here is proposed to use the term 'outer attachment area', in contrast to the 'inner attachment area' (= basal pit) (Fig. 1). The term basal pit deserves preference to the term inner attachment area. In conodonts possessing a basal cavity no distinction can be made between an inner and outer attachment area (see Clark & Müller, 1968).

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The studied material has been collected in the Spanish Pyrenees. The specimens of *S. lobata* are from sample 0190, which has to be placed in the lower *S. crenulata* zone, from the top of the Compte Formation (Hartevelt, 1970) at La Guardia de Arés, Prov. Lérida. The fauna contains 34 specimens of *S. lobata*, of which 26 could be measured. The specimens of *S. cooperi* are from sample 0281 from the top of the Mañanet Griotte (Mey, 1967, 1968) at Castells, Prov. Lérida. This sample can be placed in the lower *S. crenulata* zone. The fauna contains 2080 specimens of *S. cooperi*, of which 200 have been measured. More data about stratigraphy and locations will be given in a later paper.

Acknowledgements

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THE BASAL STRUCTURE OF SIPHONODELLA COOPERI AND SIPHONODELLA LOBATA

Siphonodella cooperi Hass, 1969

Morphological observations

Adult and juvenile specimens of *S. cooperi* have a strikingly different basal structure (Fig. 1A). In adult specimens a basal pit fading out towards the posterior is visible, approximately at the place of maximal down-bending of the platform. At the extreme posterior a short 'keel' may be present, while between the basal pit and the 'keel' a thin groove may be observed (Klapper, 1966, p. 15). There is a broad outer attachment area. Juvenile specimens on the contrary, have a more simple basal structure. The symmetrical basal pit runs nearly over the whole platform; only in the extreme posterior part of the platform the groove is not visible. The deepest part of the basal pit is situated in its anterior part. Juvenile specimens do not possess an outer attachment area and a 'keel', while the whole basal pit is elevated above the platform.

In juvenile specimens (Pl. 1, Figs. 1, 2) we see that the last lamella forms the lower surface of the conodont, the crimp, and turns downwards to a subvertical position, in such a way that the basal pit increases in size. The lamel-

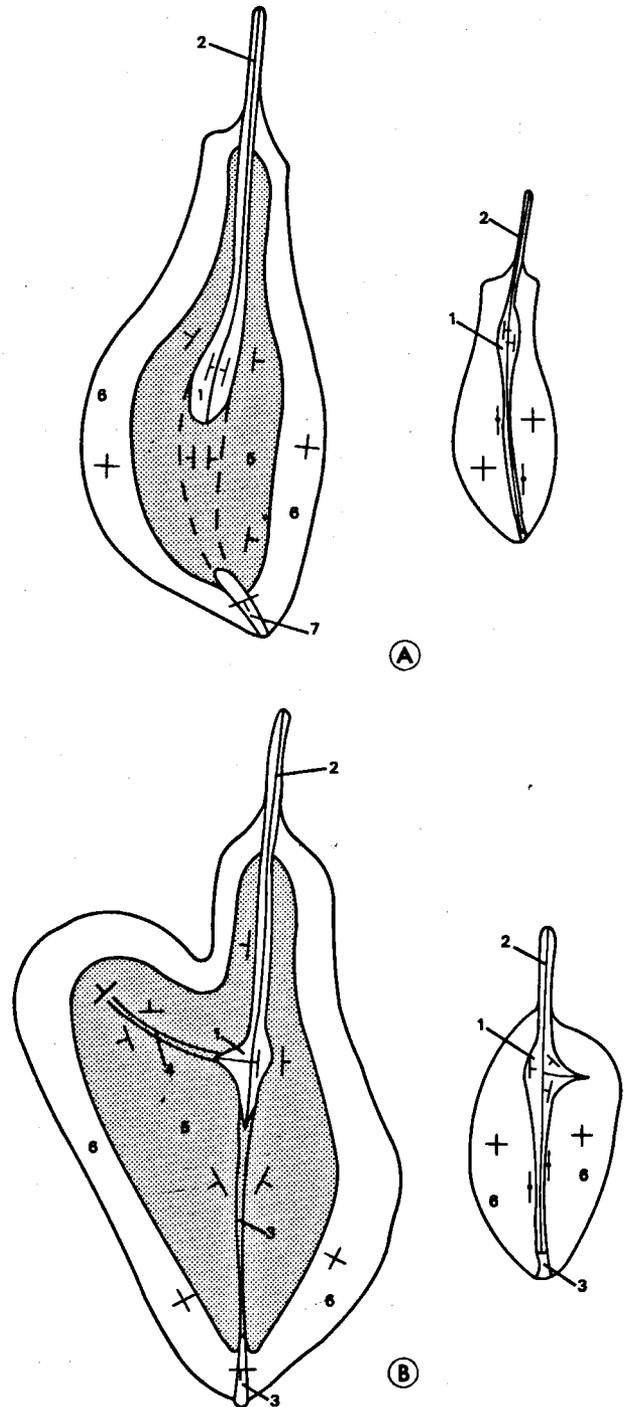


Fig. 1. A: Morphology of the basal structure of an adult and a juvenile specimen of *Siphonodella cooperi*. B: Morphology of the basal structure of an adult and a juvenile specimen of *Siphonodella lobata*.

- 1 = basal pit (= inner attachment area)
- 2 = groove
- 3 = keel
- 4 = secondary keel
- 5 = outer attachment area (shaded area)
- 6 = crimp
- 7 = secondary inverted basal cavity

lae dip towards the interior of the basal pit. It is evident that the basal pit is formed by the free back-turned ends of the lamellae. Towards the posterior the depth of the basal pit decreases. At the extreme posterior side of the platform the last lamella closes the basal structure and dips gently towards the posterior.

In comparing the illustrated juvenile specimen with a more adult one (Pl. 1, Fig. 3), we see that at a certain growth stage the lamellae keep their position parallel to the lower surface of the platform, without turning downwards to a subvertical position so that the outer attachment area is initiated (Pl. 1, Fig. 4). Until this stage the whole lower platform surface was covered by the last lamella, but from now on the crimp relatively decreases in width by the offlapping of each lamella on the former.

If we compare an adult specimen (Pl. 2, Figs. 1, 2) with the one of Pl. 1, Fig. 3, we see that an outer attachment area is present in which the lamellae make a small angle with the lower side of the platform. Only in the axial part do the lamellae keep their steep position and turn around at the posterior. We probably have to assume that some of the lamellae of the basal pit, which are parallel to the axis of the basal pit in juvenile specimens, are closed in adult specimens. This idea is supported by biometrical analysis.

The 'keel' at the posterior part of the platform is formed by an increasing down-bending of the lamellae towards the posterior into a normal position (Pl. 2, Fig. 3). The last lamella closes the basal structure. The 'keel' is a structure quite different from the true keel of *S. lobata* (Pl. 4, Fig. 2), and can better be described as a

secondary inverted basal opening. Since its size is only determined by the size of the platform and increases during ontogeny, it should be called a secondary inverted basal cavity, according to the definitions of Müller & Clark (1967).

