Norsk Geologisk Tidsskrift

THE MIDDLE ORDOVICIAN
OF THE OSLO REGION, NORWAY

8. Brachiopods of the Suborder Strophomenida.

BY

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    A b s t r a c t. 79 Strophomenid brachiopods are described from the Middle
Ordovician of the Oslo Region in Norway. They belong to 27 different genera
and subgenera. 46 species or subspecies and 6 genera or subgenera are new.
The structure of the valves is studied by serial sectioning and the results discussed.
Fairly complete ontogenetic series of three species are described. The Middle
Ordovician brachiopod fauna is rather different in the areas within the Oslo
Region. In the Oslo—Asker and Ringerike districts the fauna is of a British—
Irish type, and in the Langesund—Gjerpen, Hadeland and Mjøsa districts it
shows Baltic affinities. In the Ringsaker district there are some species of
American type.

PREFACE

The present paper is one of several being published by different
authors on the Middle Ordovician of the Oslo Region. This team work
was initiated and is led by Professor L. Størmer (Palaeontological
Institute, Oslo).

The Strophomenids of the Oslo Region were described by HOLTE-
DAHL (1916). This paper, which, to a certain degree has been neglected

by later authors, is of very high class to have been written so early
— in fact it was the first modern paper on the Strophomenids. HOLTE-
DAHL discovered the simple cardinal process in the early Plectambo-
nitids, and also noticed that the convexity is an unstable feature,
even within one species. He used the internal features (cardinal pro-
cesses, teeth and muscle impressions) as the base for the classification,
and pointed out that the division of the Strophomenids into Rafines-
quinidae and Orthotetidae was completely artificial, and that the
natural groups were the Plectambonitids and the Strophomenids. Later
these ideas were further developed by JONES (1928), KOZLOWSKI
(1929) and ÖPIK (1930, 1933, 1934).

Before 1916, there are no papers of palaeontological value on the
Strophomenids of this region. It is worth mentioning that both KJE-
RULF (1864) and BRØGGER (1887) briefly described *Kiaeromena kjerulfi*
(HOLTEDAHL) and were aware of its value as a guide fossil, even if they
did not give it a name.

KIÆR (1926) described a new species, *Leptaena minuta*, and JONES
(1928) gave some information on the Norwegian Sowerbyellinids.

Due to the considerable collecting which has taken place during
the later years, the present material is much more extensive than that
available to HOLTEDAHL, and the number of species is therefore much
larger in this paper.

Mauritz for photographing the specimens, Miss R. Gulliksen and Miss
I. Lowzow for drawing the figures and diagrams, and Mrs. A-C.
Brenna for revising and typing the manuscript.

Material and methods.

The present material of Middle Ordovician brachiopods from
the Oslo Region is mostly preserved in shale, marls and limestone.
Comparatively few specimens come from siltstones. Shale material
usually is suitable for studying the internal structures. The specimens
are either found as natural casts, or the shell substance can easily be
dissolved in dilute hydrochloric acid to form casts. This procedure has
been used extensively on the present material, especially with speci-
mens preserved in shale, but also with those from marls and marly
limestones. The latter specimens were usually very brittle when all
carbonates had been dissolved, and they were therefore strengthened
by spraying the specimens with celluloid or plexiglass (methylmeta-
crylate) dissolved in acetone. Usually, six to eight sprayings were
enough, even with very brittle specimens.

In some species, where the interior could not be studied by dis-
solving the valves, it was necessary to make serial sections in order
to reconstruct the interior. Serial sectioning was also used when stu-
dying the histological structure of the valves of some species. All
serial sections, as well as most of the ordinary thin sections were made
by the dry peel method. The procedure was as follows: The specimen
was ground with fine carborundum powder until the desired surface
was obtained. It was then etched for a few seconds with dilute hydro-
chloric acid, after which it was dried. The dry surface was pressed
against a small piece of celluloid moistned with a few drops of acetone,
until the acetone evaporated. When the specimen was freed from the
celluloid, the latter showed an impression of the structure of the
specimen. The celluloid casts had to be mounted on an ordinary
object glass as soon as possible in order to prevent the celluloid from
curling. When preparing a serial section, the grinding of the etched
surface was continued until a new surface was reached, and then
the etching was repeated. In long serial sections, it is necessary to
protect the sides of the specimen against corrosion. This was done by
giving the specimen a thin coating of wax or plexiglass.

The quality of the peel, compared to ordinary thin sections, was amazingly high. In well preserved specimens, they could be magnified up to 200x, and, in most cases, they show the histological details just as clearly as the thin sections. In order to verify this, the last surface of some of the serial sections were made into ordinary thin sections. For studies in polarized light, the thin sections are of course indispensable.

For this paper, about 25 serial sections were made, and about 450 additional dry peels and 35 ordinary thin sections.

A number of photomicrographs were made from dry peels, and no special measures were needed in order to obtain good pictures. Both thin sections and peels were photographed with the same light and optics (pl. 13, figs. 1, 3, 5).

During the preparation of the plates, it became evident that it is difficult to compare casts and positive specimens. Some features can be seen more plainly in the casts, while others only are clearly visible in the positives, as for instance the cardinal processes. Dr. Jaanusson of Uppsala has also kindly called my attention to the fact that scientists working exclusively with positive material (United States and the Baltic Region) generally have great difficulty in comparing their material with material which only is represented by casts. Authors working with cast material generally have experience both with casts and positives, and they do not so often have these difficulties.

The figures in this paper have, as far as possible, been made from positives. In some specimens, however, this was impossible, either because the original specimens (casts) were too brittle, or because the shape of the specimens made it difficult (the *Leptaena* species, with the angle between the fringe and the disc less than 90°).

Several casting substances were tried. Latex emulsion proved to be the most suitable, and, when carefully applied, gave casts showing all details, even those from deep cavities. Furthermore, they are elastic, can be handled easily, and adhering rock substance can be removed simply by washing the latex cast with soap and water.

Good photographs were not obtained from casts made by latex emulsion only, as they were semitranslucent and of a brownish-yellow colour. A large number of dyes were tried by the author, assisted by Miss L. Monsen and Miss B. Mauritz, in order to find a substance,

which, added to the latex, would give an opaque surface, and a colour
which gave good photographs. Different types of photographic nega-
tive material usually gave different results with different colours.

AGFA orthocromatic plates were used for the photographs in
this paper, and the casts were made from latex emulsion with 10—20%
pale blue commercial latex paint. These casts were of a very pale
bluish-green colour. The addition of the latex paint did not affect
the casting properties of the pure latex.

Besides the material from the Middle Ordovician of the Oslo
Region, some specimens from other regions are introduced for com-
parison. Most of them belong to Paleontologisk Museum, Oslo. The
lectotype of *Leptaena rugosa* and the specimen of *Strophonella euglypha*
figured (pl. 12 fig. 7) belong to Naturhistoriska Riksmuseet, Paleozoo-
logiska Avdelingen, Stockholm, Sweden.

General part.
THE SHELL STRUCTURE

The shell structure of the Strophomenids has been studied by
CARPENTER (in DAVIDSON 1856), KOZLOWSKI (1929), ÖPIK (1930,
1933, 1934), WILLIAMS (1953, 1953a), and a number of other authors.

The Strophomenid valve consists of two layers, the primary,
external one, secreted by the edge of the mantle, and the secondary,
inner one, secreted by the whole mantle. The secondary layer is,
in most cases, much thicker than the primary one in adult specimens.
The external sculpture is reflected on the inside of the external layer,
as vascular or ciliar grooves. Later this sculpture is obliterated by the
deposition of secondary tissue. The secondary tissue shows impressions
of muscles and vascula, and specimens lacking the secondary layer are
often devoid of these important diagnostic features. Young specimens,
in which these features are not completely developed, may often show
the diagnostic features of different species or even genus (cf. ÖPIK
1930, p. 32). The two layers are generally distinctly defined, except
in a few species, as for instance *Ptychoglyptus valdari* (cf. p. 60).

The external layer is sculptured on both sides. It is generally
very thin, and only grows laterally and not in thickness. The inner
secondary layer increases in thickness as the animal grows older, and
is therefore much thicker in gerontic specimens than in young ones.

In some species the inner layer is only slightly developed if deposited at all, and in others the majority of the adults are very thick-shelled. It is obvious that the ecological features, such as the temperature and the amount of calcium carbonate dissolved in the sea-water, will have affected the amount of material deposited in the inner layer. In many cases it is difficult to discriminate between these ecological variations, and real genotypical varieties within a species.

There seems to be a certain histological difference between the inner and the outer layers, but the fact that the latter are so thin, makes difficult to study them in detail. The tissue of the inner layer seems to be histologically uniform, except for the pseudodeltidium and the teeth in some species. In pseudopunctate species, the muscle impressions and their immediate surroundings seem to be impunctate. The tissue itself, however, is not differentiated, the only difference being the absence of the pseudopuncta. In some cases the tissues seem to be unlaminated in ordinary thin sections. Probably this is usually due to the angle under which the laminae are cut by the section. In dry peel sections, the laminae can generally be seen much more clearly, and in these all the parts of the valve appear to be laminated, with the exception of the teeth in some species, and possibly also some of the minor parts of the cardinal region.

PSEUDOPUNCTA

The shells of the Strophomenacea differ from those of all other brachiopods (with the exception of the Estlandidae) in having pseudupuncta in the valves.

They were regarded as open pores by CARPENTER (1856) and BEECHER (1891), and as internal calcareous spines by KOZLOWSKI (1929) and WILLIAMS (1953).

The pseudopuncta consist of a series of cone-shaped sheets, generally meeting at an angle of 90° or less, and a central axis of variable diameter (0,1 mm and less). The cone-sheets are continuations of the growth lines of the tissue of the valves (pl. 14 fig. 5). The apex of the cones can always be seen on the interior surface of the valves. They appear as dots, or as small cones with rounded ends (pl. 7 fig. 15).

The central axis is generally filled with clear calcite. This has led

a number of authors into believing that the axes represented massive calcareous spicules in the valve. It is, however, difficult to explain how these spicules could have grown, and why they were formed as discrete spicules. A detailed study of the pseudopuncta in *Leptaena depressa* shows that they are evenly distributed over the interior surface of the valves. The size increases towards the margin. In the case of complete specimens filled with calcite, it is impossible to decide whether the pseudopuncta are spicules or not, as the pseudopuncta in both cases would be filled with clear calcite, and there is no way of discriminating between the unlaminated tissue of the shell and the calcite which fills the space between the valves. The fact that some of the calcite crystals in the pores have the same optical orientation as the calcite fibres in the valve does not indicate that they were formed inside the animal. Such orientated growth of calcite on calcite is common, and does not point to a contemporaneous formation of the two crystals. Orientated crystals are usually just as common on the inner surface of the shell as in the pores. This paper therefore only describes the study of complete specimens where the interspace between the valves was filled with clay or marl, or, in some cases, with marl and calcite. In these specimens it was evident that all the pseudopuncta were filled with matrix, and did not contain any calcareous spicules. In some old specimens the pseudopuncta nearest to the centre of the valve did not have a central axis, and probably this was because they were closed by the growing of the secondary tissue. The possibility of the spicules having loosened from their position or been worn off, can be excluded in these cases, since the specimens show no signs of wear, and the pseudopuncta generally are curved in such a way that massive spicules could not escape. The presence of matrix in the pseudopuncta was proved by colouring the clay minerals with aniline dyes. The contents of the pseudopuncta were coloured in just the same way as the matrix between the valves, and the rest of the specimen remained unstained.

It is worth mentioning that in one of the 67 sectioned specimens, the pseudopuncta are filled with a substance which differs from the matrix in being of a brownish-yellow colour. Tests with aniline dyes show possible traces of clay minerals. The specimen in question was filled both with clay and clear calcite. In both cases the pseudopuncta were filled with the same brownish-yellow substance. This is the only

deviating specimen which has been found in the author's material of this species. In some well preserved specimens, the protruding ends of the pseudopuncta in the interior of the valve are perforated. This may be due to wear, but the fact that there usually are perforations, and the absence of all other signs of wear, indicate that the pseudopuncta were hollow.

The pseudopuncta, at least those found in *Leptaena depressa*, must therefore be regarded as cavities for protuberances of the mantle. As for the structure, they resemble the acanthopores of the Trepostomateous bryozoans (CUMMINGS & GALLOWAY 1913) which are regarded as being transformed zooids. Cone sheets similar to those of the pseudopuncta are found in the acanthopores as well (text fig. 1).

Pseudopuncta are found in almost all Strophomenid species. The only exceptions which the author has seen are the genus *Ukoa* ÖPIK (cf. ÖPIK 1932, p. 33), and *Christiania oblonga* (PANDER). In these species, no puncta at all have been observed, in spite of a large material of thin sections.

In most species the pseudopuncta are arranged according to a certain pattern. In specimens with a thin secondary layer, the larger ribs of the external sculpture will often direct the pseudopuncta, so that they are placed in radial rows or segments. This can also be seen in other specimens, and generally in those with large pseudopuncta. The size of the puncta varies considerably, even within the same species. In most species the size even varies in each single valve. *Oepikina dorsata* has large pseudopuncta in the central part of the valves, and smaller ones towards the margin. In *Leptaena depressa* (cf. textfig. 4) it is the other way around.

The largest pseudopuncta are found in *Leptaena*, the smallest in *Oepikina* and in some *Plectambonitids*. These small puncta can scarcely be distinguished from the Dalmanellid endopuncta, even under high magnification, and on well preserved material. It has therefore as yet not been ascertained whether endopuncta can be found in primitive Plectambonitids, such as *Plectambonites*, *Ingria* and others. The material of these genera (from the Lower Ordovician of the Baltic Region) which have been sectioned are all slightly recrystallized, and it is therefore impossible to discriminate between very small pseudopuncta and the endopuncta. The difference between the two types of pores, as defined here, is that the pseudopuncta have cone sheets which

A	B	C	D
LEPTAENA INVERSELLA	KJAERINA SOWERBYELLA	PTYCHOGLYPTUS KULLERVO	DALMANELLA a.o
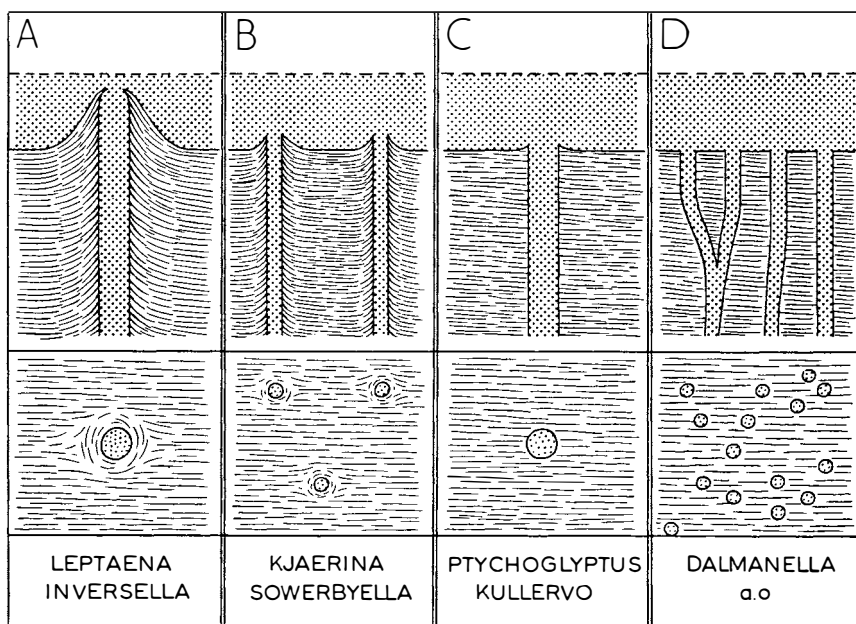
Fig. 1. Diagramatic figures of different types of puncta. *A*. Large pseupo-puncta with highly elevated margins. *B*. Small pseudopuncta with elevated margins. *C*. Puncta without, or with only slightly elevated margins. *D*. Endo-puncta. The names below the figures indicate typical representatives.

make them protrude from the inner surface of the valves. The apertures of the endopuncta are level with the surface and appear as depressions.

Puncta without, or with only slightly developed cone sheets are found in a number of Plectambonitids, especially *Ptychoglyptus*, while *Leptaena*-like puncta can be found in others, as for instance *Inversella* and *Sampo*. The «eingestochened puncte» described by ÖPIK (1933, pp. 32, 34—35 pl. 6 figs. 1—2) from *Leptelloidea leptelloides* and *L.*(?) *musca*, are also intermediate between the pseudopuncta and the endo-puncta. According to ÖPIK, they are filled with matrix right to the bottom (to the external layer). After having studied a large material of specimens belonging to these two species, it appeared that the punctate tissue spread over the whole valve as the animals grew older, and while young specimens were almost devoid of it, old specimens were completely covered. This punctate tissue is probably the in-

ternal shell layer. Unfortunately, bad preservation of the histology of these species does not allow a closer study of these interesting structures. The pores found in the Estlandiidae, are of the same type as those in the primitive Plectambonitidae, and the cone sheets are either only slightly developed, or not at all. The amount present of the latter shows the limesecreting capacity of the mantle protuberances which filled the pores.

A gradual transition therefore exists between the endopuncta and the pseudopuncta, and no sharp line of division can be drawn between the two types. If this transition had not been known to exist, the pores found in several Plectambonitids would have been referred to as undoubted endopuncta (pl. 13 fig. 7).

PSEUDODELTIDIUM AND CHILIDIUM

The pseudodeltidium is generally (BEECHER 1890, 1891, 1892, ARBER 1945) described as a thin plate covering the apical part of the delthyrium. In the material studied by the author, the pseudodeltidium is of a quite different structure. This may be due to the fact that the author has studied older species than those which previously have been described. The species in which the pseudodeltidium has been studied in detail, are *Kiaeromena kjerulfi* (HOLTEDAHL), *K. juvenilis* (ÖPIK), *Oslomena osloensis*, *Christiania holtedahli* and *Strophomena norvegica*, all from the Middle Ordovician.

The pseudodeltidium of these species consists of an obliquely pyramidal block of calcareous laminae, with sharp edges outwards, and smooth ones inwards. Because of the thin edges, the frontal part of the pseudodeltidium consists of interfingering layers of calcareous tissue and sediment. The fragile edges are easily worn off, and they are rarely preserved in free specimens. In many cases they were probably destroyed before the specimen was buried in the sediment. The material dealt with in this paper consists of specimens preserved in rock, and the pseudodeltidia have been studied either in thin sections, or in artificial casts made by dissolving the calcareous parts in dilute hydrochloric acid.

The lamellae of the pseudodeltidium are parallel to the hinge line, and seem to be part of the area. There is nothing to indicate that the pseudodeltidium was a separate plate different from the ventral valve

as indicated by KOWALEWSKY (cf. BEECHER 1891, and ARBER 1945). The growthlines on the area are confluent with those of the pseudo-deltidium and in *Kiaeromena kjerulfi* no histological difference can be detected between the area and the pseduodeltidium.

The pseudodeltidium increases in thickness, so that the last, lowest lamellae are deeper than the others. In one species, *Oslomena osloensis*, this growth even isolates the cardinal processes, which seem to be concealed in the pseudodeltidium. The external surface of the pseudodeltidium is generally convex, in *Christiania holtedahli* and *Oslomena osloensis*, it is flat and slightly raised above the area.

The edges of the lamellae are, when they can be observed, bent down towards the dorsal valve. (In specimens with a sharp angle be-tween the areas, the edges point towards the dorsal valve without bending.) They correspond to the similar, generally more fragile edges of the chilidium.

The latter structure is found in many species with well developed pseudodeltidium. It consists of a thin, curved plate which covers the parabolic nothothyrium, and conceals the cardinal processes. It is continuous with the chilidal plates. The strong growth lines with edges pointing towards the ventral valve, are found on the external surface only.

The presence of strong lamellae on the pseudodeltidium and the chilidium and the fact that the edges of these lamellae bend down towards each other, indicates that they were united, probably with a ligament. The presence of a brownish-yellow substance in the frontal part of both the pseudodeltidium and the chilidium adds to the pro-bability of this theory. It might be interpreted as remains of the origi-nal ligament tissue. The species in which the pseudodeltidium and chilidium are strongly developed, often have only slightly developed diductor muscles (i. a. *Oslomena osloensis*) or heavy valves (i. a. *Kiaeromena kjerulfi*).

It is evident from the description given in this paper of the pseu-dodeltidium of the above mentioned species, that at least two types of structures can be found. In the type mentioned, which might be referred to as the b-pseudodeltidium, the growing edge is parallel to the hinge line, while in the other, the «conventional» type, it is roughly parallel to the sides of the delthyrium. This type is called the a-pseu-dodeltidium. The taxonomic importance of the presences of the dif-

ferent types of pseudodeltidium has as yet not been made clear, owing
to the limited material which has been studied. In several cases
closely related genera have different types, as for instance *Oepikina*
(a)- *Oslomena* (b) and *Leptaena* (a)- *Kiaeromena* (b).

This shows that the presence of a special type of pseudodeltidium
probably is of no great importance. The a-pseudodeltidium was very
likely a simple cover for cardinal processes and the diductor muscles,
while the b-pseudodeltidium served as an attachment for a ligament.
It is very improbable that the species with a b-pseudodeltidium should
be a related group, opposed to those with the a-type. The taxonomic
importance of this feature must therefore be regarded as being at the
generic level or lower. The chilidium is also modified in some of the
Strophomenids, but not to the same extent as the pseudodeltidium.
It generally consists of a thin, curved plate, which more or less com-
pletely covers the nothotyrium. Histologically it differs from the rest
of the valve in being less fibrous. In the most primitive species (i.a.
Ptychoglyptus valdari) the chilidium is similar to that found in *Ingria*,
and also in the Orthids. In the Leptestidae it is generally very small,
if present at all. The so-called «chilidal plates», which form parts of the
cardinal process in this family, probably have no connection with the
chilidium. In more highly developed Strophomenids, these plates
possibly develop into cardinal processes, and in spite of this, these spe-
cies have a chilidium, which is histologically identical with that of
the primitive Plectambonitids. The «chilidal plates», therefore, can
hardly represent a reduced chilidium.

In the species with double cardinal process (Strophomenidae),
the chilidium usually has a thin median fold, corresponding to the
slit between the cardinal processes. In primitive species, this fold
is hardly developed (*Oepikina*), and in others the fold is present, but
the distance between the chilidium and the cardinal processes is com-
paratively large (i. a. *Kiaeromena juvenilis*, pl. 7 fig. 17 and *K. kjerulfi*,
text fig. 41). In the more highly developed species, the chilidium is
very thin, and the distance between the cardinal processes and the
chilidium is extremely small, so that the fold fits into the slit. Be-
cause of the small interspace between them, it is difficult to ascertain
the presence of the chilidium, except in thin sections because it forms
a perfect cast of the posterior side of the cardinal processes (i.a.
Leptaena depressa, pl. 14, fig. 8).
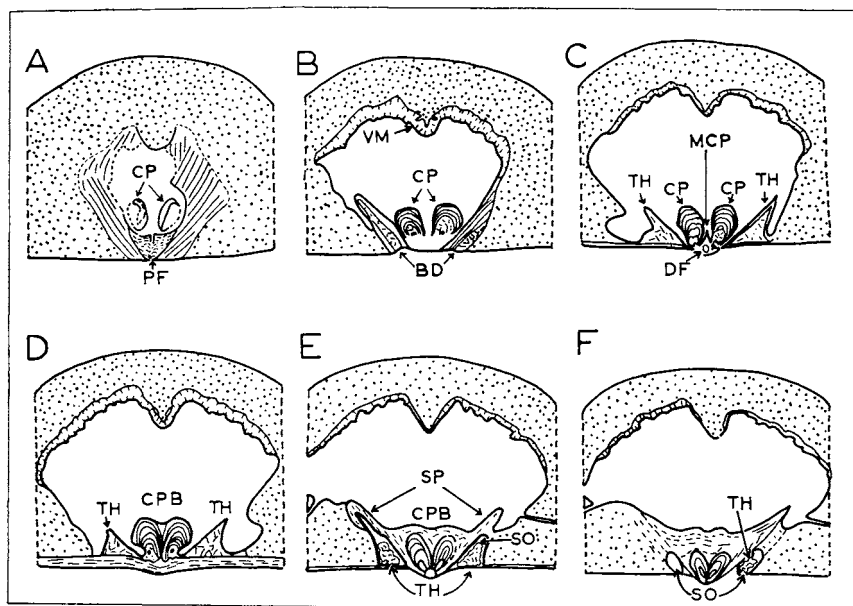
Fig. 2. *Oepikina dorsata* (BEKKER). Six horizontal, parallel sections of a small specimen from zone C2 in Esthonia, showing the structure of the teeth and the cardinal processes. *Abbreviations:* CP — Cardinal processes. CPB — Posterior shaft of the cardinal processes. BD — Base of the teeth. DF — Dorsal foramen. MCP — Median cardinal process. FF — Ventral pedicle foramen SO — Sockets. SP — Socket plates. TH — Teeth. VM — The special tissue of the ventral muscle impressions. Magnification about 5x.

THE TEETH

The teeth are defined as the secondary tissue deposited in the corners between the hinge line (area) and the dental plates.

In many thin-shelled species, and in most young specimens, the teeth are not developed, or they are present only as an inconspicuous thickening of the anterior part of the dental plates.

The histological structure of the Strophomenid teeth has previously not been well known. Except for the Stropheodontidae, which have been described in detail by WILLIAMS (1953), most others were supposed to have had teeth built up of laminated tissue. The teeth are subject to considerable wear, and it can be expected that some differentiation has taken place to compensate this.
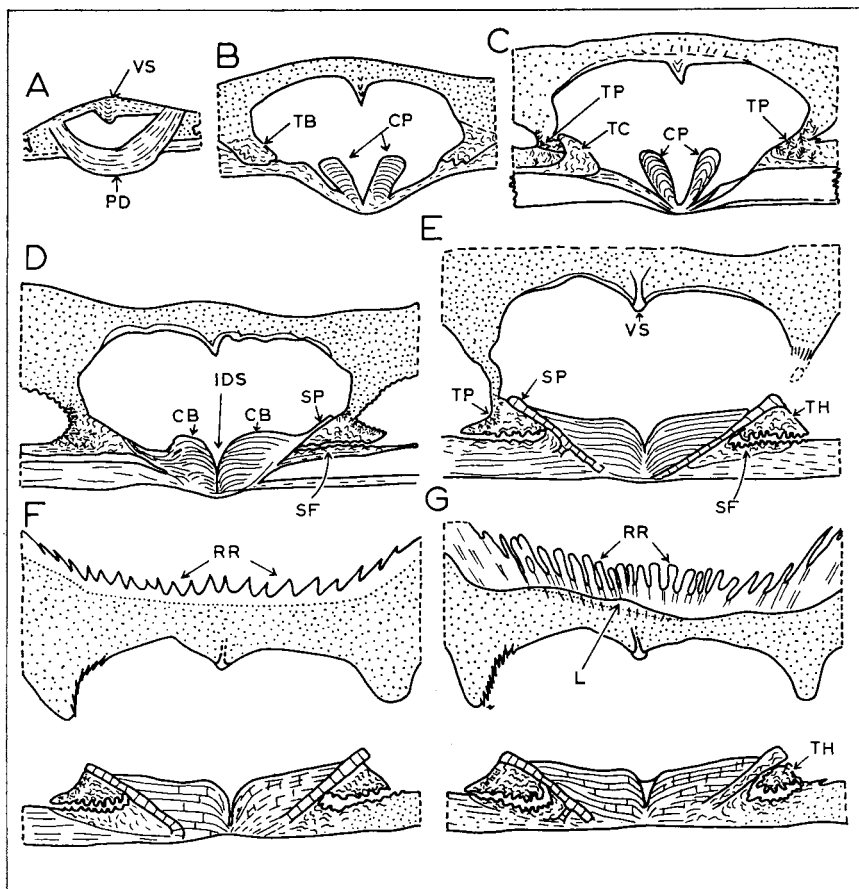
Fig. 3. *Strophomena planumbona* HALL. Seven horizontal, parallel sections of a specimen from the Maysvillian at Blanchester, Ohio, U.S.A. Section *A* cut only through the ventral valve, near the apex, the other sections cut through both valves. Note the assymetric development of the teeth, especially that the left one consists of both punctate and fibrous tissue, whereas the punctate tissue is found only in the upper, basal part of the right one.

Abbreviations: CP — Cardinal processes. CB — low, posterior shafts of the cardinal processes. IDS — furrow between the cardinal process continuing posteriorly. L— Growth-lamella with matrix in a pocket. PD—Pseudodeltidium RR — Radial ribs of the external sculpture. SP — Socket plates, well differentiated from the rest of the dorsal valve. TB — Bases of the teeth. TC — Teeth tissue consisting of irregular fibres without puncta. TH — Teeth. TP — Teeth tissue consisting of laminated tissue with small pseudopuncta. SF — Lining of socket walls consisting of tissue similar to that found in the teeth. VS — Ventral septum. Magnification about 5x.
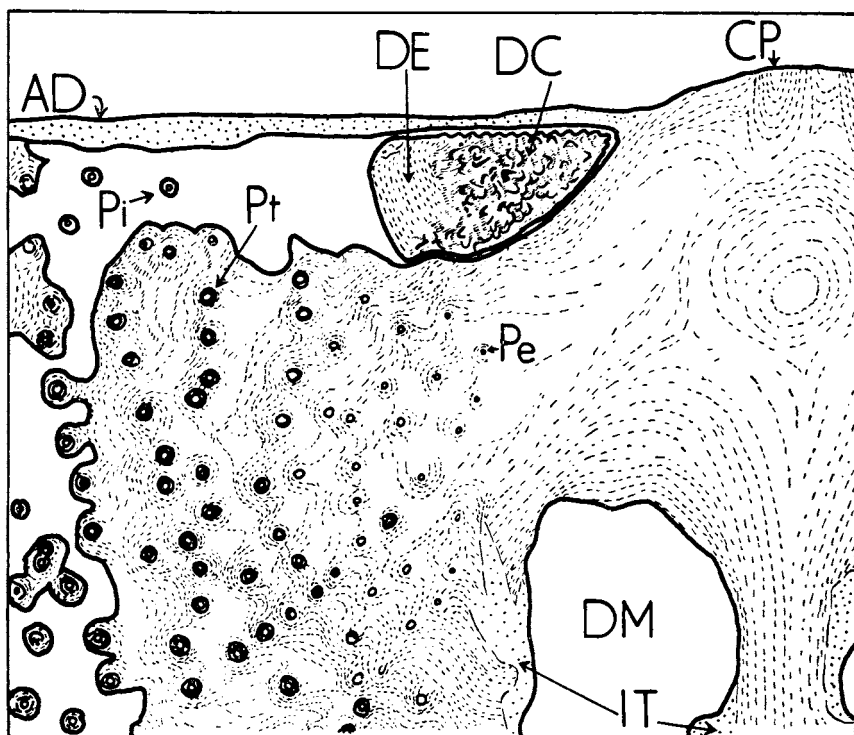
Fig. 4. *A section parallel with and near to the inner surface of the dorsal valve of Leptaena depressa*. The figure shows the structure of the teeth, and the shape and distribution of the pseudopuncta. The specimen is from the Mulde Marl (Upper Wenlock) at Tegelbruket, Frøjel, Gotland.

Abbreviations: AD = Dorsal area. CP = Cardinal process. DC = Central portion of teeth, composed of irregular vertical elements. DL = Laminated, lateral portion of teeth. DM = Dorsal muscle impressions (above the plane of the section) IT = Nonlaminated tissue around the muscle impressions. Pe = Small, central pseudopunctae. Pi = Protruding pseudopunctae, which appear isolated in the section. Pt = Large, distal pseudopunctae.

A number of species, mostly Plectambonitids, have simple teeth consisting of laminated tissue, with the laminae parallel to the sides of the more or less triangular teeth. In this group the wear seems to be compensated by double teeth in some genera, or denticulations along the hinge line.

Real specializations of the tissue of the teeth seem to be restricted
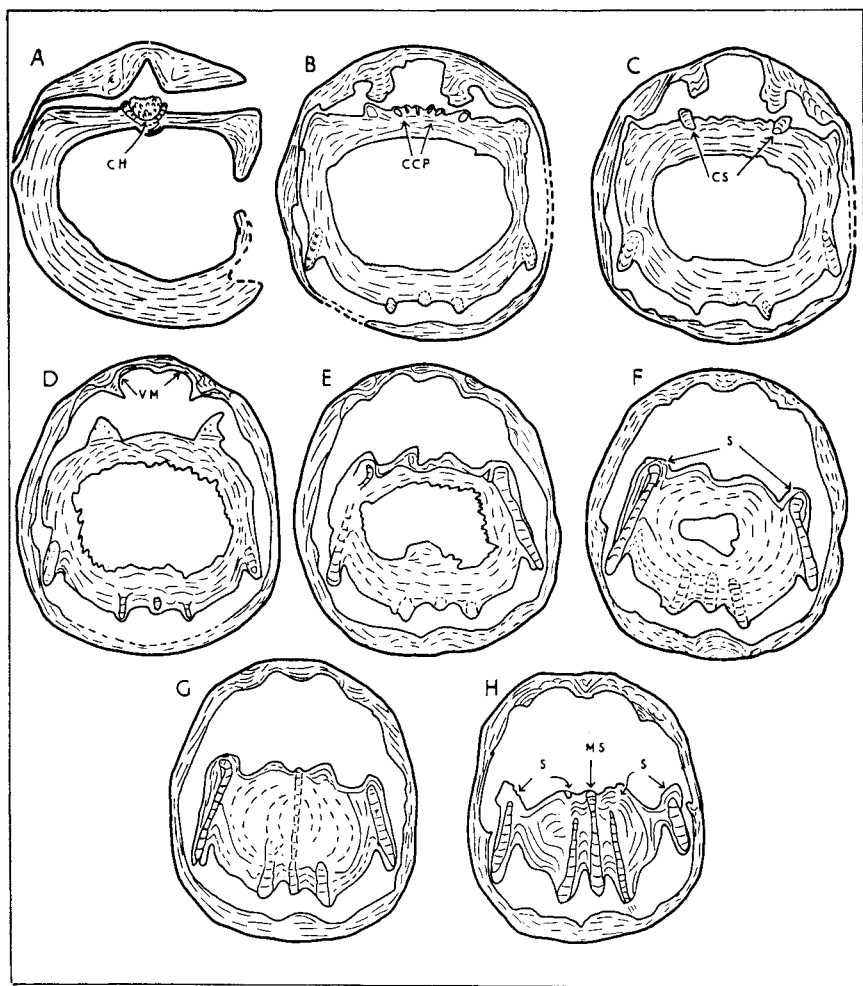
Fig. 5. *Christiania oblonga* (PANDER). *8* parallel section of one specimen. From zone B3 (?) at Popovka, near Leningrad. (cf. textfig. 26B).

   Abbreviations: CCP = Cardinal processes, denticles on the socket plates. CH = Chilidium (Most of these structures are destroyed by recrystallisation) CS = Socket plates. MS = Median septum. S = Lateral septa. VM = Ventral muscle impressions.

to the Strophomenacea. In fact, none of the species which for certain are known to belong to this superfamily, seem to have teeth consisting of laminated tissue only. When only the laminated tissue is found, it is

from the dental plates, and the teeth themselves are not developed. In all the species which have been studied. (*Oepikina dorsata*, text fig. 2, *Kiaeromena kjerulfi*, text fig. 41, *Strophomena planumbona*, text fig. 3, and *Leptaena depressa*, text fig. 4), the teeth consist of specialized fibrous tissue. Only in the latter species (and possibly *Kiaeromena kjerulfi*) parts of the teeth consist of laminar tissue. In *Kiaeromena kjerulfi*, the teeth are elongate, parallel to the hinge line, and consist of irregular lamellae and layers of calcareous tissue, perpendicular to the area. The teeth are small in proportion to the size of the valves.

In the other species which have been studied, the teeth are triangular, and consist of irregular fibrous tissue, with curved dark lines, parallel to the surface, and some small pseudopuncta. The border between the dental plates and the teeth is sharp. The side of the teeth facing the socket plate is smooth, whereas that facing the inner side of the area generally has irregular raised ridges which are especially strong in gerontic specimens. The «semidenticles» do not seem to correspond to any histological structure in the interior of the teeth (as for instance the Stropheodontid denticles), they are merely ridges on the surface of the teeth.

The anterior wall of the socket is smooth, and generally has no furrows corresponding to the «semidenticles». At the very apex of the teeth, the side facing the socket plates might also be «semidenticulated» (pl. 12 fig. 8). In some species (*Strophomena planumbona* a.o.) the sockets are lined with tissue similar to that found in the teeth. In this case, a gradual transition is found from the ordinary, pseudopunctate laminated tissue to the fibrous with smaller pseudopuncta.

Since the typical structure of the teeth is fully developed in adult specimens only, and as the histology only has been studied in a limited number of species, it is difficult to use this feature in the systematics at present, even if it obviously is of high potential value.

CRENULATIONS OF THE HINGE LINE

The crenulations of the hinge line in the Strophomenids have recently been thoroughly described by SCHMIDT (1951) and WILLIAMS (1953). The former author is of the opinion that a crenulated hinge line can be found in several groups, and that the family Stropheodon-

tidae is polyphyletic. WILLIAMS regards this family as being strictly monophyletic. This difference of opinion is due to the fact that SCHMIDT has compared all types of crenulation of the hinge line, even those of the Plectambonitacea, whereas WILLIAMS only has considered the crenulated teeth plates which are secondarily ancylosed to the hinge line.

The author's studies of this feature have made it possible to distinguish between several types of crenulation within the Strophomenids. Some of the types have been described by previous authors.

1) The *Plectambonites*-type, in which the whole hinge line is uniformly denticulated in all specimens, whether young or old. The denticles seem to be formed by small pseudopuncta strengthened by deposition of secondary calcareous tissue. (*Plectambonites, Ingria*).

2) The *Plectodonta*-type. Denticles decreasing in size from the deltidium towards the cardinal angles, which seldom or never are reached by the denticulation. The young specimens are generally not denticulated, or considerably less than the older ones. The denticles seem to consist of simple protuberances from the hinge line. No central body has been observed, and this indicates that they are not homologous with the pseudopuncta. (*Plectodonta, Eoplectodonta, Alwynella, ?Sampo*).

3) The *Sowerbyella ringsakerensis*-type, which consists of large pseudopuncta along the hinge line. The size of the pseudopuncta decreases from the cardinal angles towards the central part of the hinge line, which is not denticulated. There may be some relationship between this type and the spines of *Chonetes*. It is worth mentioning that some species of *Chonetes* have the deep ventral muscle impressions which are typical for the members of the Sowerbyellinae, and in some Sowerbyellas the ventral interior shows a strong median septum and indistinct muscle impressions, resembling the interior of *Chonetes*. The material available is too limited to prove whether these species are homeomorphs of *Chonetes*, or if they are the ancestors of that group.

It is doubtful whether these crenulations really acted as supports for the articulations of the valves. (*Sowerbyella ringsakerensis* sp. n., p. 94, and *Sowerbyella* sp. of SCHMIDT 1951, pl. 51, fig. 8).

4) The *Stropheodonta*-type. This type has been described in detail by WILLIAMS and SCHMIDT (l.c.), and it is not necessary to repeat their description here. In contrast to the types mentioned

above, the denticules are found only on the dental plates in Stropheo-
dontidae, which, however, may be extended nearly to the cardinal
angles. In the dorsal valve, there are grooves in the socket plates to
accomodate these denticles. In this type, too, the denticulation in-
creases with the age of the specimens. The type appears to be restricted
to the family Stropheodontidae, with the exception mentioned below.

These four types of crenulation must be regarded as genetically
different trends of development. The first three types also differ from
the last one in that the crenulations are restricted to the hinge line
in the former, while there is a crenulation of the teeth plates in the
latter. The Stropheodontid type can therefore rather be compared
to the double teeth of the Leptestininae, than to the three other types
of denticulation described here. The Stropheodontid crenulations are
probably homologues of the «semidenticulations» in the other Stro-
phomenacea, and these crenulations are therefore not a characteristic
feature of the family Stropheodontidae. It is the coalescence of the
dental plates (and the socket plates) with the hinge line which distin-
guishes this family from the rest of the Strophomenacea. One can find
Strophomenidae which have much more strongly denticulated teeth
than the primitive members of the family Stropheodontidae.

The above shows that there is a gradual transition between the
more primitive Stropheodontids and the Strophomenidae. This
might to a certain degree affect the validity of the family Strophe-
odontidae. It appears that all the known stropheodontid lineages lead
back to comparatively simple uniform types (WILLIAMS 1953a, p.
19), and this seems to support the theory of the family being of a
monophyletic origin. The presence of Middle Ordovician species which
are more highly developed than the previously oldest known species
from the Uppermost Ashgillian and Llandovery, and the widespread
occurrence of semidenticulation in the Strophomenidae, might, how-
ever, indicate that the Stropheodontidae are polyphyletic.

Owing to the lack of material of the younger (Devonian) species,
the author is unable to determine which lineages of the family Stro-
pheodontidae are polyphyletic. After having studied the material
described in this paper, it seems fairly evident that the majority of
the genera included in the family (as defined by WILLIAMS 1953)
belong to a genetically homogenous group. Some minor groups may
prove to be homeomorphic real strophomenids.

CARDINAL PROCESSES

The cardinal processes of the Strophomenida have been exten-
sively used for classification of the group (cf. WILLIAMS 1953, pp.
6—10). The Plectambonitacea have simple (Plectambonitidae and
Taffinidae) or complicated, trifid cardinal processes (Leptestidae) or
none at all. The Strophomenacea and Christianidae generally have
bifid cardinal processes. Some Leptestids (i. a. *Leptelloidea*(?) *musca*
ÖPIK) also have this structure.

The simple cardinal process of the Taffinidae and Plectamboni-
tidae does not show any special features, but in some Leptestids the
cardinal process is perforated by a dorsal foramen (cf. text figs.
21, 23), and it is ancylosed to a pair of chilidal plates, so that it
appears to be trifid. The dorsal foramen is discussed below (p. 51).
In the Christianidae and in *Oepikina* the bifid cardinal processes have
developed from this trifid structure. This is proved by the gradual
transition between the two types found in *Christiania oblonga,* and
by the rudimentary median cardinal process and dorsal foramen
found in *Oepikina.* It is not yet clear whether the bifid cardinal pro-
cesses developed from the chilidal plates themselves, or from small
denticulations on them.

In some Strophomenidae (*Rafinesquina* a.o.) one finds another
type of cardinal processes which cannot have been developed directly
from that of the Leptestidae. It consists of a pair of long, thin,
subparallel ridges strengthened by secondary tissue. The author
believes that this type was developed as septa on both sides of the dor-
sal groove, (cf. text fig. 7). The presence of a dorsal groove in several
larval valves of Strophomenids (pl. 7 fig. 5) gives good support of this
theory. However, there is at present not enough proof of the theory
to justify its use as a basis for the classification of the Strophomenida.
It is worth mentioning that the oldest true Strophomenids (except
Oepikina), *Rafinesquina* (?) *llandeiloensis* and *R.* (?) *maccallumi* REED,
belong to this group, with long, plate-like cardinal processes. A conti-
nuous line of development seems to lead from these species to *Kjaerina,*
Hedstroemina and to the earliest Stropheodontids.

The diductor muscles are attached to the cardinal processes. Their
effectiveness is increased if the cardinal processes are high, and incli-
ned posteriorly (cf. p. 42). One therefore often finds species with
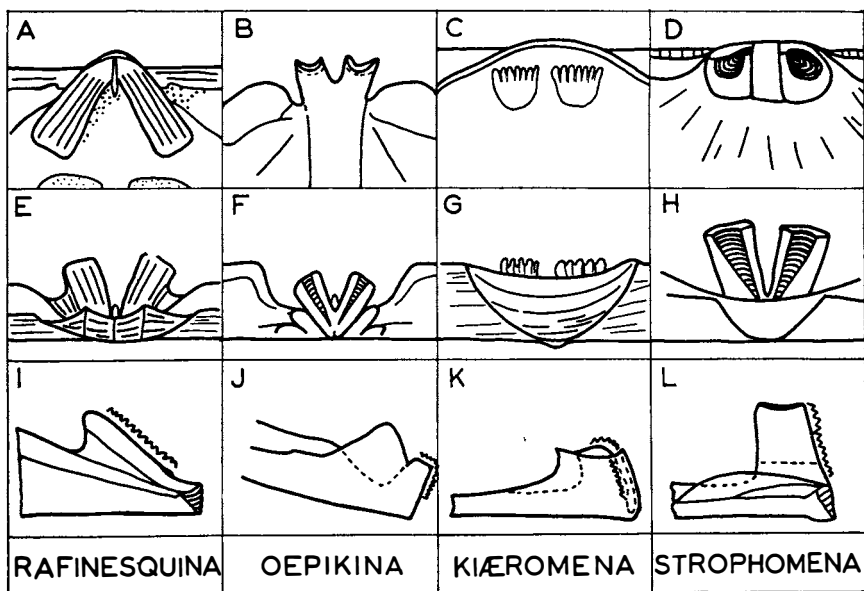
Fig. 6. Diagramatic figures of the cardinal processes in some Strophomenid genera. Figs. *A*, *B*, *C*, *D* are seen from above, *E*, *F*, *G*, *H* from the anterior side of the specimens, and *I*, *J*, *K*, *L* from the side. *A*, *E*, *I* are from *Rafinesquina alternata*, from the Maysvillian, at Cincinnati, Ohio, U. S. A. *B*, *F*, *J* are from *Oepikina dorsata* (BEKKER) from zone C2 in Esthonia. *C*, *G*, *K* are from *Kiaeromena kjerulfi* from zone 4bβ in the Oslo—Asker district, Norway. *D*, *H*, *L*. are based mainly on *Strophomena steinari* sp. n. from the Coelosphaeridium beds in the Ringsaker district, Norway. The actual muscle attachment is indicated by a zig-zag line.

high cardinal processes, curved posteriorly, and with the muscle attachments on the posterior side (cf. text fig. 6 B, F, J.). This feature is generally connected with the development of «forked» cardinal processes. Since the muscle was bent over the top of the processes, lateral ridges were necessary to keep the muscle in position, so that it should not slip off. Seen from above, these lateral ridges give the cardinal processes a forked appearance (text fig. 6 B). Seen from the notothyrium (text fig. 6 F), the lateral plates converge downwards. When the cardinal processes are built in this way, it is only a mechanical adjustment of small systematic value, as it can be found in several, probably unrelated groups (*Oepikina, Strophomena, Kjerulfina*, and the Stropheodontids).
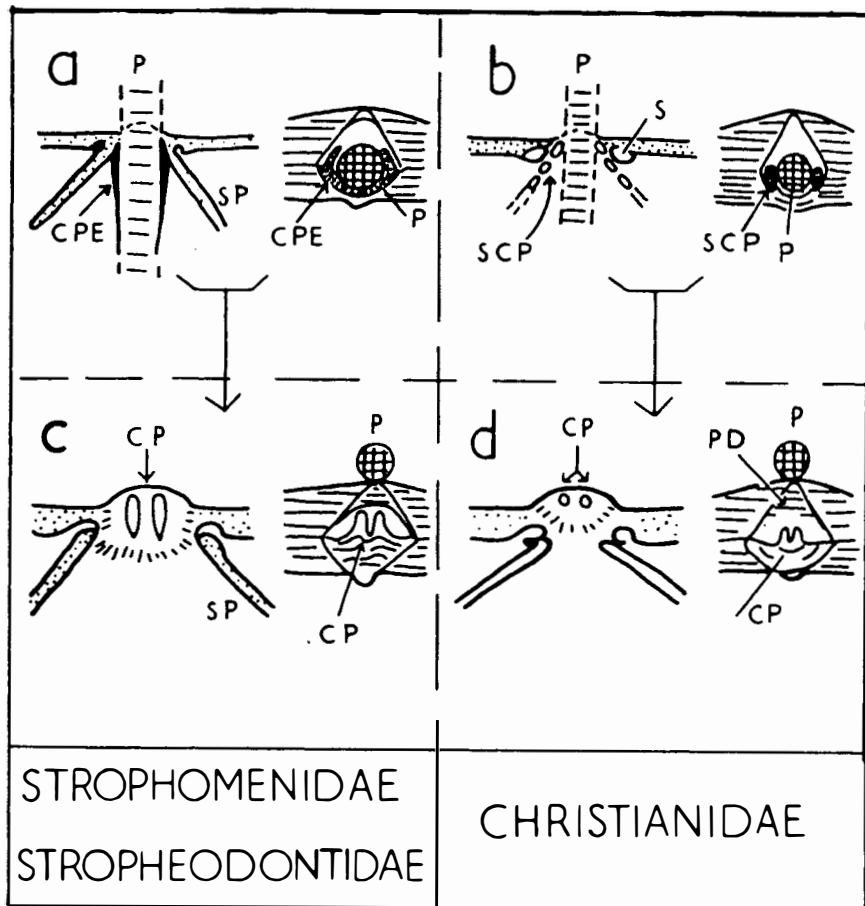
Fig. 7. The development of the cardinal processes. A—B. Larval stages. C—D. Adult forms. (It is possible that also the CPE developed from the socket plates, and the difference between the two types is smaller than supposed).

Abbreviations: CP = cardinal processes, CPE = Larval cardinal processes, formed along the sides of the pedicle. P = Pedicle, PD = Pseudodeltidium, S = Sockets, SP = Socket plates, SCP = Nodes on the socket plates, later developed into the cardinal processes.

In *Rafinesquina* (text fig. 6 A, E, I) the muscle attachment surface is inclined at 30—45°, and is broad and finely longitudinally striated. Because of the very low a/a' balance (1) (see below, p. 43) in this genus, the muscle attachments had to be large.

In *Kiaeromena*, and probably also in *Leptaena*, the muscle attachment surface was steeply inclined, and, instead of being kept in place by lateral ridges, the muscles were secured by a number of deep furrows which widened out towards the bottom (text figs. 6 C, G, K, pl. 14 fig. 9).

THE VASCULAR SYSTEM

Several authors have described vascular systems both of recent and fossil brachiopods. In spite of this, little systematic work has been done on this subject, although many authors have stressed the importance of the vascular system for the taxonomy. This is partly due to the incomplete knowledge of the vascular system in most fossil brachiopods. The vascular system is only found in gerontic specimens, and even in most of these the impressions of the vascula are incomplete. The individual and interspecific variations of the vascular systems have not been studied either.

Because of these difficulties, our knowledge of the vascular systems of the brachiopods and their taxonomic importance is still very limited. The author will therefore not attempt to make important changes in the present systematics of the brachiopods on the basis of the vascular system alone.

The vascular systems of recent brachiopods have been studied by i.a. DESLONGCHAMPS 1864, LACAZE-DUTHIERES 1864, and DAVIDSON 1886—88. However, none of these papers are primarily devoted to the study of the vascular system. TERMIER & TERMIER (1942), and especially ÖPIK (1934) have studied the vascular systems of fossil brachiopods, and there are a large number of figures and notes in SCHUCHERT & COOPER (1931), HALL & CLARKE (1892), DAVIDSON (1851—1886), REED (1917) and in several other papers. In addition to the author's own observations, which mainly are based on British and Scandinavian material, the above mentioned papers are the main sources for the following notes.

The terminology for the vascular system of recent brachiopods is due to DESLONGCHAMPS (1864). It is based on the Terebratulids which have two pairs of vascula in each valve. The marginal vascula which generally are the largest, are the lateral venous sinuses, and the central ones are the median venous sinuses. All vascula emanate from
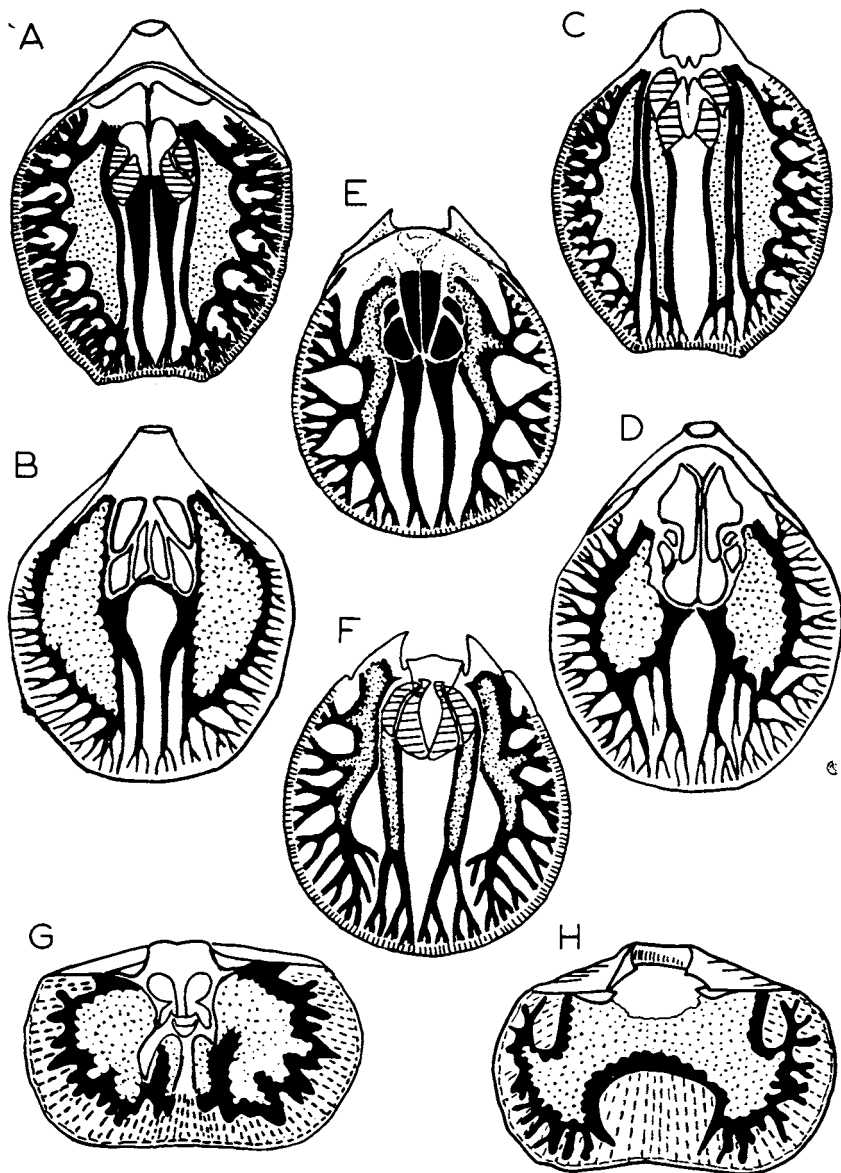
Fig. 8. *The vascular system of some recent brachiopods.* A—B. *Waldheimia fla-
vescens.* dorsal and ventral view. From DAVIDSON 1886—1888, pl. 7, figs. 15—16.
B.D. *Terebratulina caputserpentis*, dorsal and ventral view. From DAVIDSON
1886—1888, pl. 4, figs. 8—9. E—F. *Waldheimia cranium*, dorsal and ventral
view. From DAVIDSON 1886—1888, pl. 13, figs. 1—2. G—H. *Megerlia truncata*,
dorsal and ventral wiew. From DAVIDSON 1886—1888, pl. 19, figs. 18—19.
Ovaria are dotted, vascula black in all figures.

a point near the apex of the shell, and terminate in a large number of minor branches all along the margin of the shell.

ÖPIK's terminology for the vascular system of the fossil brachiopods is mainly based on the possibly primitive vascular system of the Clitambonitids. In this group, there are three pairs of vascula which are different in the dorsal and ventral valves. (In all described recent brachiopods, the vascular system is identical in both valves). ÖPIK's three pairs are termed vascula media, vascula myaria (spondylaria), vascula cruralia (dentalia); the terms in brackets refer to the ventral valve.

The vascula media seem to correspond to the median venous sinuses, and the lateral venous sinuses to the vascula myaria or the vascula cruralia, or both.

According to ÖPIK (1933, 1934) the vascular system of the most primitive articulated brachiopods was polypalmate, and consisted of a comparatively large number of radiating vascula, corresponding to the ribs of the external sculpture. The number of main vascula was then reduced to six, that is three pairs, and later even to two (one pair). In the latter case, the terminal vascular branches are formed either as an arch (vascula arcurata) parallel to the margin of the valve, or by bifurcation of the vascula (vascula bifurcata). The importance of this feature has not been studied in detail, and transitional forms are quite usual. Vascula arcurata are common in connection with ovarian impressions while vascula bifurcata generally are found in specimens devoid of such.

There is good reason for revising the terminology as regards the number of main vascula. The author therefore propose to restrict the term polypalmate to forms with more than six radiating main vascula, and to term the forms with reduced vascular system, hexapalmate, tetrapalmate and dipalmate respectively. Using this terminology, most terebratulids have a tetrapalmate system, while some, like *Krausina rubra* have a dipalmate one. Compared to ÖPIKs terminology, his polypalmate comprises polypalmate and hexapalmate of the present terminology, and his oligopalmate tetra- and dipalmate.

The so-called ovarian impressions are very common. In most recent brachiopods the ovaria are found inside the main vascula, and, as far as the author has seen, they seldom leave impressions in the calcareous valve.

In some cases there is a possibility of structures described as ovarian impressions really being the impressions of other organs. However, since we have no proof of the existence of such organs, all the impressions of this kind are regarded as being ovarian in this paper.

The ovaria are always intimately connected with the vascula. The ovarian impressions found are generally bounded by a groove, which is confluent with the vascular grooves. The development of the ovaria is different in the various groups of brachiopods, and might even be different within the same group (see the vascular system of the Orthacea).

ÖPIK (1934) believed that the ovaria of the ventral valve of the Orthacea (and probably similar ovarian impressions in other groups) were transformed vascula spondylaria. After having studied the development of the ovaria of the Orthacea and other fossil brachiopods, the author does not agree with him on this point. The ovaria are probably differentiated from the vascula, and are always found within them. The ovarian impressions are not, like the muscle impressions, devoid of pseudopuncta, if such are present in the valve (as for instance in *Leptaena*).

The ovarian impressions are generally ovoid or elliptical, or circular. Sometimes they are of an irregular shape, with ridges parallel to the sculpture of the exterior of the valve. Some of them have a complicated net of vascula inside. They are often bounded by an elevated ridge with a vascular groove on the outside.

Vascula terminalia: In recent brachiopods, the vascula terminalia ends at the base of the cilia. (Text fig. 9, L, M.). Generally there is a large number of cilia, and each of them has a special vascular branch. The ciliar grooves are smooth and uniform. Now and again the basal ends are swollen, corresponding to the shape of the base of the cilia.

In the fossil brachiopods we are dealing with, there are several types of cilia, or, to be correct, ciliar grooves. In the Clitambonacea the ciliar grooves are simple, like those of the Terebratulids, except that they are stronger. Each groove seems to correspond to a rib in the external sculpture. The ciliar fringe, the part of the inner margin of the valve where the ciliar grooves replace the vascula terminalis, is rather broad in most Clitambonitids, and a gradual transition is found from the vascular grooves to those of the cilia.

At least most of the Orthacea have fewer ciliar grooves than ribs in the external sculpture. In some cases (such as *Orthis kuckersianus*
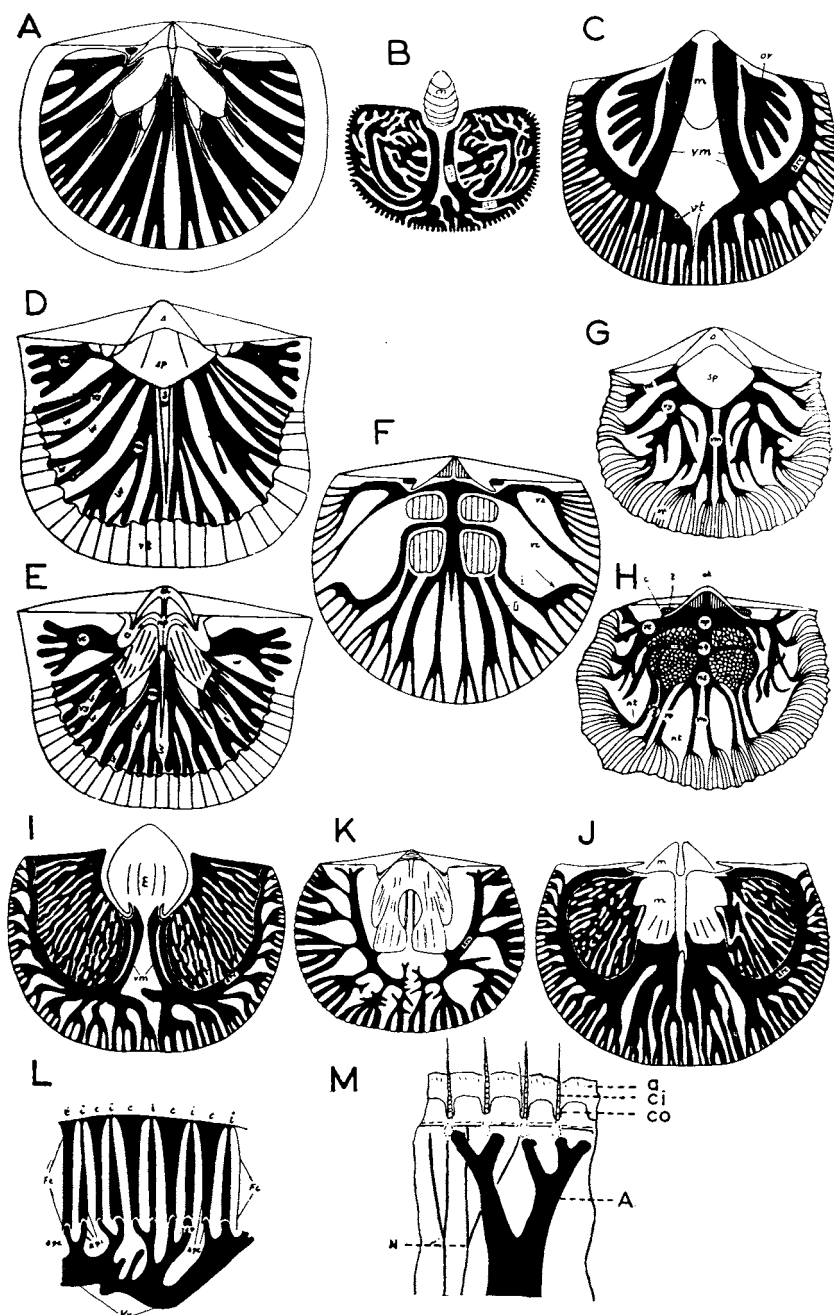
Fig. 9.

cf. ÖPIK 1934, textfig. 54) the cilia were probably differentiated into two types, placed alternatively around the margin, each of them corresponding to 1—2 vascular branches. These cilia were probably much more highly specialized than those of the recent brachiopods.

In the Strophomenids there are usually no vascula terminalia close to the margin. Generally the external sculpture also continues for a short distance on the inner surface, until it is concealed by the secondary tissue. Possibly the grooves formed by the ribs were the ciliar ones. In some species, *Eoplectodonta acuminata*, *Grorudia?* *glabrata* and *Ptychoglyptus valdari*, very strong and deep ciliar grooves are found along the margin, impressed not only in the primary valve, but also in the secondary tissue. In *Ptychoglyptus valdari* every ciliar groove corresponds to one of the terminal branches of the vascular system. In *Grorudia? glabrata* only every other or every third ciliar groove corresponds to a vascular branch. (Pl. I, figs. 1, 2, 12, Pl. III, fig. 9.) In *Eoplectodonta acuminata* the vascula terminalia are not developed. In all three species the ciliar grooves seem to correspond to the major ribs of the external sculpture.

LAMONT (1934) believed that the external sculpture, which reflected the dimensions of the cilia, also showed the grain-size of the sediment in which the specimen lived.

Fig. 9. *The vascular system of some Orthids and Clitambonitids, and the terminal vascula.* A. *Finkelnburgia* sp. dorsal valve. From ÖPIK 1934, textfig. 23. B. *Paurorthis parva* (PANDER), ventral valve. From ÖPIK 1939, textfig. 2. C. *Billingsella lindströmi* (LINNARSON) ventral valve from ÖPIK 1934, textfig. 15. D—E. *Estlandia marginata*, dorsal and ventral valve. From ÖPIK 1934, textfig. 14. F. *Orthis calligramma*, dorsal valve. From ÖPIK 1934, textfig. 16. G—H. *Clitambonites schmidti epigonus*, dorsal and ventral valve. From ÖPIK 1934, textfig. 8. I—J. *Dolerorthis osiliensis* dorsal and ventral valve. From ÖPIK 1934, textfigs. 17—18. K. *Dinorthis* sp. ventral valve. From ÖPIK 1934, textfig. 21. L. *Cyrtonotella kukersianus* terminal vascula. From ÖPIK 1934, textfig. 54. M. *Terebratulina caputserpentis*. Terminal vascula. From DESLONGCHAMPS 1864, pl. 1, fig. 5.

Abbreviations: A =: Arteries. a = growing edge of shell. Arc, ac = vascula arcurata. c = costae. Ci = cilia. Co =: muscular attachment of the mantle. iv = intervascular septa. i = intercostal spaces. Fe = marginal vasculae (?). M.m. =: Muscular impressions. N = veins. ov. = Ovarian (?) impressions, vd = vascula dentalia. vm = vascula media. vt,Vv = vascula terminalia. vy =: vascula myaria and vascula spondylaria. vc = vascula cruralia. apc = costal apophyses. api = intercostal apophyses.

However, we must remember that the size and number of cilia do not always correspond to the coarseness of the external sculpture. The Orthids have already been mentioned, and *Eoplectodonta acuminata* also had fine sculpture, but coarse cilia.

<div align="center">

THE DEVELOPMENT OF

VASCULAR SYSTEM IN THE BRACHIOPODA

</div>

Inarticulata. Several different vascular systems are found among the inarticulate brachiopods. A detailed study of this subject is outside the scope of this paper. A point worth mentioning, however, is the marked difference between *Lingula* and *Obolus*. WALCOTT (1912, p. 311) believed the vascular systems to be similar. This assumption was based on the erroneous interpretation of the species *O. appolonis* given by MICKWITZ. Figures of other, less derived species of *Obolus* (i. a. *O. (Broeggeria) salteri* cf. WALCOTT 1912, pl. 13 fig. 1 m) show that this genus has 4 vascula in the valve, and not 2 badly defined arches like *Lingula*. The difference between *Obolus* and the articulate brachiopods only lies in details as to the branching, while the vascular system of *Lingula* is fundamentally different. This brings to mind PERCIVAL's assumption (1944), that *Lingula* does not belong to the brachiopoda proper.

Clitambonitacea. (Textfig. 9). The complicated vascular systems of the Clitambonitacea have been described in detail by ÖPIK (1934). He points out the resemblance to *Finkelnburgia*, which he believes to be an ancestor of the group. The vascula which were found were hexapalmate to polypalmate. No differentiated ovarian impressions could be seen, and they are probably placed in the broad irregular vascula. In the Estlandidae (textfig. 9 D—E) the vascula cruralia do not terminate into ciliar grooves, and this may indicate that they were specialized into ovaria. The fact that the vascula cruralia are so strongly developed in contrast to the other vascula in *Rauna* also seems to indicate that the vascula cruralia had a function which was different from that of the other vascula.

Orthacea. (Textfigs. 9—10). In the Orthacea the vascular systems vary considerably. In the fully developed normal type, the ventral system consists of two large ovoid ovarian impressions, surrounded by a fringe of terminal vascula. Probably there are no differentiated vascula media at all. In some cases the median branches of the

terminal vascula are longer than the others. That, however, is probably due to the shape of the ovaria, and not to the presence of separate vascula. In the dorsal valve there are usually three pairs of vascula. In some species only one or two of them are developed. Ovarian impressions are found in most younger species, two lateral ones, placed near the hinge-line and a third, which is more rarely developed, between the forking branches of the vascula media.

The development of the dorsal ovaria through fusion of the vascula myaria and vascula cruralia has been described in detail by ÖPIK 1934. A number of beautifully preserved specimens were used to illustrate this (l.c. pl. 48, textfig. 55). It has therefore definitely been proved that the lateral dorsal ovaria were developed in the vascular arch formed by the fusion of the two vascula. It is probable that the third, posteromedian ovarium was developed in a similar way, by the fusion of the median branches of the vascula media. There is, however, no definite proof for this theory.

The distribution of the various types of vascular systems among the Orthacea will require much further study. Species with either two or three dorsal ovaria or none at all, are found in closely related groups, and the rather limited material dealt with in this paper does not indicate any sexual dimorphism which might explain this feature. Most Orthids seem to have either two ovaria or none at all, and the Dalmanellids generally have three.

The development of the ventral vascula of the Orthacea is quite different from that of the dorsal one. The oldest known species (of *Billingsella* and *Oligomys* (textfig. 9 C, 10 A)) have vascular arches. In some younger possibly more primitive species of *Nicolella* (cf. DAVIDSON 1871, pl. 36 fig. 14) and *Orthis* s.s., there is a different system, consisting of a large number of radiating vascula which do not branch until near the margin. Each of the radiating vascula in this polypalmate system corresponds to one of the ribs in the external sculpture. Some of the species which have this type of ventral vascular system, might also have a similar, polypalmate dorsal system. However, the material does not give any definite proof of this, since it often is impossible to discriminate between the vascula and the sculpture showing on the internal surface of the valves in the material available.

Through intermediate forms, found i.a. in *Dolerorthis psygma* LAMONT & GILBERT and species of *Glyptorthis*, this «*Nicolella*»-type
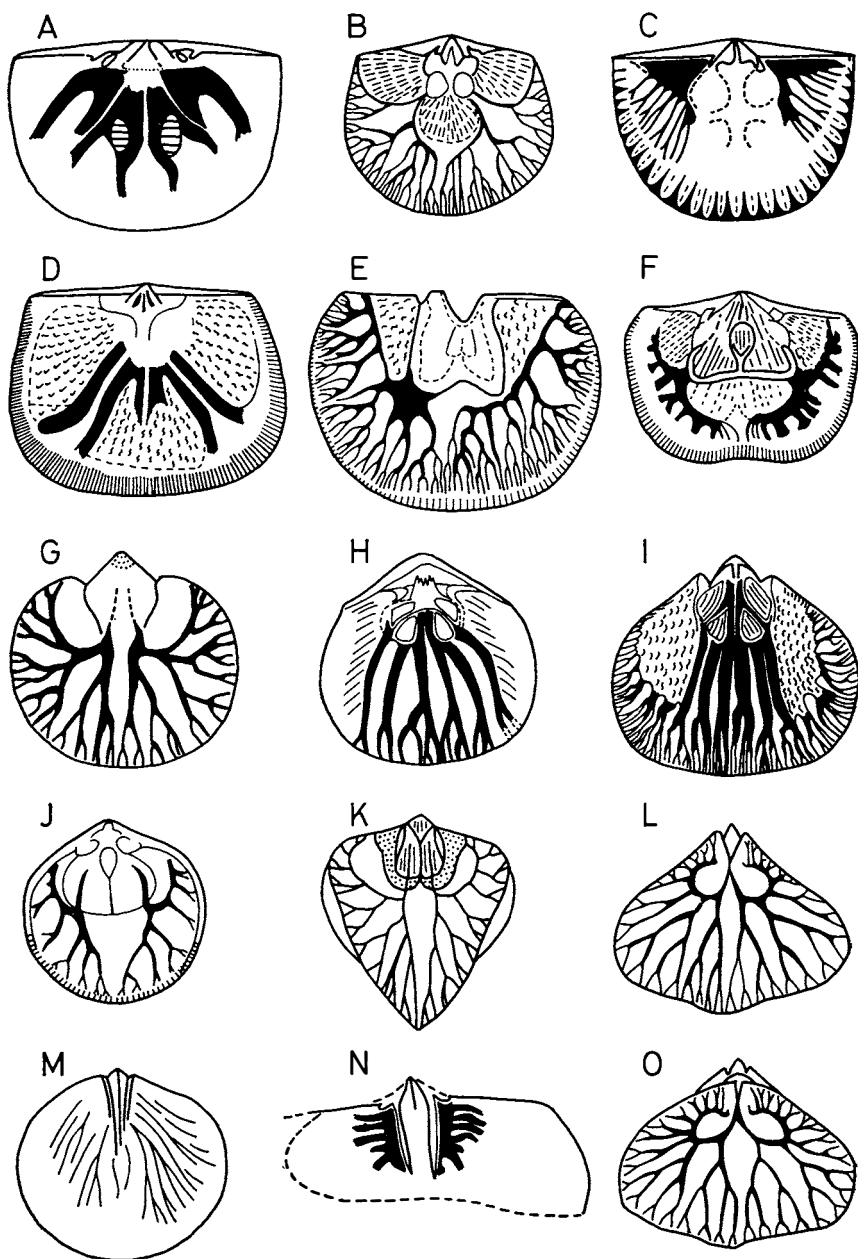
Fig. 10.

is united with the ordinary one. These intermediate species have comparatively small radially striated ovarian impressions around the ventral muscle impressions, fringed with long terminal vascula. The ovaria in the dorsal and ventral valves of the Orthacea have therefore developed in different ways.

The development of the ventral vascular system seems to have been «slower» than that of the dorsal one. In a specimen of *Orthis* cf. *calligramma* from the Baltic Lower Ordovician, with a dorsal system similar to that figured by ÖPIK (1934, textfig. 16), with the vascula myaria and vascula cruralia on the point of fusing, the ventral system is still on the «*Nicolella* stage». In a *Glyptorthis* species from the zone 4bα, in the Oslo Region, the ventral system is in the intermediate stage, with small, indistinct ovaria, and long terminal vascula. The dorsal system of the same specimens are completely developed with three ovaria. It is also worth mentioning that in *Dolerorthis osiliensis*, the ventral ovaria cover most of the internal surface of the valve even in young specimens, whereas the relative size of the dorsal ovaria increases rapidly as the specimens grow bigger. The specimen figured by ÖPIK (1934, textfig. 18) represents the maximal stage of development in a highly gerontic specimen. In ordinary ones, the ventral ovaria are considerably larger than the dorsal ones.

Fig. 10. *The vascular system of some Orthids, Atrypids, Rhynchonellids and Porambonitids.* A. *Oligomys exporrecta*, Middle Cambrian, Sweden. From WALCOTT 1912, pl. 88, fig. 1k. Dorsal Valve. B. *Orthostrophia strophomenoides*, dorsal valve. From HALL & CLARKE 1892 pl. 6, fig. 34. C. *Hesperorthis tricenaria* (CONR.) dorsal valve. From HALL & CLARKE 1892, pl. 5, fig. 14. D. *«Dalmanella» rankini* REED, dorsal valve. From REED 1917, pl. 9, fig. 32. E. *Retrorsistria retrorsa*, ventral valve. From HALL & CLARKE 1892, pl. 5A, fig. 14. F. *Plaesiomys subquadrata* ventral valve. From HALL & CLARKE 1892, pl. 5A, fig. 17. G. *Levenea subcarinata.* Ventral valve. From HALL & CLARKE 1892, pl. 5C, fig. 32. H. *Schizophoria impressa*, dorsal valve. From HALL & CLARKE 1892, pl. 6A, fig. 27. I. *Schizophoria striatula*, dorsal valve. From DAVIDSON 1853, pl. 7, fig. 133. J. *Atrypa reticularis*, ventral valve. From DAVIDSON 1853, pl. 7, fig. 90. K. *«Rhynchonella» acuminata* MARTIN, ventral valve. From DAVIDSON 1853, textfig. 34. L, O. *Camarophoria multiplicata*, dorsal and ventral valve. From DAVIDSON 1853, textfig. 35—36. M. *Porambonites riberoi* SHARPE. From DAVIDSON 1853, pl. 7, fig. 125. N. *Porambonites* sp. from zone 4bγ, Billingstad, Asker District. The ovarian (?) impressions are black in fig. C, and dotted in figs. B, D. E. F, I and K.

Compared to the Clitambonitids, the Orthid vascular systems represent a longer range in development, from really polypalmate vascula which directly reflect the external sculpture, to highly differentiated types with five ovaria of two different types. As mentioned above, the Clitambonitids did not develop ovaria which impressed themselves into the calcareous tissue of the valves. The Orthids differ both from the Clitambonitids and the recent Terebratulids (textfig. 8) and Rhynchonellids in having different numbers of vascula in the dorsal and ventral valves.

Strophomenida. (Textfigs. 11, 12). In the Strophomenacea there are also several types of vascular systems. In the Strophomenacea, the vascular system is fairly uniform, and quite resembles that of the highly developed orthids, as it has two large ovaria in the ventral valve, and two slightly smaller ones, and vascula media in the dorsal one. The size and shape of the ovaria vary considerably. Generally large flat-valved species have comparatively small ovaria, and consequently have long terminal branches. In geniculated species, such as *Leptaena* (textfig. 12D—G), the ovaria cover the whole disc, and terminal vascula are confined to the geniculated fringe. In several species the median branches of the vascular arches are not impressed, so that it looks as if there only was one large ovarium. In gerontic specimens there are always median branches.

It is difficult to trace a development in the vascular system of the Strophomenids. Even the oldest ones (*Oslomena osloensis*, *Oepikina* of the *dorsata* group) seem to have large ovaria, and only short terminal branches. The oldest Strophomenids generally have thin shells, and the vascular systems are not known in detail. An exception from the rule is *Kjerulfina* which has very strong median vascula, and where neither ovaria nor other vascula have left any impressions in case they did exist. In fact, apart from having a pedicule foramen and simple teeth, the ventral interior of *Kjerulfina* very much resembles that in *Paleostrophomena*.

As far as can be judged from the material dealt with in this paper, there is no difference between the vascular system of the Strophomenidae, and that of the Stropheodontidae. The younger families have not been studied. The family Christianidae, however, has quite a different vascular system, with three pairs of vascula. Two of them go from the ventral muscle impressions to the posterior margin and

are parallel to a thin intervascular septum which lies between them. They give off a number of branches near the margin. The third pair has with certainty only been seen in a few, gerontic specimens. It is short and broad, and gives off a large number of branches towards the sides of the valve. Because of the width of these vascula, they might be believed to contain ovaria, but there is no proof of this. The width might easily be due to the large number of lateral branches. This type of vascular system is similar to that found in many Plectambonitids, and the fact that it is found in the Christianidae, is one of the arguments for referring that family to the Plectambonitacea. The dorsal vascular system of *Christiania* is unknown.

In contrast to the Strophomenacea, the Plectambonitacea show considerable variation as to types of vascular systems. In the Plectambonitacea, too, the ventral vascular systems are the best known. The material of the dorsal vascula is much smaller than that of the ventral ones. (Text fig. 11.)

A common type is that found in *Paleostrophomena*, *Grorudia*, *Ptychoglyptus* and possibly *Inversella* and other genera. In this, the ventral vascula consist of two ovarial impressions placed near the hinge-line, from which two bundles of vacula spread to all the margins of the valve. The vascula are often fairly broad, even if their proximal ends always are thin. The ovarian impressions can scarcely be distinguished from the inner surface of the valve and from the vascula. They are also considerably larger in more highly developed species of *Paleostrophomena* than in the probably more primitive *Grorudia*.

In most other Plectambonitids, there are three pairs of vascula. However, it is a characteristic feature that one pair is dominant, the other, smaller ones, are easily overlooked since they are only found in gerontic specimens. One very rarely finds three pairs of vascula of about the same strength as for instance in *Diambonia anatoli* (textfig. 11R). In *Sowerbyella* and a number of related genera, and in *Leptelloidea*, the vascula spondylaria are strongly developed (textfig. 11H). There are only a few specimens where the median vascula appear as two thin strings along the median line of the specimens. The vascula dentalia are developed as more or less triangular ovarian impressions with a fringe of thin vascular branches (textfigs. 11I).

In *Leptelloidea leptelloides*, the vascula spondylaria are weakly developed and one can only see the ovaria with their fringe of vascula
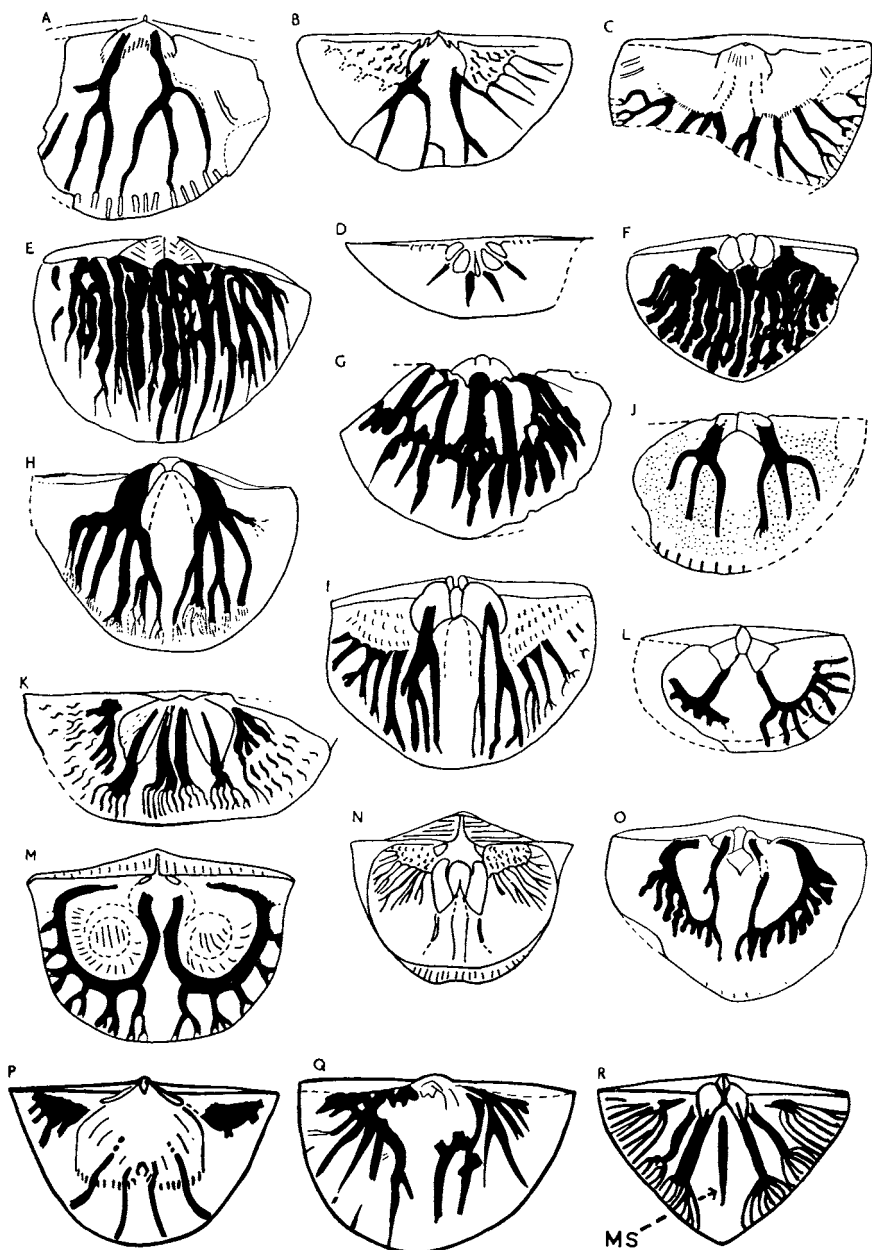
Fig. 11.

(judging from ÖPIK 1930, textfig. 14). *Leptestia* apparently had vascular arches and it is unknown whether they developed from the vascular system found in the other Plentambonitacea.

In *Sampo* and *Leptellina* the vascula dentalia are strongly developed, and the other vascula are considerably less so. In *Leptellina* they form arches, reaching almost to the median line of the valve. The vascula are broad and irregular in shape, and this indicates that they contained the ovaria. The vascula spondylaria, which only are found in gerontic specimens, are very thin, and in some cases they seem to be united with the vascula dentalia. There is no sign of the

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Fig. 11. *Vascular system of the Plectambonitacea.* A. *Grorudia* (?) *glabrata* sp. n. ventral valve. Zone 4bα, Oslo district. cf. pl. 1 fig. 12. B. *Paleostrophomena concava* SCHMIDT, ventral valve. Kukruse Stage, Esthonia. From ÖPIK 1933, pl. 2, fig. 2. C. *Ptychoglyptus valdari* sp. n. ventral valve. Zone 4bα, Billingstad, Asker district. cf. pl. 1, fig. 1. D. *Grorudia grorudi* sp. n. dorsal valve. Zone 4aβ, Tåsen, Oslo district, cf. pl. 1, fig. 10. E—F *Sampo indentata*, two ventral valves. F. is tilted to show the marginal vasculae. Zone 4bγ, Hvalstad, Asker district. cf. pl. 4, fig. 8. G. *Sampo indentata* ventral valve with less strongly developed vascular impressions. Zone 4bγ (lowest part), Hvalstad, Asker district. H. *Sowerbyella millinensis* JONES, ventral valve, SM, A40662, Gas Works, Llandovery, Haverfordwest, Pembrokshire. I. *Sowerbyella ringsakerensis*. ventral valve. From lower part of the Coelosphaeridium zone, Ringsaker district. (cf. pl. 6, fig. 4) J. *Sowerbyella sericea askerensis* (SOW.) ventral valve, zone 4bγ, Hvalstad, Asker district. K. *Sowerbyella* cf. *rhombica conspicua* (REED) dorsal valve. SM. A40671. Upper Bala, Gelli Grin, Bala, Merionetshire. L. *Leptelloidea llandelioensis* (DAV) ventral valve, Balclatchie Group, Ardmillan, Girvan district, Scotland. (From REED 1917, pl. 13, fig. 34). M. *Leptestia jukesi*. Ventral valve. (From HALL & CLARKE 1892, textfigs. 19—20). N. *Leptelloidea leptelloides* (BEKKER). Kukruse Stage, Esthonia, Ventral valve. From ÖPIK 1930, textfig. 14. O. *Sampo* (L.) *oepiki* ventral valve, PMO 57733, zone 4bα—β, Hadeland district. (cf. pl. 4, fig. 6). P. *Sampo indentata* sp. n. dorsal valve, zone 4bγ, Hvalstad, Asker district. (cf. pl. 2, fig. 15). Q. *Leptelloidea* sp. ventral valve, SM, A40669a. Basal Ashgillian, Pen-y-garnedd, 4 miles S.E. of Llanfyllin, Montgomeryshire. R. *Diambonia anatoli* sp. n. ventral valve. Zone 4bα, Nesøya, Asker district. (MS = median septum).