The faint groove, reported by Klapper (1966, p. 15), is identified as a line of rupture through the zone of bending of the lamellae (Pl. 2, Fig. 3). This conclusion confirms that of Müller & Nogami (1971) (see e. g. their Pl. 15, Fig. 4).

Biometrical analysis

In juvenile specimens the anterior margin of the basal pit is situated closer to the anterior side of the platform than in adult specimens, so that the basal pit shifts posteriorly in the platform during ontogeny (Fig. 2). This correlation fits best to an isometric regression.

If we compare the width of the attachment area (basal pit + outer attachment area) with the length of the platform, we see that its width increases with the length of the platform (Fig. 3). First only a basal pit is present, and regression is isometric with a low coefficient, but where attachment areas are measured (sizes above 0.40 mm), the relationship is anisometric and the coefficient increases.

If we compare the length of the platform with the length of the basal pit, the distribution of the measurements seems rather confusing (Fig. 4). The specimens, however, were separated into two groups: one group of specimens with an incomplete basal pit, where the posterior margin of the basal pit reaches the posterior of the platform, and the other group of specimens with a com-

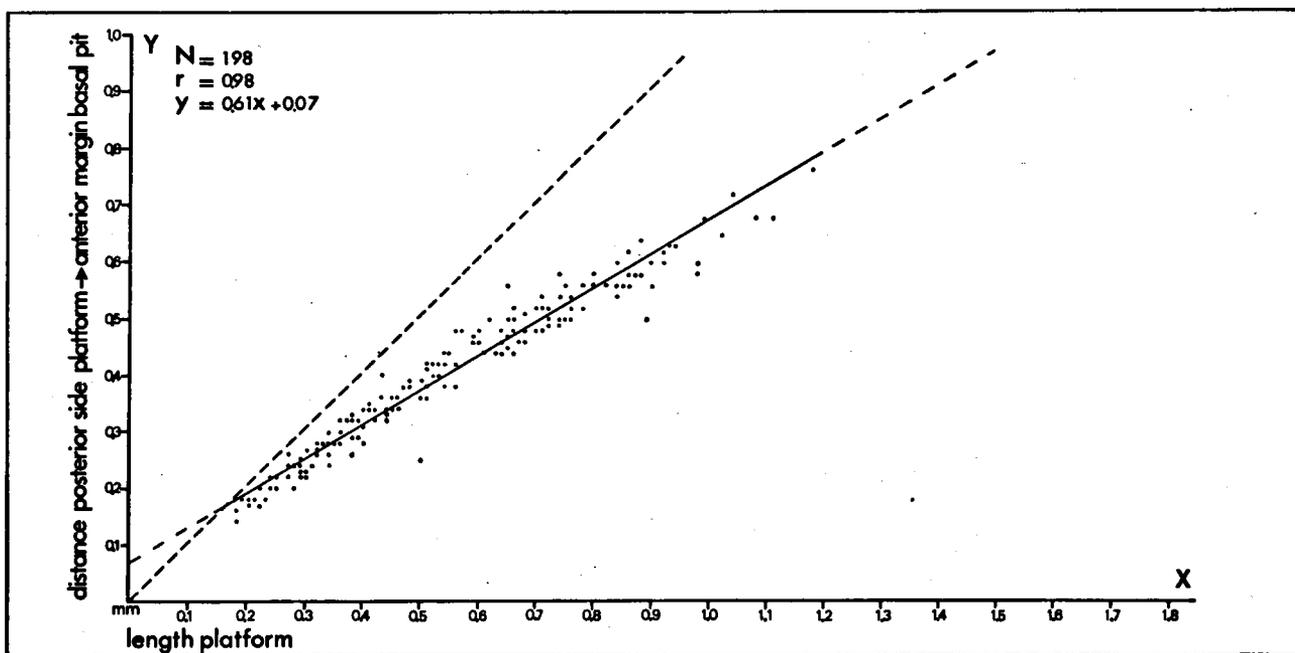


Fig. 2. Position of the anterior margin of the basal pit in the platform of *S. cooperi*. Where the computed regression line crosses the dashed line (45°) the anterior margin of the basal pit coincides with the anterior margin of the platform.

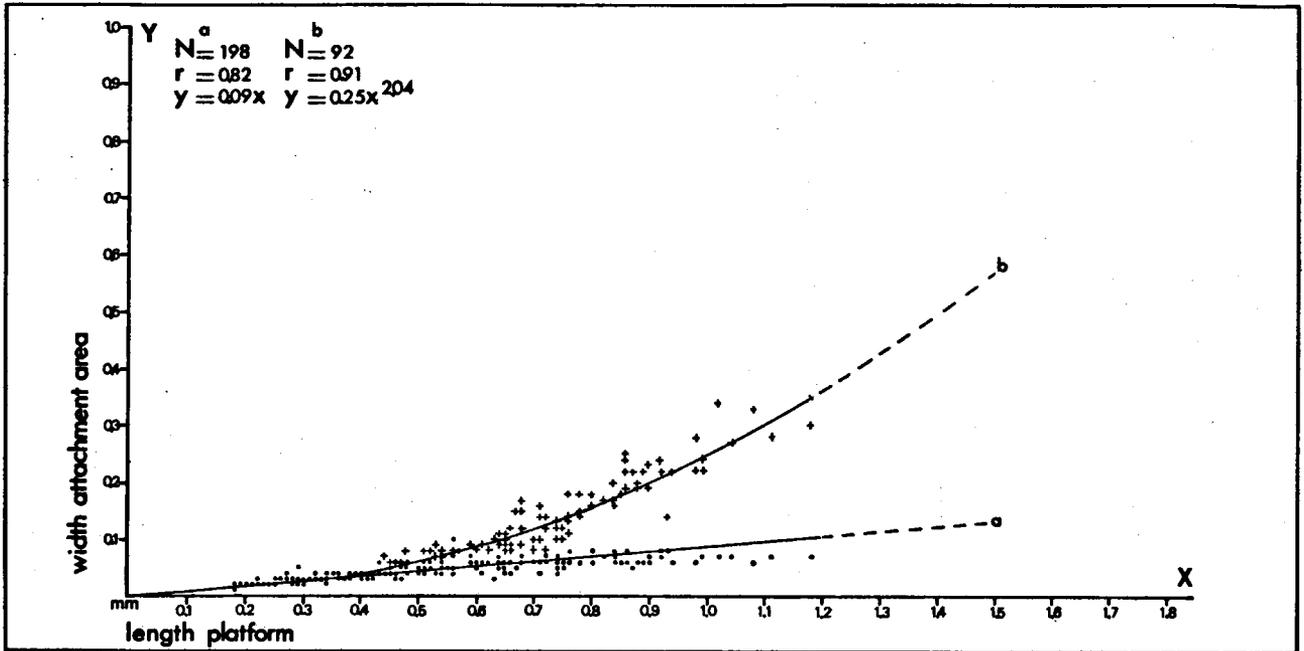


Fig. 3. Width of the attachment area of *S. cooperi* compared with the length of the platform during ontogeny. Regression line a (-) indicates the width of the basal pit (= inner attachment area), regression line b (+) indicates the width of the outer attachment area. Specimens with a platform smaller than the place where regression line b crosses regression line a possess no outer attachment area.

plete basal pit, where the posterior margin of the basal pit does not reach the posterior of the platform. In this way two regression lines can be obtained, crossing each other at about 0.43 mm. This means that until the platform is about 0.43 mm, the basal pit increases in length

with an isometric relationship, but that it decreases in length in the next growth stages with an anisometric relationship to a minimal value.

The same procedure can be applied in comparing the length of the basal pit with its width (Fig. 5). First the

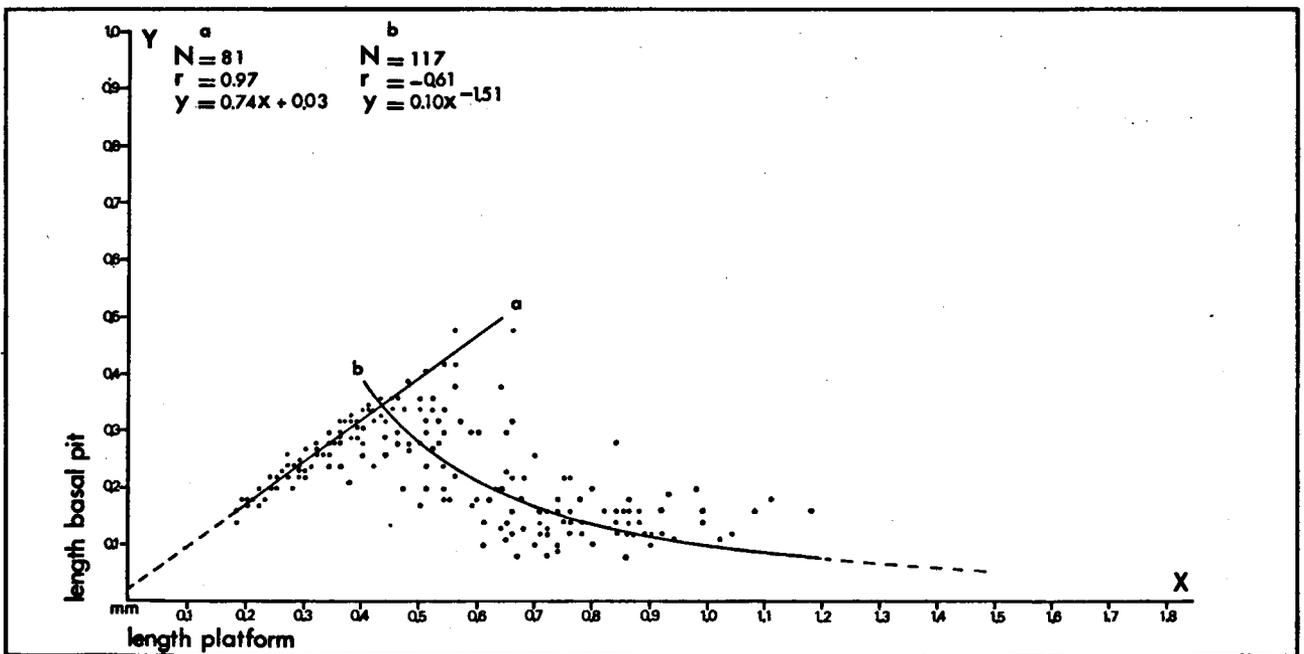


Fig. 4. Length of the basal pit of *S. cooperi* in relation to the length of the platform during ontogeny. Regression line a is based on specimens in which the posterior margin of the basal pit extends to the posterior of the platform, regression line b is based on specimens in which the posterior margin of the basal pit does not extend to the posterior of the platform.

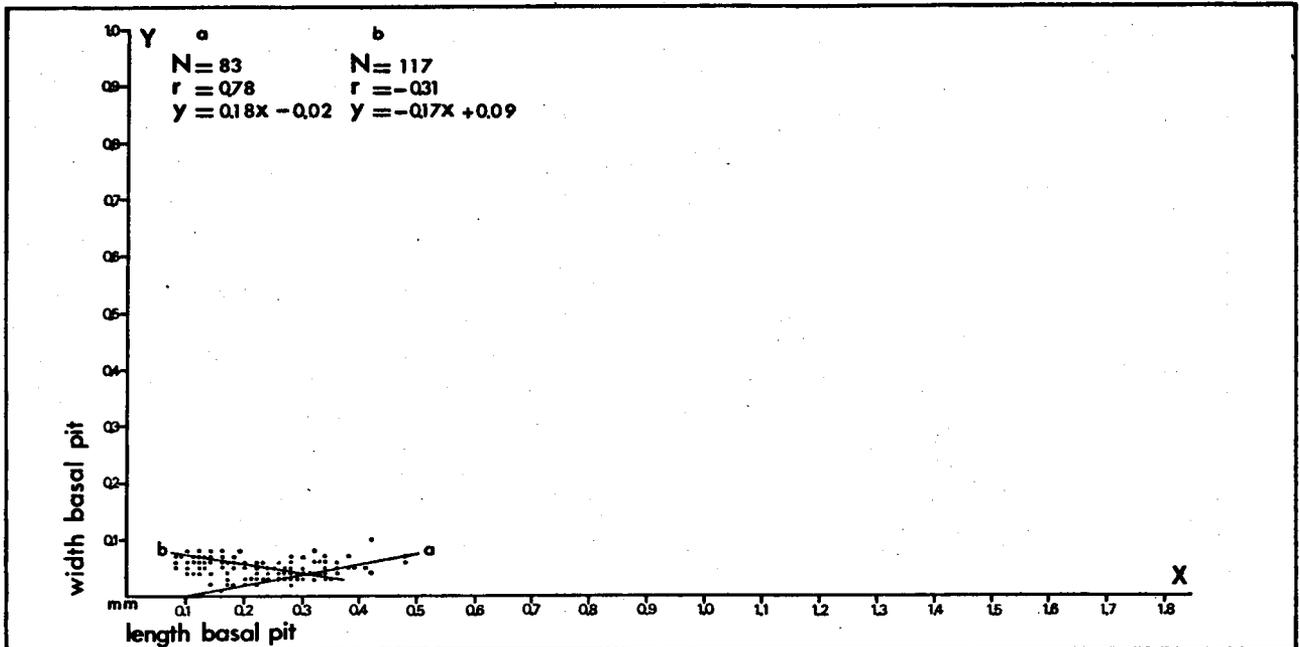


Fig. 5. Size of the basal pit of *S. cooperi* during ontogeny. Regression line a is based on specimens in which the posterior margin of the basal pit extends to the posterior of the platform, regression line b is based on specimens in which the posterior margin of the basal pit does not extend to the posterior of the platform.

length of the basal pit increases, in later growth stages the length decreases whereas the width increases. Both relationships are isometric.

Siphonodella lobata (Branson & Mehl), 1934

Morphological observations

The basal pit of *S. lobata* is strongly asymmetrical. The outer side of the basal pit displays a sharp angle, about perpendicular to the main axis of the basal pit. Juvenile and adult specimens have a different basal structure (Fig. 1B). Very juvenile specimens only possess a basal pit and a short keel, while in adult specimens a secondary keel and an outer attachment area are also present.