The figures are drawn from casts, except B, M and N which are from valves, and D, K and P which are drawn from latex impressions of casts.

The magnification is variable. Ovarian (?) impressions are striated in figs. B, I and N, and black in fig. P.

Numbers starting with SM, A... indicate that the specimen belong to Sedgwick Museum, Cambridge.
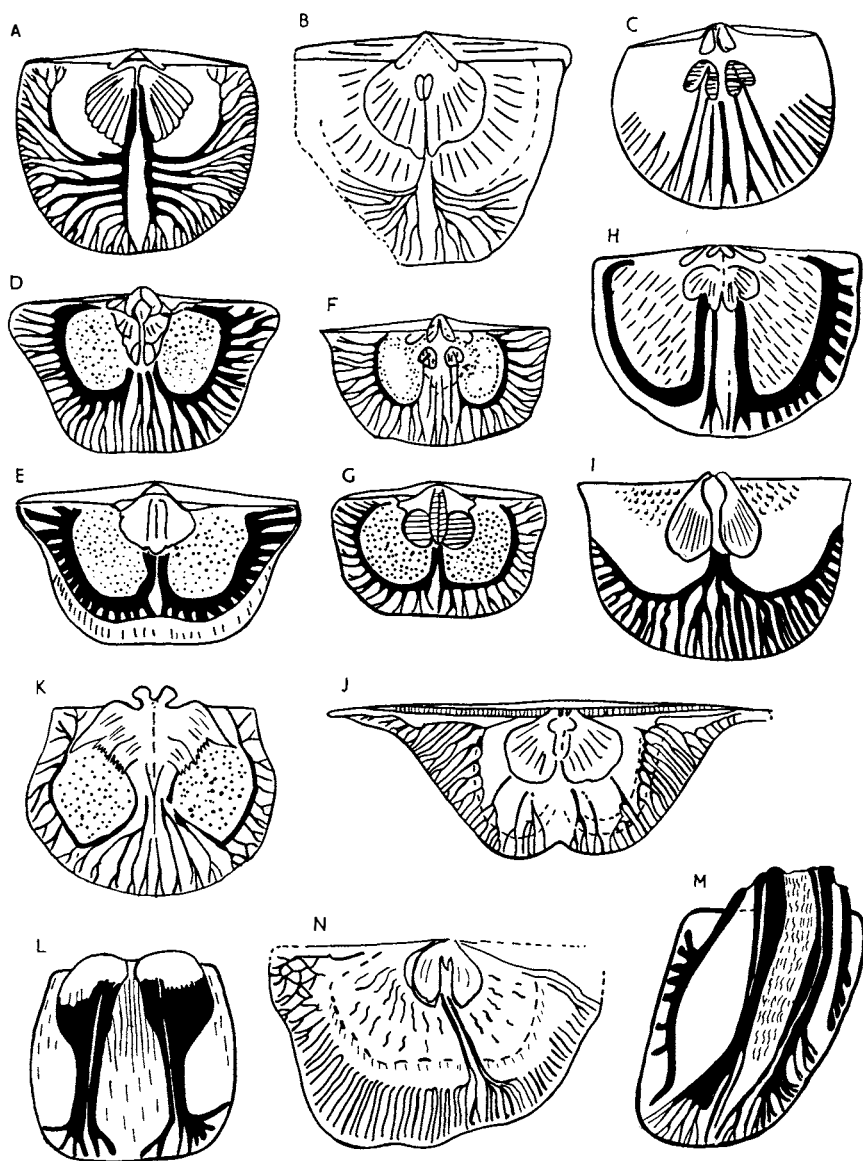
Fig. 12.

vascula media. In *Sampo*, the greater part of the interior of the ventral valve is filled with broad anastomosing vascula. Because of the large number of branches and the numerous anastomoses, it is difficult to see which vascula are developed. In *S. indentata*, the vascula dentalia seem to be dominant, but there are also vascula spondylaria, although they are not as strong as the vascula dentalia. The anastomoses seem to start as a concentric ring about half-way to the margin (textfig. 11 C). In younger species (*S. hiiuensis* and *S. ruralis*) the vascula spondylaria are strongly developed. The majority of the branches of these species also appear to belong to vascula dentalia. Because of the complicated net of vascula, one cannot be absolutely certain that there were no vascula media.

In the dorsal valve of the Plectambonitacea, the variations in the vascular system are not as great as in the ventral. Generally all three pairs of vascula are present. In some species the vascula cruralia have small triangular ovaria, as for instance *Sampo indentata*. In this species there is a marked difference between the broad, frequently branching and anastomosing vascula in the ventral valve, and the thin, unbranched vascula in the dorsal. It is also worth noting that the vascula media and the vascula myaria continue through the branchial lamellae in narrow furrows. In other species where there are two branchial lamellae, as for instance in *Sowerbyella*, the vascula media are placed between the lamellae, and the vascula myaria cut

Fig. 12. *Vascular system of the Strophomenacea*. A. *Strophomena expansa*, ventral valve. From DAVIDSON 1853, pl. 8, fig. 162. B. *Strophomena filitexta*, ventral valve. From HALL & CLARKE 1892, pl. 9A, fig. 15, C. *Rafinesquina alternata* (?) dorsal valve. From DAVIDSON 1853, pl. 8, fig. 160. D—E. *Leptaena analoga* PHILLIPS, ventral and dorsal valves. From DAVIDSON 1861, pl. 28, fig. 10, 9. F—G. *Leptaena depressa* SOW. ventral and dorsal valves. From DAVIDSON 1853, pl. 8, figs. 171, 170. H. *Strophomena filitexta* HALL, dorsal valve. From HALL & CLARKE 1892, pl. 9A, fig. 10. I. *Douvillina inaequistriata*, ventral valve. from HALL & CLARKE 1892, pl. 14, fig. 13. J. *Strophonelloides caelata*, dorsal valve. From HALL & CLARKE 1892, pl. 15A, fig. 10. K. *Oepikina dorsata* (BEKKER). Dorsal valve. Kukruse Stage. Esthonia. From ÖPIK 1930, textfig. 22. L. *Christiania holtedahli* sp. n. ventral valve, zone 4bα, Billingstad, Asker district. M. *Christiania* sp., ventral valve Geol. Surv. 10913, Ashgillian Cynwyd, Wales. N. *Leptaena* sp. ventral valve. From zone 8c, (Wenlock) Malmøya, Oslo district. The figures L. M and N are drawn from casts, the rest from valves. The specimen in fig. M belongs to the Geological Survey and Museum, London.

through them, dividing them into two subequal parts. Even in specimens where the dorsal vascula are not developed, this diagonal groove is found in the branchial lamellae (cf. pl. 3 fig. 4). Also in *Sowerbyella*, ovaria-like areas are formed by the vascula cruralia near the hingeline.

Conclusion: The taxonomic importance of the vascular system has been stressed by several authors. The fact that completely develloped, characteristic vascular systems only are found in a few old adult specimens, reduces the diagnostic value of this feature. In some groups, the vascular system proves to be very useful, as for instance in the Clitambonacea, where the families Estlandidae and Clitambonitidae have different vascular systems. This difference corresponds to a just as important difference in shell-structure and spondylium.

The vascular system of the Orthids is highly variable, and it is probable that further studies will show that it is of considerable taxonomic value. It is, however, outside the scoope of this paper to deal with this in detail.

In the Strophomenacea, the vascula are too uniformly developed to be of much taxonomic importance.

The Plectambonitacea can easily be divided according to the vascular system and the· various groups seem to be identical with systematic units based on other features. The author made extensive use of the ventral vascular system in this group as a taxonomic guide, because this feature seems less variable as to external influences than most features used in the taxonomy of this group. One reason for placing the family Christianidae in the Plectambonitacea is the resemblance as to vascular systems.

The study of the vascular system of the palaeozoic braciopods is still in its early stages, but through further studies and patient collecting it might give a more natural classification than many other features.

<center>THE MUSCULAR SYSTEM</center>

The muscular system of the Strophomenids is known to consist of adductors and diductors. All the muscles were obliquely conical. The small attachments of the adductor muscles are in the ventral valve, and the larger ones in the dorsal valve. The diductors have their
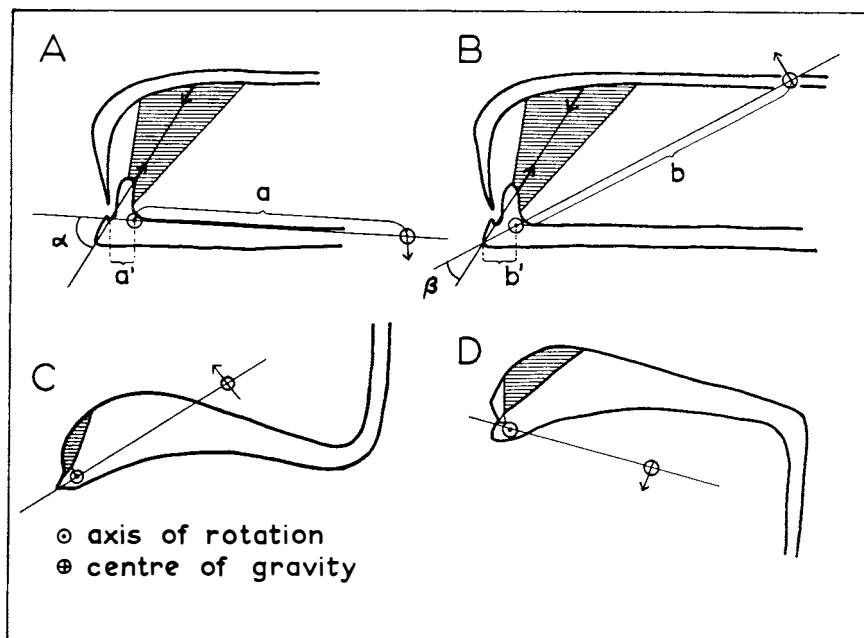
Fig. 13. Illustrating the structure of the muscle system of the Strophomenidae. For explanation, see the text.

small attachments on the cardinal processes, and the larger ones in the ventral valve. In some instances the larger muscle impressions are bilobed, indicating that the muscles were paired. In all other cases there are only two adductors and two diductors.

The mechanism of the adductor muscles is quite simple, and it is not necessary to describe it here. That of the diductors, which work according to the lever principle is more complicated. The force necessary to open the valves of a specimen resting on the ventral one, is:

$$K = \sin. \alpha g \frac{a'}{a} \qquad (1)$$

where K is the force, α the angle between the plane of rotation and the direction of the diductor muscles, and a' is the distance between the axis of rotation and the centre of gravity. a is the projection of the distance between the axis of rotation and the muscle attachments on the cardinal processes. g is the weight of the valve (see textfig. 13).

The corresponding equation for a specimen resting on the dorsal
valve, is

$$K' = \sin. \beta g' \frac{b'}{b} \qquad (2)$$

The effect of the diductor muscles is therefore a function of the
angle a (or β), which should approach 90° to make the muscle effective.
These angles in their turn are dependent on the position of the centre
of gravity of the valves. Since the position of this point will change
as the valve grows, the angles a and β will change correspondingly, if
the muscle impressions are unaltered. A number of species have shown
that the shape and size of the ventral muscle impressions change
during the growth of the individual, and this is obviously a conse-
quence of the mechanisms described here.

The change in the position of the centre of gravity will be espe-
cially prominent in species with geniculated valves. In many of these
the centre of gravty lies outside the valves. Textfig. 13 shows diagrama-
tically the change in shape and position of the ventral, muscle im-
pressions in flat specimens, dorsally geniculated and ventrally geni-
culated ones. It appears that dorsally geniculated specimens will have
longer muscle impressions than those which are ventrally geniculated,
if the valves have the same shape and weight.

The general convexity of the valves also has an influence on the
shape of the muscles. Strongly convex specimens generally have broad,
flabellate muscles, while flat or geniculated ones have more elongate
muscles.

It is interesting to note that there is an intimate connection
between the convexity of the valve, and the muscle attachments.
Generally the convexity of the valves is not regarded as being a fea-
ture of great systematic importance. The author's studies have, how-
ever, led to the conclusion that the umbonal convexity is intimately
connected with the development of the muscles, and must be consi-
dered as a stable feature in most species. The convexity of the central
and marginal parts of the valves seem to be much more variable,
and can not be correlated with internal features.

Furthermore the umbonal part was the first one to be developed
and it seems reasonable that the features found in this region were
less subject to fenotypical variations than the marginal parts of the
valve.

In specimens with strong umbonal convexity, the angle α (or β) is large and the muscle impressions smaller, while in specimens with flatter umbo, the muscles are attached further behind, and the angle α (or β) is smaller (cf. textfig. 13). Generally this results in larger muscle impressions.

Regarding the geniculation, at least some species (or genera) seem to have a great plasticity, and the change in shape of the muscle impressions due to the geniculation (cf. textfig. 13 C-D), are probably only mechanical adjustments which are not of any great systematical significance.

The muscular system of *Oepikina* and related genera is slightly different. Here the dorsal adductor muscle impressions seem to be replaced by septa. No special impressions of the adductor muscles are visible in ordinary specimens. In some especially well preserved interiors from the Kukruse Stage in Esthonia, the muscle impressions appear as dark, semitranslucent spots contrasting against the white, opaque substance of the rest of the valve. In dorsal interiors of this type, there are muscle attachments both in front of the lateral septa (textfig. 28A), and between the median and lateral septa. The latter are the smallest. All impressions are of irregular shape, indicating that the muscles consisted of a bundle of fibres. The edges of the septa are also translucent, but that might be due to the fact that the branchiae were attached to them.

Double dorsal adductor muscles are found in several primitive species (*Oslomena* spp. and *Kiaeromena juvenilis*). In *Kiaeromena kjerulfi*, too, there is a pair of small posterocentral impressions (pl. 10 fig. 2). Generally, all Strophomenacea have only one pair of dorsal adductors. In the transitional species mentioned above, the formation of visible impressions of these muscles is connected with the loss of branchial septa (pl. 12 fig. 12, pl. 7 fig. 17). Because of the small material available, it is impossible to know definitely if the septa had some connection with the muscles, or if the correlation in development was accidental.

From equation (1) it is obvious that a' and a must be on opposite sides of the axis of rotation ($=$ the line through the apex of the teeth). If not, the diductors will act in the opposite direction, as adductors. In several species, the muscle attachments on the cardial processes is on the same side as the centre of gravity, but the distance a' is

still positive, because the cardinal processes are high, or the angle
a is comparatively small (textfig. 13).

The forces necessary to open the valve, is a function of the balance
'a/a in (1). In most specimens this value is about 1/5—1/7. In other
species, especially among the Rafinesquinas, it is as low as 1/20 or
even less. In these cases, the diductor muscles alone could scarcely
have opened the valves.

The presence of a strong pseudodeltidium and a chilidial plate in
many specimens without functional diductors or very high a'/a seems
to indicate that these species had a ligament uniting the pseudodel-
tidium and the chilidium, which served to open the valves. In many
species the diductor, at least partially, took over at a later stage of
growth. The structure of the pseudodeltidium, described above, seems
to give support of this theory. It is also worth noting that most
species with strong cardinal processes and diductor impression do
not have a well developed pseudodeltidium or chilidium. This negative
correlation between the development of the cardinal processes and the
pseudodeltidium is found in many groups within the Strophomenacea,
as for instance the Stropheodontidae, where the development of the
cardinal processes in the direction of higher efficiency can be directly
correlated with the gradual loss of the pseudodeltidium and chilidium
(cf. WILLIAMS 1953a, textfigs. 2—3). In *Strophomena norvegica* and
Kiaeromena kjerulfi, both the cardinal processes and the pseudodel-
tidia are strongly developed. In the first mentioned species, the growth
lines are much less prominant than in the pseudodeltidia of most
species. The fact that the cardinal processes project over the chili-
dium, and the pseudodeltidium is sharply angular, indicates that no
ligament was developed in this species. In *Kiaeromena kjerulfi*, both
the pseudodeltidium, the chilidium and the diductor muscles were
strongly developed. This is probably due to the fact that the valves
of this species are extremely heavy so that both muscles and ligament
were needed to open them. The ratio a'/a is also very large in this
species.

In *Oslomena* and *Oepikina* also a negative correlation is found
between the development of the pseudodeltidium and the cardinal
processes and the diductor impressions. In *Oslomena* the diductors are
comparatively small (cf. textfig. 34 D—E), and the cardinal processes
are not fully developed either. The pseudodeltidium (described above) is

very strong, with prominent growth lamellae. This species has no real chilidal plate, but the callosity on which the cardinal processes are placed, have strong growth lemellae, corresponding to those of the pseudodeltidium. The cardinal processes of *Oepikina* are among the largest to be found in the brachiopoda, and the ventral diductor impressions are very big, filling most of the ventral interior (cf. textfig. 34 A). The pseudodeltidium is small and smooth, and the chilidium is scarcely developed.

The muscles of the Plectambonitacea are not by far as well known as those of the Strophomenacea. Generally the muscle impressions do not seem to be well defined from the rest of the valve in many Plectambonitacea. There are several types of muscular systems, and they are found in most stages of development or differentiation of the impressions.

In some of the Leptestinids, the muscular system of the ventral valve is similar to that of the Strophomenacea, with one large double impression (diductors?) and a small, generally double one in the middle of the large one (adductor?). All the muscles are placed near the hinge line in the often very convex specimens. In the dorsal valve, the muscle impressions are seldom developed. The adductor muscles might have been attached to the branchial lamellae, or to the «x-plate» (cf. ÖPIK 1933).

In *Paleostrophomena* and some other genera, even the ventral muscles have left no impressions. There is a striking resemblance between the ventral interior of some of these species and young or primitive Strophomenids, and it is most probable that they did have muscles, but that these for some reason did not leave impressions on the valve. (Compare *Grorudia* (?) *glabrata*, Pl. 1 fig. 12 to *Leptaena ennessbe*, Pl. 10 fig. 9). The cardinal process of the Plectambonitacea varies considerably. Generally it is triple, but sometimes bifid, simple or quintuple, or absent altogether. This indicates that the diductors were more variable than in the Strophomenacea. The distance a' is generally very small. This is partly compensated by the strong convexity of many species, which makes the distance a correspondingly shorter.

In *Sowerbyella* and related genera, the ventral diductor muscles are to a great extent filled with the impressions of the vascula, so that there might be some doubt as to whether they are muscle im-
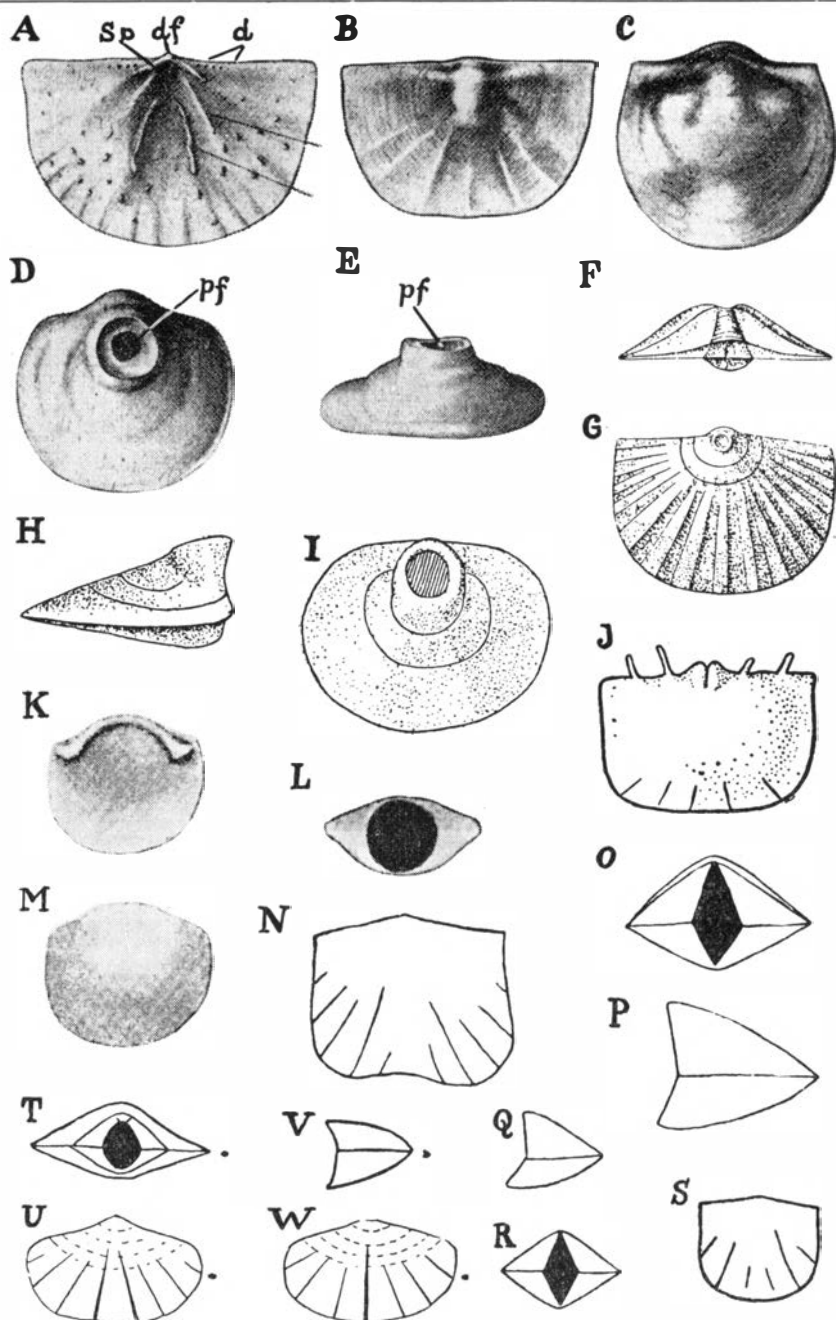
Fig. 14.

pressions at all. The impressions are large, elongate diverging at about
90°, and continue gradually into the vascula. In old, well calcified
specimens, the vascular impressions continue almost to the hinge line.
The adductor impressions reported from the Sowerbyellinids (cf.
ÖPIK 1930, 1933), have an interesting structure. They consist of two
conical cavities reaching almost to the exterior of the valve (text-
fig. 23). These ventral cavities, which can clearly be seen in casts, is
a characteristic feature of the Sowerbyellinae, and it is not found in
adult specimens outside that family. Generally, the laminated tissue
in the muscle impressions grew in thickness together with the rest
of the valve, but in the case of the ventral cavities, the muscles seem
to have been attached to the interior surface of the external layer
of the valve during the growth of the animal.

GROWTH AND ONTOGENY

The ontogeny of the palaeozoic brachiopods has been described
especially by BEECHER (1891, 1891a, 1892, BEECHER & CLARKE 1889).
More recently KOZLOWSKI (1929), ARBER (1940), IVANOVA (1949),
SARYTSCHEVA (1948), and others have published papers on this subject.
These papers show that there are two widely different types of
ontogenetic development in the «Protrematous» brachiopods. In the
Orthacea, the larvae had high areas, open delthyrium and notothy-

Fig. 14. Larval valves of brachiopods. A—B. *Plectodonta mariae* KOZLOWSKI
1929, Interior and exterior of a dorsal valve. 30x. from KOZLOWSKI 1929, fig.
36, B—C, p. 116. C—D—E. *Leptaena emarginata* (BARRANDE), C. exterior of
dorsal valve, D—E. two different views of the exterior of the ventral valve.
From KOZLOWSKI 1929, textfig. 25, p. 93. F—G—H—I. *Leptaena «rhomboidalis»*
F—G a relatively large larval form seen from the areas, and from the ventral
side. H—I a small larval form seen from the side, and from the ventral valve.
From BEECHER 1891. J. *Chonetes (Chonetes) carboniferus* KEYSERLING, the cast
of a larval ventral valve, showing double ventral cavities. 16x. From
SOKOLSKAJA 1950, textfig. 20, p. 56. K—L—M *Enteletes lamarckii* (FISCHER)
Ventral exterior and interior, and a complete specimen seen from the area. 35x.
From IVANOVA 1949, textfig. 1, 1 a—c, p. 245. N—O—P—Q—R—S. *Dicoelosia
biloba* (L.) Two specimens, seen from the side, the ventral valve, and the areas.
Note the angular pedicle foramen. From BEECHER 1892, pl. 1. T—U—V—W.
Platystrophia sp. Dorsal, areal and side of two specimens. From CUM-
MINGS 1903.

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rium with no chilidium or deltidium. The pedicle probably was thick
and placed between both valves, filling both the delthyrium and the
nothothyrium. This type of larval development is found in a large
number of species belonging to different genera, ranging from Ordo-
vician to Permian. The difference between the species and genera is
small, they vary as to the details of the sculpture and in the outline
of the pedicle foramen, which is rhomb-shaped in most forms, and
rounded, circular or oval in others. (Textfig. 14).

In the Strophomenidae, the larvae are quite different. Both
valves are smooth, and the ventral one has a very dominant pedicle-
tube, which is subcentral in the youngest larva, and more peripheric
in the older one. There is no foramen in the dorsal valve. This type
of structure is found in *Leptaena*, and some other genera.

The material studied by the author includes fairly complete
ontogentic series of three species from the Middle Ordovician of the
Oslo Region, *Kjerulfina foliovalve* (p. 155), *Christiania holtedahli* (p.
117) and *Sowerbyella sericea soudleyensis* (p. 91). In addition the
author has studied a number of larval valves of *Parmorthis elegantula*
and *Leptaena depressa* from the Silurian of Gotland. The study of the
last mentioned specimens, however, only confirmed the results of
the previous authors, and they are therefore not considered further.
The larval valves of *Sowerbyella sericea soudleyensis* do not provide
any additional material on the development of the species. Even
the smallest larvae are surprisingly like the adults. (Pl. 3 figs. 1—4).

A ventral pedicle foramen in the Sowerbyellinids is reported by
ARBER (1940) and KOZLOWSKI (1929). The author has studied a large
number of well preserved specimens of Sowerbyellinids, but none of
them had a ventral foramen. Many slightly worn specimens, however,
show one or both the ventral pits, probably the deep attachments
for the adductor muscles. These almost reach to the exterior surface
of the valves, and in semi-translucent specimens they can often be
seen when the valves are worn. The pedicle foramen described by
the authors mentioned above, might be pits from such specimens.
They can be distinguished from the pedicle foramen in that there
are two of them, and in not being placed centrally but slightly to
the side.

The fact that *Christiania oblonga*, which has a ventral pedicle
foramen, has a cardinal process similar to that of the Sowerbyellinids,

could indicate that there are two different foramina, a dorsal and a ventral which seem to occur alternatively. If the pedicle had moved from the dorsal to the ventral valve, that would evidently have caused some modifications to the cardinal processes.

The final proof of the presence of both foramina is the fact that they are both found in *Oepikina dorsata* (textfig. 2, pl. 14, fig. 7). In that species, the cardinal processes correspond to the lateral branches of the cardinal process in *Sowerbyella*, and the median branch, which is the largest one in *Sowerbyella*, is reduced to a very low, thin septum between the two very large, forked processes.

The dorsal foramen was called the notothyrial cavity by earlier authors (i. a. WILLIAMS 1953). It differs from the pedicle foramen, which is cylindrical, in being conical. In at least *Alwynella* and *Eoplectodonta acuminata*, it is definitely a real perforation in the calcareous shell. It can be seen both in thin sections, and as an external opening. In *Sowerbyella sericea* (subsp. div.) the internal opening is very broad, while the external one is extremely small, if present at all. Structures similar to the dorsal foramen are also found of the Sowerbyellinae, but here they only appear as traces. At the base outside the cardinal processes in *Leptaena depressa*, there is a whirl in the growth laminae which might be an atrophied foramen. The foramen found in *Oepikina* is mentioned above.

Because of the conical shape, it is improbable that the dorsal foramen was a pedicle one. The fact that it mainly is found in the Sowerbyellinae, indicates another possibility. In this subfamily the ventral adductor muscles are deep, conical and almost reach right through the valve. It is therefore possible that the dorsal foramen is the impression of a muscle or another organ, which was attached to the exterior side of the cardinal process, or to the periostracum. To the author's knowledge, no such muscles are known from recent brachiopods. The interpretation of the dorsal foramen must therefore be highly provisional.

In the larval valves of a number of Strophomenids, there is a distinct dorsal cavity (cf. *Christiania holtedahli*, textfig. 30 A—F, pl. 5 figs. 2, 5, 8, *Plectodonta mariae*, textfig. 14 A—B), which, at least in *Christiania* terminates in a foramen. This grove which probably has nothing to do with the dorsal foramen in Sowerbyellinids, is cylindrical, and has the same diameter as the pedicle foramen, which is

constant during growth in this species (*C. holtedahli*). This grove may therefore be the pedicle foramen. It is not bridged by the chilidal plates (= socket plates), and the ontogenetic development shows that the pedicle gradually is transferred to the ventral valve. In *Oepikina*, which both had a pedicle and a dorsal foramen, the trifid cardinal process with its foramen was probably formed after the pedicle was transferred to the ventral valve.

This dorsal grove is found also in a number of Middle Ordovician Strophomenidae, and it is therefore not restricted to the Plectambonitacea. The material of larval ventral valves is rather small, but not a single specimen similar to *Leptaena* (with large pedicle tube) is found. Judging from the direction of the hemicylindrical pedicle groove in the dorsal valve, the pedicle opening must in some cases have been completely in the that valve.

It is very difficult to explain these contradictory observations. A possibility is that the mantle was reversed during the larval development, such as in the Terebratulida (cf. PERCIVAL 1944), and that this reversion took place later in the development in the older species than in the Silurian and Devonian Leptaenas studied by the earlier authors.

At present, there are, however, no definite proofs for this hypotesis.

It is obvious that both the ontogeny and the presence of a dorsal foramen is of considerable systematical value. The fact that the ontogeny only is known from comparatively few species, and it is unknown, or almost unknown, in large groups make the use of these features difficult. No larvae are known from such important groups as the older Plectambonitida and the *Kjaerina-Rafinesquina-Stropheodonta* lineage, and it is therefore too early to split the groups according to the ontogeny. However, it would seem natural to divide the Plectambonitacea into two groups, one consisting of the older forms, Taffinidae and Plectambonitidae, and the other including Christianidae, Chonetidae, and Sowerbyellidae.

As mentioned below (Trends of evolution in the Strophomenidae), the Strophomenids might also be divided into two main groups, based on the structure of the cardinalia. Since both the ontogeny and the detailed histological structure of the majority of the Strophomenids are unknown, one cannot draw any conclusions from the fragmentary material available.

GROWTH: Detailed studies have been made of variations both in size and growth. For this purpose extensive material is required, and this has limited the study to a few species only. It is also difficult to find a sufficient number of specimens for studying each population statistically. Strict mathematic methods have therefore not been applied. A large percentage of the specimens are distorted, due to growth anomalies or tectonic pressure. This decreases the number of specimens on which measurements can be made even further, and may possibly introduce a bias.

The studies were concentrated on the variations within one population, within a set of contemporaneous, or at least nearly contemporaneous populations, and populations of different age, all of the same species.

The number of species was very small, the only ones in which all variations were studied were *Christiania holtedahli* and *Oslomena osloensis*.

Generally the variations within one population were small. In a few cases there was considerable variation (the exterior of *Kjerulfina foliovalve*, and the ventral muscle impressions of *Oslomena osloensis*). In some populations there was an amazingly great number of abnormal specimens, generally thin-shelled Strophomenids with healed fractures.

The study of contemporaneous populations showed that the mean size and the proportions are very variable. The variations could generally be correlated with the average size of the other species in the fauna. In *Oslomena osloensis* for instance, the typical form is found together with other species of moderate size. In some localities in the Oslo—Asker district, a smaller form occurs, together with the same fauna, the species being on a smaller scale. In this case, too, the proportions vary and the smaller specimens are slightly broader than the typical form. In the Oslo—Asker district the geographical distribution of the types is very complicated. In most localities there is only one type, while in a few one can find some intermediate forms. Both types are never found together. In the Ringerike district the species, in this case slightly larger than the typical forms, is found together with large, thin-shelled species. The difference in size, however, is small (see textfig. 37). In the Mjøsa districts (Toten and Ringsaker), the specimens are considerably larger than the typical form.

They occur together with other specimens, which also are much larger than those found in the Oslo—Asker district.

A similar variation is found in *Christiania holtedahli*, and to a smaller extent also in *Chonetoidea gamma*. In other species, such as *Eoplectodonta acuminata*, the size hardly varies at all, even in localities were the other species show considerable variation. In *Ptychoglyptus valdari* the species vary, and in the population where the largest specimens are found, there are also specimens which are dorsally geniculated. This is not found in the otherwise smaller populations. Possibly the geniculation only took place when the disc had grown to a certain size, which was not reached in the other populations.

Probably all the varieties described above should be regarded as being ecological variations only, and do not merit subspecific rank. In many cases it is of course difficult to discriminate between closely related, genotypically different forms, and fenotypical varieties.

A number of populations of *Christiania holtedahli* from different horizons have also been studied. A gradual increase in size has been observed from older to younger populations, and also a change in shape, from specimens with equal width in the oldest population, to specimens which are widest behind in the younger ones. This line of development leads from *Christiania elongata*, and specimens resembling *Christiania oblonga* in zone 4aβ and the lower part of zone 4bα, to the typical specimens of *Christiania holtedahli* in the middle and upper part of zone 4bα. (The vertical and geographical distribution of the *Christiania* species is shown in textfig. 31, p. 121).

The studies of the relative growth-rate have been concentrated on the rate HL/L (Hingeline/greatest length). Measurements were made both of samples of specimens, and of series of growth-lines, in single specimens. Several correlations show that the two methods give identical results (cf. textfig. 35). It has to be mentioned, however, that specimens in which the growth-lines are accentuated by healed fractures can not be used for these studies.

The species studied fall into two main groups, those in which the ratio HL/L is constant during the growth (except in the youngest larval valves), and those in which the ratio change considerably. Representatives of the first group, with isometric growth, is *Sowerbyella sericea soudleyensis* and *Strophomena norvegica* (Textfigs. 22, 35). In species of this group, the growth is isometric and radial,
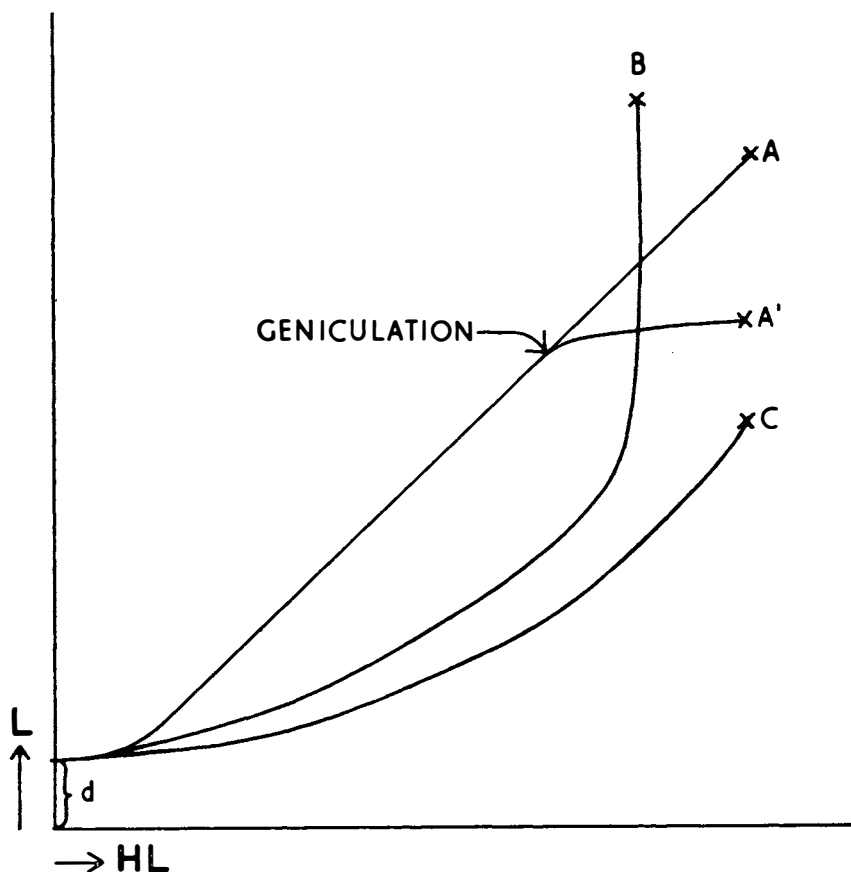
Fig. 15. The development of the Length/Hinge-line ratio in the different types of growth. (See text) A = Isometric growth. A' = Isometric growth and geniculation. B = Christiania-type of allometric growth. C = Alwynella-type of allometric growth. d = Diameter of smallest larval valve.

from a centre at the hinge-line. The ratio HL/L is therefore 2 or more.

The second group, which show allometric growth, might be divided in several subgroups. The first one include the geniculated species. In the early stage of growth, they resemble the species with isometric growth, but at a certain total size, the valves turn abruptly, and the growth continue allometrically. If the angle between the disc and the fringe is 90° or less, the observed length will cease to grow, and if it

is between 180° and 90°, the observed addition in length is considerably smaller then the actual growth of the fringe. The hinge-line might or might not continue to grow. In the first case it forms long pointed cardinal angles.

The critical size for the geniculation might be constant for the species, but it is likely that it is different in different populations, at least in some species. In *Ptychoglyptus valdari* (p. 58) only a fraction of the generally small specimens from the Oslo--Asker district reach the size necessary for geniculation. In the Ringerike district where most brachiopod specimens are larger, all the comparatively few specimens known are geniculated. In this species, therefore, the critical size seems to be constant for the species, and independant of the ecology.

The development of the geniculation in the Strophomenids is therefore probably similar to the development of the horns of the titanotheries discussed by HUXLEY (1944). It might be suspected that the possibility of geniculation was present in all Strophomenids, but that the critical size was not reached in a number of species.

A second type of allometric growth is found in *Christiania* (Text-fig. 29) and probably some species of *Oepikina*. Here the hinge-line reaches a maximal size rather early in the development of the specimens, and all the later growth is in the transversal and vertical directions. The maximal width of the hinge-line is different in the different populations, and closely connected with the maximal size of the specimens, so that the HL/L ratio of the adult specimens is constant in all populations, when the absolute size vary.

This constant development gives a certain scale for the relative individual size in the different populations, because when the *Christiania* populations show large specimens, the other brachiopod species will show the same, even if smaller variations occur.

The third type of allometric growth is found in the new genus *Alwynella*. From the study of the growth-lines of a large number of specimens, it appears that the increase in length is more rapid than that of the hingeline. Since the ratio HL/L is rather high in most specimens belonging to this genus, the growth rates must have been opposite to those observed in the early stages of development of the valves. This indicate that the hingeline growed rapidly till the HL/L ratio was 5—6 or even more, and later it decreased slowly till it reached
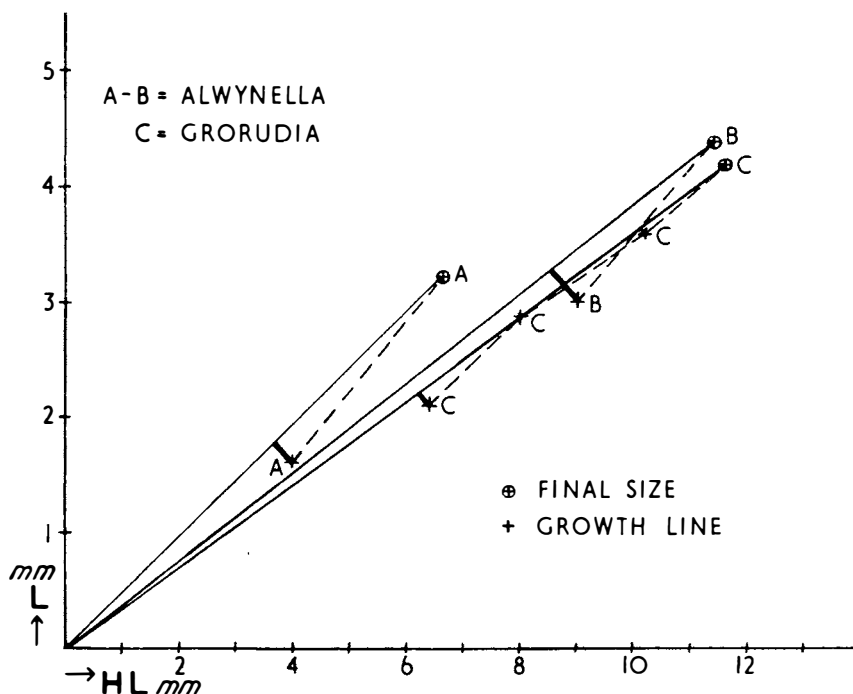
Fig. 16. Diagram showing the correlation between the L/HL index in growth lines and outline in species with allometric growth (A/B) and isometric growth(C).

the value for adult specimens (2,5—3,5). This type of growth may be called elliptical allometric growth, because the directions of growth form an ecclipse with the longest diameter along the hinge-line in the earliest stages, and later with the shortest axis along the hinge-line. (Textfig. 15).

The material of measurements is still much too small to be treated statistically, but it certainly has some significance. It also has some practical value, because this allometric growth is not found in the genus *Grorudia*. Exteriors of *Alwynella* and *Grorudia*, which occur together, and are very similar, might be distinguished by measuring the growth-lines. If the growth is isometric, the valve belong to *Grorudia*, if it is allometric, the valve belong to *Alwynella*. (Cf. Textfig. 16).

The data presented here are at the moment to few, and too fragmentary to allow any important biological conclusions. They are

mentioned because further investigations along these lines might give important facts, and because already these small attempts have given some results of practical and diagnostic value.

Description of Fossils.

Suborder Strophomenida ÖPIK 1934 EM. WILLIAMS 1953.

Superfamily Plectambonitacea (JONES 1928) nom. transl. COOPER & WILLIAMS 1952.

Family Sowerbyellidae (ÖPIK 1930) nom. transl. nov.[1] (= Leptestiidae (ÖPIK 1933), nom. transl. WILLIAMS 1953).

Subfamily Leptestina ÖPIK 1933.

Ptychoglyptus WILLARD 1928.

This genus was originally described as a Rafinesquinid, but later studies have shown that it is a Plectambonitid, probably belonging to the family Sowerbyellidae. In the new species described below, the ventral interior is similar to that of *Paleostrophomena*, whereas the dorsal is quite different from that genus.

Most species of *Ptychoglyptus* are fonded upon the exterior only, and it is possible that some of them are homeomoorphs, with deviating interior.

Ptychoglyptus valdari. sp. n.
Plate 1, figs. 1—3. Textfigs. 17 and 19 K-L.

Type data: The holotype, PMO 18853, is the cast of a dorsal interiorfrom zone 4bα at Slependen, Oslo—Asker district. (Pl. 1, fig. 2).

Material: About 30 exteriors of valves, 4 complete specimens, 3 ventral and 3 dorsal interiors.

Diagnosis: A *Ptychoglyptus* species with thick valves, numerous ribs and variable geniculation.

Description: A specimen of average size is 30 mm wide and 18 mm long. In most specimens the valves are flat, with a very slight

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[1] This family is formed by the union of the two subfamilies Sowerbyellinae ÖPIK 1930 and Leptestiinae ÖPIK 1933, and should therefore, according to the new rules on zoological nomenclature, have the name of the oldest subfamily.
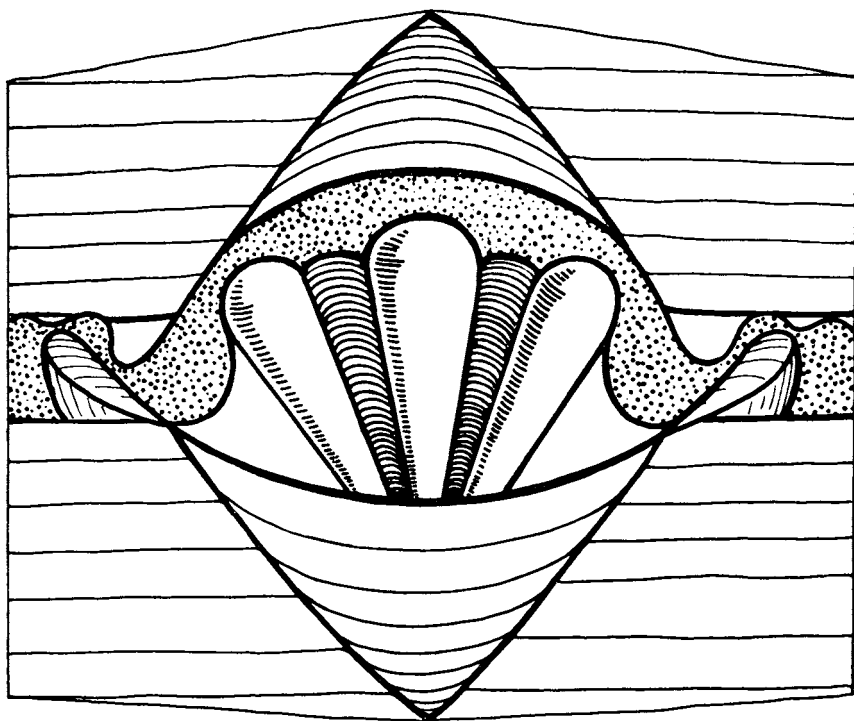
Fig. 17. *Ptychoglyptus valdari* sp. n. Somewhat diagramatic figure showing the median parts of the areas. The valves are separated to show the interior. The drawing is based on a specimen from zone 4bα at Slependen, Asker district.

marginal geniculation, which is opposite in both valves, and in this way provides space for the soft parts of the body. In some specimens the valves are subequally biconvex, and others are dorsally geniculated (cf. p. 54).

The areas are high, triangular, and meet at sharp angles even in young specimens. The pseudodeltidium is comparatively large, and much protruding. A strongly convex chilidium covers the notothyrium (Textfig. 17).

As it is usual in this genus, the sculpture consists of prominent radial ribs which cut the strong concentric rugae. In addition to this, there are fine striae, which in contrast to the ribs, follow the undulations of the rugae. There are 5—8 of them between each rib. In the central part of the valve, and in young specimens, the concentric

rugae are continuous, being broken at an angle of less than 180° at each rib. In the rest of the disc, the rugae are not continuous. Each segment between two ribs seems to have developed rugae independant of the other segments. In other specimens the rugae are more continuous, but they are broken sharply so that they form angles pointing posteriorly and anteriorly at every other rib. The differences as to sculpture have not been compared with variations other of features, because all specimens of which the interior of the valves is known have the first mentioned type of sculpture, which is the one usually found. The marginal parts of the valve, which are geniculated, have no concentric rugae. In a few specimens, this nonrugated area include the marginal part of the disc too.

The ventral interior very much resembles that of *Paleostrophomena*. It has a similar vascular system and slightly developed muscle impressions. The teeth are strong, and there is also a pair of small lateral accessory teeth. The accessory teeth themselves have only been observed in one ventral interior, and their existence is mainly proved by the presence of accessory sockets in the three dorsal interiors.

The dorsal interior (Pl. 1, fig. 2) shows small, finely striated branchial lamellae, a large, complex x-plate (cf. ÖPIK 1933), very strong crural plates which are fused to the chilidium, and a prominent cardinal process consisting of three parts, one central, subcircular and two lateral ones, formed as thick, diverging plates. It grows vertically from the notothyrial platform, and is not supported by septa posteriorly, as for instance in the Sowerbyellinids. The vascular system is unknown, only the marginal vasculae are developed in one specimen.

The shell structure is punctate, no cone-sheets are observed (p. 12, Pl. 13, figs. 6—7). The large ribs of the sculpture are found not only on the surface, as in most species with a thin external layer, but continue as bars down in the tissue of the valve, almost to the inner surface. The interspaces between the ribs are filled with punctate tissue. (Pl. 13, fig. 6).

Remarks: Ptychoglyptus valdari differs from *P. virginensis* WILLARD 1928 and *P. rugosa* REED 1932 in the noncontinuity of the concentric rugae, and in having more ribs and thicker valves than the two other species. It appears to be closely related to a species occuring

in the Middle Ordovician Lower Reef Limestone in Dalarne, Sweden, which has the same type of sculpture as *P. valdari*, and a more regular convexity, always being flat with sligth opposing geniculation.

A small specimen with *Ptychoglyptus* sculpture is found in zone 4ba at Gåsøya, Oslo—Asker district. There is a sinus in the ventral valve of the specimen, and it might belong to another species. However, the occurence of *P. valdari* in the same layer, and the variable shape of that species, indicates that this deviating specimen belongs to it.

«*Rafinesquina*» *ringerikensis* HOLTEDAHL (1916 p. 30, pl. 3, fig. 7) has a *Ptychoglyptus*-like sculpture, differing from that of *P. valdari*. As the interior of «*R.*» *ringerikensis* is unknown, it is impossible to determine the generic position of that species.

Distribution: Ptychoglyptus valdari is common in the upper part of zone 4ba in the Oslo—Asker district. In the same zone in the Ringerike and Hadeland districts there are some few large specimens belonging to this species.

Genus *Grorudia* gen. nov.

Diagnosis: Leptestiids with paucicostate ornamentation. Ventral interior similar to that of *Paleostrophomena*, with no clearly defined muscle impressions, only two diverging vascular impressions almost from the apex and double teeth. Dorsal interior with strong, bilobed branchial lamella, which are not elevated, triple median septum, and absent or large, flat cardinal process. Hinge-line apparently not denticulated. Shells generally flat, or slightly convex-concave.

Type species: Grorudia grorudi sp. n. from the lower Middle Ordovician (zone 4aβ) of the Oslo Region.

Remarks: Grorudia is probably related to *Paleostrophomena* and *Ptychoglyptus*. It differs from the latters in being smaller, having different ornamentation, no geniculation. The dorsal interior is also different in the three genera (*Grorudia*, Pl. 1, figs. 10—11, *Ptychoglyptus* pl. 1, fig. 2, *Paleostrophomena* cf. WHITTINGTON & WILLIAMS 1955, pl. 39, figs. 68—70, textfig. 4b). The teeth and the ventral interior is essentially the same in all three genera.

Distribution: Grorudia is found in zones 4aβ and 4ba (lowest part) in the Oslo region, and in the Tramore Limestone, County Waterford, Eire.

Grorudia grorudi sp. n.
Pl. 1, figs. 7, 10—11, textfigs. 11D, 16.

Type data: The holotype is PMO 66939, the cast of a dorsal interior from zone 4aβ, Tåsen, Oslo district.

Material: More than 25 casts of the interiors and complete specimens. The exact number of exteriors can not be given as they occur together with *Alwynella osloensis* which is of similar shape and size and has the same type of ornamentation.

Description: A specimen of average size is 10 mm wide, and 4 mm long. Valves with sharp cardinal angles and slight convexity. The sculpture shows traces of differentiation, every third to fifth rib is generally stronger than the rest. This differentiation is differently developed, in many specimens all ribs seem to be of equal size. The areas are comparatively high, semiequal. There is no apical foramen. The ventral interior does not have any distinct muscle impressions, a pair of diverging vascular impressions are prominent, and between them there are a few thin septa. The dorsal interior has branchial lamella divided by a diverging pair of vascular impressions. The cardinal process is not developed, and there is only a large swollen area on the top of the notothyrium. The teeth are double, the hinge-line is not denticulated. The shell substance is finely pseudopunctate.

Remarks: G. *grorudi* differs from G (?) *glabrata* in being much smaller, in the slight differentiation of the sculpture, and in the branchial lamella being more strongly developed. As to the exterior it is difficult to discriminate it from the contemporaneous *Alwynella osloensis*, which has a similar sculpture and is of the same size, convexity and shape. The growth-lines are, however, differently developed (cf. p. 57), and the interior of the two species are of course very different.

A similar species is found in the Tramore Limestone (stage III, with *Trinucleus hibernicus*), county Waterford, Eire. It differs from the species described here in being extremely wide (hingeline/length ratio more than 4).

Distribution: G. *grorudi* is found in zone 4aβ of the Oslo district. Probably this species occurs in other districts too, but since the interior cannot be studied in any of the specimens, it is difficult to distinguish this species from *Alwynella osloensis*.

Grorudia (?) *glabrata* sp. n.

Pl. 1, figs. 4, 8, 18, Textfig. 11A

Type data: The holotype, PMO 66929, is a cast of a dorsal interior from the transitional layers between zones 4aβ and 4bα at Sentralinstituttet, Blindern, Oslo district.

Material: 2 dorsal interiors, 2 ventral interiors and a large number of fragmentary exteriors.

Diagnosis: Large, flat *Grorudia* with differentiated sculpture, high areas, strong, diverging vascular impressions and small, circular branchial lamella.

Description: Comparatively large species (the holotype is 15 mm wide and 10 mm long). Both valves are rather flat, outline hemicircular, cardinal angles right. Sculpture differentiated, 6—7 more delicate ribs between each stronger one. The areas are comparatively high, the ventral one is the largest. The delthyrium is narrow, with an angle of about 60°. There does not seem to be a pseudodeltidium.

The ventral interior is, just as in *Grorudia grorudi*, dominated by the strong, diverging vascular impressions. The muscle impressions can not be seen, but a number of subparallell septa between the vascular may have some connection with them. The margin of the valves have strongly marked ciliar grooves, for a space of about 0,75 mm from the margin. It is remarkable that the vascular branches all terminate into such a groove, although all grooves are not provided with a vascular branch.

The dorsal interior is dominated by the branchial lamella, which are smaller and more uniformly circular than in *G. grorudi*. There is no real cardinal process, only an undifferentiated swelling of the notothyrial floor. The teeth and sockets are double, the distalmost being the smaller ones.

Remarks: The differences as to internal structures between this species and *G. grorudi* are mentioned above. They also differ considerably as to size, shape and ornamentation. There may be some doubt as to whether *G.* (?) *glabrata* should be referred to *Grorudia* at all. Probably it is closer to *Paleostrophomena*, and at least it is a transitional link between the two genera. It differs from *P. concava* and other species of *Paleostrophomena* in not having concentric rugae and geni-

culation, in having comparatively larger branchial lamella and in the lack of a cardinal process.

Distribution: As yet this species has only been found at the type locality and some localities in the neighbourhood. They are all in the transitional layers between zones 4bα and 4aβ. Most of the specimens occur in layers which should be regarded as belonging to zone 4bα, since they occur together with *Ullerella holtedahli* (HENNINGSMOEN) and *Chasmops* sp. Probably the holotype itself also comes from these layers, but it is impossible to date it as accurately as the other specmens.

Genus *Paleostrophomena* HOLTEDAHL 1916 (em. ÖPIK 1933)

Paleostrophomena (?) *majori* sp. n.

Pl. 1, fig. 13.

Type data: The holotype, PMO 64790, is the cast of a ventral interior from the middle part of the Bryozoan zone at Saltboden, Frierfjorden, Langesund-Gjerpen district.

Material: 5 ventral interiors (casts).

Diagnosis: Paleostrophomena species without geniculation and well defined ventral muscle impressions, and with sharp cardinal angles.

Description: Fairly large species, the holotype is 26 mm wide and 17,5 mm long. The valve is almost flat, without any geniculation. The sculpture is not known, but judging from the grooves on the margin of the interior, the distance between the major ribs was about 1,5 mm. Concentric rugae (4—7) are strong at the hinge-line. The area is high, with a narrow delthyrium (about 45°) covered with a strongly arched pseudodeltidium. The muscle impressions are small, badly defined, and nearly filled with the large vascular impressions, which are of the usual *Paleostrophomena*-type. The teeth are small, and double. Both pairs are of about the same size. The interior surface is finely pitted, indicating a punctate structure of the valve, possibly of the same type as that found in *Ptychoglyptus*. There are long, undifferentiated ciliar grooves along the margin.

The dorsal valve is unknown.

Remarks: P (?) *majori* differs from the type species, *P. concava* (SCHMIDT) in the absence of geniculation, in being smaller, having a

narrower delthyrium, and in the concentric rugae of *P.* (?) *majori* appearing to be restricted to the area near the hinge-line. It differs from *P. magnifica* WILLIAMS (1955) in the short and badly defined muscle impressions.

Together with *Grorudia* (?) *glabrata*, *P.* (?) *majori* forms a continuous series of species from the typical *Grorudia* to *Paleostrophomena* (*G. grorudi* — *G.* (?) *glabrata* — *P.* (?) *majori* — *P. concava*). The stratigraphic occurrence of the species is also in accordance with this theory.

Distribution: P. (?) *majori* is found in the Echinosphaerites and Bryozoan zones in the Langesund—Gjerpen district. A very small specimen is found at the base of the Echinosphaerites zone, while the majority of the specimens are collected 85 m. higher, in the middle part of the Bryozoan zone.

Genus *Leptestia* BEKKER 1922.

Leptestia aff. *jukesi* (DAVIDSON 1871).

Pl. 4, fig. 4.

For synonymy, see HARPER (1952, p. 101) and ÖPIK (1930, p. 125—129).

Material: 5 ventral interiors (casts).

Description: The moderately convex specimens are about 25 mm wide and 19 mm long. The area is high, the dental plates short, and the teeth strong and triangular. The muscle impressions are ovoid, with longitudinal septa, probably between the adductors and diductors. The large rounded ovarian impressions are strongly impressed in the valves, and show a number of radial, high, thin septa. The vascular arches are less developed than in typical specimens of *L. jukesi* (and *musculosa*). The interior surface of the valves is strongly pitted, indicating that the shell structure was coarsely pseudopunctate.

Remarks: The present material is too small to throw any light on the relationship of *L. jukesi* and *musculosa*, but they differ from them only in the marginal branches of the vascular arches not being so strongly developed. The ventral interiors are rather like those of certain Orthids as to the shape of the muscle impressions, and especially those of the ovaria. The presence of pseudopuncta, however,

shows that the specimens belong to the Strophomenida, and in this group they can only be placed in the genus *Leptestia*, as no other Strophomenid genus has these features.

Distribution: In Norway in the Bryozoan zone in the Langesund/Gjerpen district. In Esthonia *L. musculosa* is found in zones C_1–$C_{2\beta}$. In Eire *L. jukei* is found in beds of similar age.

THE GENUS *Leptelloidea* JONES *1928* AND RELATED GENERA

The genera of the subfamily Leptestina belong to three distinct groups. The first has flat, generally large valves, double teeth, constant ventral interior (of the *Paleostrophomena*-type) and variable dorsal interior. (*Paleostrophomena* HOLTEDAHL 1916, em. ÖPIK 1933, *Ptychoglyptus* WILLARD 1928, and *Grorudia* gen. nov.).

The second group has small, generally very convex valves, distinct ventral muscle impressions, elevated branchial lamella. The development of the cardinal process and the denticulation of the hinge-line is very variable. (*Leptella* HALL & CLARKE 1892, *Leptelloidea* JONES 1928, *Sampo* ÖPIK 1933, *Leangella* ÖPIK 1933, *Leptellina* ULRICH & COOPER 1938, *Diambonia* COOPER & KINDLE 1939, *Benignites* (*Benignites*) HAVLICEK 1952, and *Benignites* (*Leptestiina*) HAVLICEK 1952). The third group consist only of the type genus *Leptestia*.

Within the second group, *Leangella*, and *Diambonia* are well defined, and are discussed below. *Leptella* in not well known, and is not considered here.

There are probably synonyms among the other generic names mainly because the opinions of the taxonomic value of certain structural features have differed considerably.

In the present material two species belonging to this group are represented by a very large number of specimens from several localities and horizons. The variation has been studied in order to find which features were constantly variable, and which were variable during the individual growth and with changing ecology.

The sculpture, outline, size, angle between and curvature of areas, outline of ventral muscle impression and size and frontal outline of branchial lamella were all too variable too be used as taxonomic features at the generic and subgeneric level. In most cases they could

not be used to distinguish species. The only feature which is both caracteristic and constant for the genus or subgenus, seems to be the ventral vascular system. Three types are found in the groups of genera considered here. a) the *Leptelloidea* type, with triangular ovaria along the hinge-line in the vascula cruralia, large frequently branching vascula spondylaria, and reduced vascula media (= the *Sowerbyella* type, cf. p. 37).

b) the *Sampo* type, with almost the whole interior surface covered with the broad anastomosing vascular branches. Most of the branches belong to vascula cruralia, vascula spondylaria present, but seldom prominent, vascula media not observed. In young specimens an irregular vascular arch is often formed (textfig. 11G).

c) the *oepiki* type, with vascula arches formed by vascula cruralia in old specimens united with the broad, unbranching vascula spondylaria, vascula media reduced.

HAVLICEK (1952, p. 426) indicated that the ventral muscle impressions in *Leptelloidea leptelloides* are different from those found in other species referred to *Leptelloidea*. Although this difference is not so prominent in normal specimens as in the particular one figured by ÖPIK (1933, Pl. 5, fig. 1), it may be convenient to use *Benignites* HAVLICEK as a subgenus for species with the same ventral vascular system as *L. leptelloides*, and with diductor impressions with a rounded outline and not surrounding the adductors.

All species with the *Sampo* type of vascular system are included in *Sampo* (*Sampo*), and those with the *oepiki* type are placed in *Sampo* (*Leptellina*) (ULRICH & COOPER 1938).

This arrangement is provisional, since the ventral vascular system is unknown in the type species of *Leptellina* and *Benignites*. It is, however regarded to be more convenient to use these names in a new sense than to introduce new names.

The species which can be refered to the different genera as defined here, are:

Leptelloidea (*Leptelloidea*) — *leptelloides* (BEKKER 1922)
Leptelloidea (*Benignites*) — *llandeiloensis* (DAVIDSON).
Sampo (*Sampo*) — *hiiuensis* ÖPIK 1933, *ruralis* (REED 1917) *tra-
     beata* (ANGELIN & LINDSTRÖM 1880), *indentata* sp. n.,
          ? *derfelensis* (JONES 1928).
Sampo (*Leptellina*) — *oepiki* WHITTINGTON 1938, *elevata* sp. n.
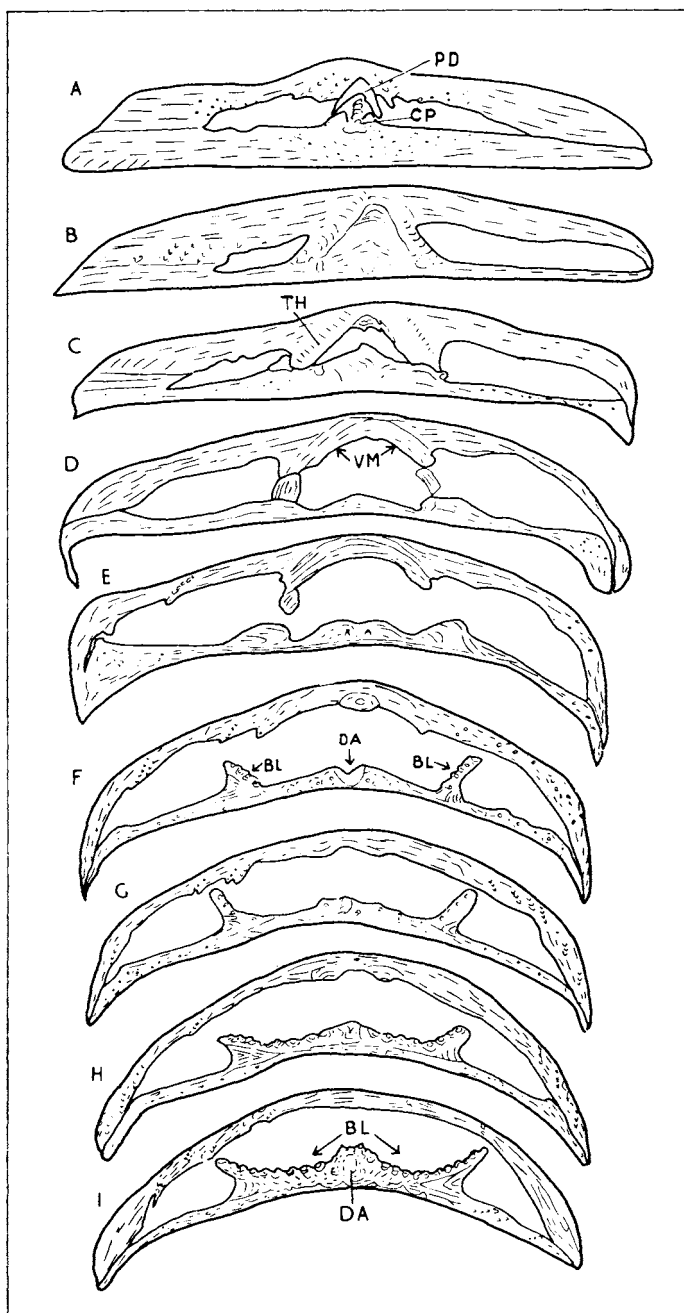
There are still some «Leptelloideas» which do not fit into any of these genera as for instance *L. (?) rosendahli*, which has ventral muscle impressions like *Sampo* and *Benignites*, but long, narrow and pointed branchial lamella. A similar species is found in the Balclatchie Group in Scotland. Further material will be needed in order to decide if these species should be included in a new genus or subgenus.

Some of the oldest species in this group of genera, *L. (?) humboldti* and *L. (?) heintzi* sp. n. are not well known, and cannot with absolute certainty be refered to any of the above mentioned genera.

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Genus *Sampo* ÖPIK 1933
Subgenus *Sampo (Sampo)* ÖPIK 1933
Sampo (Sampo) indentata sp. n.
Pl. 2, figs. 15—16, Pl. 4, fig. 8 Textfigs. 11EFG, P. 18, 19E.

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Type data: The holotype, PMO 67135, is the cast of a ventral interior from zone 4bγ, west of Billingstad st. Asker district.

Diagnosis: Strongly curved *Sampo* species with slightly developed vascula spondylaria, no denticulation of the hinge-line, and compara-tively large branchial lamella.

Material: About 50 complete specimens, 85 ventral and 30 dorsal interiors and a large number of fragmentary specimens and valves in rock.

Description: Strongly concave convex valves, some specimens almost cylindrical. Cardinal angles acute. Sculpture consisting of few ribs with 8—14 stria between each. The areas are triangular, with rounded ends, and the delthyrium is covered with a slightly convex pseudodeltidium. The notothyrium is filled with the chilidal plates and a strong cardinal process.

The ventral interior shows the characteristic vascular system of the genus, the only difference from the other species, is the slightly developed vascula spondylaria. In the younger species (*hiiuensis* and

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Fig. 18. *Sampo indentata sp. n.* A—I, 9 sections of one specimen. The sections are not parallel. The specimen is from the upper part of zone 4bγ, at Hvalstad, Asker district.

Abbreviations. BL = Branchial lamella composed of flat lying pseudo-puncta. CP = Cardinal process. DA = Dorsal axis. PD = Pseudodeltidium. TH = Teeth. VM = Ventral muscle impression.

ruralis) these vascula are much stronger. The muscle impressions are divided into central-anterior small adductors, which migrate anteriorly as the specimen grow older, and large paired diductors with strong growth-lines parallel to the posterior margin. The muscle impressions are deeply impressed in the valve.

A specimen of average size is 17 mm wide and 9,5 mm long.

The vascula in the dorsal valve differ from those in the ventral one in being narrow and unbranching (textfig. 11P). The cardinal process and the chilidal plates are strongly developed. The branchial lamellae are of a rounded outline with a prominent sulcus, and it is longitudinally striated by pseudopuncta parallel to the surface. In adult specimens the lamellae are supported by deposition of secondary tissue. The muscle impressions are not defined. There is a central axis, which at least in young specimens, possibly is open posteriorly (DA in textfig. 18, F. I). It can be traced through the whole length of the branchial lamellae, and can be compared to the structure described by ÖPIK (1933, textfig. 7. *T*) from *Leangella*.

The shell structure is finely pseudopunctate. The puncta seem to be of the same size all over the valves. Along the hinge-line there is a row of pseudopunctae corresponding to the denticles in the younger *Sampo* species. In *S. indentata*, they do not reach the surface of the valve, not even in gerontic specimens. (cf. textfig. 18, B, left side).

Remarks: Sampo indentata differs from its congeners in having no developed denticulations along the hinge-line. The vascula spondylaria is slightly developed in contrast to the younger species. It also differs from *S. hiiuensis* in having comparatively large branchial lamellae. Features of less importance, is the fact that *S. indentata* generally is smaller, and more strongly convex than the other species.

S. (L.) derfelensis resemble *S. (S.) indentata* both as to exterior and dorsal interior. The ventral vascular systems are, however, different, (cf. WHITTINGTON & WILLIAMS 1955, pl. 39, fig. 73) and the latter species is therefore refered to the subgenus *Sampo (Leptellina)* as defined here.

Distribution: S. (S.) intendata is quite common in zone 4bγ in the Oslo—Asker district, in the shelly facies of this zone. In the same horizon in the Ringerike district there are some strongly curved specimens of which the interior is not known, and they might also belong to this species. It also occurs in the Cyclocrinus Shale and the Cyclo-

crinus Limestone at Gran, Hadeland district. A smaller variety, with a broad, more or less prominent sinus in the ventral valve is common in zone 4bδ in the Oslo—Asker district, and probably also in zone 4bδ$_2$ (of *Tretaspis kiaeri*) in the Ringerike district. The interiors found in zone 4bδ in the Oslo—Asker district, are identical with those from zone 4bγ, and they are therefore regarded as belonging to the same species in spite of the difference in external shape.

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Subgenus *Sampo* (*Leptellina*) ULRICH & COOPER 1938 em. nov.

Sampo (*Leptellina*) *oepiki* WHITTINGTON 1938

Pl. 2, figs. 18—19, pl. 4, fig. 6, textfig. 19G, 11O.

</div>

1938 *Sampo oepiki* sp. n. — WHITTINGTON, pp. 255—257, pl. 10, figs. 15—16, pl. 11, fig. 10.

Material: More than 100 ventral interiors, 17 dorsal interiors and a large number of free complete specimens, complete specimens and valves in rock. As usual in species of this kind, the number of ventral valves is much higher than that of dorsal ones.

Description: A specimen of average size from the Oslo—Asker district is 5,5 mm wide and 2,5—3 mm long. The larger specimens from the Hadeland district are about 11 mm wide and 8 mm long.

The size and convexity is variable. The specimens are generally rounded triangular in outline, and widest along the hinge-line. The sculpture consists of some delicate ribs, and in a few cases a number of scarcely visible stria (6—9) are found between each. Most specimens appear to be smooth. The areas are very high, especially the ventral one, with broad delthyrium and notothyrium. The pseudodeltidium is comparatively small, as is also the cardinal process. The «chilidal plates» are developed such as in *Sowerbyella*.

The ventral interior is dominated by the vascular impressions, and the muscles. The vascular system consists of a pair of vascula media, which are very thin, and directed posteriorly. It is only found in gerontic specimens. A strong pair of vascula (v. spondylaria) are parallel to them, but much broader. (Pl. 4, fig. 6 and textfig. 11 O). The vascula dentalia run from the anterior side of the muscle impressions, parallel to the hinge-line, and turn posteriorly, parallel to the margin of the valves .These vascula are very broad, with irregular, short branches with rounded ends. They are therefore supposed to

contain the ovaria. In old specimens these vascula meet the vascula spondylaria, so that a vascular arch is formed. In young specimens, only the vascula dentalia are developed. In older specimens, the vascula spondylaria are observed, and then the fusion of the vascula. The thin vascula media are only observed in highly gerontic specimens.

The muscle impressions are comparatively small, and tripartite, as for instance in *Sampo indentata*, and most other Leptestiinids. The teeth are strong, and accessory teeth, which were very small, have only been seen in a few specimens.

The dorsal interiors show the cardinal process, which is low, rounded and wide. The sockets are prominent, and those of the accessory teeth can be seen in most of the specimens. The branchial lamellae are large, with pointed anterior flanks, and they are radially striated, indicating that they consist of parallel pseudopuncta, such as in other Leptestiids. The median sulcus in the branchial lamella varies as to strength and width. The vascular system of the dorsal valve is only slightly impressed in the valve, and it seems to be similar to that of *Sampo indentata*.

Remarks: S. (*L.*) *oepiki* differs from S. (*L.*) *derfelensis* in the sculpture, convexity, and the size of the areas (cf. textfig. 19, G). The interiors are quite like, and the specimens are undoubtedly nearly related.

There are several different types of growth of this species in the material dealt with in this paper. One type, which is found in the Oslo—Asker district, is small, strongly convex, and distinctly triangular in young specimens. The other type which occurs in contemporaneous or slightly younger layers in the Hadeland district (and possibly Ringerike) is larger, not so convex, and with a more rounded outline. The two types are not separated into different species or subspecies, because the author is inclined to believe that the first type is an ecological form found in clay and clay-silt environment with little or no lime, and that the other type is restricted to marl and limestone environment. The first type is also in most cases accompanied by a microfauna (see below), while the second is found with a macrofauna.

Distribution: This species appears to be a good guide-fossil. It occurs in the zone 4ba in the Oslo—Asker, Ringerike and Hadeland districts. The small type seems to be restricted to the middle part

of the zone in the Oslo—Asker district, where it occurs together with *Steusloffia costata* and dalmanellids. The larger type is found in Hadeland, and possibly also in Ringerike, together with large Strophomenids and Orthids. Transitional forms are found in the more calcareous upper part of zone 4ba in the Oslo—Asker district, and in the middle part of the zone in Ringerike. It is also found in the Coelosphaeridium beds of the Ringsaker district. This species also occurs in the Lower Longvillian of Shropshire and Wales, together with i.a. *Eoplectodonta acuminata*.

Sampo (*Leptellina*) *elevata* sp. n.
Pl. 6, figs. 11—12.

Type data: The holotype, PMO 7513, is the cast of a ventral interior from the lower portion of zone 4ba at Gomnes—Rud, Ringerike district.

Diagnosis: Small *Leptellina* species with valves higher than long, and with a prominent marginal groove.

Material: 3 casts of the ventral interior, 4 complete, free specimens and some casts of exteriors and fragments.

Description: The holotype (pl. 6, figs. 11—12) is 7 mm wide and 4,5 mm long. This species is remarkable in being higher than it is long. The specimens are very small, and at the later stages of growth, the margin was almost hemicylindrical, flattening out at the latest stages of growth. In cross-section, the hingeline is found above the middle of the specimens. The vertically striated medio-marginal groove is slightly lower than the hinge-line. The muscle impressions are small, subpentagonal, rounded posteriorly. The areas are low, and the angle between them is generally less than 180°. The vascular system is similar to that of *S.* (*L.*) *oepiki*. The dorsal valve and the shell structure is unknown.

Remarks: This species is closely related to *S.* (*L.*) *oepiki*, but differs from it in the peculiar vertical growth. It is possible that further research may show that it is a subspecies of *oepiki*.

Small specimens of *S.* (*L.*) *elevata*, in which the marginal fringe is broken off, resemble species of *Leangella* and *Diambonia*. If a diaphragm is present in the dorsal interior, the species may be refered to the first genus with some doubt. Because of the absence of the

septum in the ventral interior, it cannot be a *Diambonia*. The vascular system is of the type found in *Leptellina*, indicating that the species should be referred to that subgenus.

Distribution: The species is with absolute certainty only known from the type locality, and zone 4bα. In other localities in the same zone in the Ringerike and Oslo—Asker districts, there are some specimens, which might be referred to this species. The marginal fringes are, however, at least partly broken off, and the specimens can therefore not be definitely determined. In this species, the vascular system (most of the vascula dentalia) is found in the part which is easily broken off.

Genus *Leptelloidea* JONES 1928
Subgenus *Benignites* HAVLICEK 1952, em. nov.
Leptelloidea (*Benignites* ?) *heintzi* sp. n.
Pl. 4 figs. 10—11.

Type data: The holotype is PMO 66651, the cast of a ventral interior from zone 4aα$_3$, at Ravaldsjøelven, Sandsvær/Eiker district.

Material: 4 ventral interiors, and some casts of the exteriors of valves.

Diagnosis: A small *Benignites* (?) species, with subtriangular outline, small, well defined muscle impressions in the ventral valve, diverging vascula spondylaria, and sometimes a small disc.

Description: A ventral valve of average size 7 mm wide and 4,5 mm long. The valves are moderately convex, and appear to be smooth, a feature which might be due to the mode of preservation of the specimens. The outline of the valves is somewhat variable, generally rounded triangular. The areas are comparatively low, with clearly visible chilidium. The ventral interior shows small muscle impressions, bluntly pointed posteriorly, and with strong vascula spondylaria diverging from their ends. In some interiors there is a small disc. but without a real geniculation. The dorsal interior is unknown. Judging from the pits found in the casts of the ventral interior, the shell structure was coarsely pseudopunctate. The shell substance itself is not preserved.

Remarks: This species resembles *L.* (*B.*) *llandeiloensis* as to the vascular system and shape, but it has no bilobed muscle impressions, and is much smaller. Except for the coarse pseudopuncta and the

disc, it is also quite like *Leangella*, although it is larger than usual for that genus.

L. (B.?) heintzi is interesting, being among the oldest species of this group of genera (*Leptelloidea* s.l.).

Distribution: In the zone $4aa_3$. In the type locality it is associated with *Trinucleus* cf. *foveolatus*, *Ogygiocaris dilatata dilatata* and small dalmanellids and ostracods.

Leptelloidea (s. l.) *rosendahli* sp. n.
Pl. 2, figs. 4—5, textfig. 11D.

Type data: The holotype, PMO 66984, is the cast of the interior of both valves, from the Coelosphaeridiumbeds, Fangberget, Ringsaker district.

Material: 2 complete casts of the interior of both valves, 6 ventral interiors (casts), and a number of casts of the exteriors of valves.

Diagnosis: Leptelloidea (s. l.) species with posteriorly pointed branchial lamellae, strong crural plates, ventral muscle impressions bounded by parallel lateral ridges, and with coarsely pseudopunctate valves.

Description: A specimen of average size is 6,5 mm wide and 6 mm long. The valves are strongly convex, with rounded triangular outline. Sculpture on the holotype consisting of about 16 ribs with indications of fine striae between them. In other specimens, these striae are stronger, almost of the same strength as the ribs. There are 4—5 between each rib. The areas are comparatively high, and concave. The delthyrium is broad, and the chilidal plates are developed just as in *Sowerbyella*.

The ventral interior shows the muscle impressions, which have parallel lateral sides. The adductor impressions is placed further in front, and is small. The boundaries of the muscle impressions are smooth laterally and spinose posteriorly. The teeth are small.

The dorsal interior shows the large, posteriorly pointed branchial lamellae, and very strong crural plates which seem to be double. The interior of the valve is striated longitudinally, and has a pair of vascula media between the branchial lamellae.

The shell substance is not preserved, but the pits in the casts show that the valves were coarsely pseudopunctate. In the middle

of the valves, the pseudopuncta were almost parallel to the surface, as for instance in *Christiania*.

The cardinal processes seem to be double in one of the dorsal interiors, in the other, this feature is destroyed. The presence of a double cardinal process is also known from *Leptelloidea* (?) *musca* ÖPIK (1933, pl. 6, fig. 2), and is probably a feature of less importance.

Remarks: This species differ considerably from all other species of the genus, especially in having pointed branchial lamella. *L. musca* ÖPIK has similar ventral muscle impressions, but the adductors are placed more posteriorly in *L. rosendahli*, and the branchial lamellae are also much larger, and more well defined than in *musca*. The shell structure is different too. Because of the absence of a diaphragm, and the coarse pseudopuncta, it cannot belong to *Leangella*.

The author has observed a dorsal valve from the Balclatchie Group of the Girvan district, Scotland, which is rather similar to that of *L. rosendahli*.

Distribution: *L. rosendahli* is found in the Coelosphaeridium zone of the Ringsaker district only. It has been collected from two localities in this district, and seems to be common in both.

Leptelloidea (s.l.) sp.
Pl. 4, fig. 5.

Material: One fragmentary cast of a dorsal interior, and a cast of a dorsal exterior.

Description: The exterior is 6 mm wide and 4 mm long. The interior was considerably larger, about 12 mm wide and 5—6 mm long. The valves are rather flat, and appears to be smooth. The branchial lamellae are turned outwards anteriorly, such as for instance *L. llandeiloensis*, and they are longitudinally striated. The crural plates are thin, short and rather high. The sulcus on the branchial lamellae is sharp and high. The specimens were thinshelled.

This species is mentioned here because of its stratigraphic occurence. The material is too limited for a specific determination.

Distribution: The two specimens were collected in the transitional layers between the zones $4a\alpha_4$ and $4a\beta$ in Muggerudkleiva, Sandsvær— Eiker district. This is an unusually low horizon for species of this type in Norway.

THE GENERA
Leangella ÖPIK 1933 AND *Diambonia*
COOPER & KINDLE 1936.

The type species of *Leangella* is *L. scissa* (SALTER) (The type selected by ÖPIK 1933 was *L. scissa* var. *triangularis* (HOLTEDAHL 1916). This form is identical with the typical *scissa*. The species described by ÖPIK (l.c.) as *L. triangularis* (HOLTEDAHL 1916), however, is another species. The type species of *Leangella* is therefore *L. scissa*).

The differences between *Leptelloidea* and *Leangella* are: the muscle impressions in the ventral valve have an indentated margin, and are elongate in *Leptelloidea* while they in *Leangella* are subcircular, and have a smooth margin. *Leptelloidea* also has open puncta while *Leangella* only has ordinary strophomenid pseudopuncta.

In the dorsal valve, *Leangella* has a diaphragm, which is not found in *Leptelloidea* and *Sampo*. The branchial supports are thicker in *Leangella*, and they are smaller than in most species of *Leptelloidea*, with the exception of *L. musca*, which probably is the ancestral form of *Leangella*.

The genus *Diambonia* was made to include species intermediate between *Leangella* and *Leptelloidea musca*. The ventral valve is largely similar to that of *L. musca*. The muscle impressions are in some species more elongate and diverging in *Diambonia*. The dorsal interior is similar to that of *Leangella*. A median septum is found in the ventral valve. ÖPIK (1933, p. 42) included one of the species now refered to *Diambonia* in *Leangella*, in spite of the median septum in the ventral valve. It therefore seems correct also to include species without this median septum in *Diambonia*.

The position of *Leptelloidea musca* is still uncertain. It is doubtful whether it should be included in *Diambonia* as defined here, or if it shall remain in *Leptelloidea*, as a deviating species of that genus. *L. (?) musca* is from the lower Middle Ordovician, *Diambonia* appears to be restricted to the Middle and Upper Ordovician, and *Leangella* is recorded from the Upper Ordovician and Silurian, with the exception of one species from the upper part of the Middle Ordovician of Norway (*L. hamari*).
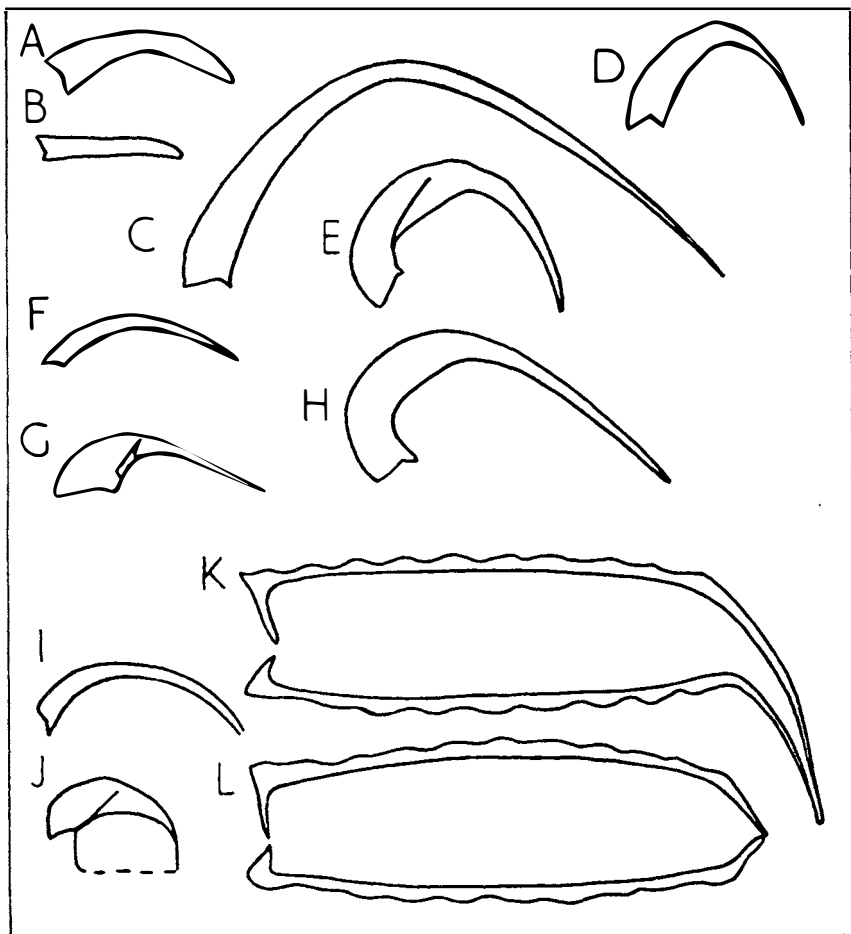
Fig. 19. Cross-sections of some Plectambonitid species. Magnification about 9/10. A. *Eoplectodonta acuminata* (HOLTEDAHL 1916), from zone 4bα in the City of Oslo, Oslo district. B. *Alwynella osloensis* sp. n. from zone 4aβ at Tåsen, Oslo district. C. *Eoplectodonta* (?) *rhombica* (McCOY 1852), from zone 4bδ in the Hadeland district. D. *Leptelloidea* (s.l.) *rosendahli* sp. n. from the Coelosphaeridium Beds of Brummundal, Ringsaker district. E. *Sampo* (*Sampo*) *indentata* sp. n. from zone 4bγ at Hvalstad, Asker district. F. *Sowerbyella serica askerensis* subsp. n. from the Lower part of zone 4bγ at Hvalstad, Asker district. G. *Sampo* Leptellina) *oepiki* WHITTINGTON 1938, from the middle part of zone 4bα in the City of Oslo, Oslo district. H. *Eoplectodonta* (?) *percedens* (HOLTEDAHL 1916). from zone 4bβ at Arnestadtangen in the Asker district. I. *Sowerbyella sericea*

Diambonia (?) *leifi* sp. n.