In juvenile specimens (Pl. 3, Figs. 1, 2) the last lamella turns down, bends over the keel and turns upwards again at the other side of the platform. More to the anterior the last lamella may even turn downwards to a subvertical position. It is evident that the basal pit is formed by the free ends of the lamellae. The lamellae are dipping towards the interior of the basal pit.

Adult specimens of this species also suggest that the basal pit increases in size up to a certain stage and that afterwards the outer attachment area begins to form (Pl. 4, Figs. 1, 4). Up to this stage the whole lower surface of the platform, except the basal pit, was apparently covered by the last lamella. The width of the crimp decreases relatively by the offlapping of each lamella on the former.

Only adult specimens possess a well developed main

keel which is formed by sharply down-turning lamellae, gently dipping to the posterior and offlapping each other (Pl. 4, Fig. 2). Consequently the keel increases a little in height and width towards the posterior.

In very juvenile specimens no secondary keel is present. Of the 26 measured specimens only those with a platform longer than 0.44 mm consistently possess a secondary keel. There seems to be no relation between the angle between the two keels and the size of the platform. The angle varies from 50–110°, with a mean value of 83°. The secondary keel grows by a down-bending of the lamellae, offlapping each other and dipping towards the outer side of the platform (Pl. 4, Fig. 3). The secondary keel never reaches the crimp; however, it increases in length with increasing size of the platform. Apparently the lamellae of juvenile stages do not form a secondary keel, whereas the same lamellae of adults do.

Biometrical analysis

The position of the basal pit in the platform changes during ontogeny. In juvenile specimens the anterior margin of the basal pit is located closer to the anterior side of the platform than in adult stages, and may even reach the anterior side of the platform in very juvenile specimens (Fig. 6). This relationship is isometric.

Comparing the length of the basal pit with its width, we see that there is no strong correlation (Fig. 7). The data are not conclusive but anisometric relationship is postulated following the results for *S. cooperi*.

If we compare the length of the basal pit with the length of the platform, we see that the length of the

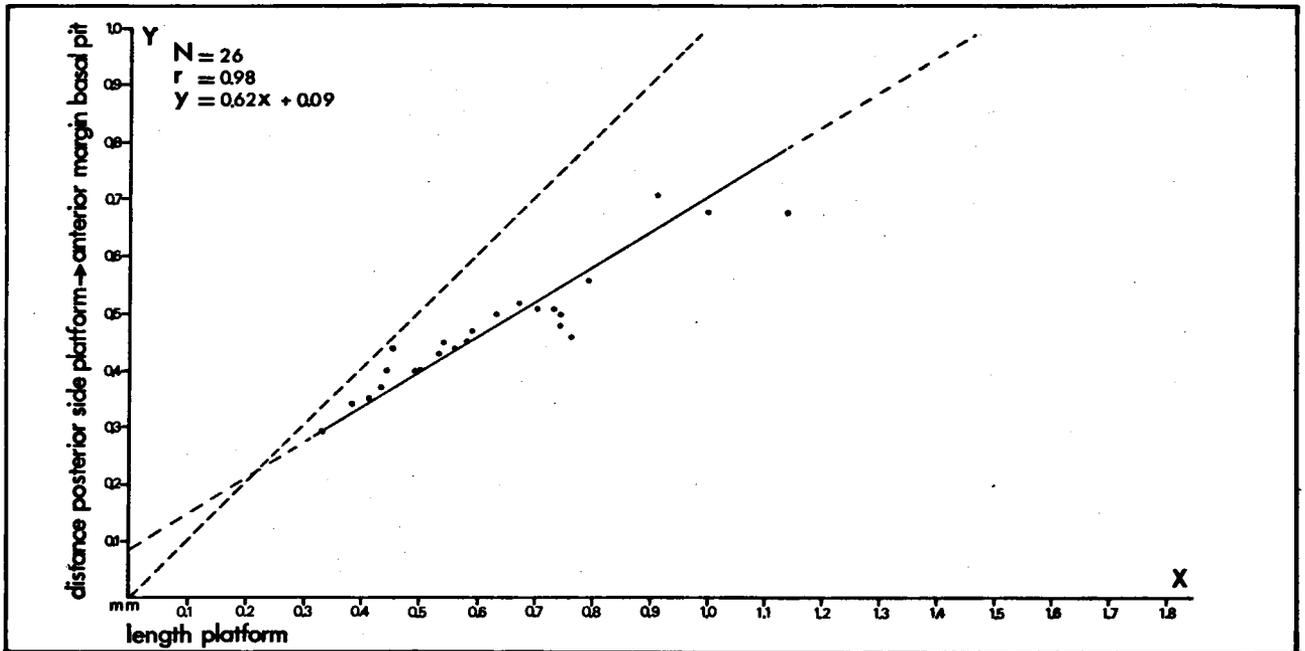


Fig. 6. Position of the anterior margin of the basal pit in the platform of *S. lobata*. Where the computed regression line crosses the dashed line (45°) the anterior margin of the basal pit and the anterior margin of the platform coincide.

basal pit decreases with an increase of the size of the platform with an anisometric relationship (Fig. 8). In *S. lobata* no separation of the measurements was possible as in *S. cooperi* since even in small specimens the posterior margin of the basal pit does not reach the posterior side of the platform, so that an increase in size of the basal pit during the earlier growth stages can only be

concluded from the photographs and not from biometrical analysis.

DISCUSSION

The following features need further explanation:

- 1) In both *S. cooperi* and *S. lobata* the size of the basal

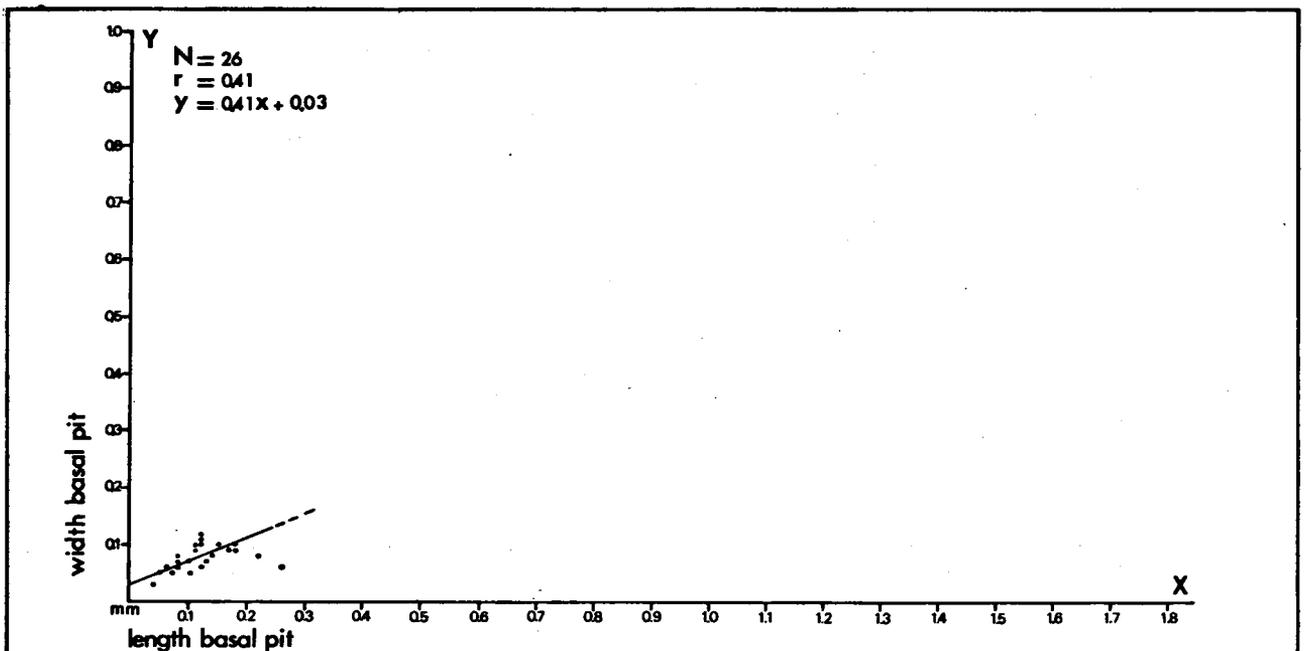


Fig. 7. Size of the basal pit of *S. lobata* during ontogeny.

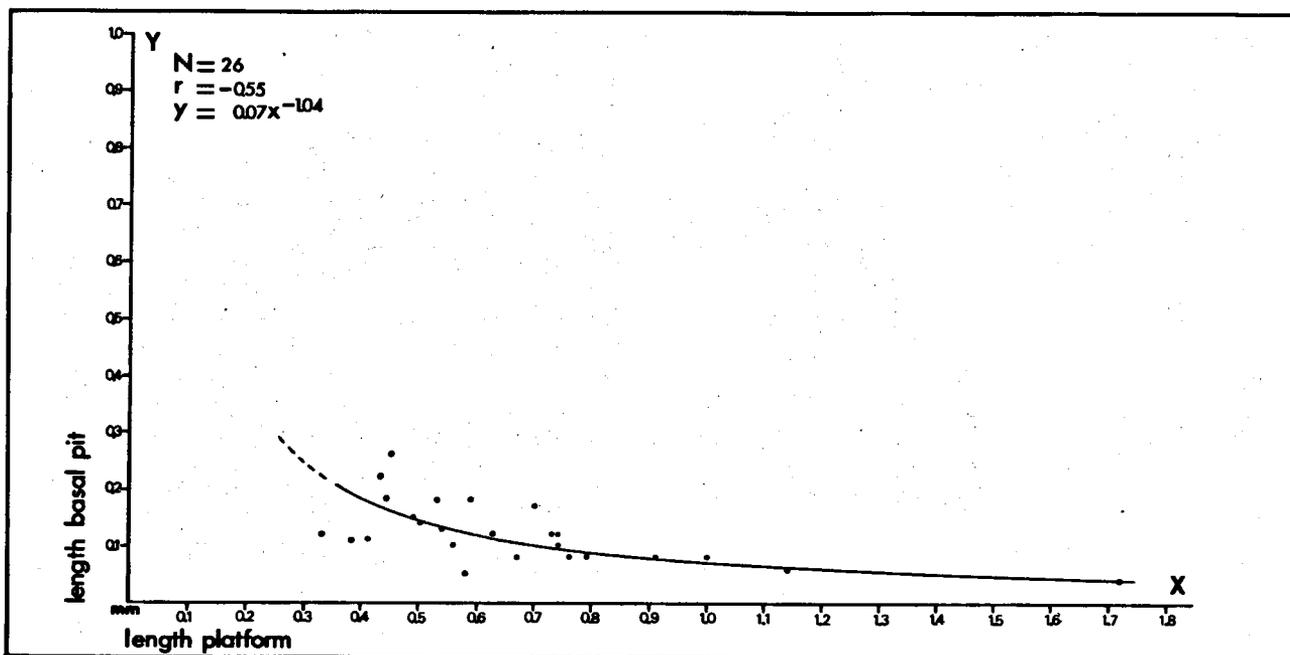


Fig. 8. Length of the basal pit of *S. lobata* in relation to the length of the platform during ontogeny.

pit, after increasing in the first growth stages, decreases at a certain stage (toward a minimal value), in contrast to the theoretical expected behaviour which predicts growth to a standard size.

2) The last lamellae in *S. lobata* do not aid in building of the secondary keel in juvenile specimens, while the same lamellae do so in adult specimens.

These features cannot be explained by supposing secondary growth, as the basal pit is closed off from the exterior in later growth stages by the basal plate. The only way to explain these features is by assuming that at a certain stage a part of the material of the basal plate is transformed into 'normal lamellar material'. This process may be called a downward directed migration, in the holoconodont, of the plane of separation between conodont and basal plate. As a consequence of this process a part of the lamellae of the basal plate would have been taken up in the conodont, so that the length of the basal pit would decrease (Fig. 9).

In a discussion on the possibility of a basal filling of the gnathodids, Lindström (1964, p. 28) stated: "In view of the general similarity between the material of the filling and that of the conodont itself one may perhaps assume that the conodont might occasionally have taken over some of the space and morphology of the filling during evolution". Müller & Nogami (1971) came to the same conclusion after studying thin sections of Cambrian conodonts (p. 53): "Bei ihnen bestehen in der Tat die später vom Basiskörper eingenommenen Teile aus noch nicht weiter differenzierter Substanz".

Pierce & Langenheim (1970) explained the difference between the lamellae of the conodont and of the basal

plate by "... either differences in the secreting cells", or by "... the passage of a progressive mineralisation front" (p. 3235).

The present results seem to conform Lindström's original suggestion. However, as the lamellae of the conodont and of the basal plate differ mainly in the arrangement of the crystallites in the lamellae (Pietzner et al., 1968) (which might also be the cause of the difference of colour, of the difference of hardness and of minor chemical differences), the process can be described more appropriately as a process of recrystallization, resulting in the downwards migration of the separation plane.

It seems probable that this process of migration might also be observed on other platform genera as *Polygnathus* and *Palmatolepis*. During his visit to Bonn the author got the impression that on some of the sections of the collection studied by Müller & Nogami (1971), the recrystallized part of the basal plate could be observed, e.g. on UB 276 (Pl. 8, Fig. 2), UB 286 (Pl. 11, Fig. 1) and UB 337.

It seems hard to understand what really happened. How is it possible that lamellae have been partly recrystallized while they were isolated from the surrounding secreting cells? We probably have to assume that there was still some connection with the exterior. Two known features could have formed such a connection:

- a) the canalules running through the basal plate, as described by Müller & Nogami (1971, p. 56, 57), although these authors have interpreted these structures as living places for organisms (Müller & Nogami, 1972, p. 73, 74);
- b) the groove running through the free blade, which is connected with the basal pit.