Pl. 2, figs. 9—11.

1916 *Plectambolites convexa* PANDER 1830 — HOLTEDAHL, p. 78,

pl. 14, fig. 9.

Type data: The holotype, PMO 57536, is the cast of a dorsal interior from 18 m above the base of the Mastopora zone, just N. of the pier at Stranda, Frierfjord, Langesund—Gjerpen district.

Material: 43 casts of valves, 3 of the dorsal and 12 of the ventral interior.

Description: Small, strongly concave-convex species. Three specimens are 7,5—6,5—5,5 mm wide, and 4,0—4,5—4,5 mm long. Ventral area high, triangular with open delthyrium. Dorsal area low, subparallel. The sculpture is only seen on a few specimens. Generally it is not preserved, because of the contactmetamorphosis of the rocks in which the specimens occur. When preserved, the sculpture consists of a number (about 3—4) striae. No radii can be seen on the material available. The outline of the specimens is generally subtriangular, with sharp cardinal angles. Some with a more rounded outline and right cardinal angles does also occur. In some specimens the diaphragm in the dorsal valve is reflected as a faint ridge on the exterior of the valves.

The dorsal interior has a pair of sharply pointed, triangular branchial lamellae, a median septum and a complex, not bifid cardinal process. The socket plates are parallel to the hinge-line. There is a distinct diaphragm parallel with and near to the margin of the valves.

The ventral interior is similar to that of *L.* (?) *musca* (ÖPIK 1933, pl. 6, fig. 3, textfig. 15) as to the shape of the muscle impressions. However, in most specimens there is a groove corresponding to the diaphragm in the dorsal valve.

The shell-structure is unknown, because of the state of preservation of the material. No traces of pseudopunctae or punctae can be seen in the casts, as was the case with *Leptelloidea* (?) *musca*, but this might be due to the coarse surface of the cast.

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soudleyensis JONES 1928, from the Mjøsa Limestone, at Helgøya, Hamar—Nes district. J. *Leangella hamari* sp. n. from the Cyclocrinus Beds at Furuberget, Hamar—Nes distrikt. (cf. textfig. 18). K, L. *Ptychoglyptus valdari* sp.n. from zone 4bα at Billingstad, Asker district. L. is a large, normal specimen, and K. is a specimen with dorsalwards geniculation.

Remarks: This species was referred to *Plectambonites convexa* PANDER by HOLTEDAHL because of its similarity to material so labeled from the Kurkuse beds. However, these Esthonian specimens belong to *Leptelloidea (?) musca*.

The ventral interior of *Diambonia (?) leifi* is similar to that of *Leptelloidea (?) musca*, except for the teeth being slightly stronger in *L. (?) musca*, and the ventral area being considerably higher in *Diambonia (?) leifi*. It differs from all other species of *Diambonia* in not having a median septum.

The dorsal valve differs from those of most Diambonias and Leangellas in the branchial lamellae being far apart, so that the low median septum is placed between the lamellae, without being fused to them, as in *L. (?) musca* and other species. In this feature *Diambonia (?) leifi* resembles *Leptelloidea (?) etheridgei* (REED 1917). This species, however, has no diaphragm, and the ventral interior is quite different.

Because of the structure of the branchial lamellae and the diaphragm, *Diambonia (?) leifi* cannot be referred to *Leptelloidea* (or *Sampo*), and it cannot be included in *Leangella* because of the shape of the ventral muscle impressions. It is referred to *Diambonia*, but the sharp separation of the branchial lamellae, and the absence of a median septum in the ventral valve makes it uncertain whether this is correct.

Distribution: In the Langesund—Gjerpen district only. It ranges from the upper part of the Bryozoan zone to the top of the Mastopora layers.

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Diambonia anatoli sp. n.

Pl. 2, figs. 6—8, texfig. 11R.

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Type data: The holotype, PMO 66985, is the cast of a dorsal interior from zone 4b*a*, in a roadside section just N. of Halsen, Nesøya, Oslo—Asker district.

Material: 4 casts of the dorsal interior, 12 of the ventral interior and a large number of casts of the valves, and partly exfoliated valves.

Description: An adult specimen of average size is 5 mm wide and 4 mm long. The specimens are strongly concave-convex, of variable shape, mostly rounded triangular. Ventral area low triangular, delthyrium narrow, 45°, the development of the pseudodeltidium depends on the age of the specimen, being hardly visible in young ones, and large in the older. The dorsal area is rectangular and com-

paratively high. Chilidal plates small, cardinal process trifurcate. Both areas are slightly concave, the angle between them is about 180° in young specimens, and considerably less in older ones.

The sculpture consists of 5—7 radii. Striae are only faintly indicated on a few specimens.

The ventral interior is dominated by the diverging muscle impressions, the border of which is dentated in most specimens. The adductor muscle impressions are elongated pyriform. There is always a median septum, but it varies as to length and depth. In old specimens it tends to be flatly wedge-shaped. In most specimens there is a groove parallel to the margin of the shell, corresponding to the diaphragm of the dorsal valve. One gerontic valve has a strong, smooth bounding ridge around the muscle impressions, and a very narrow adductor impression. In this it resembles *Leangella*, but it differs from it in the elongated outline of the diverging muscle impressions. The vascular system is remarkably similar to that of certain dalmanellids (textfig. 11R). It consists of two pairs of main vascula, the v. dentalia, which have two large branches, and v. spondylaria. All four vasculae branch frequently without forming a vascular arch. No ovarian impressions are found.

Dorsal interior with coherent branchial lamellae with a strong median sulcus, and rounded outline. Socket plates strong, highest at the ends. Diaphragm strongly developed, placed comparatively far from the margin. It has a slightly more triangular outline than the valve.

Remarks: Diambonia anatoli differs from *D. gibbosa* (WINCHELL & SCHUCHERT), the type species, in having a shorter median septum, and from *D. septata* (COOPER) in having no spines on the diaphragm and narrow, long and diverging muscle impressions.

Distribution: This species is found from several localities in zone 4ba in the Oslo—Asker district. It is also found in the same zone in one locality in Ringerike.

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Leangella hamari sp. n.

Pl. 2, figs. 1—3, textfig. 19J, 20.

</div>

Type data: The holotype, PMO 37879, is an etched complete specimen from the Cyclocrinus Shale of Furuberget, Hamar—Nes district.

Material: 32 free specimens, some of them etched to show the interiors, one cast of the dorsal interior, and a large number of valves in rock.
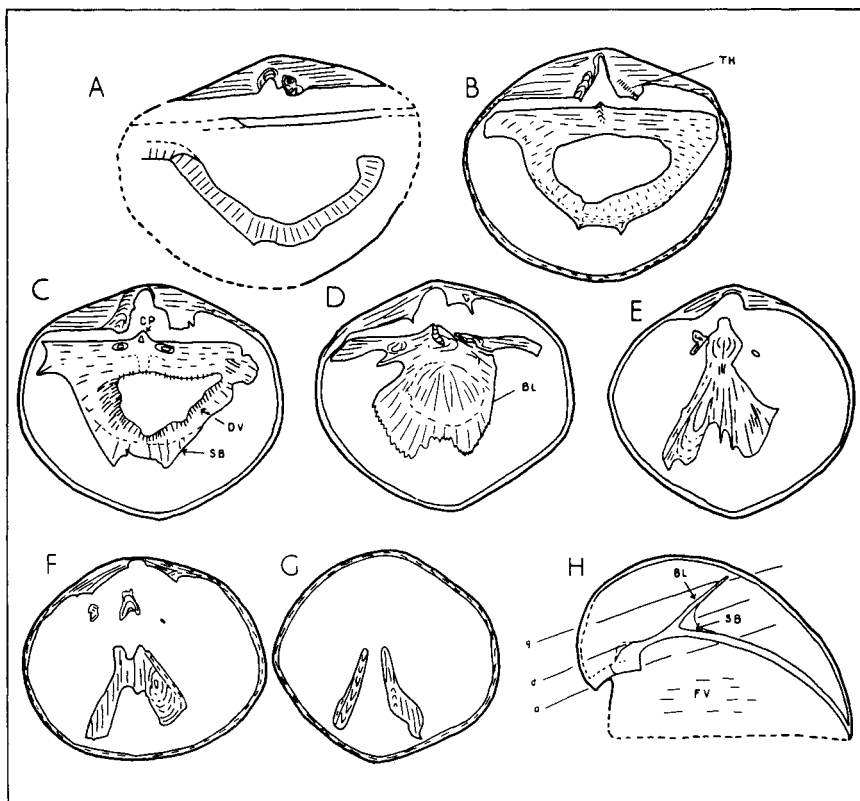
Fig. 20. *Leangella hamari sp. n.* A—G, 7 parallel sections of a specimen. The approximate position of the sections are shown in fig. H (a—d—g). H. Longitudinal section of another specimen. The ventral flange (FV) is not visible in the section, and is indicated by a broken line in order to show the outline of the specimen.

    Both specimens are from the Cyclocrinus shale, at Furuberget, Hamar— Nes district.

    Abbreviations. BL = Branchial lamella. CP = Cardinal process. DV = External surface of dorsal valve, with fine striation. FV = Lateral ventral flange. SB = Supporting tissue in connection with the branchial lamella. TH = Teeth.

Description: A specimen of average size is 7 mm wide and 5,5 mm long. The valves are rounded triangular in outline, strongly concave-convex. Ventral area low, triangular, the delthyrium has an apical angle of about 90°. Dorsal area rectangular, low, both areas

strongly concave. The sculpture consists of a large number of striae (18—22) with 5—7 radii between each.

The ventral interior has small, rounded muscle impressions bounded by a smooth ridge. The dorsal valve has branchial lamellae with two sharply pointed ends, each supported by a septum, as in the specimen of *Leangella scissa* figured by JONES (1928, pl. 25, fig. 10). There is a strong diaphragm near the margin of the valve.

The shells are pseudopunctate. The numerous, comparatively large puncta are arranged in radial rows.

Remarks: This species is a typical *Leangella*, as indicated by the muscle impressions in the ventral valve, and the shape of the branchial lamellae and the diaphragm in the dorsal one. It is rather like *L. scissa*, the type species, from which it differs as to the sculpture (more striae), and in addition to the ventral muscle impressions being smaller, and the diaphragm being placed closer to the margin of the valves. It differs from other species of *Leangella* in the shape of the branchial lamellae, and the outline of the diaphragm.

L. hamari is the oldest typical *Leangella* species known. *L. scissa* is recorded from the uppermost Ordovician, and the other members of the genus are known from the Lower and Middle Silurian. However, a dorsal interior, similar to that of *L. hamari* has been collected by the author in the Balclatchie Group in the Girvan district, Scotland.

Distribution: In the Cyclocrinus Shale in the Hamar—Nes district exteriors of *Leangella*-like brachiopods are found in a large number of localities in the Oslo Region, but only those which can be determined with absolute certainty are included here. Further collecting will definitely extend our knowledge of the distribution of the three last mentioned species.

Subfamily *Sowerbyellinae* ÖPIK *1930.*

As defined here, this subfamily comprise Sowerbyellidae with a dorsal foramen (= Sowerbyellen-grube of ÖPIK 1933), which may be atrophied in some young specimens, simple teeth, a double ventral cavity, and generally without raised branchial lamellae.

Two, or three lineages are found in this subfamily. The first one is that of the genus *Sowerbyella* itself. In this paper it is restricted to species with branchial lamellae bordered by radially arranged,

more or less flatly inclined pseudopuncta. There is generally a pair of submedian septa. The earliest representative of this lineage is *Sowerbyella llandeiloensis* WILLIAMS (1949)[1]. Other typical members are *S. sericea* with sub-species, and *S. semiluna* ÖPIK. *Eochonetes advena* REED, *S. ringsakerensis*. *Eoplectodonta* (?) *rhombica* (McCOY) and *E.* (?) *percedens* HOLTEDAHL may also belong to this lineage. They differ from the typical members in having denticulated hingelines of different structure.

The second Sowerbyellind lineage consists of species with branchial lamellae bounded with oval, smooth ridges, not composed of pseudopuncta. There are seldom septa between the lamellae, but they are divided by a diagonal vascular septum or groove. If it looks as if the median septa are present, it is in most cases the median margin of the branchial lamellae, which is elevated. In some younger species, both margins are raised, so that the species has 6 septa. In contrast to the previously mentioned group, most of these species have a denticulated hingeline of an uniform type. The structure of these denticulations are described below (cf. *Eoplectodonta acuminata*). The earliest representative of this lineage, is «*Sowerbyella*» *antiquata* JONES[2], and other members are some from the «*S.*» *rhombica* and *quinquecostata* groups, and most species which previously were grouped under *Thaerodonta* WANG, *Plectodonta* and *Eoplectodonta*. The difference between the two latter genera lies in the development of the branchial lamellae, which are level with the surface of the valve in *Eoplectodonta*, and have strongly elevated lateral margins, while they are pointed laterally in *Plectodonta*. *Thaerodonta* WANG (1948) was founded on species which were supposed to have denticles in the dorsal valve, and sockets in the ventral. It was assumed that the opposite was the case in *Plectodonta* and *Eoplectodonta*. The author's studies has shown that there are denticles both in the dorsal and ventral valves in all these genera,

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[1] As mentioned below, *S. antiquata* JONES might belong to another lineage. *S. llandeiloensis* (= *S. antiquata llandeiloensis*) WILLIAMS (1949) is therefore regarded as being a separate species, provisionally including the older forms of the genus, with less developed interior.

[2] As figured by JONES (1928, pl. 21, fig. 11). Another species also appears to have been described under this name, since specimens with a dorsal interior like *S. llandeiloensis* have been included in this species. If therefore a lectotype is not chosen, the author select the specimen figured by JONES 1928, pl. 21, fig. 11 as the lectotype of «*S*» *antiquata*. (Sedgwick Museum nr. A 32152b).

and the sockets are merely the interspaces between the denticles. *Thaerodonta* must therefore be regarded as a synonym of *Eoplecto-donta* as defined here.

Beside these typical lineages, two minor groups are also included in this subfamily, although it is not certain whether this is correct. The first one is *Chonetoidea*, which differs from the typical members as to the structure of the branchial lamellae, which consist of two arches of very large pseudopuncta. The structure of these lamellae is not unlike that of the *Sowerbyella*-group, but the pseudopuncta are much larger and fewer. The dorsal foramen is not known from this genus. The double ventral cavity found in all species of *Chonetoidea* (pl. 2, figs. 21—22), is a feature which points towards placing it in the Sowerbyellinae. According to ÖPIK (1933) has *Aegiria*, with well developed and raised branchial lamellae, developed from *Chonetoidea*. However, the trend of development in *Chonetoidea* is from older species with well defined branchial lamellae to younger ones without them. *Aegiria* also seems to lack the double ventral cavities. *Sericeoidea* LINDSTRÖM 1952, might, however, be included in the group without doubt, either as a subgenus of *Chonetoidea* or as an independant genus.

The other minor group consists of the new genus *Alwynella*, which has a dorsal interior largely similar to that of *Eoplectodonta*, but with unpaired ventral muscle impressions, a feature which distinguishes it from most Strophomenids. Since the genus is so old (Llandvirn—Llandeilo), it is natural to suppose that this is a primitive feature.

It is too early to decide whether the two major groups of this subfamily, that of *Sowerbyella*, *Eochonetes* and *Chonetoidea*, and that of *Plectodonta*, *Eoplectodonta* and *Alwynella* are monophyletic or not. At their first, contemporaneous appearance (zone of *Did. geminus*) they are quite distinct, and no intermediate forms have been found in younger layers. On the other hand, the peculiar structure of the dorsal foramen and the double ventral cavities indicates a common origin.

Genus *Alwynella* gen. nov.

Type species: Alwynella osloensis sp. n., from zone 4aβ in the Oslo Region.

Diagnosis: Sowerbyellinids with simple, not bilobed ventral
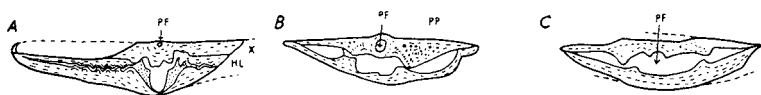
Fig. 21. *Alwynella osloensis sp. n.* A—C, 3 parallel sections of one specimen, showing the dorsal foramen (PF), and the denticulated hinge-line. The specimen is from the lower part of Zone 4aβ, at Ildjernet, Oslo district.

Abbreviations: DE = Denticles of the hinge-line. HL = Hinge-line proper. PF = Dorsal foramen. PP = Pseudopunctae. X = Line of junction of the valves. (external).

muscle impression, dorsal valve with large foramen, small, elevated branchial lamellae median septum and crenulated hinge-line.

Distribution: Upper Lower to Lower Middle Ordovician (zones $4a\alpha_1$—$4a\beta$).

Remarks: In spite of the unlobed and probably primitive structure of the ventral muscle impressions, *Alwynella* is included in the Sowerbyellinae because of the dorsal interior being of the same structure as in this subfamily.

Besides the type species, *Alwynella* includes *A. ildjernensis* sp. n. and *A. intermedia* sp. n. It does not look as if any of the previously described species will have to be included in the genus. Some of the specimens figures by JONES (1928, pl. 21, fig. 11) as *Sowerbyella antiquata* apparently belong to *Alwynella* or an early member of the *Eoplectodonta*-group. The latter possibility seems the more probable, since the species has two ventral muscle impressions, instead of one in *Alwynella*. «*S.*» *antiquata* might also represent an intermediate stage between *Alwynella* and *Eoplectodonta*.

Alwynella osloensis sp. n.
Pl. 1 figs. 5, 9, 14, textfigs. 19B, 21.

Type data: The holotype, PMO 66940, is a cast of a dorsal interior from zone 4aβ at Tåsen, Oslo district.

Material: 16 casts of interiors, 8 casts of exteriors, and about 50 complete specimens and valves in rock.

Diagnosis: Alwynella species with acute cardinal angles, slightly differentiated sculpture, large, rounded branchial lamellae. Hinge-line denticulated for about 1/2 to 1/3 of the length in adult specimens.

Description: A specimen of average size is 10 mm wide and 4 mm long. Sculpture consisting of coarse, subequal ribs. Cardinal angles acute. Growth distinctly allometric, young specimens have a higher width/length ratio than the older ones (cf. p. 56). Areas high, triangular. The dorsal one is higher than the ventral, with a large subapical foramen. This opening (cf. textfig. 21) pierces the dorsal valve just behind the socket plates, and is quite big. Serial sections (textfig. 21) prove that the foramen really exists and that it is not merely a deep notothyrial cavity.

Branchial lamellae strong, elevated and evenly circular in outline. A median septum is found between them. The hinge-line is crenulated by denticles which do not appear to be transformed pseudopuncta, since they do not have a central axis. The real teeth are much larger than the denticles, which occur both in the dorsal and ventral valve. The ventral muscle impression is not bilobed, and it is deeply impressed. The shell substance is pseudopunctate, with puncta of moderate size.

Remarks: The difference between this species and *A. ildjernensis* and *A. intermedia* are the shape of the valves, the outline of the branchial lamellae, and the amount of crenulation of the hinge-line. The exterior is quite similar to that of *Grorudia grorudi*, which occurs in the same beds. They might be discriminated by the growth-lines (cf. p. 57, and textfig. 16). The interiors are also quite different.

Distribution: *A. osloensis* is a guide fossil for the zone $4a\beta$, at least in the Oslo—Asker district. It is also found in the Ringerike district, and probably in Langesund—Gjerpen and Hadeland. From the two latter districts only exteriors are known, so that the identity of the specimens could not be ascertained.

A. osloensis ranges from the very base of zone $4a\beta$, where it overlaps with *A. intermedia*, to the top of the zone, where it does not seem to occur in the transitional layers to zone $4ba$.

Alwynella intermedia sp. n.
Pl. 1 figs. 15—16.

Type data: The holotype is PMO, 66935, a dorsal valve from the transitional layers between zone $4a\alpha_4$ and $4a\beta$ at the NW-ern end of Ildjernet, Oslo district.

Material: 3 dorsal and 2 ventral interiors, and some (about 25) exteriors of valves.

Diagnosis: Alwynella species with right cardinal angles, branchial lamellae which vary as to shape and size, generally rounded triangular.

Description: Thick, robust valves with right cardinal angles. An average specimen is 8 mm wide and 3,5 mm long. Sculpture coarse, in some cases every other rib is stronger than the rest. The areas are high, the ventral one higher than in the other *Alwynella*-species. The ventral interior is similar to that of *A. osloensis*. Because of the heavily calcified valves, the marginal restriction of the body-space found in gerontic specimens of other species is found also in ordinary adult specimens of *A. intermedia*. The dorsal interior has branchial lamellae intermediate between those of *A. osloensis* and *A. ildjernensis*. Generally they show a closer resemblance to those of the latter, being triangular.

Remarks: As indicated by the name of this species, it is intermediate between the two other species of the genus. Further studies may prove that it is not a valid species, but only a transitional form between the two others. The right cardinal angles, however, seem to indicate that *A. intermedia* is a separate species. As was the case in the two other species, the growth-lines indicate that the width/length ratio was larger in the young specimens.

Distribution: A. intermedia is found in the transitional layers between zone $4a\alpha_4$ and $4a\beta$ in the Oslo—Asker district. The species is only found in a few localities, and appears to have a very restricted stratigraphical range, probably less than 2 m. In all localities it seems to be accompanied by *Ogygiocaris dilatata sarsi* and *Reedolithus carinatus*.

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Alwynella ildjernensis sp. n.
Pl. 1, fig. 6.

</div>

Type data: The holotype, PMO 66928, is the cast of a dorsal interior from the lower part of zone $4a\alpha_4$ at the NW-ern side of Ildjernet, Oslo district.

Material: About 100 casts and valves in rock.

Diagnosis: Alwynella species with acute cardinal angles, coarse sculpture, small, triangular branchial lamellae and 2/3 of the hinge-line denticulated in adult specimens.

Description: An adult specimen of average size is 9 mm wide and 3,5 mm long. The sculpture is coarse, with ribs of nearly equal size. Cardinal angles very acute in adult specimens. Growth-lines indicate that the cardinal angles of the younger specimens were considerably less acute, in some cases almost 90°.

Areas triangular, the ventral one low, the dorsal one much higher, with a large, open foramen at the apex.

The ventral interior can not be distinguished from that of *A. osloensis.* Dorsal interior with small, triangular branchial lamellae and high, thin median node. Teeth and cardinal processes like those of *A. osloensis.*

Remarks: A. ildjernensis differs from *A. osloensis* as to the shape of the shell (which has more acute cardinal angles), as to the outline and size of the branchial lamellae, and partly also as to the amount of denticulation of the hinge-line. The latter feature can only in few cases be used to determine the species, as the material is seldom well enough preserved to show the real amount of denticulation without making a thin section.

Distribution: A. ildjernensis is found in the zones $4a\alpha_{2-4}$ in the Oslo—Asker and Sandsvær—Eiker districts. It might occur in other districts too, but no specimens which can be definitely discriminated from *A. osloensis,* have been found.

This species ranges through a considerable period of time, and a number of different sediments without any noticeable change. It occurs in graptolitic shales, mudstones, muddy siltstones and calcareous mudstones and siltstones. The specimens found in calcareous rocks have a tendency towards having thicker shells than those occuring in noncalcareous rocks.

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Genus *Sowerbyella* Jones 1928

Sowerbyella sericea soudleyensis Jones 1928

Pl. 3, figs 1—4, pl. 6, textfigs 19, I and 22

</div>

1916 *Plectambonites sericea* (Sow.) — Holtedahl (parte), p. 81, pl. 14, figs 1—3.
1928 *Sowerbyella sericea soudleyensis* var. nov. — Jones, pp. 417—418, pl. 21, figs. 5—6.

Material: More than 50 dorsal interiors, 70 ventral ones, and a large number of exteriors.

Description: The specimens are rounded rectangular in outline, slightly convex, and of moderate size (see diagram, textfig. 22). The
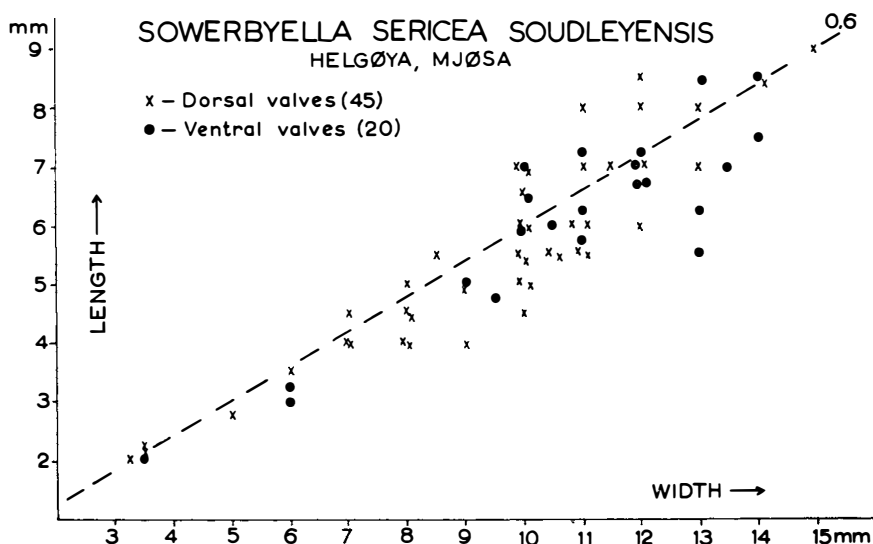
Fig. 22. Diagram showing the variation is size of specimens of *Sowerbyella sericea soudleyensis* JONES 1928, from the Mjøsa Limestone at Helgøya, Hamar —Nes district. The dorsal valves are from the slab figured by HOLTEDAHL (1916, pl. 14, fig. 3, PMO L0085), and the ventral ones are from HOLTEDAHL, pl. 14, fig. 2, (PMO 66977). The dorsal and the ventral valves belong to two different populations.

sculpture is hardly differentiated, with one or two finer striae between each stronger one. The cardinal angles are right or slightly less in adults, and about 60—70° in young specimens. The areas are in one plane in all but gerontic specimens.

The ventral interior shows the diverging muscle impressions with a median septum between them, comparatively strong teeth, and deep ventral cavities, one on each side of the median septum. The muscle impressions are small, and bounded by sharp, smooth ridges.

The dorsal interior shows the wedge-shaped branchial impressions, which are divided into two unequal parts by a pair of vascular grooves. The median borders of the branchial lamellae are raised, forming two slightly diverging septa. The chilidal plates are strongly developed, and the dorsal foramen is large, but does not penetrate

the valve. Just as in most other *Sowerbyella* species, the pseudopuncta visible on the interior surface of the valve, are largest around the branchial lamellae, and decrease in size towards the margin. The hinge-line is straigth, and slightly raised, and the margin is thickened in all adult specimens.

A number of young specimens show the development of this subspecies. The outline changes from subtriangular or hemicicular in the young specimens to rounded rectangular in the adult ones. The ratio Width/Length is remarkably constant during the growth of this species (cf. textfig. 22). Most other brachiopod species have allometric growth. The convexity increase slightly with age. In very small specimens (pl. 3, fig. 2), the median septum and the ventral cavities are found in the ventral interior. The youngest dorsal interiors (pl. 3, fig. 1) show a strongly developed dorsal foramen and chilidal plates, and the two median septa of the branchial lamellae are always present. In the youngest specimens, the external sculpture is found in the interior. In the dorsal valve the branchial septa seem to be continons with the ribs of the sculpture. In young specimens, the pseudopuncta are arranged in radial rows, which seem to continue into a rib of the external sculpture.

Remarks: S. s. *soudleyensis* differs from the subspecies *askerensis* and *hadelandica* in having a marginal thickening of the valves, and in having wedge-shaped triangular branchial lamellae instead of oval ones. The sculpture is also more clearly differentiated in the other two subspecies. According to JONES (1928, p. 418), the subspecies *soudleyensis* differs from the typical subspecies in always being smaller, and having a marginal thickening, and in the shape of the branchial lamellae (rounded in *sericea*, triangular in *soudleyensis*), and the size of the ventral muscle impressions which are smaller and shorter in *soudleyensis*.

Distribution: In Norway this subspecies is very common in the Cyclocrinus zone in the Hamar—Nes district, in Toten, and the northern part of Hadeland. Some specimens from the corresponding layers in the Langesund—Gjerpen district might belong to this species, or to S. *ringsakerensis*. The subspecies may probably also be found in the corresponding layers in the Sandsvær—Eiker district, but no interiors are preserved.

In the Ringsaker district it is represented by S. *ringsakerensis*,

which is quite similar, and in the Oslo—Asker and Hadeland districts by *S. s. askerensis* and *S. s. hadelandica*.

In Great Britain it is found in the Horderley Sandstone in Shropshire, and probably in N. Wales (JONES 1928, p. 418).

Sowerbyella sericea askerensis subsp. n.
Pl. 6, fig· 5, texstfigs. 11 J and 19F.

Type data: The holotype, PMO 66954, is the cast of the interior of a ventral valve from the lower part of zone 4bγ, N. of Hvalstad st. Asker district.

Material: 11 ventral interiors, 4 dorsal ones, and a large number of casts of the exterior of both valves.

Diagnosis: Subspecies of *Sowerbyella sericea* with well differentiated sculpture, slight convexity of the valves, high width/length ratio (more than 3). Ventral muscle impressions short, no marginal thickening of the valves.

Description: A comparatively small species with slightly convex valves and long hinge-line. A specimen of average size in 15 mm wide and 4,5 mm long. The width/length ratio is generally between 3 and 3,5. The sculpture consists of numerous ribs, about 1 mm between each at the margin, and 3—5 fine striae between each rib. The areas are high, and the pseudodeltidium and chilididal plates are developed in the same way as in most Sowerbyellas.

The ventral interior shows small muscle impressions, wide ventral cavities and usually a well developed vascular system. The branching is variable, in some specimens the main vascula send off a number of branches at almost 180° just in front of the muscle impressions, and in others the vascula bifurcates at a smaller angle, and nearer to the margin of the valve.

In the dorsal interior the branchial lamellae are oval in the adults, and wedge-shaped, radially striated in the young ones. The whole interior is covered with coarse pseudopuncta and the chilidal plates and the dorsal foramen are strongly developed. No crenulations are found at the hinge-line.

Remarks: Sowerbyella sericea askerensis resembles *S. s. sericea* as to size and ventral interior, and differs from it in the sculpture, convexity and the more clearly differentiated branchial lamellae in

the dorsal valve. It differes from the other subspecies of *S. sericea* as to shape, size, ornamentation, and in having no marginal thickening.

The subspecies of *Sowerbyella sericea* mentioned here differ from one-another as to sculpture, shape, and in having a marginal thickening or not. All these features may be influenced by the environment, obviously *S. s. soudleyensis* which has coarse sculpture, lived in a siltstone environment, while the finely sculptures *S. s. askerensis* and *hadelandica* lived in a calcareous-muddy environment. It might therefore be more correct to regard them as ecological or geographical races rather than subspecies.

Distribution: This subspecies is found in the Asker district, mainly in the upper part of zone 4bγ. No specimens which with certainty can be identified as belonging to this subspecies, have been found in other districts.

Sowerbyella sericea hadelandica subsp. n.
Pl. 4, figs. 7, 7.

Type data: The holotype, PMO 67138, is the cast of a dorsal interior from the Lower Cyclocrinus Beds in a section between Jonsrud and Stensrud in the northern part of Hadeland.

Material: 3 dorsal interiors, 15 ventral ones, more than 50 complete specimens, and a large number of valves and fragments of valves.

Diagnosis: A *Sowerbyella sericea* subspecies with well differentiated sculpture, strongly convex valves, and triangular outline.

Description: Outline rounded triangular, valves strongly convex and high, sculpture consisting of 10—13 ribs with about 7 striae between each. The size and proportions of the specimens are somewhat variable, one specimen is for instance 15 mm wide and 9 mm long, and another 13 mm wide and 11 mm long. The areas meet under a large angle (140—160°), the dorsal one is generally in the plane of junction of the valves.

The interior is similar to that of *S.s. sericea*, with rounded branchial lamellae, and with a long median septum between the ventral muscle impressions.

Remarks: This subspecies differ from the others described here as to outline of the valves, and sculpture, and from *askerensis* in

having a long median septum in the ventral valve. See also remarks to the other subspecies.

Distribution: S. s. *hadelandica* is found in the Lower Cyclocrinus Beds in the northern part of Hadeland, where it is very common. Some specimens from the southern part of that district, and from Ringerike, may belong to this subspecies. However, no interiors have been found from these areas. It is worth mentioning that this species externally resemble *Sampo (Leptellina) oepiki,* and these two occur together in some localities.

Sowerbyella ringsakerensis sp. n.
Pl. 6 figs. 1—4.

Type data: The holotype, PMO 66951, is the cast of a dorsal interior from the Coelosphaeridium beds between Tørud and Bratberg, Ringsaker district.

Material: About 20 casts of the dorsal interior, and 6 of the ventral, and a large number of casts of the exterior.

Diagnosis: A small *Sowerbyella* species with sculpture and interior like that of *S. sericea sericea,* apart from that it has a number of large pseudopuncta, forming nodes along the hinge-line. These decrease in size towards the notothyrium.

Description: An average adult specimen is about 13 mm wide and 7 mm long. The specimens are small, moderately convex with hemicircular to trapezoidal outline.

The interior is largely similar to that of *S. sericea sericea,* with comparatively large muscle impressions and a median septum in the ventral valve, and oval branchial lamellae in the dorsal. Just as in young specimens of *sericea sericea* and in *sericea soudleyensis,* the formation of the branchial lamellae start with two median septa, each forming the medianmost side of the lamellae, which are badly defined and triangular in the young specimens (and in the adults of *S. s. soudleyensis*). Later the lateral borders of the lamellae are formed, but still the median septa are much stronger than the rest of the lamellae. Occationally (pl. 6, fig. 1) a median septum is found between the two ordinary ones. Most probably it is an intervascular septum, dividing the two median vascula. It is not a constant features, and except in young specimens, it is much lower than the branchial septa.

The dorsal foramen seems to be only slightly developed in this species. It is considerably smaller than in *S. sericea*. Instead, the inner surface of the chilidal plates are united with secondary tissue in adult specimens. The foramen appears as a thin furrow in the notothyrial floor.

The denticulation of the hingeline consists of large pseudopunctae, decreasing in size from the cardinal angles towards the notothyrium. They are described on p. 21.

Remarks: This species differ from all other species of the genus in having these nodes on the hinge-line. They are known also from another species, *Sowerbyella* sp. of SCHMIDT (1951, pl. 51, fig. 8). If it was not for the nodes, *S. ringsakerensis* would definitely have been a subspecies of *S. sericea*. It is remarkable that this species is more highly developed when it comes to the structure of the branchial lamellae, than the later *S. s. soudleyensis*.

Distribution: This species is found in the Coelosphaeridium Beds in the Ringsaker district, where it appears to be very common, at least in some localities. A considerable material has been found in the lowest part of the Encrinite Limestone of the Langesund—Gjerpen district. The interiors are not well preserved. They are all of the *S. sericea*-type, but no nodes can be seen. The trapezoidal shape of some of the specimens might indicate that some of them are *S. ringsakerensis*. The horizon is the same as the one with the rich layers with *S. s. soudleyensis* at Mjøsa. Without better material it is impossible to tell which form occurs at Langesund.

Sowerbyella (?) sp.

Material: About 15 exteriors of valves, mainly of the ventral ones.

Description: A small species, moderately convex, with sharp cardinal angles. It is much wider than it is long, the largest specimen present being 15 mm wide and 6 mm long. The sculpture consists of fine ribs with 4—7 striae between each. Some distinct concentric rugae are present near the hinge-line, strongest at the umbo. In the ventral valve there is a pair of diverging ridges with a shallow sulcus between them. These ridges are very prominent in some species, and not so marked in others. The interiors are not known.

Remarks: The diverging ridges found in this species distinguish it from all others in the Oslo Region. It is quite similar to *Sowerbyella sublobata* (REED 1917, pl. 14, figs. 20, 23), but differs as to sculpture and size. As long as the interior is not known there is no reason to give it a separate specific name.

Distribution: In zone 4bγ in the Ringerike district.

Genus *Eoplectodonta* (KOZLOWSKI 1929).
Eoplectodonta acuminata (HOLTEDAHL 1916.
Pl. 3, figs. 6—12, textfigs. 19A and 23.

1916 *Plectambonites trabeata* LINDSTR. var. *acuminata* n. var. — HOLTEDAHL
          pp. 79—80, pl. 14, figs. 6—7.
1916 *Plectambonites* sp. — HOLTEDAHL, p 80, pl. 14, fig. 8.
1917 *Plectambonites sericea* var. *semirugata* n. var. — REED, p. 884, pl. 15,
          figs. 18—26.
1928 *Sowerbyella semirugata* (REED) — JONES, p. 464.
1938 *Sowerbyella sericea* (J. de C. SOWERBY) var. nov. *brynensis* — WHITTING-
          TON, pp. 253—255, pl. 11, figs. 6—9.

Type data: The lectotype, chosen here, is PMO 5279, the cast of the exterior of a dorsal valve and both areas. The specimen was figured by HOLTEDAHL (1916, pl. 14, fig. 7) and is figured in this paper, pl. 6, fig. 11. HOLTEDAHL gives 4b as the horizon, and «City of Oslo» as the type locality. A restudy of the labels and the accompaning fauna shows that the specimen come from zone 4bα (associated with *Sampo* (L.) *oepiki* and *Steusloffia costata*) and that the type locality is the site of the Royal Palace in Oslo. This locality is not longer accessible and the specimens were probably collected more than 100 years ago, when the Palace was being built.

Material: More than 50 ventral interiors, more than 30 dorsal ones, and a very large number of exteriors and complete specimens.

Description: Slightly convex to almost flat species, with sharp cardinal angles. An average specimen is 17 mm wide and 9 mm long. The areas are of about equal size, and the angle between them is 150—120°. The sculpture generally consists of 11—13 ribs with 8—10 striae between each of them. A number of concentric rugae are found, especially near the hinge-line. The strength of the rugation varies. It is found in all specimens, and is prominent and continuous in most

of them. In most adult specimens there is a slight marginal thickening of the valves.

The ventral interior has small, rhomboidal muscle impressions, with strong vascular grooves. The large teeth are triangular and broad. The whole surface is pitted with coarse pseudopuncta, and there are short, but very deep ciliar grooves all around the margin (Cg. in pl. 3, fig. 9), each of them corresponding to one of the ribs of the external sculpture. The ventral cavities are thin and deep (textfig. 23 C—D).

The dorsal interior has oval branchial lamellae, with a marked septum. There is no vascular groove as in the Sowerbyellas. The cardinal process is high, the chilidal plates small, and the dorsal foramen large, supported posteriorly by two strong plates. Behind the middle of the branchial lamellae there is a large, high callosity (DA in textfig. 23, I—K, O—Q), which consists of pseudopunctate tissue, which is lined with laminated tissue in the central and anterior part. Owing to this callosity, the branchial lamellae bend forwards, and the effective body volume of the species was extremely small, and the valves very massive. The margins of the branchial lamellae are raised, and in many specimens form high, elevated ridges. In some specimens, mainly in adult ones with a large callosity, the branchial lamellae are depressed into the valves, and are lower than the surface of the valves. This feature is not known from other Sowerbyellinids.

About 2/5 of both the dorsal and ventral hinge-lines are denticulated. The denticules are probably transformed pseudopuncta, and just behind the hinge-line, the strong pseudopuncta are found just to the cardinal angles. Young specimens, where the denticulation is not visible, show in thin sections that there are pseudopunct-like denticulations just below the surface of the hinge-line, even if they cannot be seen on the surface. The denticulations are only clearly visible in fairly old specimens, and in many specimens they can not be seen because of the bad state of preservation. In specimens from silty beds, the denticulations are generally more distinct. This might be due to a selective development of the denticles in that particular environment. On the other hand, specimens from slightly contact metamorphic, hardened rocks always have denticulation, even if the rock was not silty. The selective occurrence of the denticulations is therefore probably due to selective preservation, and not to selective development.

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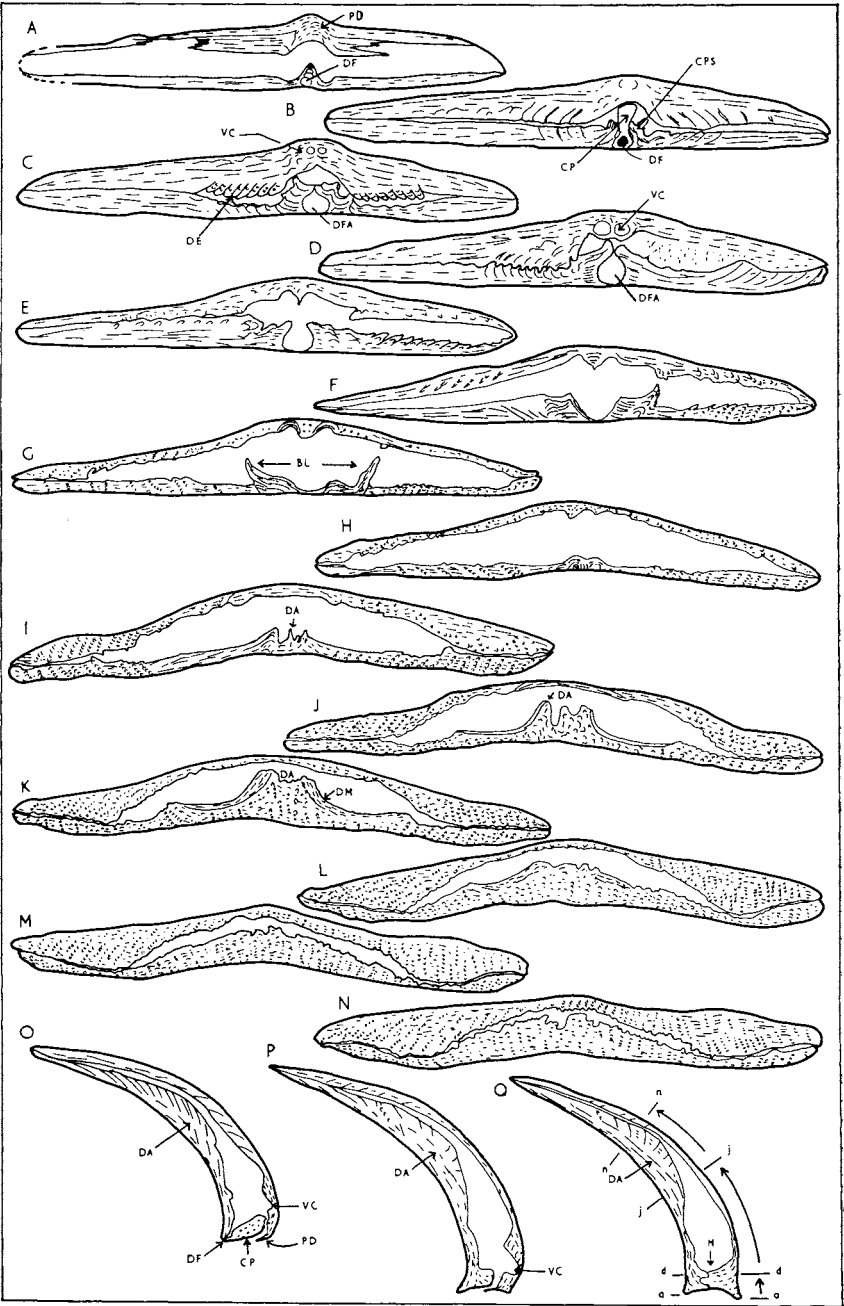
Remarks: *E. acuminata* differs from most other Eoplectodontas as to sculpture, and being so flat. If differs from the younger species as for instance *E. praecursor,* in the massive valves, and in having a dorsal callosity. The points in which it differs from the closely related and almost contemporaneous *E. karina* are described below.

HOLTEDAHL's material of this species was rather limited, but further studies have shown that it is very common in the Oslo—Asker district. Because of the sculpture, he referred it to *Leptaena trabeata* LINDSTRØM (in ANGELIN & LINDSTRØM 1880, p. 30, pl. 17, figs. 1—4). This species, however, seems to be a *Sampo,* and HOLTEDAHL's variety must be given specific rank. The Scottish species referred to as *Sowerbyella semirugata* (REED) seems to be identical with HOLTEDAHL's species. The author has not studied REED's types, but has seen material from the Balclatchie Beds of the Girvan district, and these cannot be distinguished from the Norwegian specimens. The variety described by WHITTINGTON (1938) of *Sowerbyella sericea* from the Berwyn Hills, also appears to be identical with HOLTEDAHL's species. According to WHITTINGTON, there are no denticulations, but this is probably because of the denticulations of this species is not preserved in casts. Mr. Richard Cave, Cambridge, has kindly informed me that he has found denticulations in some of the specimens, and the author has seen a specimen in Sedgwick Museum, Cambridge, which definitely was denticulated.

Distribution: In Norway this species seems to be restricted to the Oslo—Asker district, where it occurs in the upper part of zone 4ba,

Fig. 23. *Eoplectodonta acuminata* (HOLTEDAHL) A—N 14 transversal sections. The approximate position of the sections are shown in fig. Q, (a—d—j—n). They are, therefore, not parallel. O—Q. 3 longitudinal sections. O. is in the median line of the valves, P. is through one of the ventral cavities, and Q is still further to the side.

The specimens (two different were used, one for figs A—N, and the other, smaller one for figs O—Q) are from the middle part of zone 4ba, at Billingstad, Asker district.

Abbreviations: BL = Branchial Lamellae. CP = Cardinal process, CPS = Side branches of cardinal process. DA = Dorsal central callosity. DE = Denticles along the hinge line. DF = Dorsal foramen. DFA = Dorsal foramen with slit in front of cardinal processes. DM = Dorsal muscle impression, or branchial lamellae, fused to DA. H = Hinge. PD = Pseudodeltidium. VC = Ventral cavities.

but does not reach the upper limit of that zone. Specimens from Ringe-
rike and the southern part of Hadeland might belong to this species
or to *E. karina*. The exteriors of the specimens are intermediate be-
tween the two, and the interiors are unknown or badly preserved.

Apart from the Oslo region, the species is found in the Balclatchie
Group in the Girvan district, Scotland, in various districts in North
Wales and western England, and in the midlands of Eire (cf. HARPER,
1952, p. 88).

The wide horizontal distribution of this species is remarkable,
and coincides with the appearence of other species in the same areas
(*Sampo* (*L.*) *oepiki* and *Chonetoidea alpha*).

Eoplectodonta karina sp. n.

Pl. 3, fig. 5.

1916   *Plectambonites quinquecostata* (McCoy) — HOLTEDAHL, p. 78, pl. 15, fig. 9.

Type data: The holotype, PMO 66978, is the interior of a dorsal
valve from the uppermost part of zone 4bα at the southern end of
Nakholmen, Oslo district.

Material: About 20 dorsal interiors, 6 ventral ones, and a large
number of exteriors and complete specimens (several hundred).

Diagnosis: Small *Eoplectodonta* species with a dorsal callosity,
branchial lamellae with highly elevated boundary ridges, and a very
high septum.

Description: Small, hemicircular species (average width 11—12
mm., length 5,5—6 mm). The outline may vary, in some specimens
the cardinal angles are right, in others they are about 60°. The con-
vexity is low, slightly stronger than in most specimens of *E. acuminata*.
The sculpture also resembles that species, but the concentric rugae
are always less prominent in E. *karina*.

The ventral interior is not well known, it has a number (6—8)
prominent ridges, and is different from most other Sowerbyellinids,
except *E. multiseptata* (WILLIAMS 1955). The ridges are subparalell,
not diverging.

The dorsal interior shows high boundary ridges around the bran-
chial lamellae. There is a dorsal callosity, but it is generally less pro-
minent than in *E. acuminata*. The septa in the branchial lamellae

are very strong, and are both broad and high. Judging from the thickness of the complete specimens this septum must have touched the ventral valve then the valves were closed, just like the septa of *Christiania*. The septum does not reach the posterior margin of the branchial lamellae as do the vascular grooves found in this position in most Sowerbyellinids. The development in *E. karina* do more resemble that found in *Christiania oblonga* (cf. textfig. 27, 28).

The valves are comparatively thin in this species, and the pseudopuncta appear to be fairly small. The hinge-line shows denticulation, which is of the same type as in *E. acuminata*. Because of the state of preservation it is generally observed in thin sections only. Traces of the denticulation is seen on the left side of the hinge-line of the holotype (pl. 3, fig. 5).

Remarks: E. karina differs from *E. acuminata* as to outline, sculpture, thickness of the valves, development of the branchial lamellae, and in the ventral interior. It is nearly related to *E. multiseptata* (WILLIAMS 1955), from which it differs in having a well developed dorsal foramen, parallel instead of diverging ventral ridges, and in having a denticulated hinge-line. Further studies may show that these two species should be included in a new genus. They show a close resemblance to *Christiania* and *Oepikina*, especially in the development of the branchial lamellae. (textfig. 28).

Distribution: E. karina is found in the uppermost part (4–5 m) of zone 4bα in the Oslo—Asker district. In some localities it might possibly be found also in the lowest beds of zone 4bβ. As mentioned above, some specimens found in the Ringerike and Hadeland districts in corresponding horizons, might belong to this species or *E. acuminata*.

Eoplectodonta (?) *percedens* (HOLTEDAHL 1916).
Pl. 4, fig. 9, pl. 6, fig. 7, textfig. 19H.

1916   *Plectambonites Schmidti* TQU. var. *percedens* n. var. — HOLTEDAHL, pp. 81—82, pl. 15, figs. 10—11.

1928   ? *Sowerbyella rhombica* var. *conspicua* (REED) — JONES, pp. 508—509.

Type data: The lectotype, chosen here, is PMO LO132, the specimen figured by HOLTEDAHL, pl. 15, fig. 10 (this paper pl. 6, fig. 7), the exterior of a ventral valve from zone 4b (probably the uppermost part of 4bα or the lower part of 4bβ) at Bratterud, Ringerike district.

Material: 4 ventral interiors, and about 20 exteriors.

Description: A strongly convex, rather large species. The width is between 22 and 25 mm, and the length between 13 and 15 mm in average adult specmens. The sculpture consists of a small number of fine ribs, with 6–7 striae between each of them. The areas form an angle of about 90° in adult specimens, and the apexes, especially that of the ventral valve, are bent over the areas.

The dorsal interior is unknown.

The ventral interior has small, angular muscle impressions, divided into unequal parts by the broad vascular grooves. Just in front of the muscle impressions the vascula widen, and become nearly as broad as the muscles. The ventral cavities are comparatively shallow, and wide. The inner surface of the valve has extremely long ciliar grooves, a feature which seem to be characteristic for this species and *E.* (?) *rhombica.* In adult specimens about 3/4 of the hinge-line is finely denticulated. In the present material the denticulation can only clearly be seen in one specimen. The other three ventral interiors are either badly preserved, or so small that they cannot be expected to show denticulation.

The shell substance is coarsely pseudopunctate.

Both *percedens* and *rhombica* have a peculiar type of denticulation. About 1/3 of the hingeline show denticules increasing in size from the denthyrium. The lateral parts of the hinge-line show smaller denticles, which are all of uniform size.

Remarks: This species was first described by HOLTEDAHL (1916). Judging from the exterior of the specimens figured by HOLTEDAHL, JONES (1928, pp. 508—509) was of the opinion that the species might be related to *Sowerbyella rhombica* var. *conspicua* (REED 1917). The author is inclined to believe that the form described from Gelli Grin by JONES (l.c.pl. 22, figs 3—4) is not identical with that described by REED (1917) from the Girvan district. The vascular system in the Welsh form has many, distinct and irregularly branching vascula, resembling the impressions of a *Sampo*, whereas the vascular system is only slightly developed in the Scottish form. Both differ from the Norwegian specimens in not having long ciliar grooves and also in sculpture and size (the Scottish form). The author is therefore inclined to believe that all three forms are separate species, at least until the dorsal interior of *percedens* is better known.   The species

differs from *rhombica*, as defined here, as to size and sculpture and the smaller ventral muscle impressions. Both these species are included in *Eoplectodonta*, but it is questionable whether this is correct as they appear to be related to *Sowerbyella*. The two species resemble the others referred to *Eoplectodonta* both in the muscle impressions being of a rhomboidal shape, and in having prominent ciliar grooves.

Distribution: HOLTEDAHL (1916) reports this species from the zones 4bα and 4bβ. The author's studies show that *E.* (?) *percedens* is confined to the uppermost part of zone 4bα, and to 4bβ. In the lowest part of 4bγ, there are some specimens which might belong to this species.

It is recorded from the Oslo—Asker, Ringerike and Langesund—Gjerpen districts. JONES (1928, p. 509) records this species from the Mjøsa district. However, there are no specimens from that district in the material at the authors disposal.

Eoplectodonta (?) *rhombica* (McCoY 1852).

Pl. 4, figs. 2—3, textfig. 19C.

1916 *Plectambonites sericea* var. *rhombica* (McCoY) — HOLTEDAHL, pp. 80—81, non pl. 14, figs. 4—5 = *Sowerbyella* cf. *thraivensis* (REED 1917).

1928 *Sowerbyella rhombica* (McCoY) — JONES, pp. 426—430, pl. 22, fig. 1. See this paper for further references and discussion.

Material: One ventral interior, two complete specimens, and a number of fragmentary exteriors.

Description: Moderately convex species with hemicircular to rounded triangular outline. Valves large, an average specimen is 32 mm wide and 19 mm long. Sculpture consisting of closely placed, sharp ribs with 3—5 prominent striae between each. Areas high, delthyrium and notothyrium broad.

The dorsal interior is not known in the Norwegian material.

The ventral interior has small, rhomboidal muscle impressions, broad vascula, and strong, broad and rather shallow ventral cavities. At least 3/4 of the hingeline is crenulated with denticles of the same type as found in *E.(?) percedens*. The internal surface is striated, and pitted with pseudopuncta arranged in radial rows. There are ciliar grooves which are not so long as in *E.* (?) *percedens*, and not so strong as in *E. acuminata*.

Remarks: This species differs from all other Norwegian Eoplectodontas and Sowerbyellas in size and ornamentation. It seems to be closely related to *E* (?) *percedens*, and together with that species it forms an intermediate group between *Sowerbyella* and *Eoplectodonta*.

The species *rhombica* is not well defined, and the interior is not known in the type material. There is therefore a possibility of the Norwegian material belonging to another species. It resembles the type in size and ornamentation. The convexity is slightly stronger in the type than in the specimens described here. According to JONES (1928, p. 428), the only specimen from Cynwyd of which the interior is known and which can be referred to this species have a structure similar to that of «*Sowerbyella rhombica* var. *conspicua* from Gelli Grin. As mentioned above, this species does not differ much from *E*. (?) *percedens* except for the vascular system. The present material is therefore, at least at provisionally included in *E*. (?) *rhombica*.

Distribution: The Norwegian specimens are found in zone 4bδ, probably mainly the upper part of that zone, in the Oslo—Asker district, and in the southern part of the Hadeland district, near Grindvoll.

Genus *Chonetoidea* JONES 1928.
cf. textfig. 24.

A number of species from the Middle Ordovician of the Oslo region is included in this genus. A distinct trend of evolution can be followed in the species described here, from *C. stoermeri* with large, regular branchial lamellae over *C. alpha* with smaller, triangular ones, and over *C. gamma* with regular small arches, and strong spines also outside the lamellae, to the typical Upper Ordovician species *C. papillosa* (REED) and *C. iduna* ÖPIK (1933), which have small indistinct branchial arches, and numerous spines on the rest of the surface (textfig. 24).

It is therefore necessary to alter the diagnosis of *Chonetoidea* so that it will include species with differentiated sculpture (*C. gamma*) and species with regular branchial arches (*C. stoermeri* and *C. alpha*). The ventral interiors are generally also more strongly developed in the older species, and especially the muscle impressions can be seen more clearly, also posteriorly.
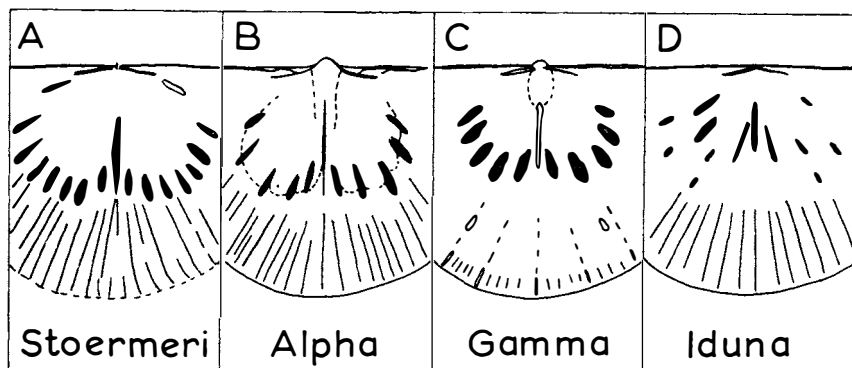
Fig. 24. The dorsal interior of some species of *Chonetoidea*. A. C. *stoermeri* sp. n. from zone 4aα₃ in the Asker district. B, C. *alpha* sp. n. from zone 4bα, at Billingstad, Asker district. C, C. *gamma* sp. n. from zone 4bγ, at Blakstad Road Junction, Asker district. D, C. *iduna* ÖPIK 1933, from zone 4cα, of *Tretaspis seticornis*, from just South of Billingstad railway station. The figures are drawn from casts, they are reduced to the same size, and are magnified about 7 times.

Because of the prominent ventral cavities (cf. pl. 2, figs. 21—22) found in *Chonetoidea*, this genus is included in the subfamily Sowerbyellinae though there is some doubt as to whether this is correct. Especially in the structure of the branchial arches (corresponding to the branchial lamellae) it shows a resemblance to the Leptestinae.

Chonetoidea can be distinguished from *Aegiria* ÖPIK (1933) because of the distinct branchial lamellae in the latter genus, but otherwise they are quite similar. Formerly it was believed that only *Aegiria*, and not *Chonetoidea* had a median septum. It is, however, found in most specimens belonging to the older species. This is also the case with the strongly developed muscle impressions. HAVLICEK (1952) has described some species, which seem to be intermediate between *Chonetoidea* and *Aegiria*.

Sericeoidea LINDSTRÖM (1952) is definitely closely related to *Chonetoidea*, but lack the well defined branchial arches. It is still doubtful whether the three Middle Ordovician species described here should be referred to *Chonetoidea*, or to *Sericeoidea*. WILLIAMS (1955) referred his species *abdita*, which is rather like *C. alpha* to *Sericeoidea*. In this case it would not be necessary to alter the diagnosis of *Chonetoidea*.

Chonetoidea gamma sp. n.

Pl. 2, figs. 12—13, textfig. 24C.

Type data: The holotype, PMO 66988, is the cast of a dorsal interior from the middle part of zone 4bγ at Blakstad Road junction, Asker district.

Material: About 75 casts of interiors and exteriors of both valves, and a small number of fragmentary valves.

Diagnosis: Chonetoidea species with strong ventral muscle impressions, small, regular branchial arches with some few spines in the marginal parts of the dorsal interior, and a differentiated sculpture.

Description: Small, flatly planoconvex species with right or slightly less than right cardinal angles. Sculpture consisting of numerous fine ribs with 3—5 striae between each at the margin. The holotype is 7 mm wide and 5 mm long, and is a specimen of average size in the Oslo—Asker district. Those from the Hadeland district are often considerably larger, up to 10 mm wide.

The dorsal interior has small, rounded branchial arches, and in most specimens there are also some spines in the marginal areas of the dorsal interior (cf. pl. 2, fig. 13). The spines are believed to be homologous with the pseudopuncta. In thin sections one can see that they are of the same histological structure. The spines of the branchial arches are directed inwards against the centra of the arches, and not as those in the branchial lamellae of *Leptelloidea* (s.l.), towards the margin of the valves. The ordinary pseudopuncta, which are abundant in this species, are much smaller than the spines.

The socket plates are strong, and long, diverging at about 150°. The cardinal processes are not clearly visible in the dorsal interiors, but judging from what can be seen in casts of the areas, they are similar to those of *Sowerbyella*.

In the ventral interiors, the muscle impressions can be seen quite clearly, also posteriorly. They are comparatively small in this species.

Remarks: As mentioned above, *C. gamma* differs from the younger species of *Chonetoidea* in having distinct ventral muscle impressions, regular branchial arches, and in the differentiated sculpture. There are, however a number of the Chonetoideas where the sculpture is undifferentiated on the exterior of the valve, which show indications of differentiation in the interior, where the sculpture usually is visible

to the branchial arches. *Gamma* differs from *stoermeri* and *alpha* as to the sculpture, in having smaller branchial arches, and occational spines outside the arches in the dorsal interior.

Distribution: This species is found at the type locality, in the railway section between Billingstad and Hvalstad in Asker, and at Grefsen and Nakholmen in the Oslo district. At all localities it is found in zone 4bγ, generally in the middle part of the zone. It appears to be relatively most abundant in localities where the facies is euxinic (Grefsen, Nakholmen) or intermediate between euxinic and ventilated (Blakstad). It also occur in the Cyclocrinus Shale (layer B of KIÆR 1926, p. 5) at Tønnerudodden, Hade˙and district. This species might also occur in other districts, from which no interiors are known. It is usually referred to as «young specimens» of *Sowerbyella*, because of the resemblance as to shape and size. The specimens from Hadeland are slightly larger than the typical ones, and come from beds with a ventilated facies.

<h3 style="text-align:center">*Chonetoidea alpha* sp. n.</h3>

<p style="text-align:center">Pl. 2, figs. 20—22, textfig. 24B.</p>

Type data: The holotype, PMO 67027, is a natural cast of a dorsal interior from zone 4bα, about 8 m below 4bβ, in the roof of the second tunnel W. of Billingstad st. Asker district.

Material: About 30 casts of the dorsal interior, 18 of the ventral, and a large number of casts of exteriors.

Diagnosis: Chonetoidea species with undifferentiated sculpture, no spines outside the subtriangular branchial lamellae and with a median septum.

Description: Small planoconvex to unequally biconvex specimens with right cardinal angles. Sculpture consisting of numerous equal or subequal ribs. In a few cases every third or fourth rib is slightly more prominent than the others. The areas are comparatively high. A specimen of average size is 6—7 mm wide and 2,5—3,5 mm long.

The dorsal interior is similar to that of *C. gamma*, except for the branchial lamellae being more triangular in outline, especially in old specimens. There is always a medium septum, which generally is prominent. In some specimens it is double.

The ventral interior is like that of *C. gamma* and *Aegiria*, with two prominent muscle impressions, and ventral cavities.

Remarks: This species differs from *C. gamma* in the undifferentiated sculpture, and the shape of the branchial lamellae, and from *C. stoermeri* in having smaller branchial lamellae composed of fewer spines. It differs from *C. iduna* and *C papillosa* in not having any spines outside the branchial lamellae, and in the more regular outline of the latter, and in the distinct muscular impressions in the ventral interior. It differs from *Sericoidea* in having well developed branchial lamellae.

It differs from *Sericoidea* (?) *abdita* WILLIAMS (1955) in having more spines in the branchial lamellae (5—6 instead of 3), and in the undifferentiated sculpture.

Distribution: It is found in zone 4ba, upper part. Very common in the northern part of the Asker district. Sporadic in the rest of that district, and in Oslo.

Chonetoidea stoermeri sp.
Textfig. 24A.

Type data: The holotype is a natural cast of a dorsal interior from zone $4a\alpha_3$, of *Ogygiocaris dilatata sarsi* and *Glossograptus hincksi*, in a road section 500 m N. of Dalbø Road junction, on the road between Bø and Heggedal in Røyken, Asker district.

Material: About 25 casts of the exterior and interior of both valves.

Diagnosis: Chonetoidea species with coarse, undifferentiated sculpture, no spines outside the large branchial lamellae, which are composed of 7—9 pairs of spines.

Description: Small, thin-shelled, planoconvex species with right, or slightly less than right cardinal angles. An average specimen seems to be about 8 mm wide and 3,5—4 mm long. It is difficult to give exact measurements for this species, because all specimens occur crowded on small spots, where they overlap.

Sculpture consisting of subequal coarse ribs. Ventral interior similar to those of *C. gamma* and *C. alpha*, but generally less calcified. Dorsal interior with large branchial lamellae, composed of 7—9 pairs of spines. No spines are found outside the lamellae. Shell structure unknown.

Remarks: This species is the oldest one of the genus. It differs from all younger ones in having very large branchial lamellae, and from *Sericoidea* in the stronger and more numerous spines in the branchial lamellae. The ventral interior is similar to that of *Sericoidea*, *C. gamma* and *C. alpha*.

Distribution: Interiors of this species are found only in the type-locality, and a few other localities in the Røyken facies of zone 4aα. It is, however, very difficult to distinguish this species from *Alwynella ildjernensis* if the interiors of the specimens are not known. The size, shape and sculpture of the two species are remarkably alike, and they partly occur in the same layers. It may therefore be possible that *C. stoermeri* also occurs outside the Røyken district.

Family Christianidae WILLIAMS 1953.

As mentioned above (p. 37), this family is tentatively included in the Plectambonitacea, (near the Leptestidae) because of the new observations on the ontogeny, and the structure of the cardinalia in *Christiania oblonga* (PANDER 1830).

Genus *Christiania* HALL & CLARKE 1892.

Type species: Leptaena subquadrata HALL 1883, Middle Ordovician of Tennessee.

A number of species of *Christiania* have been described, but only three or four of them are well known. In Norway a common Middle Ordovician species was called *Ch. tenuicincta* (McCOY). There is, however, some difficulty as to the taxonomy of this name. McCOY used the specific name *tenuicincta* for two different species, *Producta tenuicincta* McCOY 1846, and *Leptaena tenuicincta* McCOY 1849. McCOY himself (1852, p. 239) stressed the fact that the two species were different. The first species (from the Kildare Limestone in Eire) is not well known, and it can hardly be regarded as a valid species, at least not before the types have been restudied. *Leptaena tenuicincta* is from the Bala rocks of Wales. It is generally (DAVIDSON, HOLTEDAHL a. o.) regarded as a synonym of *Producta tenuicincta*, and is usually referred to as *Christiania tenuicincta*. The author had the opportunity of studying the types of *L. tenuicincta*, and discovered that it is a *Sowerbyella*, probably of the *sericea*-type. The figured specimen is a

fragmentary cast of the exterior of a specimen, where both sides are broken off. The artificial cast, made from sealing wax which was used by McCoy, was unable to «take» the sculpture and the finer details of the hinge-line, and the species was therefore described as smooth. Both the sculpture, fine ribs and striae, and the hinge-line structure is like that of *Sowerbyella sericea*. The specimen as well as the original artificial cast are preserved in the Sedgwick Museum, Cambridge.

The author prefers to regard *Leptaena tenuicincta* McCoy as a synonym of *Sowerbyella sericea*, and *Producta tenuicincta* as a nomen dubium for the time being, until the types of the latter have been restudied.

This will mean that the *Christiania* species, which up to now have been called *Christiania tenuicincta* (McCoy) will have to have a new name.

Christiania holtedahli nom. nov.

Pl. 5, figs. 1—11, 15—16, Pl. 6, fig. 10, textfigs. 12L, 25, 26A, 27B, 28C, 29—31
1916   *Christiania tenuicincta* (McCoy)—HOLTEDAHL, pp. 85—86, pl. 16, figs.
4—8.

Type data: The holotype, PMO L 0071, is the cast of a ventral interior from zone 4bα at Bratterud, Ringerike district. The specimen was figured by HOLTEDAHL, (1916, pl. 16, fig. 7).

Material: A large number of complete specimens and casts of separate valves, and some free specimens, from several localities in the Oslo region. From at least three localities, the number of specimens exeed 200.

Diagnosis: Christiania species with small, bifid cardinal processes, diagonal branchial septum ancylosed both to the lateral and central branchial septa, forming a transverse septum between them. The socket plates are thin and ancylosed to the lateral branchial septa. The median septum is thin, and weakly developed in most specimens. The valves are pseudopunctate mainly in their lateral parts.

Description.

Exterior: Generally this species is elongate and strongly curved. In the anterior part the central portion is globose, while the corners of the hinge-line are nearly flat. These triangular, flat corners are often

broken, and it is therefore often difficult to evaluate the variations in width. Posteriorly the valves flatten out, and are generally slightly broader than the hinge-line.

The convexity of the ventral valve is strongest near the apex, and gradually fades out posteriorly (Cf. textfig. 26A). The dorsal valve is rather flat near the hinge-line, at least in the central parts, and the convexity appears later in the development often starting as a slight geniculation. At the margin, the two valves are parallel. This indicates that the young valves were rather flat, especially the dorsal one, and that the convexity appeared in a later period of growth, together with a rapid increase in body-volume.

The dimensions of the specimens can be seen in textfig. 29, and the variation in size is discussed above (p. 54).

The ornamentation of the surface consists of fine concentric lines, which sometimes are accenturated by weathering. There are no radial striae. Just behind the cardinal processes, in the dorsal valve, there is a small node, the structure and purpose of which are discussed below. There is a pedicle foramen just above the apex of the ventral area.

Dorsal interior: Dorsal area narrow, almost rectangular. The angle between the areas is 120—150° in young specimens, decreasing to less than 90° in gerontic ones.

Cardinal processes double, very small in adult specimens, and relatively more prominent in the younger ones. The sockets are remarkably small, and in a few specimens there are also traces of an additional pair of sockets, nearer to the cardinal processes.

The branchial lamellae consist of two elongated loops cemented to the valve. Each lamella has a transverse septum. These transversal septa divide the branchial loops into two parts, a large posterior, and a smaller anterior one. The ontogenetic development of the branchial lamellae is discusse below.

There is a certain amount of variation in the development of the branchial lamellae. The central pair of septa (cb)[1] are subparallel, and rather uniform. Between them one usually finds a median septum (ms), particularly well developed in old specimens. The lateral branchial septa (lb) are in most cases ancylosed to the socket plates (sp.). In most specimens they are continuous, but in others, a distinct

[1] The abreviations used for the septa, refer to the corresponding terms in textfigs. 27 end 28.
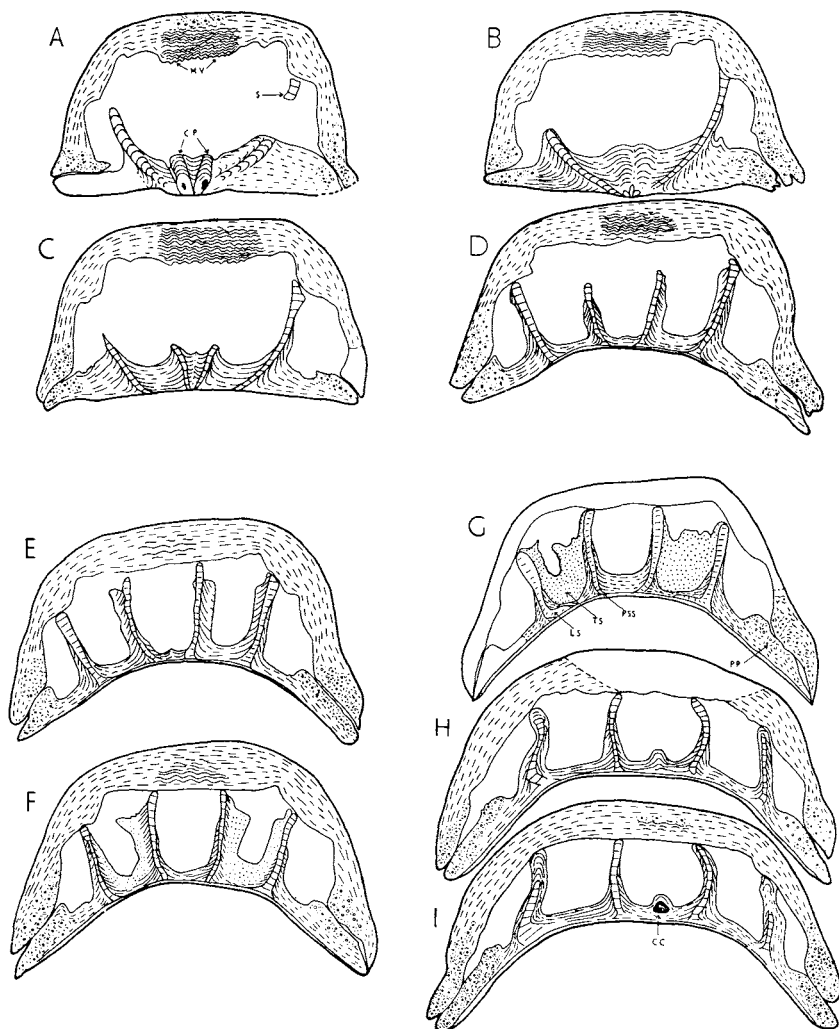
Fig. 25. *Christiania holtedahli.* Nine parallel thin sections (peels) through a specimen from the upper part of zone 4ba at Billingstad, Asker district. A. is nearest to the hinge-line.

Abbreviations: CC = Central body of median septum. CP = Cardinal processes. LS = Lateral branchial septum. MV = Impressions of vascula ? PP = Pseudopuncta. PSS = Central branchial septum. S = Septum, probably a part of the lateral branchial septum. TS = Transverse septum.
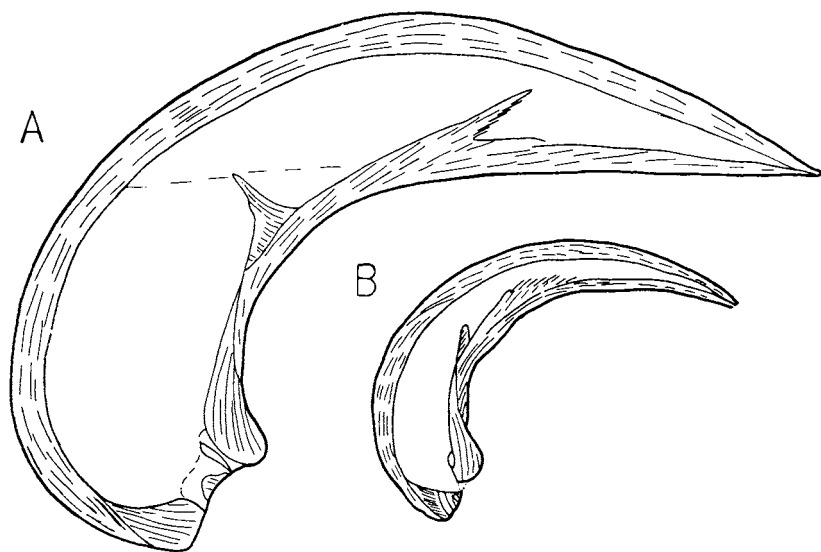
Fig. 26. *Christiania*. Longitudinal sections of *A*. *Ch. holtedahli* from the upper part of zone 4bα at Billingstad, Asker district. 7x. B. *Christiania oblonga* (PANDER) from the Lower Ordovician at Popovka, near Leningrad. 7x.

angle is observed at the point of coalescense. In the young specimens (pl. 5, fig. 2) they do not touch at all.

Posteriorly the lateral and central branchial septa join to form the elongated branchial loops. In a few specimens (pl. 5, fig. 15) the lateral septa seem to meet behind the central ones, without being connected with them. This may be due to the strong development of a concentric ridge, joining the lateral septa. Even if this is the case, the posterior part of the branchial loops in those specimens are less developed than usual. This is the case with one of the largest specimens known from the Oslo region.

The transverse branchial septum is a striking feature in all species of *Christiania*. In *Ch. holtedahli* they form a concave ridge, which is only slightly developed in the young specimens, but almost of the same strength as the other septa in adults. In this species it is difficult to homologize the structure with those of other brachiopods. In *Ch. oblonga* (PANDER), a more primitive species, these structures are differently developed, and here it is not so difficult to explain the formation of the transverse septa (cf. textfig. 27 and 28).

8
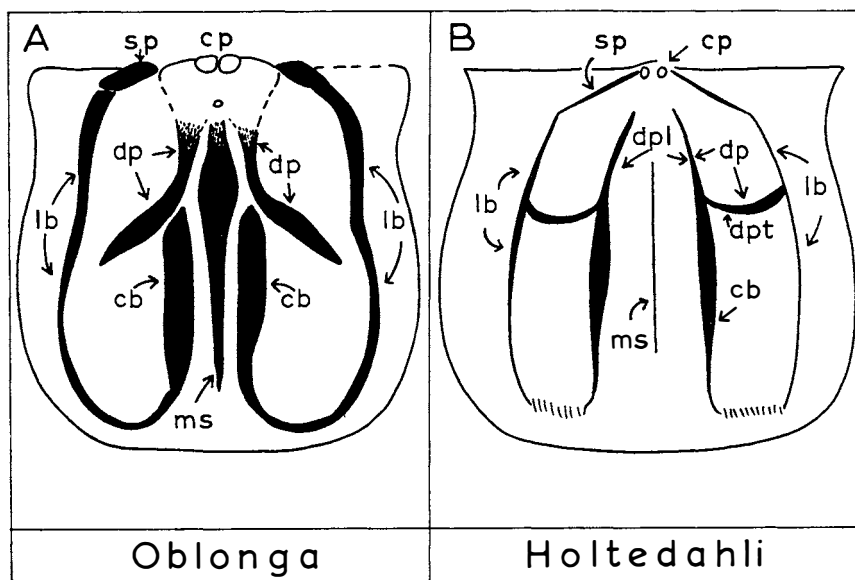
Fig. 27. Diagramatic figures of the dorsal interior of *Christiania oblonga* (PAN-
DER 1830), from zone B3 at Popowka near Leningrad, (A) and *Christiania
holtedahli*, from zone 4bα, at Blakstad, Asker district, Norway. The figures are
reduced to the same size, A is magnified about 10,5 times, and B is magnified
about 6,5 times.

Abbreviations: cb- central branch of branchial loop. *dp* — diagonal sep-
tum. *dpl.* — longitudinal part of diagonal septum. *dpt.* — transversal part of
diagonal septum. *cp* — cardinal processes. *lb* — lateral branches of branchial
loop. *ms* — median septum. *sp* — socket plates.

In *Ch. oblonga* the lateral branchial septa are connected with the
socket plates, just as in *Ch. holtedahli*. The central branchial septa
are, however, formed by two elements, the first of which is the posteri-
or part of the central septa. The second element consists of a pair of
diverging septa, commencing just behind the cardinal processes, and
terminating where the transverse septa are found in *Ch. holtedahli* and
Ch. subquadrata. At this point the septa are strongly swollen, but they
are not, or at least generally not fused to the central septa, and never
to the lateral ones.

It is therefore very probable that the central and transversal
septa in *Ch. holtedahli* also consist of two elements, one (dp) forming
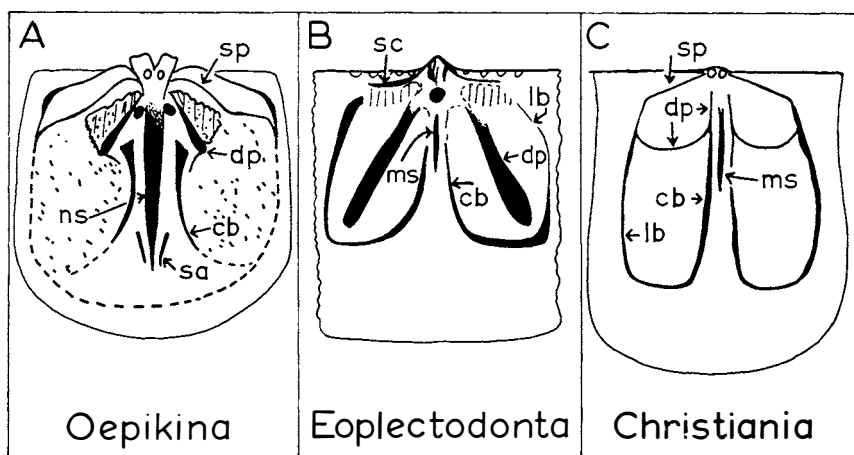
Fig. 28. The dorsal interiors of *Oepikina, Eoplectodonta* and *Christiania,* to show the development of the branchial septa. A. *Oepikina dorsata* (BEKKER) from zone C2 in Esthonia. B. *Eoplectodonta karina* sp. n. from zone 4bα in the Oslo district. C. *Christiania holtedahli* sp. n. from zone 4bα in the Asker district

Abbreviations: cb — central branch of branchial loop. dp — Diagonal septum. lb—lateral branch of branchial loop. ma—muscle attachments. ms —median septum. sa — intervascular septa. sp. — socket plates.

the anterior part of the central septum and the transversal septum, and the other (cb proper), forming the posterior part of the central septum.

This interpretation of the structure of the branchial lamellae of *Christiania,* makes it possible to homologize them with those of some of the Sowerbyellinids, as for instance *Plectodonta, Eoplectodonta,* and the *quinquecostata*-group of *Sowerbyella* (cf. textfig. 28).

In *Ch. subquadrata,* the transversal septum and the anterior part of the central septum are distinctly lower than the other septa, thus confirming the interpretation of the development of the septa given above.

Ventral interior: The triangular ventral area is comparatively high. Teeth strong, with oblique supporting plates.

The muscle impressions are subovate, and are not well limited posteriorly. In adult specimens, they continue into two semiparallel vascular grooves. The distance between the branchial lamellae and the interior surface of the ventral valve is less than 0,1 mm, and they
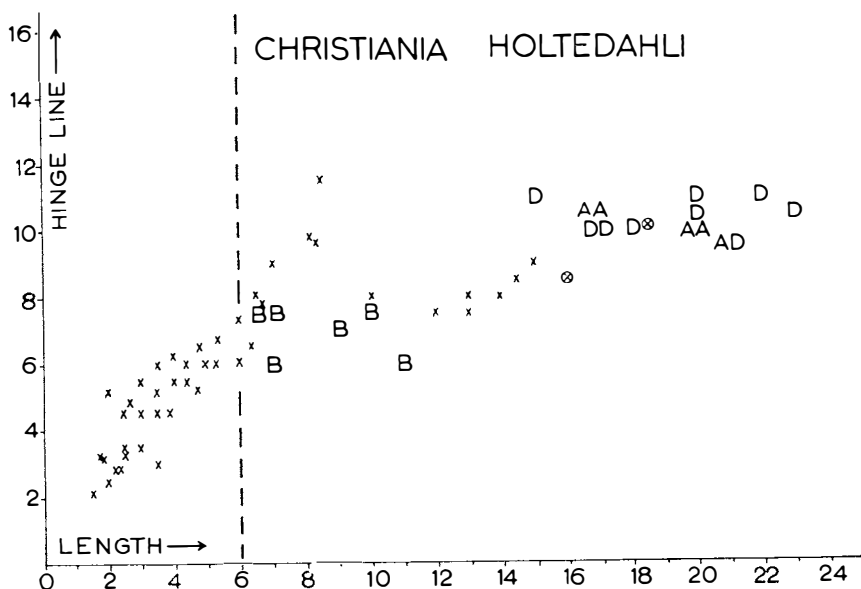
Fig. 29. Diagram showing the variation of the size in *Christiania holtedahli* sp. n. from various populations in the Oslo Region. x. are specimens from the typical populations, Billingstad and Blakstad in the Asker district. ⊕ are two large specimens found together with the typical ones. B. are small specimens from the lower part of sone 4bα at Gomnes, Ringerike district, probably intermediate between *Ch. holtedahli* and *Ch. elongata*. (cf. textf'g. 31). A. are specimens from the Bratterud population (upper part of zone 4bα, and possibly lowest part of zone 4bβ). D. are specimens from the Coelosphaeridium Beds (?) of the Toten district. The broken line at 6 mm length, is the arbitary border between the larval and adult specimens in the Billingstad and Blakstad populations.

therefore divide the interior of the animal in five unequal parts, one central, two «interbranchial», and two lateral ones (cf. textfig. 25). The central and the lateral parts are longitudinally striated in the ventral valve. In the depressed «interbranchial» areas the main vascula are found (cf. p. 36, textfig. 12LM).

In young specimens, the branchial grooves are not developed, and the muscle impressions are well limited posteriorly.

The pseudodeltidium is found in all specimens with a supraapical foramen. The development varies considerably in specimens of the same size. Even very large specimens may have a small pseudodelti-

dium, and small specimens may have a comparatively large one. Gerontic specimens, however, always have a large one. The pseudo-deltidium is built as a triangular to rectangular pyramid, consisting of horizontal lamellae. The surface of the lamellae is smooth inwards, and outwards (in the delthyrial opening) they are long and pointed, so that the cross-section of the pseudodeltidium is like a saw-blade. The lamellae seem to be continuous with the growthlines of the area, with which they are intimately connected. In the gerontic specimens the pseudodeltidium reaches almost to the cardinal processes.