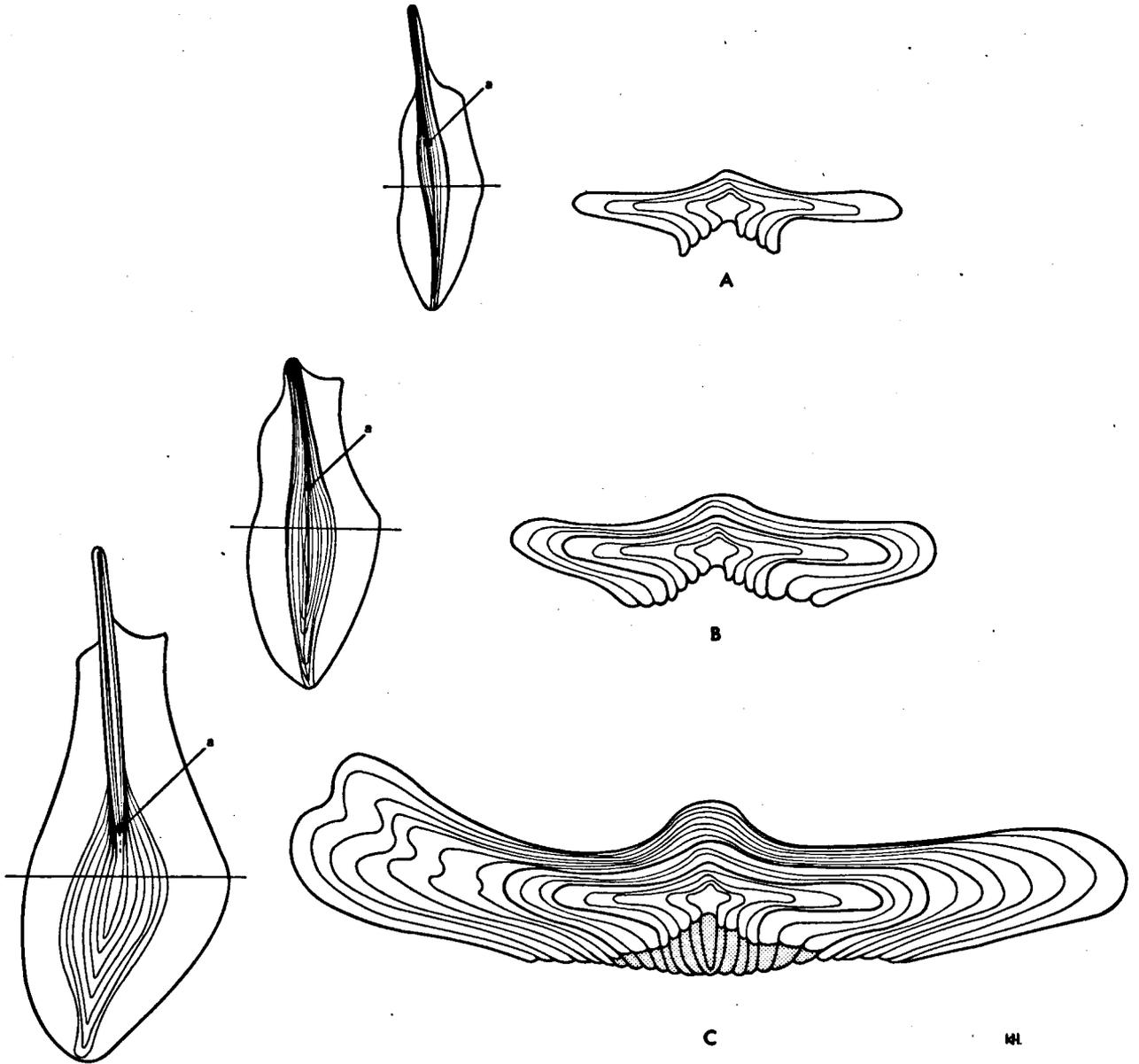


Fig. 9. Schematical cross-sections through the central part of the platform of *Siphonodella*, demonstrating the change of the basal structure during ontogeny. The three cross-sections have been made at identical places with respect to the oldest part of the conodont (i. e. the deepest part (a) of the basal pit). The three stages A, B, C are corresponding with the three photographed specimens of *S. cooperi* (Pl. 1, Fig. 1; Pl. 1, Fig. 3; Pl. 2, Fig. 1). The part of the basal plate which has been transformed into 'normal lamellar material' in section C is shaded.

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PLATES

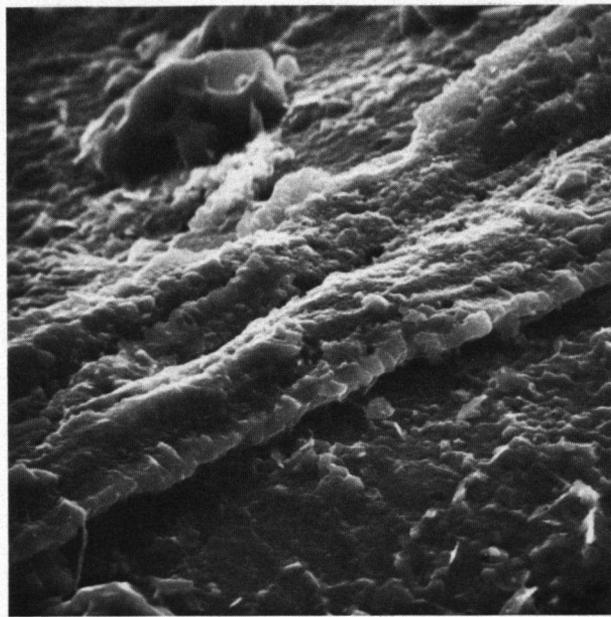
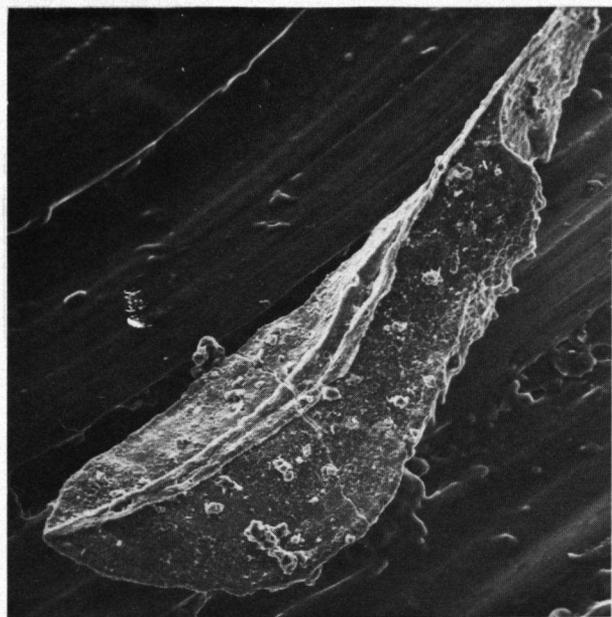
PLATE 1

Fig. 1. Lower side of a juvenile specimen of *Siphonodella cooperi*. x 175.
Specimen 03-096, sample 0281.

Fig. 2. Detail of the central part of the basal pit of the same specimen. x 1800.