The chilidium seems to be continuous with the cardinal processes, and has very strong growth-lines, the edges of which in some cases are turned upwards, against the pseudodeltidium. Also in the chili-dium, the growth-lines seem to be continuous with those of the area. It is also interesting to note that the notothyrium is elliptical to hemi-circular, and not triangular such as the delthyrium.

Structure of the shell: The author has seen typical strophomenid puncta in all sectioned valves of *Christiania holtedahli* (cf. textfig. 25). In contrast to most other Strophomenids, this species has pseudo-puncta which are almost parallel to the surface of the valves. They are restricted to lateral and centromarginal parts of the ventral valves. In the dorsal one, they are only found along the margin. The fine stri-ation in the central parts of the ventral valves, may be due to vascula (textfig. 25, mv, and pl. 5, fig. 10). In tangential sections of the valves, the puncta are cut longitudinally. The strongly inlined pits of the puncta can be seen on most casts of the ventral interior (pl. 5, fig. 16).

Boring organisms are observed in many specimens as fine threads penetrating the shell, especially at the umbo. Probably this is a post mortem feature, but it is mentioned here as it seems to be more common in this species, than in other brachiopod species from the same localities.

Ontogeny: Larval valves are found abundantly from two local-ties, and a continuous series from very small to adult specimens are present (pl. 5, figs. 1—9, cf. textfig. 29). The development of the dor-sal interior has been studied in detail.

In specimens 6—7 mm wide and 6 mm long, the transversal branchial septum is not developed, and the lateral and central septa are not united into loops. In still smaller specimens, the branchial septa are diverging, not subparallel, and the lateral ones can clearly
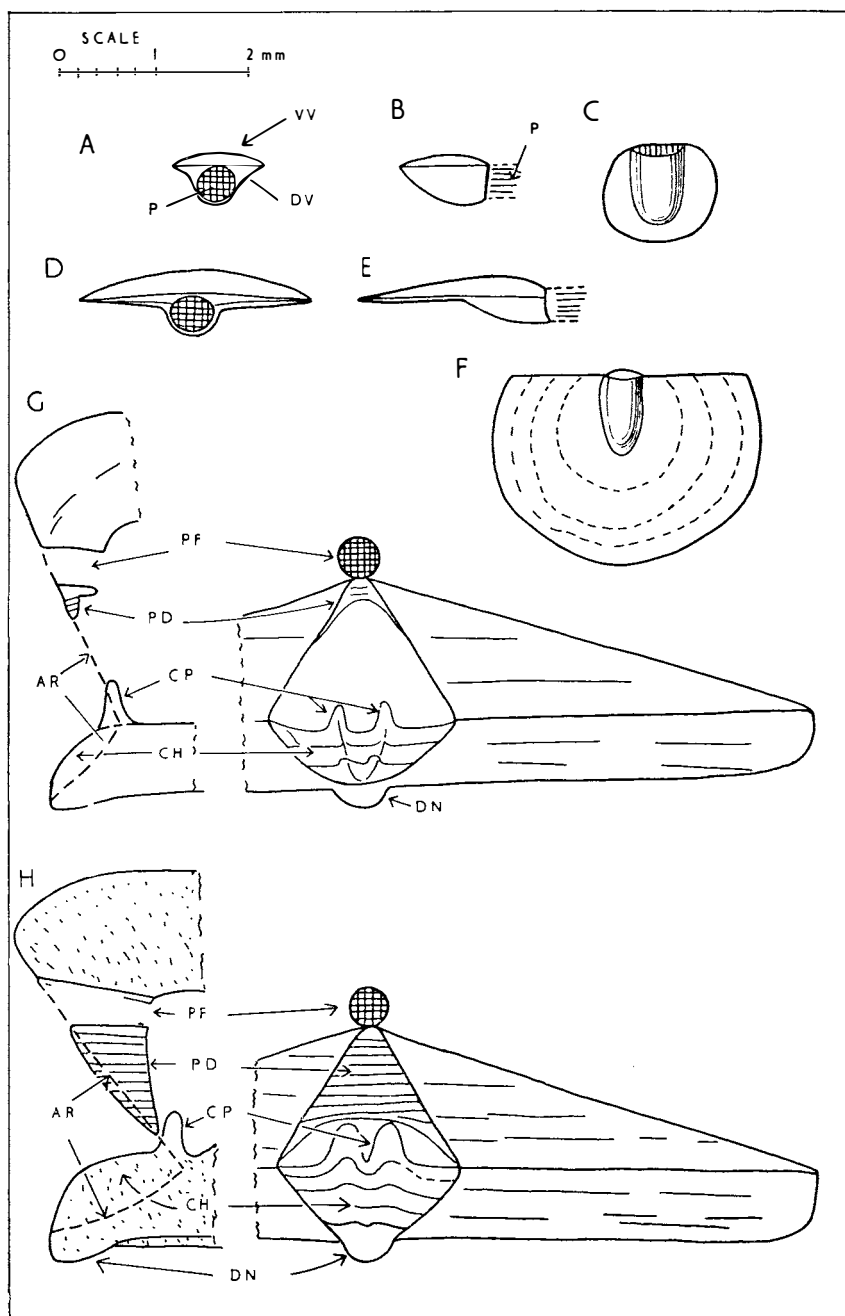
be distinguished from the socket plates. In specimens less than 5 mm wide (4 mm long) the cardinal processes are fused to the socket plates. In still younger specimens they are nodes on the proximal end of the socket plates, and in the youngest specimens, there is no cardinal process at all.

In all young dorsal interiors, there is a longitudinal groove with hemicylindrical bottom, tapering towards the area. This groove, which is supposed to be the pedicle groove, is of the same size in all specimens (0,3—0,4 mm). It is therefore more prominent in the smaller specimens than in the larger ones. It is also remarkable that the groove has the same diameter as the pedicle foramen in the ventral valve of the adult specimens. Some specimens showing the area of the dorsal valve, indicate that the groove really terminated in a foramen, which in most specimens was placed in the dorsal valve, even if it in the larger ones also invaded the ventral area. External impressions of some very small dorsal valves, indicates that in these specimens, the whole of the supposed pedicle foramen was in the dorsal valve (text-fig. 30 A—C). The presence of branchial septa and socket plates, and of associated ventral valves, indicates that the valve in which the pedicle foramen is found, really is the dorsal one.

All these facts points towards the pedicle of *Christiania holtedahli* being in the dorsal valve in the young larvae, and migrating during the ontogeny into the ventral valve, where it in the adult specimens passed through a supraapical foramen. It is remarkable that it was of the same size both in the larvae and adults. This may indicate hat the larvae lived in a vertical position, with the areas down, fixed to the bottom with the pedicle. Later, they turned over, and rested on the ventral valve.

Fig. 30. *Christiania holtedahli sp. n.* A—C very small larva seen from the area (A), the side (B) and the dorsal valve (C). D—F. A larger larva seen from the area (D) the side (E), and the dorsal valve (F). G. Section through the median line, and areal view of a young, adult specimens. H. Similar views of a gerontic specimen. All the figures are semidiagramatic, and based on several specimens from the same population in the upper part of zone 4bα at Blakstad, Asker district.

Abbreviations: AR = Projection of area into the sections. CH = Chilidium. CP = Cardinal process. DN = Dorsal node (pedicle scar?) DV = Dorsal valve. P = Pedicle, and pedicle foramen. PD = Pseudodeltidium. PF = Pedicle foramen. VV = Ventral valve.

The outline of the larval specimens was, during the later part of the ontogeny, rounded quadratic, with right cardinal angles, and with about the same width and length. The convexity was considerably smaller than in the adults. In the youngest valves, the outline was more circular, the hinge-line being smaller than the maximum width of the specimens (pl. 5, fig. 7). Judging from the growth-lines in the smallest specimens, this tendency was stronger in the still smaller larvae, which seem to have been almost perfectly circular, with only a large foramen in the dorsal valve (textfig. 30, A—C).

The development of the ventral interior is not as well known as that of the dorsal, partly because of the material of the ventral valves not being so well preserved, and partly because of the ventral interior lacking diagnostic features. In the larger larvae, the muscle impressions are somewhat stronger than in the adults, in particular they are better limited posteriorly. In smaller specimens, the muscle impressions will as usual fade out gradually. No traces of diagonal septa, like those found in *Ch. oblonga* and *Ch. subquadrata* can be observed in the larvae. The supraapical pedicle foramen is observed in comparatively small specimens (length more than 4—4,5 mm). The pseudodeltidium is found in all specimens longer than 6 mm. At this size, therefore, the pedicle was completely transferred to the ventral valve.

Ecology: Christiania holtedahli lived on clay bottom only. Just a very small amount of silt and a little calcareous matter is found in the sediments where this species is present.

From the ontogeny, it seems probable that the larvae rested on the comparatively very strong pedicle, and later turned over, and rested on the ventral valve. The fact that the dorsal valve is much lighter than the ventral one (according to a rough estimate 8–12% of the total weight of both valves), and that it is mechanically strengthened by the longitudinal branchial septa gives good support for the theory of the animal living in that position.

When the valves are closed, the branchial septa will be almost in contact with the ventral valve. The animals must therefore have had some special arrangement for the soft parts of the branchia in order to close the valves.

The variable size of this species in the different districts are shown in textfig. 29, and it is discussed above (p. 56).

ZONE	EIKER-S.	RINGERIKE	OSLO-A.	MJÖSA
			W E	
4bβ				? Coel. ?
4bα				
4aβ	?			
4aα				

	holtedahli		elongata		oblonga
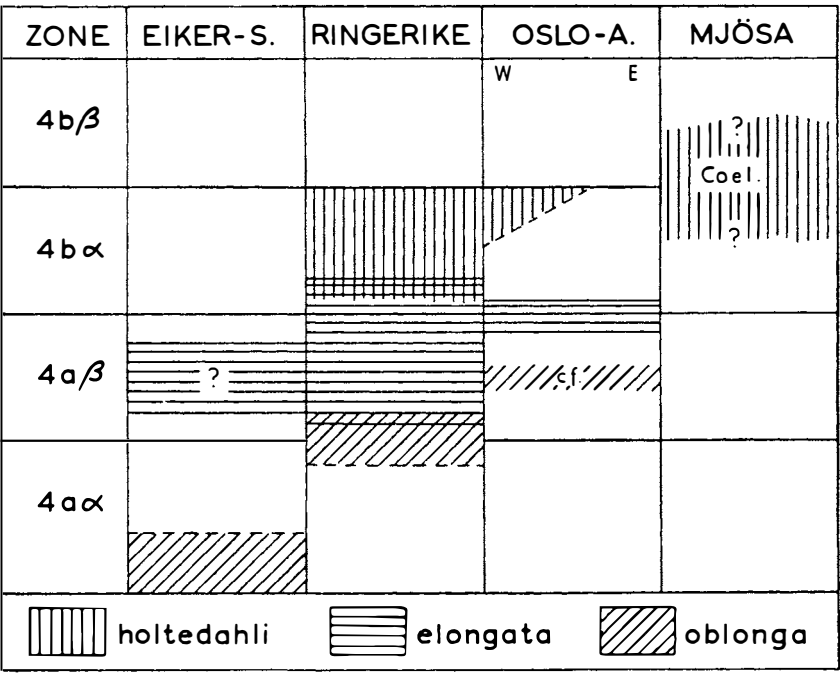
Fig. 31. Diagram illustrating the horizontal and vertical distribution of the *Christiania* species in the Oslo Region.

Remarks: The differences between this species and the other, comparatively well known ones of the genus are mentioned above, or below, under *Ch. elongata* and *Ch. oblonga*.

Distribution. (cf. textfig. 31).

This species is found in zone 4bα and possibly the lowest part of 4bβ in the Ringerike district, in the uppermost part of zone 4bα in the Asker district, where it is very common. In the Oslo district, it seems to be absent. It is also found in the Coelosphaeridium zone in Toten, and in the Ringsaker district.

Except in Norway, this species is also common in the Balclatchie group in the Girvan district, Scotland. The records of *Ch. tenuicincta* from Tyrone, N. Ireland, (REED 1953) and N. Wales refer probably to another, younger Ashgillian species which also occur in zone 5a

in the Oslo region (cf. HOLTEDAHL 1916, p. 86). GAERTNER (1930) records *Ch. tenuicincta* and *Ch. oblonga* from the Ordovician of the Carnic Alps. Only exteriors are known, and at least some of them might belong to this species.

Christiania cf. *holtedahli* sp. n.
Pl. 6, figs. 8—9.

In the material of *Ch. holtedahli*, there is a ventral interior with some deviating features.   Just behind the middle of the valve, at the point of strongest convexity, there is a comparatively large «pocket» in the median line (pl. 6, figs. 8—9). The opening is elliptical in cross section. The cast shows that the pocket is tongue-shaped. The whole specimen is very assymetrical, one side of the valve being much more strongly developed than the other.

This feature is probably due to some damage to the animal in vito. Since, however, a considerable number of assymetrical ventral exteriors have been found from this district, and they are practically all oblique in the same way (the right side is stronger than the left), this may not be an accidental feature. No other interiors of the oblique specimens are observed, and no other specimens showing the ventral interior are oblique. The dorsal valves can not be expected to be assymetrical in the same way, since the hinge-line and outline is symmetrical in all the oblique specimens.

Distribution: All specimens come from zone 4bα (lower part?) at Bratterud, Ringerike district.

Christiania oblonga (PANDER 1830).
Pl. 5, figs. 17—22, pl. 6, fig. 14, textfigs. 5, 27, 26B, and 31.
1830   *Plectambonites oblonga* sp. n. — PANDER, p. 92, pl. 19, fig. 10. '
1830   *Plectambonites ovata* sp. n. — PANDER, p. 92, pl. 19, fig. 9.
1845   *Leptæna oblonga* (PANDER)—VERNEUIL, in MURCHISON, KEYSERLING & VERNEUIL, pp. 228—229, pl. 15, fig. 2a—f.

Material: 2 ventral interiors, one dorsal, one complete exterior, and a number of fragmentary casts of exteriors, all from the same layer, probably from the same slab.

Description: Comparatively small species, 3½ mm wide and 3 mm long. Convexity moderate for a *Christiania*. Cardinal angles right,

the angle between the areas is 150° in the only specimen in which this feature is preserved. The delthyrium, notothyrium and chilidium is badly preserved, and the pseudodeltidium cannot be observed.

Dorsal interior with strongly developed lateral branchial septa (cf. textfig. 27A), which are fused to the socket plates. The posterior part of the central septa (cb) are only slightly developed, and the loops are not complete. The median septum is very strong, but short. Instead of the anterior part of the central septum, and the transversal septum in *Ch. holtedahli*, there is a pair of wedge-shaped ridges (dp), the pointed ends of which are near the hinge-line, and the blunt, round ends where the median septum begins, at the point of strongest convexity of the valves. No cardinal processes are found in the only dorsal interior present.

The ventral interior has very strong vascular grooves, divided by a pair of intervascular septa. Muscular impressions only slightly developed, and can hardly be distinguished from the posterior end of the vascular grooves. The teeth are badly preserved in the material available, but they appear to be strong. No diagonal septa can be seen, and there is a fine supraapical pedicle foramen (0,3 mm in diam.).

A large number of specimens of *Ch. oblonga* from the type locality, Popovka near Leningrad, have been studied in order to obtain some information on this very interesting strophomenid. The Russian material is probably from zone C1, perhaps also from B3. PANDER applied two specific names to this species, *ovata* for the young ones, which are about as wide as they are long, and with the maximum width at the hinge-line, and *oblonga* for specimens which are considerably longer than they are wide, with the maximum width behind the hinge-line. VERNEUIL (1845) and subsequent authors united the two species, which most probably was correct. All transitions can be found, and sometimes the interior of the *ovata*-type is not fully developed (the branchial loops are not complete). This type is therefore regarded as being the young specimens of the species. There is, however, a possibility of the types occuring in different layers, so that *ovata* might be regarded as a chronological subspecies. The Norwegian material should in that case be referred to *ovata*. The present material is not sufficiently labelled as to zone to give any information on this

point. The ventral interior of the Russian specimens are similar to those of the Norwegian ones, except for the vascular grooves being more shallow in most specimens, and the presence of some faint diagonal septa in some of them.

The dorsal interiors vary considerably as to height and thickness of the septa. Their position, however, is stable, and just like the same as in the Norwegian specimen. The cardinal processes also show a considerable variation. In most specimens the cardinal process is triple, with one strong median process, and two smaller ones flanked by the socket plates (pl. 5, fig. 22). This is exactly the same as the cardinal process in the Leptestidae, and some specimens also have a pair of small extra sockets, indicating that the teeth were double. There is no dorsal foramen below the cardinal proce::ses, the pedicle foramen is supraapical in the ventral valve. Behind the cardinal processes, there is a small depression in the valve just where the dorsal foramen is seen in the Sowerbyellinids. Even in thin sections, there is no trace of such foramen. In some specimens (about 25 %) the median cardinal process was reduced, and replaced by a bilobed mass, fused to the socket plates (pl. 5, fig. 20). It is impossible to determine whether these two elements of the cardinal processes are the two smaller, lateral cardinal processes of the first mentioned type (such as in *Oepikina*), or if they are protuberances from the socket plates (such as in the ontogeny of *Ch. holtedahli*). In many specimens the socket plates have some denticles near the notothyrium, and the cardinal processes might be the distalmost of them. In other specimens, an intermediate structure can be found, where the cardinal process is a large mass, with irregular longitudinal furrows, so that it appears to be pentafid or tetrafid (pl. 5, figs. 19, 21). The internal structure is undifferentiated. The specimen figured in textfig. 5 belong to this group.

The shell structure appears to be impunctate. This is probably not due to the state of preservation, since all other features are clearly shown.

Remarks: The fact that most specimens of this species have a complex cardinal process, seems to exclude it, not only from the genus *Christiania*, but also from the whole superfamily Strophomenacea. It is however, evident that it is closely related to the other *Christiania*-species, and the taxonomic consequenses of this observation is discussed above (p. 195).

Ch. oblonga differs from the other species of the genus in a number of features, of which the structure of the cardinal processes is the most striking. Nor is the development of the anterior part of the dorsal central branchial septum and the transversal septum as a special ridge found in any other *Christiania*-species.

Distribution: The Norwegian specimens are from zone $4a\alpha_1$ or the lowest part of $4a\alpha_2$ (zone of *Did. bifidus*, or lowest part of zone of *Did. geminus*). Associated fauna: *Ullerella triplicata* HENNINGS-MOEN, *Tallinella trident* HENNINGSMOEN, and *Alwynella* cf. *ildjernensis*. The locality is 12 m above zone 3cγ, at Muggerudkleiva, Sandsvær—Eiker district. Some additional specimens which may belong to this species have been found in 4aα at Gullerud, Norderhov, Ringerike district.

Christiania cf. *oblonga* (PANDER 1830).
Pl. 5, fig. 13.

Only one specimen has been found of this peculiar form. It is a partly exfoliated complete specimen, showing the dorsal interior. It is small, 4,5 mm wide, and 3,5 mm long, the convexity is just the same as in small specimens of *Ch. oblonga*. The ventral interior and the areas are not known. The dorsal interior is not quite the same as that of *Ch. oblonga* as the septum forming the anterior end of the central septum and the transverse septum is of even thickness, thin, and curved so that it resembles the branchial system in the younger Christianias. It seems, however, to be a discrete plate. The other branchial septa are also high and thin, and there is no difficulty in seeing the complete branchial loops, as is the case with the small specimens of *Ch. oblonga* and *Ch. holtedahli*. The cardinal processes are not preserved, and it is impossible to see whether the lateral branchial septa are fused to the socket plates or not.

If there had been a larger material of this form, it would probably have been made into a new species, intermediate between *Ch. oblonga* and the younger species of *Christiania*.

This only specimen was found in the upper part of zone 4aβ, about 10 m below 4ba, on the southern side of Vassholmen outside Snarøya, Oslo district. It is accompanied by an unusually rich fauna for that zone.

Christiania elongata sp. n.

Pl. 5, fig. 12, textfig. 31.

1954   aff. *Christiania oblonga* (PANDER 1830)—SOKOLSKAJA, pp. 74, pl. 4, figs. 17—18.

Type data: The holotype, PMO 66967, is a cast of the interior of both valves from the transitional beds between zones 4aβ and 4bα, at Sentralinstituttet, Blindern, Oslo district.

Material: 3 casts of the interior of the dorsal valve, 2 of the ventral, and 4 complete casts of the exterior. There are also a large number of fragments, and exteriors which probably belong to this species.

Diagnosis: Christiania species with long, narrow valves, greatest width at the hinge-line, complete branchial loops, and transverse branchial septa in all adult specimens.

Description: Specimens of moderate size, an average specimen is 5,5 mm wide and 8,5 mm long. Areas high, the ventral one triangular, the dorsal rectangular. A pedicle foramen is found in the ventral valve. Pseudodeltidium strongly developed. Dorsal interior similar to that of *Ch. holtedahli*, except for that the transversal septum being considerably less developed than the other branchial septa. The lateral branchial septa are also more evenly curved, and have no raised points at the junction with the transverse septa. The cardinal processes are strong, with a deep fissure between them. The ventral interior is similar to that of *Ch. holtedahli*, except for having some fine diagonal septa. The muscle impressions are also more distinct than in adult specimens of *Ch. holtedahli*. The shell structure is unknown, as all the specimens are either preserved as casts, or in metamorphic rocks.

Remarks: The differences between this species and *Ch. holtedahli* are mentioned above. The two are much alike, and further studies may prove that *Ch. elongata* is a chronological subspecies of *holtedahli*. It has a strong resemblance to young specimens of that species, but differs in the smooth curves of the lateral dorsal septa, and in the shape of the valves, both of which are stable features in the material available. *Ch. elongata* resembles *Ch. subquadrata*, in having diagonal septa. In the latter species, however, the corners of the lateral branchial septa (at the junction with the transversal septa) are strongly pointed, the valves more convex, and the areas lower.

Ch. elongata is united with *Ch. oblonga* (PANDER) through a number of intermediate forms, in Norway occuring in zone $4aa_4$ and $4a\beta$. The typical *oblonga* is smaller, shorter, almost quadrangular, and has a different development of the branchial septa. Some of these intermediate forms have more or less developed diagonal ventral septa, resembling *Ch. subquadrata*. Among the latter are the specimens described by SOKOLSKAJA (1954) as *Ch. oblonga* from the Echinosphaerites zone at Zvjanka near Leningrad. At present the Norwegian material of these intermediate forms is too small to allow a more detailed study.

Distribution: This species is found in zone $4a\beta$, especially in the transitional beds between this zone and $4b\alpha$. Except for the typical specimens from the Oslo—Asker and Ringerike districts, there are some specimens from zone $4a\beta$ in the Sandsvær—Eiker district, which might belong to this species.

Superfamily Strophomenacea KING 1846.

Family Strophomenidae KING 1846.

Subfamily Strophemeninae KING 1846.

A large number of generic terms have been applied to the species belonging to this subfamily.

Leptaena DALMAN 1828 has been misinterpreted by various authors. In this paper the type species is redescribed.

Hedstroemina BANCROFT 1929 and *Kjaerina* BANCROFT 1929 were included in *Rafinesquina* HALL & CLARKE 1892 by SALMON (1942), but differ from the typical members of that genus as to interior structure of the ventral valve. In this paper, they are used as subgenera of *Rafinesquina*.

Actinomena ÖPIK 1930 is probably a synonym of *Kjerulfina* BANCROFT 1929. Both genera have a *Leptaena* (or rather *Oslomena-*) like dorsal interior, but reversed geniculation. The difference between the genera is probably due to their living in different environment. *Actinomena*, which is heavily calcified, lived in calcareous-muddy to sapropelitic sediments. *Kjerulfina* is only slightly calcified, and lived in sand-silt -clay environment with no surplus of lime.

Dactylogonia ULRICH & COOPER 1942 and *Oepikinella* WILSON 1944 are probably synonyms of *Oepikina* SALMON 1942. *Dactylogonia*

is said to have only three septa in the dorsal interior, and *Oepikinella* has four, while *Oepikina* has five. In all other repects the genera appear to be identical. The author has studied a large material of the *Oepikina dorsata*-group, and at least here, the relative strength of the septa varies considerably, especially as regards the median septum.

Besides the typical *Oepikina*-species, there are some which have diverging instead of subparallel septa, just like *girvanensis*, and this species is a transition to another group intermediate between *Oepikina*, *Leptaena* and *Rafinesquina*. The dorsal valves have more or less pronounced bilobed muscle impressions, and there is usually a central triangular plate like that in *Leptaena*. These species are included in the new genus *Oslomena*.

Trigrammaria and *Microtrypa* WILSON 1945 differ from *Strophomena* in the development of the dorsal septa, and in the shell structure. The validity of these genera is doubtful, they are probably synonyms of *Strophomena*. Most of the species referred to *Trigrammaria* by WILSON (1945) have a late resupination. About one half of the valve has a «normal» convexity. However, it is doubtful whether this feature is of any taxonomic value.

The classification of the genera within the subfamily Strophomeninae is based on a large number of different features. The convexity and sculpture were used by most older authors, while modern ones have stressed the importance of the shell-structure and the dorsal interior (SALMON, ÖPIK) and the ventral interior. (BANCROFT, HOLTEDAHL). In most cases the author has tried to combine these views, all generic diagnosis are based on internal features, with one exception. As usual, a feature which is stable and of high diagnostic value in one group, might vary considerably in another. It is therefore necessary to have a large material to study the variation in order to evaluate the features to be used in the taxonomy.

Genus *Rafinesquina* HALL & CLARKE 1892.
Subgenus *Rafinesquina (Rafinesquina)* HALL & CLARKE 1892.

As defined here, the typical subgenus only includes species with large, flabellate ventral muscle impressions (different from *Kjaerina* and *Oslomena*), and with no, or not fully developed septa in the dorsal

valve (different from *Oepikina*). The genus is mainly found in the Upper Ordovician of North America, and only occurs sporadically in the Middle Ordovician of the Oslo region.

Rafinesquina (Rafinesquina) sp.

Pl. 8, fig. 8, textfig. 32C.

1916   *Rafinesquina* sp. (cf. *alternata* EM. var *loxorhytis* MEEK)—HOLTEDAHL, p. 22, pl. 1, fig. 12.

Material: Apart from the specimen described and figured by HOLTEDAHL, there is only one fairly complete cast of a ventral interior.

Description: Both specimens have typical *Rafinesquina*-like ventral muscle impressions, and the new specimen is 45 mm wide and 29 mm long. The valves are strongly convex, and the irregular convexity may be due to a distortion of the valves after burial. The geniculation is rounded, and the angle between the disc and the fringe, is about 120°. Otherwise, there is nothing to add HOLTEDAHLs description (l.c.).

Remarks: The present species undoubtedly belongs to *Rafinesquina* (*Rafinesquina*) because of the structure of the muscle impressions, but it is impossible to refer it to any known species owing to the limited material. The specimens are also rather like *Leptaena* (?) *indigena* in size and convexity, and might have been distorted specimens of that species. However, the leptaenoid geniculation, and the long, posterior ends of the muscle impressions are, however, not found in the two specimens mentioned here.

Distribution: In the Coelosphaeridium-zone in the Ringsaker district.

Subgenus *Kjaerina* BANCROFT 1929, and subgenus *Hedstroemina* BANCROFT 1929.

These two subgenera were made to include a number of Rafinesquinids from the Ordovician of Shropshire. The ventral muscle impressions are smaller than in *Rafinesquina* (*Rafinesquina*), and the cardinal processes are long, parallel plates. They also have very thin valves with slightly calcified interior features.

9

The difference between the genera is that the boundary ridges of
the muscle impressions (in the ventral valve) are narrowly diverging
(40—70°) in *Kjaerina,* and widely diverging in *Hedstroemina.* (80—
120°). *Hedstroemina* also has geniculate valves, while *Kjaerina* has
almost flat valves, or slightly geniculated ventral and flat dorsal. In
addition, the median ribs are stronger than the others in *Kjaerina.*

Most of the features mentioned above, are of small taxonomic
value, at least at the generic level. The sculpture and convexity vary
considerably, and the thin valves may be due to ecological features.
The angle of the boundary ridges does not seem to be of such an im-
portance that it can be used for separating genera. There are, however,
two well defined groups of species which correspond to the subgenera,
as defined here. The only exception from the original diagnosis observ-
ed by the author, is that the strong median ribs are found in
some species with a *Hedstroemina*-like interior, and that they are
absent in some *Kjaerina*-species. The author regards these groups as
subgenera of *Rafinesquina.*

SALMON (1942) regarded both *Kjaerina* and *Hedstroemina* as
synonyms of *Rafinesquina.* Among the species described by that
author as a *Rafinesquina,* is *R. robusta* WILSON 1932. If *Hedstroemia*
is included in *Rafinesquina* (as a subgenus or as a synonym) this spe-
cific name is a homonym of *Hedstroemina robusta* BANCROFT 1929.
Coincidentally the species seem to be quite like (only the ventral
interiors are known).

Rafinesquina (Kjaerina) lepta sp. n.
Pl. 12, fig. 14, textfig. 32M.

Type data: The holotype, PMO 67133: is the interior of a ventral
valve from the lower part of zone 4bδ at Rauskjær, Asker district.

Material: About 15 ventral interiors, and a moderate number of
exteriors, and casts of exteriors.

Diagnosis: Kjaerina species with rounded geniculation, convex
disc, with a slight carina, and scarcely differentiated sculpture. Ventral
muscle impressions slightly variable in outline. Dorsal interior un-
known.

Description: Small, strongly convex species (average width 16
mm, length 10 mm). Valves rounded geniculated, and with right

cardinal angles. Areas low. Sculpture hardly differentiated except for the group of strong median ribs characteristic for the subgenus. The disc is strongly convex.

In most specimens, the ventral interior is of the shape which is typical for the genus (cf. textfig. 34C). Because of the geniculation, the muscle impressions are somewhat longer and broader in old specimens.

The do sal interior is unknown, and the shell structure is finely pseudopunctate.

Remarks: This species differs from other Kjaerinas in the slightly differentiated sculpture, and in the strongly convex disc and geniculation. Species with similar external appearance have been referred to *Hedstroemina,* but he present species have the strong median ribs, and the small angle between the boundary ridges of the ventral muscle impressions which are believed to be typical for *Kjaerina.* It is therefore included in that subgenus.

Distribution: Rafinesquina (Kjaerina) lepta occurs in the upper part of zone 4bγ, and the lower and middle parts of zone 4bδ in the Asker district. Exteriors probably belonging to this species are found in the Ringerike and Hadeland districts.

Rafinesquina (Hedstroemina) holtedahli sp. n.

Pl. 8, fig. 14, textfig. 32H.

1916 *Rafinesquina deltoidea* CONRAD (parte)—HOLTEDAHL, pp. 16—18, pl. 1, figs. 4—6, non figs. 2—3.

Type data: The holotype, PMO 66997, is a cast of the interior of a ventral valve from zone 4bα—β at Bratterud, Ringerike district.

Material: 3 ventral interiors, a number of exteriors, and two complete specimens.

Diagnosis: Hedstroemia species with badly defined interior structures, and strongly deflected valves. Umbonal part very convex, and irregularly triangular disc.

Description: A comparatively small species, the holotype is 18 mm wide, 15 mm long and 13 mm high. The valves are subparallel and geniculated. The fringe is long, and the umbonal part of the valves is very convex. The valves are thin, and therefore vary in shape and angle of the geniculation. The disc generally is triangular, but in some

specimens irregular, and there are strong undulations parallel to the angle of geniculation. The sculpture consists of fine ribs with 3—4 striae between each. There are also irregular, but strong concentric rugae.

The ventral interior has small teeth, short, strong dental plates, and no trace of the posterior part of the muscle impressions or the pedicle foramen.

The dorsal interior has long, subparallel cardinal processes, and strong socket plates diverging at about 120°. The shell structure is comparatively coarsely pseudopunctate.

Remarks: R. (*H.*) *holtedahli* differs from the other species of the subgenus in the shape, which appears to be a constant feature (cf. textfig. 32H.), especially the strong umbonal convexity.

Because of the triangular shape, this species was referred to the incompletely known *Rafinesquina deltoidea* (CONRAD) by HOLTEDAHL (1916). From the descriptions given of the latter species by SALMON (1942) and HALL & CLARKE (1892) the Norwegian specimens evidently are not conspecific with the American ones. They differ in several important features, both in exterior and interior.

Distribution: This species is found in zone 4bα—β in the Ringerike district. The specimens referred to *Rafinesquina deltoidea* (CONR.) by HOLTEDAHL, (1916, pl. 1, figs. 2—3, non figs. 4—6) belong probably to *Rafinesquina* (*Kjaerina*) *lepta* sp. n., and are from zone 4bδ in the Asker district.

Rafinesquina (*Hedstroemina*) *ungula* sp. n.

Pl. 8, figs. 9—11, textfig. 32B.

1916   *Leptaena undata* McCOY (?)—HOLTEDAHL, p. 75, pl. 13, fig. 12.

Type data: The holotype, PMO 7834, is a ventral valve from zone 4bγ at Vestbråten, Ringerike district.

Material: 3 dorsal and 8 ventral interiors, and a large number of complete specimens and valves.

Diagnosis: Abruptly geniculated *Hedstroemina* species with almost flat disc with concentric corrugations, and small, strong ventral muscle impressions with radial striae.

Description: A species of moderate size, average width 30 mm, length 21 mm. The ventral valve is flat, with an abruptly rounded

geniculation, which is at right angles to the disc. In some specimens, the disc is slightly convex. The geniculated fringe is generally short, 3—5 mm. The sculpture consists of fine ribs with 4—5 striae between each of them, and strong, usually regular concentric rugae. The areas are low. The dorsal valve is almost completely parallel to the ventral, and in spite of this, the body volume is comparatively large. The valves are very thin.

The ventral interiors have small teeth, dental plates diverging 110°, and ventral muscle impressions with strong boundary ridges, which meet posteriorly in adult specimens and have radial striae. The ventral interior quite resembles that of *Strophomena*.

The dorsal interior has long, blade-like cardinal processes, and strong, thin, stright socket plates.

The shell structure is finely pseudopunctate.

Remarks: This species was referred to as *Leptaena undata* Mc Coy by HOLTEDAHL (l.c.). The specimens figured, (1916, pl. 13, fig. 12) came from the Cyclocrinus Layers at Furuberget, Hamar—Nes district. The whole of the material, with the exception of that specimen, comes from zone 4bγ of the Ringerike district. The possibility of HOLTEDAHLs specimen being incorrectly labelled can therefore not be excluded.

R. (H.) ungula differs from most other species of that subgenus in the abrupt geniculation, and in the strongly developed, but small ventral muscle impressions. Apart from the sculpture, it very much resembles the not very well known *Rafinesquina (Hedstroemina ?) muensteri* HOLTEDAHL, which occurs in zone 4bα (cf. p. 135).

Distribution: This species is found in zone 4bγ of the Ringerike district, and (?) in the Cyclocrinus Layers in the Hamar–Nes district.

Rafinesquina (Hedstroemina) cf. *robusta* BANCROFT 1929.
Pl. 8, fig. 5, textfig. 32I.

Material: 4 ventral interiors, and some fragmentary casts of exteriors.

Description: An average specimen is 32 mm wide and 32 mm long. The convexity of the ventral valve is fairly strong and even. The sculpture is rather coarse, and there is not much difference between

the ribs and the striae. The cardinal angles are pointed, and the flanks are flatter than the rest of the valves.

The ventral interior has a small, rather indistinct muscle impression, with radial striation. The dental plates are strong and short, and the teeth are not fully developed.

The dorsal interior and the shell structure is unknown.

Remarks: This species evidently belongs to *Rafinesquina* (*Hedstroemina*), and is a transition between this subgenus and the typical one. The species resembles *Hedstroemia robusta* BANCROFT (1929, pl. 2, figs. 6—7) both as to shape, size and sculpture. The Norwegian form differs from the British in the stronger convexity of the latter. It also quite resembles *Rafinesquina robusta* WILSON 1932 (as figured by SALMON 1942, pl. 85 figs. 23—25). As mentioned above, these two rather similar species are homonyms. Apart from the convexity, which is stronger in the Canadian species, and the sculpture, which is coarser in the British, there is no difference between these two species. Since, however, only the ventral valve is known at present, it is possible that the dorsal valves will show more prominent differances. The British species seems to be of about the same age as the Norwegian specimens, while the Canadian species is considerably younger.

Distribution: R. (*H.*) cf. *robusta* is found in the Coelosphaeridium zone in the Ringsaker district.

Rafinesquina (*Hedstroemina*) aff. *robusta* BANCROFT 1929.
Pl. 8, figs. 1—4.

Material: 6 dorsal and 5 ventral fragmentary interiors.

Description: The exterior of the species is not very well known. The valves are rather flat, the ventral moderately convex, without geniculation. The sculpture seems to be rather coarse. The specimens are rather large, probably up to 42 mm wide, and 41 mm long.

The ventral interior have widely diverging, very high dental plates, comparatively small teeth, and rather indistinct muscle impressions. The area is moderately high, and the delthyrium broad (120°).

The dorsal interior has long, slightly diverging cardinal processes, strong, low socket plates, and a rather indistinct anchor-shaped platform, which is found in the oldest specimens.

Remarks: This species differs from *R.* (*H.*) *robusta* in the lower convexity, and in the less defined ventral muscle impressions. The dorsal interior is rather like that of *Eostropheodonta williamsi*, but differs in the angle between the dental plates being larger, and in the absence of denticles. Never the less it might indicate that *Eostropheodonta* was derived from species like this one.

Distribution: This species is found in the Coelosphaeridium zone in the eastern part of the Ringsaker district (Brumundal).

Rafinesquina (*Hedstroemina?*) *muensteri* HOLTEDAHL 1916.

1916   *Rafinesquina münsteri* sp. n. — HOLTEDAHL, p. 29, pl. 3, fig. 8.

No new material of this species is available, the holotype is still the only specimen known. It is quite like *R.* (*H.*) *ungula* sp. **n.** in all features known, except for the concentric rugae being broken by the ribs in *muensteri*, and not in *ungula*. A large number of specimens of the latter species have been studied, but none of them show the type of sculpture found in *muensteri*.

The holotype of *R.* (*H.*) *muensteri* was found in the transitional beds between zone 4bα and 4bβ in the Ringerike district.

«*Rafinesquina*« *ringerikensis* HOLTEDAHL 1916.

1916   *Rafinesquina* (?) *ringerikensis* sp. n. — HOLTEDAHL, p. 30, pl. 3, fig. 7.

Of this species, only the holotype, the specimen figured by Holte- DAHL, is available. There is nothing to add to his description, the interiors are still unknown. The sculpture is very characteristic, resembling that of *Ptychoglyptus*. The concentric rugae, however, are not broken by the ribs, and the shell structure seems to be different, with ordinary large, pseudopuncta, instead of the small, primitive ones found in *Ptychoglyptus*. The species might therefore belong to the Strophomenidae, but can hardly belong to *Rafinesquina*. Before the interiors have been studied, it is impossible to place this species in the correct genus.

It occurs in the transitional beds between zone 4bα and 4bβ in the Ringerike district.
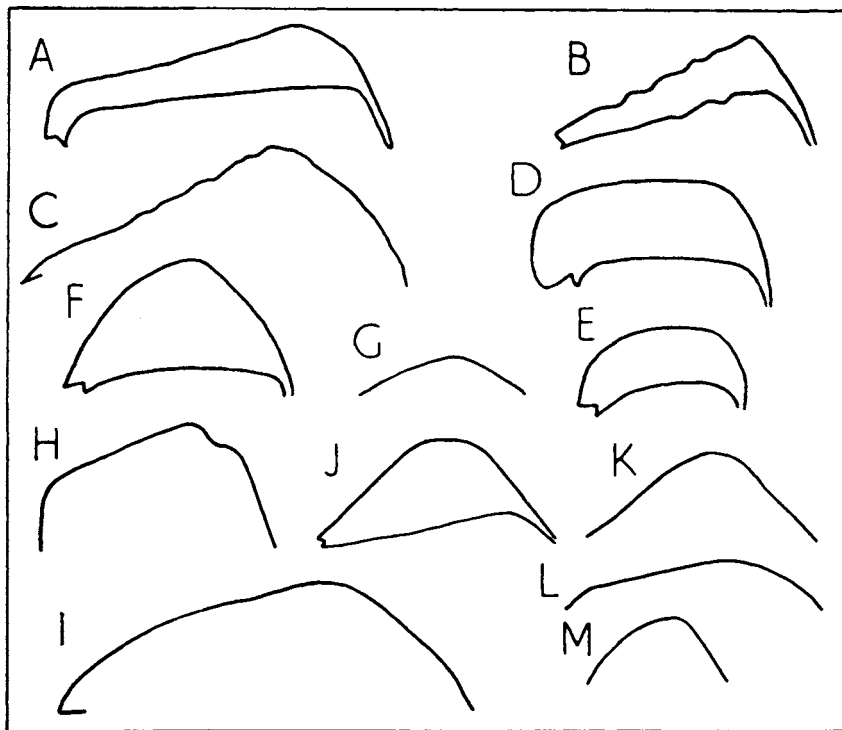
Fig. 32. *Cross-sections of some Strophomenid species.* About 9/10-th natural size. A. *Eostropheodonta williamsi* sp. n. from the Cyclocrinus Shale of the Hamar —Nes district. B. *Rafinesquina (Hedstroemina) ungula* sp. n. from zone 4bα-β at Bratterud, Ringerike district. C. *Rafinesquina (Rafinesquina)* sp. from the Coelosphaeridium Beds in the Ringsaker district. D, E. *Oslomena osloensis* sp. n. D is a large specimen from the Toten district, E, is a typical specimen from zone 4bα at Arnestad, Asker district. F. *Oepikina dorsata media* (ÖPIK 1930) from the Bryozoan Beds in the Langesund—Gjerpen district. G, J. *Mjoesina mjoesensis* (HOLTEDAHL 1916) G. Ventral valve from the Cyclocrinus Beds in the Hamar—Nes district. J. A complete specimen from the Mjøsa Limestone in the Hamar—Nes district. H. *Rafinesquina (Hedstroemina) holtedahli* sp. n. from zone 4bα-β at Bratterud, Ringerike district. I. *Rafinesquina (Hedstroemina)* cf. *robusta* BANCROFT 1929, from the Coelosphaeridium zone (boulder) at Bruflat, Ringsaker district. K. *Mjoesina* cf. *mjoesensis* (HOLTEDAHL 1916) from the Coelosphaeridium Beds of the Ringsaker district. L. *Mjoesina* (?) *gregaria* sp. n. from the Coelosphaeridium (?) Beds of the Toten district. M. *Rafinesquina (Kjaerina) lepta* sp. n. from zone 4bγ at Hvalstad, Asker district.

Mjoesina gen. nov.

Diagnosis: Strophomenid genus with convex ventral valve, flat, dorsally geniculated dorsal valve, and ventral muscle impressions limited by straight converging septa. Dorsal interior unknown.