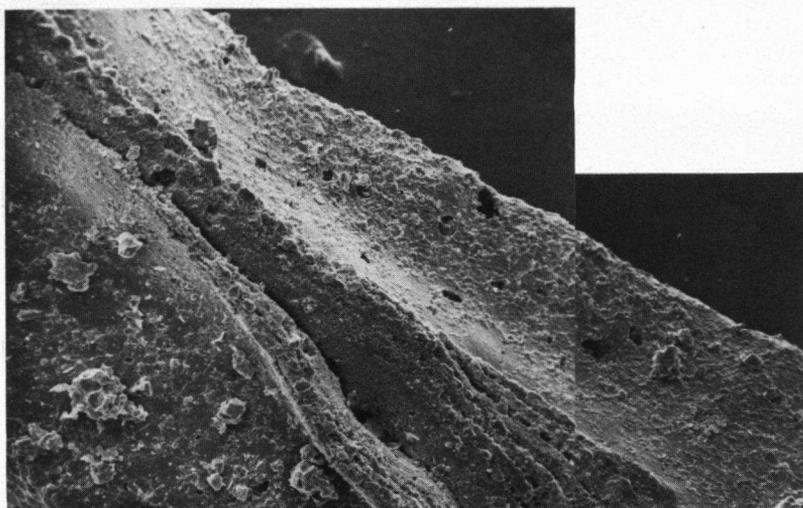
Fig. 3. Lower side of an adult specimen of *Siphonodella cooperi*. x 120.
Specimen 03-110, sample 0281.

Fig. 4. Main part of the basal structure of the same specimen. x 405.
Note that the lamellae are turned around to the posterior, and that the lamellae in the central part dip to the platform margins, while they dip to the interior of the basal pit in the anterior part. The specimen represents the stage at which the formation of the outer attachment area started.



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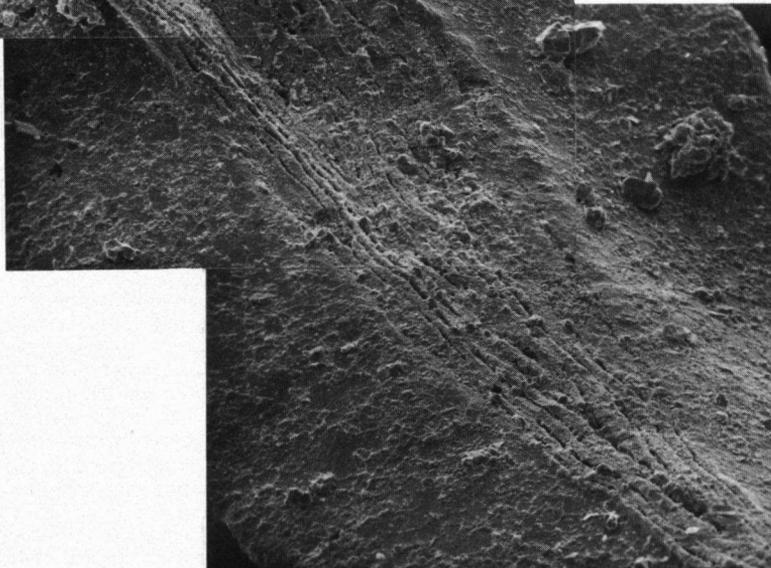
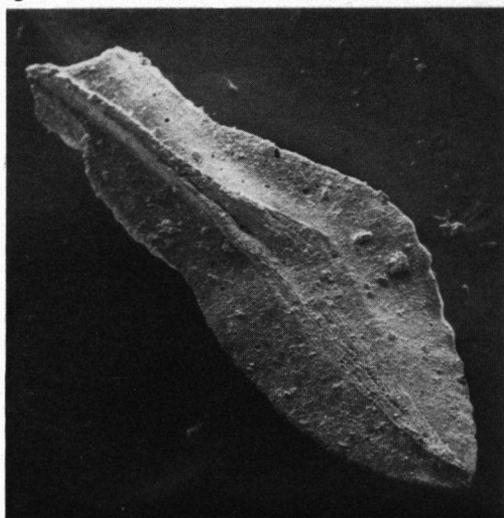
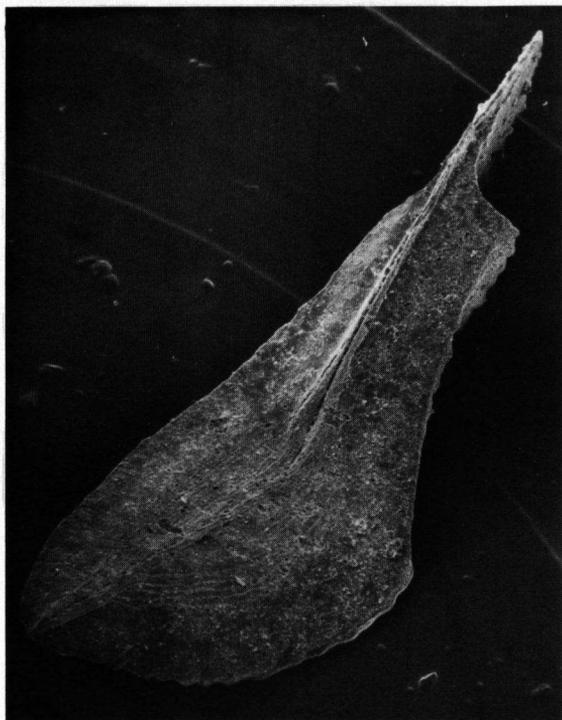


PLATE 2

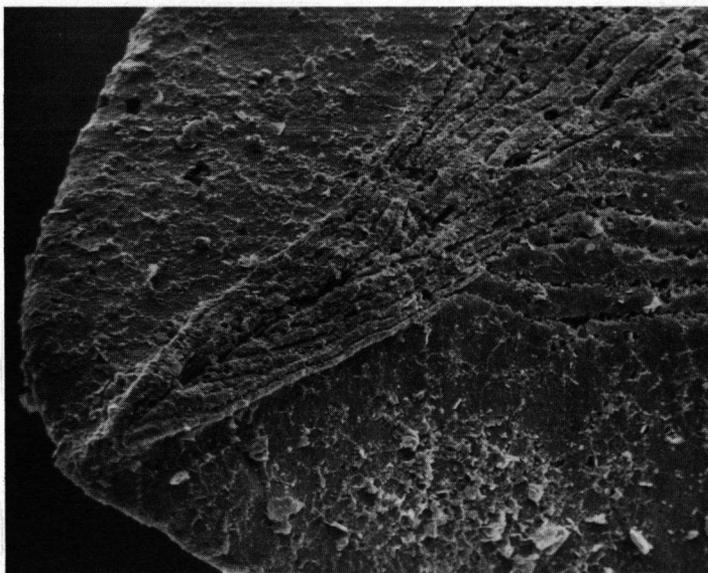
Fig. 1. Lower side of an adult specimen of *Siphonodella cooperi*. x 95.
Specimen 03-172, sample 0281.

Fig. 2. Detail of the basal structure of the same specimen. x 375.
Note that the dip of the lamellae is directed to the interior of the basal pit in the anterior part, and to the platform margins in the central part. In the central part a basal pit and an outer attachment area can be recognized.

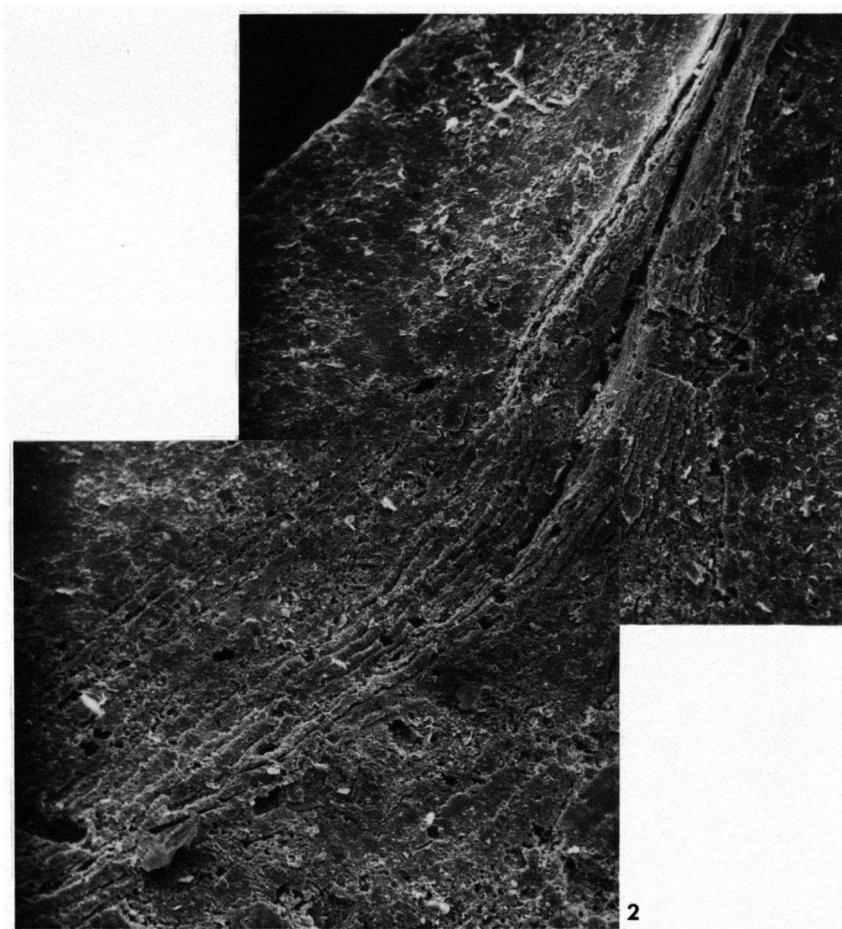
Fig. 3. Detail of the posterior part of the same specimen, showing the transition of the outer attachment area, with lamellae dipping to the exterior, and the secondary inverted basal cavity, with lamellae steeply dipping to the interior. x 470.
Note the rupture through the line of bending of the lamellae in the secondary inverted basal cavity.



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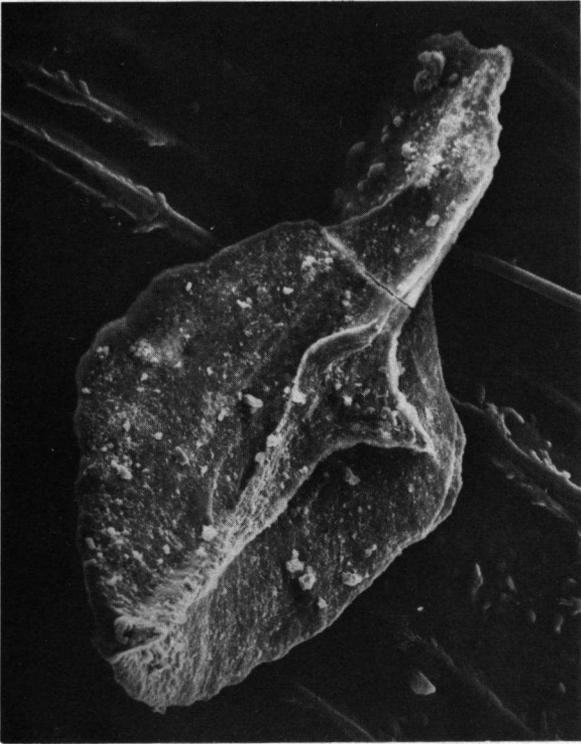


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PLATE 3

Fig. 1. Lower side of a juvenile specimen of *Siphonodella lobata*. x 200.
Specimen 04-005, sample 0190.

Fig. 2. Basal structure of the same specimen. x 785.
Note the last formed lamella, which does not enlarge the basal pit as do the former lamellae, but which starts the formation of the outer attachment area.



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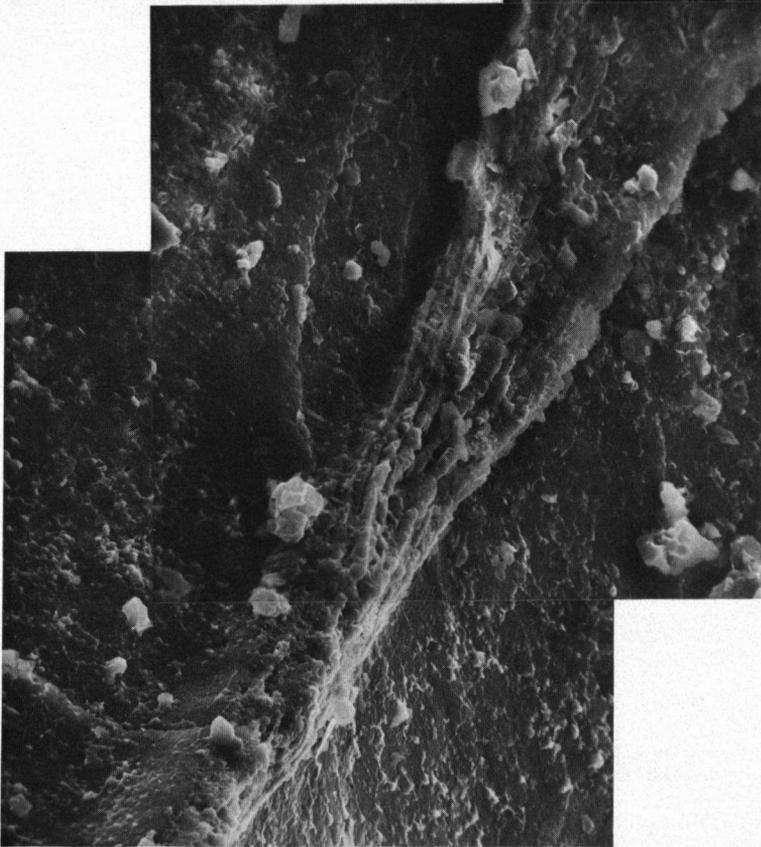


PLATE 4

**Fig. 1. Lower side of an adult specimen of *Siphonodella lobata*. x 45.
Specimen 04-002, sample 0190.**

Fig. 2. Detail of the keel of the same specimen. x 635.

**Fig. 3. Detail of the secondary keel of the same specimen. x 315.
Note that the last formed lamellae do not add to the size of the secondary keel.**

**Fig. 4. Basal pit of the same specimen. x 630.
Note that the lamellae at the anterior dip to the interior of the basal pit, while they dip to the platform margins at the posterior.**