Remarks: This genus differs from most others in the development of the ventral muscle impressions. *Kjerulfina*, which has similar, but parallel boundar ridges (or septa), has reversed orientation of the valves. The convexity and shape of the valves is similar to that of *Oslomena*. At present only the type species, *M. gregaria* sp. n. and *M.* cf. *mjoesensis* are included in the new genus.

Type species: Rafinesquina mjoesensis HOLTEDAHL 1916, pp. 19 —20, pl. 2, figs. 1—3.

Mjoesina mjoesensis (HOLTEDAHL 1916).

Pl. 8, fig. 6, textfig. 32G, J.

1916 *Rafinesquina mjøsensis* sp. n. — HOLTEDAHL ppp. 19—20, pl. 2, figs. 1—3.
1916 *Rafinesquina* cf. *mjøsensis* sp. n. — HOLTEDAHL, p. 20.
1916 *Rafinesquina parva* sp. n. — HOLTEDAHL, pp. 22—23, pl. 1, fig. 7.

Type data: The lectotype, chosen here, is PMO 38448 a complete specimen from the upper part of the Mjøsa Limestone at Helgøya, Hamar—Nes district. (Figured by HOLTEDAHL 1916, pl. 2, fig. 2).

Material: A large number of specimens, most of them preserved in limestone. Only two ventral and no dorsal interiors.

Description: An average specimen is 17 mm wide and 14 mm long. Ventral valve strongly convex without geniculation. Sculpture consisting of coarse ribs, slightly differentiated. The areas are low, and the delthyrium is very small. The evenly rounded ventral valve, and the rounded geniculation of the dorsal are characteristic features.

The ventral interior has muscle impressions limited by straight lines, the posterior ones being slightly converging, and rather long. (in old, well calcified specimens the straightness and angularity of these lines somewhat obscured by deposition of calcareous tissue at their bases, so that they appear to be rounded, at least in casts, cf. pl. 8, fig. 6). The teeth are strong, triangular. There is a pedicle foramen in all specimens.
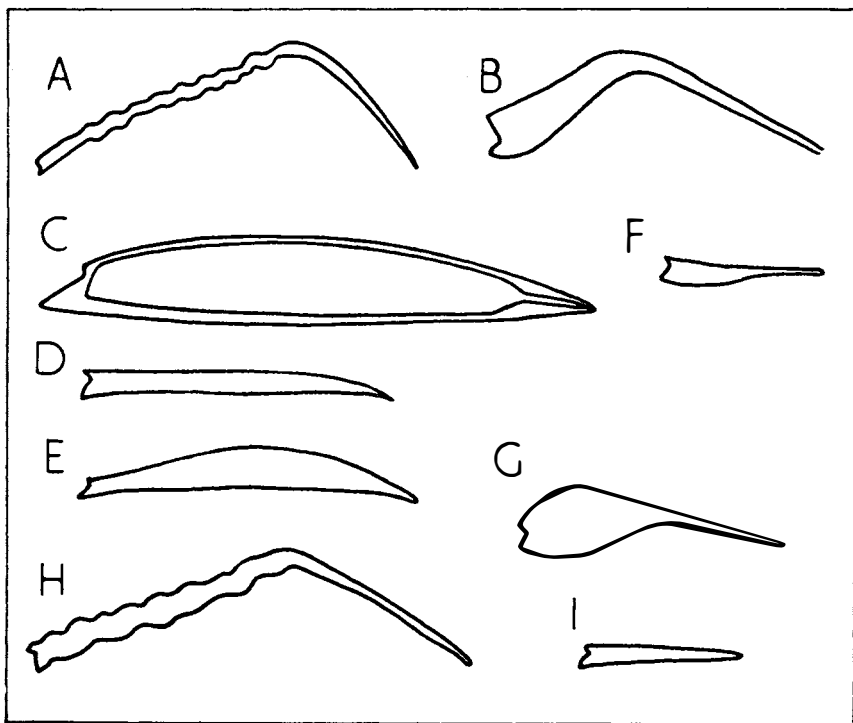
Fig. 33. *Cross-sections of some Strophomenid species.* Magnification about 9/10th. A. *Kjerulfina broeggeri* (HOLTEDAHL 1916), from zone 4bα-β at Bratterud, Ringerike district. B. *Strophomena (Gunnarella) delta* sp. n., from zone 4bδ, at Gåsøya, Oslo—Asker district. C. *Strophomena steinari* sp. n. from the Coelosphaeridium beds in the Ringsaker district. D. *Strophomena norvegica* sp. n. from zone 4bα at Bratterud, Ringerike district. E. *Strophomena hirsuta* sp. n. from the Coelosphaeridium Beds in the Ringsaker district. F. *Strophomena (Gunnarella) alpha* sp. n. from zone 4bα at Billingstad, Asker district. G. *Strophomena kjerulfi* HOLTEDAHL 1916, from the Mjøsa Limestone at Helgøya, Hamar—Nes district. H. *Kjerulfina limbata* sp. n. from zone 4bγ at Vestbråten, Ringerike district. I. *Kjerulfina lata* sp. n. from zone 4bα at Nakholmen, Oslo district.

The dorsal interior is unknown. The shell structure is finely pseudopunctate.

Remarks: The closest relative seems to be *M.* cf. *mjoesensis*, which is older and has longer, narrower muscle impressions, and differentiated sculpture. *M. gregaria* sp. n. has smaller muscle impres-

sions, coarser sculpture, lower convexity of the valves, and is larger.

Rafinesquina parva HOLTEDAHL, is included in this species, as young valves of *mjoesensis* cannot be distinguished from the type of *parva*. *Parva* was recorded from older layers than *mjoesensesis*, but specimens of *mjoesensis* are found in the same layers as the type of *parva*.

The specimens mentioned by HOLTEDAHL (1916, p. 20) as «extremely nearly related» to *mjoesensis*, from the Hadeland district, certainly belong to this species. The horizon in which they are found is now referred to as Cyclocrinus-beds.

Distribution: The types of this species are from the upper part of the Mjøsa Limestone, but it occurs in lower horizons too, in the Cyclocrinus beds at Furuberget, Hamar—Nes district, and in the same horizon in the Hadeland district.

Mjoesina cf. *mjoesensis* (HOLTEDAHL 1916).
Pl. 6, fig. 13, pl. 8, fig. 7, textfig. 32K.
(non *Rafinesquina* cf. *mjoesensis* sp. n. — HOLTEDAHL, p. 20).

Material: 3 ventral interiors, and a number of casts of the exterior.

Description: This species differs from *M. mjoesensis* in having much longer and higher plates in the ventral muscle impressions, and the sculpture being clearly differentiated, with 3—4 striae between each rib. The specimens are also slightly larger, and the ventral valve is not so evenly convex. Because of the limited material it is impossible to study the variation in this species. It appears to be considerably more variable as to shape and size than *mjoesensis*.

Distribution: In the Coelospharidium zone in the Ringsaker district. It is remarkable that this species which appear to be more highly developed than *mjoesensis* occurs in older layers.

Mjoesina gregaria sp. n.
Pl. 8, figs. 12—13, Textfig. 32L.

Type data: The holotype, PMO 66996, is the cast of a ventral interior from the Coelosphaeridium zone at Sund, Einavatn, Toten district.

Material: 4 ventral interiors and a number of more or less fragmentary casts of exteriors.

Description: A rather large species, the holotype is 29 mm wide and 21 mm long. Ventral valve moderately convex, dorsal valve almost flat. Ventral area high dorsal, low. Sculpture consisting of coarse, slightly differentiated ribs. Outline uniformly hemicircular, in some specimens, the greatest width is just in front of the hinge-line.

The ventral interior has strongly developed muscle impressions of moderate size. They are deep, and are of the usual *Mjoesina*-shape. The adductors are small, and placed in the middle of the diductors. The vascular system consists of two large ovaria, limited by broad vascula starting at the adductor muscle impressions. The marginal vascular branches are short, and the ovaria, which take up most of the inner surface of the valves, are slightly depressed with an irregularly wrinckled surface.

The teeth are strong, triangular. In gerontic specimens, as for instance the holotype, the anterior surface is vertically striated, resembling the denticulations in the Stropheodontids (cf. pl. 12, figs. 7—8).

The dorsal interior is unknown.

Remarks: This species is referred to *Mjoesina* because of the ventral muscle impressions, but differs from the type species in the low convexity, the size and the coarse sculpture. The small, regularly limited muscle impressions distinguish the species from *Rafinesquina*.

Distribution: In the Coelosphaeridium zone in the Toten district. Fragmentary exteriors with the same sculpture are found in the Hamar—Nes district.

Genus *Strophomena* BLAINVILLE

As defined here (cf. textfig. 34, F, G), this genus both includes species with a comparatively coarse undifferentiated sculpture, and those with fine, well differentiated sculpture. The latter species might perhaps be included in *Longvillia* BANCROFT 1933 (cf. BANCROFT (M S 1949). However, the type species of *Longvillia*, *L. grandis* (SALTER) is not well known, and judging from the figures and specimens seen by the author, the sculpture is not particularly fine or well differentiated.
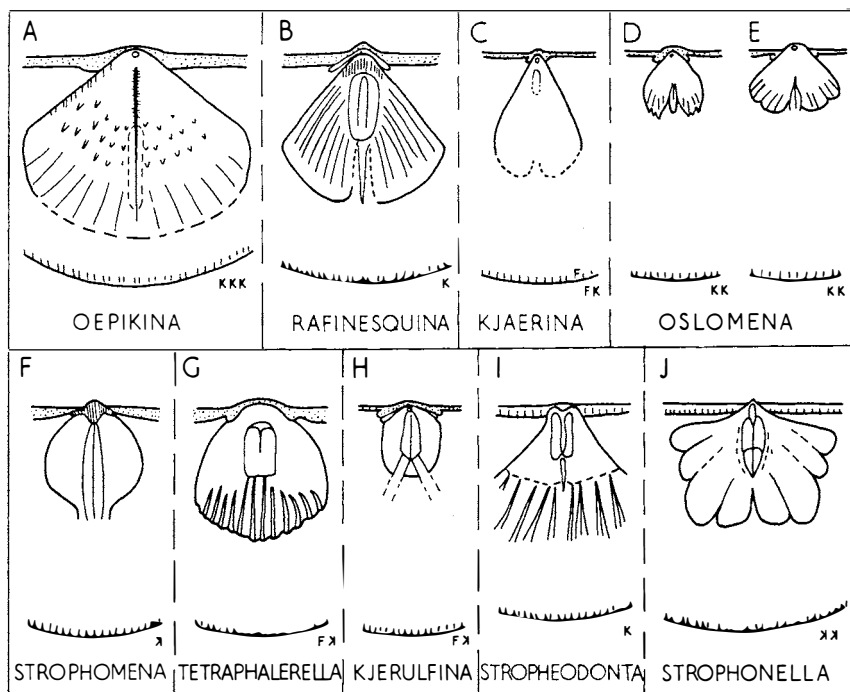
Fig. 34. *The variation of the ventral muscle impressions in the Strophomenidae and Stropheodontidae*. The sources of the figures are: A. *Oepikina dorsata media*, from the Langesund district, cf. pl. 12, fig. 10. B. From HALL & CLARKE 1892, pl. 20, fig. 28 (*R. alternata*). C. *Kjaerina geniculata* Upper Longvillian, Road section near Onny River, Shropshire, England. A exceptionally well calcified specimen. D—E. Two specimens of *Oslomena osloensis* from the same population (zone 4bα, Arnestad, Asker district). F. *Strophomena neglecta* (JAMES) Richmond (Waynesville), Blanchester, Ohio, U.S.A. G. *Tetraphalerella plano-dorsata*. From WANG 1949, pl. 9, fig. D1. H. *Kjerulfina orta* (ÖPIK) zone C2β, Kukruse, Esthonia. I. From WILLIAMS 1953a, pl. 7, fig. 11. (*Stropheodonta* ss. sp.) . J. *Strophonella* cf. *euglypha* from the Mulde Marl, (Upper Wenlock), at Tegelbruket, Frøjel, Gotland. RM. Br. 35731.

The specimens are all reduced to the same size (the curved line below each figure indicate the relative position of the margin of the valve). The letters K, KK and KKK indicate the convexity of the valves, K = slight. KKK = very strong. FK indicate that the valves are generally flat, and geniculated. An inverted K indicate that the convexity is inverse (like that of *Strophomena*).
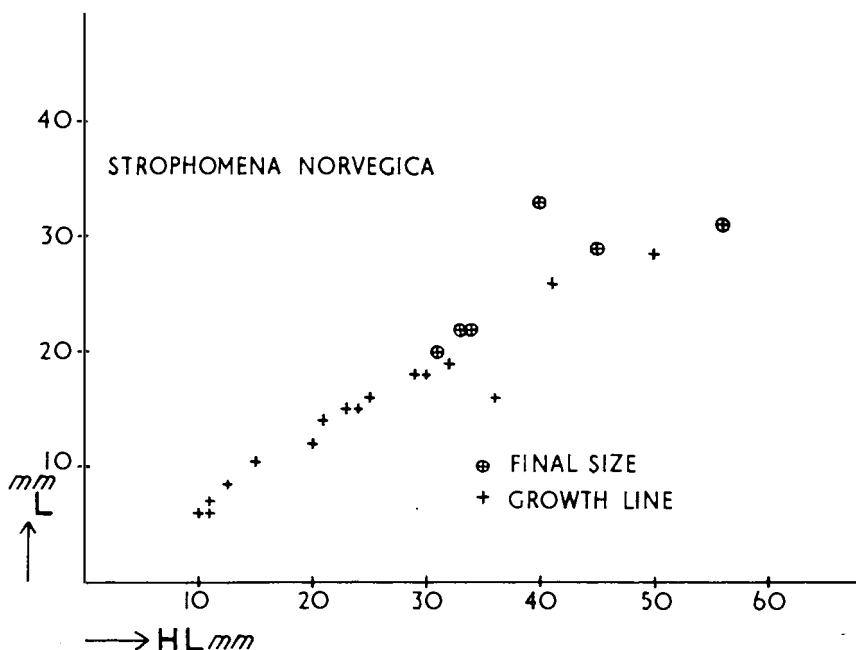
Fig. 35. Diagram showing the correlation between the final outline and the growth-lines in some specimens of *Strophomena norvegica* from the same layer in zone 4bα at Bratterud, Ringerike district.

Only species with distinct resupination, or reversed convexity of the valves are included in *Strophomena*. Species with normal convexity, and reversed geniculation in most cases belong to *Kjerulfina*.

In *Strophomena*, the socket plates are curved outwards and often pointed ventral-wards. In *Kjerulfina* the socket plates are straight, or only slightly curved, whereas they are always straight in *Rafinesquina*.

Strophomena norvegica sp. n.

Pl. 11, figs. 1—3, textfig. 33D, 35.

1916   *Strophomena asmussi* (VERN.) parte HOLTEDAHL, pp. 51—52, pl. 8, figs. 1—6, non figs. 7—8 and pl. 9, fig. 2.

1954   cf. *Strophomena asmussi* (VERNEUIL 1845)—SOKOLSKAJA, pp. 83—85, pl. 5, figs. 1—2, non figs. 3—4.

Type data: The holotype, PMO 7117, is the cast of a dorsal interior from zone 4bα at Røysetangen, Ringerike district.

Material: 5 casts of the dorsal interior, and 7 of the ventral, and a large number of complete specimens and valves in rock.

Diagnosis: Slightly convex, thin-shelled *Strophomena* species, with very long, forked cardinal processes, curved socket plates parallel to the hinge-line, badly defined muscle impressions, ventral diductors flabellate, pseudodeltidium wedge-shaped, and with well differentiated sculpture.

Description: Medium sized, almost flat, thin-shelled species. The size of the well preserved specimens from a population from the type locally is shown in textfig. 35. Surface sculpture consisting of intercalating ribs, with 6—10 striae between each. Every other rib is smaller than the others. Very fine concentric growth-lines occur regularly, about 6 pr. mm at the margin. Near the apex, both the striae, ribs and growth-lines are much finer, without much decrease in number. Coarse growth-lines occur occasionally. Nearly every valve show some irregularites in the sculpture due to fractures in the thin shells during the growth. These healed fractures are found in all parts of the valves, and are often surprisingly numerous.

The areas are high, and there is a supraapical foramen in the ventral valve. The pseudodeltidium is strongly protruding, and rounded wedgeshaped, in some specimens with a median keel. The growth-lines of the area are continuous with those of the pseudodeltidium.

The internal surface is sculptured in the same way as the exterior in young specimens, exept that the growth-lines are missing. In adult specimens, the sculpture fades out in the central parts of the valve, due to the deposition of secondary tissue, which, however, is extremely thin in this species, in spite of it occuring in calcareous rocks. In adult specimens, the fine striae of the sculpture have a wavy appearance near the margin, probably due to the differentiation of the vascular system.

In the dorsal interior, the cardinal processes are very long, thin and forked. They are placed quite close together, with a thin slit between them. The socket plates are strongly curved parallel to the hinge-line, and they are continuous with the socket plates. The muscle impressions are only slightly developed and are divided by a rounded median septum.

Ventral interior with distinct pedicle foramen, and feebly develloped, flabellate muscle impressions. The teeth are long and thin,

and they are not fused to the hinge-line, there is generally a thin slit between them.

The shell structure is finely pseudopunctate.

Remarks: The author has not seen any authentical specimens of *Orthis asmusi* VERNEUIL 1845. According to ÖPIK (1930, p. 166) this species is a *Kjerulfina* (= *Actinomena*), and since *Strophomena norvegica* show a number of important differences from the members of that genus, it seems probable that the species described by HOLTEDAHL (1916) is not identical with *asmusi* (That species is also recorded from younger layers than *norvegica*, zone D in Esthonia).

Of the specimens described by SOKOLSKAJA (1954 pl. 5) as *Strophomena asmusi* at least that on fig. 2 belong to *S. norvegica*. Those on figs. 3—4 seem not to belong to the same species, and are also from an other horizon.

Strophomena norvegica belongs to a group of species which is fairly common in the Middle and Upper Ordovician of the Oslo region. They differ from the typical *Strophomena* in the structure of the cardinal processes, which are short and thick, and often strongly curved posteriorly in most other Strophomenas, while they are long, thin and protruding anteriorly in the *norvegica*-group. The ventral muscle impressions are different too, and the typical Strophomenas are generally more convex than *S. norvegica*. The specimens figured by HOLTEDAHL (1916, pl. 8, figs. 7—8) as *S. asmusi* from zone 5a, probably belong to a closely related species, which mainly differs from *norvegica* in the shape of the socket plates. The group is remarkably stable, no important differences can be detected between the specimens from the different districts and horizons, even if they occur in different sediments.

It does not seem necessary to separate this group of species as a new genus or subgenus, even if it differs from the typical *Strophomena* in certain constant features.

S. hirsuta, which is the only contemporaneous species which might belong to this group of species, is larger, with stronger ribs, and better developed muscle impressions.

Distribution: Strophomena norvegica is found in zone 4bα—β in the Ringerike district, and also in the Cyclocrinus zone in Hadeland. (The specimen figured by HOLTEDAHL 1916, pl. 8, fig. 6, is not from stage 4c, the Cyclocrinus beds correspond to stage 4b). The species is also found in zone 4bβ in the Oslo—Asker district.

Strophomena hirsuta sp. n.
Pl. 11, figs. 9(?)—10, textfig 33E.

Type data: The holotype is PMO 67022, the cast of a ventral interior from the Coelosphaeridium beds at Fangberget, Ringsaker district.

Material: 3 dorsal and 3 ventral interiors, and a number of fragmentary casts of both interiors and exteriors.

Diagnosis: Strophomena of the *norvegica*-group, with comparatively coarse sculpture, and thick anteriorly curved cardinal processes.

Description: An adult specimen is about 30 mm wide, and 20 mm long. The dorsal valve is evenly and moderately convex, the ventral is flat, or slightly resupinate. The sculpture is clearly differentiated, but comparatively coarse. The ventral area is high, and the pseudodeltidium well developed.

The ventral interior is similar to that of *S. norvegica*, with radial septa instead of lateral ridges. It has a pedicle foramen. The teeth are small.

The dorsal interior show strong, but badly differentiated muscle impressions, which are radially striated. The cardinal processes are short, thick, curved posteriorly, and with a V-shaped muscle attachment. The socket plates are strong, and curved towards the hinge-line.

The shell structure is unknown.

Remarks: This species both resembles *S. norvegica* (as to convexity, the socket plates, and especially the ventral muscle impressions) and the typical Strophomenas (as to the sculpture and the cardinal processes). It differs from *S. keilhaui* in the convexity, and the shape of the ventral muscle impressions.

S. hirsuta also resembless *S. steinari* in many features, but differs in size (they occur together) and ventral muscle impressions. It is difficult to distinguish between young dorsal valves of *S. steinari* and adults of *S. hirsuta*.

Distribution: In the Coelosphaeridium beds in the Ringsaker district.

10

Strophomena keilhaui HOLTEDAHL 1916

Textfig. 33G.

1916   Strophomena keilhaui sp. n. — HOLTEDAHL, pp. 55—56, pl. 7, fig. 8.
1916   Strophomena asmusi (VERN.) parte — HOLTEDAHL, p. 52, pl. 8, figs. 4—5.

Type data: The lectotype is PMO 22051, the exterior of a dorsal valve figured by HOLTEDAHL (1916, pl. 7, fig. 8, the left specimen on the figure), from the top of the Mjøsa Limestone at Helgøya, Hamar—Nes district.

Material: From the type locality, the slab figured by HOLTE-DAHL is the only material available. It includes 4 dorsal and 3 ventral exteriors, a number of fragments on the side shown in the figure, and 3 fragmentary ventral interiors and some casts of exteriors on the reverse side. A number of specimens have been found in the Cyclo-crinus beds at Furuberget, Hamar—Nes district, among them two ventral and a fragmentary dorsal interior.

Description: A specimen of average size is 26 mm wide and 18 mm long. The dorsal valves are evenly convex, with the strongest convexity near the middle of the valve. The ventral valves are re-supinate, about 25 % of each with normal convexity.

The sculpture is fine for a *Strophomena*, and every other or third rib is stronger than the rest. In the specimens from Furuberget, the sculpture is well differentiated, with 3—5 striae between each rib. Areas and pseudodeltidium have not been found.

The ventral interior shows a typical *Strophomena*-development, first only the dental plates are developed, then come the lateral ridges, which are shaped like brackets (), and in the adult specimens, the lateral ridges continue into closely placed parallel vascular ridges. The teeth are small.

The dorsal interior is found in a fragmentary specimen from Furuberget. It has a low median septum and almost straight socket plates, only the ends of which are curved towards the hinge-line. The angle between the plates is 100°, considerably less than in most other Strophomenas. The cardinal processes are not preserved.

Remarks: This species differs from the other ones in the different convexity of the valves (large body-volume), in the almost straight socket plates, and the differentiated sculpture. *S. keilhaui* is inter-mediate between *S. norvegica* or *Kjerulfina limbata* and the later, Upper Ordovician and Lower Silurian species of *Strophomena*.

The specimens from Furuberget, which are included in this species, were referred to *S. asmusi* (= *S. norvegica*) by HOLTEDAHL (1916, p. 52), because of the sculpture being the same. The interiors, however, are like those of the types of *S. keilhaui*. The difference in sculpture might be due to different ecology, and is correlated with the body volume (large volume- coarse sculpture).

Distribution: In the Mjøsa Limestone and the Cyclocrinus beds in the Hamar—Nes district. In the Ringsaker district, it is represented by *S. hirsuta*.

Strophomena steinari sp. n.
Pl. 11, figs. 11—12, textfig. 33C.

Type data: The holotype, PMO 67026, is the cast of a ventral interior from the Coelosphaeridium beds near Bratberg, Ringsaker district.

Material: One dorsal interior, 6 ventral ones, and a few fragmentary casts of the exterior.

Diagnosis: Very large *Strophomena* species, with heavy valves, the ventral one almost flat, the dorsal slightly convex. Ventral muscle impressions of the *Tetraphalerella*-type.

Description: A very large species, the holotype is 61 mm wide and 46 mm long. Even larger fragmentary specimens can be found. The dorsal valve is evenly convex, and the ventral is almost flat, in gerontic specimens with a slight marginal dorsalwards deflexion. The sculpture is coarse, and almost undifferentiated. The areas are high, and the delthyrium and notothyrium narrow.

The ventral interior has strong teeth, and muscle impressions bounded by high lateral ridges. In young specimens, the ridges have the usual *Strophomena*-shape, being closely parallel posteriorly. In old specimens, the posterior part is acute, and the adductor impressions seem to be surrounded by the posterior part of the diductors.

The dorsal interior has two strong cardinal processes, which are bifurcate, V-shaped, and curved anteriorly. The muscle impressions are radially striated, small and not well developed. A short, low and broad median septum is found near the hinge-line.

Both valves have long, equal-sized ciliar grooves, and the shell-structure is pseudopunctate, with puncta of variable size.

Remarks: S. *steinari* differs from all other Norwegian Strophomenas in being so large, and in the absence of resupination. The muscle impressions of the ventral valve, point towards referring this species to the genus *Tetraphalerella* WANG 1942. The latter genus seems to include a fairly homogenous group of Strophomenas, but differs only slightly from the typical members. The adductor muscle impressions are reported to be surrounded by the diductors. Just as in many Strophomenid genera, the shape of the posterior part of the ventral muscle impressions are determined by the vascula media. In *Strophomena*, these vascula seem to start from the end of the adductor muscles, and continue unbranched towards the margin. The parallel ridges are therefore boundary ridges between the vascula media and the diductors, and not between the adductors and the diductors. In the species referred to *Tetraphalerella*, the vascula media branch just behind the adductor muscles, and the diductor muscle does in fact not surround the adductors. The posterior part of the muscle impressions are filled with the vascular impressions and the intervascular septa. It is therefore doubtful whether *Tetraphalerella* can be given more than subgeneric rank. The present species shows typical *Strophomena* features up to the very late stages of growth, and is probably intermediate between the younger *Tetraphalerella* species and Strophomenas of the *norvegica* type (cf. S. *hirsuta*). Of the American species of *Tetraphalerella*, S. *steinari* is rather like *planodorsata* (SCHUCHERT & WINCHELL) cf. WANG 1942, pl. 9, fig. D.

Distribution: All the material of this species is from two localities in the Coelosphaeridium beds in the Ringsaker district.

Strophomena sp.
Pl. 9, fig. 11.

Material: 7 exteriors and casts of exteriors.

Description: A small species, the width is about 10 mm, and the length 7 mm. The valves are resupinate, with a strong umbonal convexity in the ventral valve, and a gentle ventralwards deflection of the valves. The sculpture consists of a few ribs which are especially strong in the median sector of the valves, with 6—8 very fine striae between each. Towards the margin, some of the striae are coarser, and more like the ribs in strength. There are a large number of fine

concentric rugae, which are strongest in the lateral parts of the valves.

Remarks: This species can not be referred to any described species of *Strophomena*, although it obviously belongs to this genus. The sculpture shows that it is not a *Gunnarella*, and the roundness of the marginal deflection distinguishes it from *Kjerulfina*. The large umbonal convexity, and the variable sculpture toward the margin might indicate that the present specimens are young or dwarfed individuals of a larger species.

Distribution: In zone $4b\delta_2$ (of *Tretaspis kiaeri*) at Frognøya, Ringerike district.

Subgenus *Gunnarella* subgen. n.

Type species: Strophomena (Gunnarella) delta sp. n.

Diagnosis: Strophomenas with a sculpture similar to that of *Ptychoglyptus* (concentric wrinckles cut by radial ribs).

Remarks: This subgenus includes a group of species which have the same internal structure as the typical Strophomenas. The external sculpture, however, is like that of *Ptychoglyptus*. In some species, only the central part of the valve has this type of sculpture, while the margin has no concentric wrinkles.

Many Strophomenids have concentric rugae. In most cases they are of no taxonomic value, being an ecological feature found in a large number of unrelated thin-shelled species. In some cases, rugated specimens are found in species which generally do not have rugae, and vice versa. The type of wrinkles found in *Gunnarella*, however, is of a different kind, and are believed to be of some taxonomic importance. Because of the comparatively limited material, it is impossible to decide whether the subgenus is monophyletic or if that type of sculpture appeared several times independently in *Strophomena*.

Besides the type species, the following ones are included in *Gunnarella: S. (G.) alpha* sp. n., *S. (G.) beta* sp. n., *S. (G.)* cf. *rigida* (BARRANDE 1879, em. HOLTEDAHL 1916). *S. (G.) frognoeenesis* HOLTEDAHL 1916, and probably several others.

The *Strophomena antiquata*-group in the Silurian might be related to *Gunnarella* having the same sculpture. The genus *Drummockina* BANCROFT–LAMONT (MS) 1949 is reported to have denticulated hinge-

line (dental plates ?). Such denticulations are not observed in *Gunnarella*, and this feature is the only important difference between the two genera.

<div style="text-align:center">

Strophomena (Gunnarella) delta sp. n.

Pl. 12, fig. 11, Textfig. 33B.

</div>

1916   *Strophomena rigida* BARRANDE 1879, parte. — HOLTEDAHL, pp. 56—58.
1916   *Strophomena* sp. — HOLTEDAHL, pl. 9, fig. 9. (cf. expl. to pl. 9).

Type data: The holotype is PMO 67145, a dorsal valve from zone 4bδ (6 m below 4cα)) from the SW-side of Borøya, Bærum, Oslo—Asker district.

Material: A large number (> 50) of valves in rock, and 12 complete free specimens. The species often occur in masses.

Description: A specimen of average size is 28 mm wide and 17 mm long. The geniculation is generally rounded, and towards the ventral valve. In most specimens the disc is triangular. The shape of the disc, and the roundness of the angle of the geniculation are very variable in this species. Owing to the large populations, it is obvious that only one species occurs. Typical features of all specimens are, however, the comparatively strong convexity (due to the rounded geniculation) and the more or less triangular shape of the specimens. The typical *Gunnarella*-sculpture is found on the disc only. It disappears towards the geniculation and the marginal parts of the valves have only the ordinary sculpture, radial ribs with 4—5 striae between each.

The ventral area is very high. Ventral interior is not well known. Dorsal interior with high, strongly developed cardinal processes, curved socket plates, and three septa in the muscle area. The adult specimens are generally strongly calcified, while the majority of the young valves are extremely thin-shelled, in spite of their occuring in a limestone.

Remarks: This species was referred to the collective species *S. rigida* by HOLTEDAHL (1916). The specimens figured as *Strophomena* sp. from stage 4?, Gåsøya, by HOLTEDAHL (1916, pl. 9, fig. 9) also belongs to this species. The horizon is probably 4bδ, where this species occurs abundantly at Gåsøya.

S. (G.) delta differs from the other species of the subgenus by the dorsal interior being more strongly developed, and from *alpha* also in the convexity. It differs from *S. (G.) frognoeensis* HOLTEDAHL (1916, pl. 10,

fig. 5) in having a larger and more distinct disc, and coarser sculpture.

Distribution: In zone 4bδ in the Oslo—Asker district. A number of the specimens figured by HOLTEDAHL (1916, pl. 10, figs. 1—4) from younger layers may also belong to this species.

Strophomena (Gunnarella) beta sp. n.
Pl. 9, fig. 12.

Type data: The holotype, PMO 55427, is a specimen showing the posterior part of a dorsal interior, and the ventral exterior, from zone 4bβ at Bratterud, Ringerike district.

Material: Two dorsal interiors, and a small number of exteriors.

Diagnosis: Gunnarella species with a very low resupination, and a gently rounded geniculation.

Description: Moderately sized, long species, the holotype is 28 mm wide and 24 mm long. The length of the disc is 12,5 mm. The valves are resupinate, but the convexity of the disc is very low, so that it appears to be almost flat. The geniculation is rounded, and the fringe is curved so that only the *Gunnarella*-sculpture of the disc distinguishes it from the fringe. As usual the fringe does not have the concentric sculpture, and the radial ribs are strong, especially the median ones. 3—5 very fine striae are found between each rib in well preserved specimens. The valves are very thin, and the body-volume is small. The outline of the specimens is rounded triangular, in some ones with a marked median keel.

The ventral interior is unknown, and the dorsal one is not very well preserved either. None of the specimens have the cardinal processes or socket plates. The dorsal muscle impressions are strong, circular, with an irregular boundary ridge, and three intervascular (?) septa in front of it.

Remarks: S. (G.) *beta* differs from S. (G.) *delta* in the disc being flatter, in the small body-volume, and in the presence of a bundle of strong median ribs. S. (G.) *alpha* and S. (G.) *rigida* are flat, and generally smaller. S. (G.) *beta* is probably the preceding form of S. (G.) *delta*. Both species are of the same shape, and have a triangular outline. It is possible that the specimens from Hadeland, which are from a slightly higher horizon, represent an intermediate form between

beta and *delta*. They are generally better calcified than the specimens from the type locality, a fact which also might be due to differences in the ecology.

Distribution: In zone 4bβ in the Ringerike district, and perhaps also in the Oslo—Asker district (only fragmentary exteriors), and in the Cyclocrinus Shale, just below the Sphaeronid Limestone in the northern part of the Hadeland district.

Strophomena (*Gunnarella*) *alpha* sp. n.

Pl. 11, figs. 5—6, textfig. 33F.

1916   *Strophomena rigida* BARRANDE 1879, parte — HOLTEDAHL, pp. 56—58.

Type data: The holotype, PMO 67021, is a cast of a dorsal interior from the upper part of zone 4bα, west of Billingstad, Asker district.

Material: 6 casts of the exterior and interior of valves from the type locality, and a large number of more or less fragmentary valves and casts of valves from other localities.

Diagnosis: A small *Gunnarella* species, flat, without geniculation, with closely placed, small cardinal processes and deep, small ventral muscle impressions. Characteristic sculpture all over the surface of the valves.

Description: A small, flat species. A specimen of average size is 14 mm wide and 9 mm long. Some large specimens from Arnestad-tangen in Asker may belong to this species in spite of being much larger (length: 40 mm, width: 24 mm). See also below, distribution.

Ventral interior with high umbo, and consequently deep, but small ventral muscle impressions. A slightly convex pseudodeltidium covers approximately half of the delthyrium in adult specimens. Dorsal interior only slightly developed, cardinal processes thin, high, and placed close together. Dorsal muscle impressions probably circular, septa only slightly developed. No deposition of secondary tissue on the inner surface of the valves, so that the external sculpture is visible also on the inside of the valves. Ventral area high, triangular, the dorsal one low, rectangular.

Shell structure unknown, probably finely pseudopunctate.

Remarks: This species is the oldest of the subgenus, and it is remarkable in being so small, in not having geniculation and the shell being thin and the interior consequently only being slightly calcified.

Distribution: In zone 4bα, only in the upper and middle part of it, in the Oslo—Asker district. Exteriors of specimens probably belonging to this species are found in the Echinosphaerites zone in the Langesund—Gjerpen district. In the Hadeland district (northern facies, N. of Tønnerudodden) the specimens are considerably larger than the holotype (32 mm wide and 17 mm long). The specimens come from the Cyclocrinus Shale which probably corresponds to zone 4bβ—γ in the Oslo—Asker district.

Strophomena (Gunnarella) cf. rigida BARRANDE 1879
Pl. 9, fig. 16.

Material: Two exteriors of valves, probably one ventral and one dorsal.

Description: A small species, 10 mm wide and 6,5 mm long. Valves flat, with a small umbonal convexity in the ventral valve. The sculpture is coarse, and of the *Gunnarella*-type. Both the radial ribs and the concentric wrinkles are strong. The interiors and the shell structure are unknown.

Remarks: The present specimens differ from *S. (G.) delta* in the absence of convexity, and in having stronger sculpture. *S. (G.) alpha*, which is of about the same size, has finer sculpture and much thinner valves. The specimens are quite like the typical *S. (G.) rigida* BARRANDE 1879 (pl. 48, figs. VII) except for the size and strength of the sculpture, and they may be an early variety or an ecological type of that species.

Distribution: In zone 4bδ$_2$ (of *Tretaspis kjaeri*) at Frognøya, Ringerike district.

Genus Kjerulfina BANCROFT 1929
(= Actinomena ÖPIK 1930)

This genus was made to include species with a ventral interior similar to that of *Leptaena*, and a reversed convexity of the valves.

In most cases (*K. orta, K. asmusi* a. o.) the valves are normally convex, but with reversed geniculation. The dorsal muscle impressions are, at least in adult specimens, rather like those of *Leptaena*, and differ from those of *Strophomena*. The geniculation is not an absolutely stable feature in this genus, and in one species at least,

broeggeri (HOLTEDAHL), normally geniculated specimens are found.

It is difficult to see any difference between young specimens of *Strophomena* and *Kjerulfina*. In *Kjerulfina*, however, the ventral muscle impressions generally have parallel sides, and do not converge towards the anterior end. (Textfig. 34H). *Strophomena* usually has evenly curved sides of the muscle impressions, which converge anteriorly towards the median line. In old specimens, a narrow parallel-sided slit is found at the anterior end (cf. textfig. 34F). This difference in the anterior end of the ventral muscle impressions, is probably due to the size of the median vascula, which are very broad in *Kjerulfina* (pl. 9, fig. 6), and narrow in *Strophomena*. The adductors were placed anteriorly in Strophomena, and posteriorly in *Kjerulfina* (Just as in *Tetraphalerella*). In most Kjerulfinas the socket plates are straight, and the cardinal processes are long and slender, resembling those of *Rafinesquina*.

A feature probably of less importance is that *Strophomena* generally has a coarse, not well differentiated sculpture, while most species of *Kjerulfina* have delicate sculpture, differentiated into ribs and stria. In this feature *Kjerulfina* resembles *Gunnarella*, and still more the *norvegica*-group of *Strophomena*.

Some species referred to *Holtedahlina* (*H. hallie* (FOERSTE 1912), and *H. higginportensis* (FOERSTE 1912)), cf. WANG (1949, p.. 34—35, pl. 7F, fig. 2) and FOERSTE (1912, pl. 2, figs. 1c, 1e, 3a—b, and pl. 10, fig. 4) have the same type of ventral muscle impressions as *Kjerulfina*. The straight, parallel sides of the ventral muscle impressions are best seen in slightly calcified specimens. In strongly calcified specimens (pl. 9, fig. 6) they appear to be curved, but thin sections show that they are parallel in the deeper layers of the valve.

Kjerulfina limbata sp. n. and *K. polycyma* BANCROFT have more *Strophomena*-like ventral muscle impressions than the rest of the genus, but differ from *Strophomena* in having straight socket plates.

<center>

Kjerulfina foliovalve sp. n.

Pl. 7, fig. 5, pl. 9, figs. 1—3, 5, 8.

</center>

Type data: The holotype, PMO 67004, is the cast of a dorsal interior from the lower part of zone 4bγ in a railway section between Hvalstad and Billingstad, Asker district.

Material: 22 dorsal interiors, 17 ventral ones, few complete specimens, and a large number of casts of valves. There are also some larval valves.

Diagnosis: A large, thinshelled *Kjerulfina* species, of irregular shape and convexity, short muscle impressions, strong cardinal processes and sculpture with many fine, irregular concentric lines.

Description: This species varies considerably as to outline, convexity, sculpture and some internal feature. This is probably due to the very thin valves, which in many specimens seem to be crumbled, as if they consisted of thin paper. The specimens are generally large, up to 52 mm wide and 36 mm long. Most of them are flat, others are more or less convex. In the latter case, the dorsal valve is more convex than the ventral. The real outline is rarely preserved because of the thin shells. Most specimens seem to be rather long, such as the holotype, others are hemicircular. The sculpture consists of ribs with 3—5 stria between each, and a large number of irregular concentric rugae. In some specimens a large number is present, of about the same size, in others they are few and strong. Since the specimens have the same radial sculpture, and since the rugae are possibly due to crumbling and compression of the specimens, they are regarded as belonging to one species.

The ventral interior has small teeth, and the typical *Kjerulfina* muscle impressions, with the side ridges first diverging, then with parallel sides. In some specimens the parallel sides are not developed, and in their place there are fine oblique septa, resembling the ventral interior in *Strophomena norvegica*.

The dorsal interior has strong, parallel cardinal processes, placed on a notothyrial platform, which also has a median septum. The socket plates have an angle of about 120° and are rather high. There is a chilidium. In both valves the layer of secondary tissue is very thin, and the sculpture is visible on the interior.

There are a number of larval valves which are of the same proportions and have the same sculpture as the adults, and are always flat. In some of the valves, there is a carina or sharp fold near the hinge-line, flattening out towards the posterior end of the valve. These valves were first believed to be the ventral ones, the fold was thought to be the impression of the pedicle. Studies of the interiors of the larval valves, however, showed that in the dorsal valve there

is a strong groove between the cardinal processes, which are thin and long in these specimens (pl. 7, fig. 5, Pg). The groove is deep, and strongly impressed also on the exterior of the valve. The ventral valves are flat, and only the diverging ridges of the muscle impressions are developed. No groove is found, and no carina on the exterior. In the dorsal interior, the groove is relatively stronger in the smallest specimens, and the cardinal processes cannot be distinguished from the elevated edges of the groove in the smallest specimens.

If this groove is taken for the pedicle groove, the ontogeny of *Kjerulfina foliovalve* shows a considerable resemblance to that of *Christiania*. The smallest larvae are also quite similar, except for the sculpture (cf. pl. 5, fig. 7 and pl. 9, fig. 5).

Remarks: K. *foliovalve* differs from all other members of the genus in the closely placed ribs, the very variable rugae of the external sculpture, the absence of strong median ribs, and in the well developed notothyrial platform in the dorsal interior. *Kjerulfina lata* sp. n. seems to be the species closest related to it, although it is considerably smaller, and has flat valves of stable proportions.

Distribution: In zone 4bγ in the Oslo—Asker district. Specimens from Hadeland and Ringerike are too fragmentary to be referred to this species with absolute certainty.

<center>

Kjerulfina limbata sp. n.

Pl. 9, figs. 4, 9—10, textfig. 33H.

</center>

Type data: The holotype, PMO 67011, is the cast of a ventral interior from zone 4bγ at Hole, Ringerike district.

Material: About 15 ventral and 4 dorsal interiors, and a large number of exteriors.

Diagnosis: Large *Kjerulfina* species with curved lateral ridges of the ventral muscle impressions in adult specimens, and short, blunt cardinal processes in the dorsal.

Description: A large species. The holotype, which is among the largest preserved, is 42 mm wide and 31 mm long. The disc is slightly convex, or almost flat, and has a number of regular, weak concentric rugae. The radial sculpture consists of ribs with 3—5 striae between each. A slightly asymetrical bundle of median ribs stronger than the

others is found. The angle between the disc and the geniculated fringe
is 130—150°, and the geniculation itself is rounded. The areas are
comparatively low, the ventral is triangular, and the dorsal thinnest
near the notothyrium in adult specimens.

The ventral interior shows the muscle impressions, which are
Strophomena-like in the adult specimens, and has more parallel sides
in the younger ones (cf. Pl. 9, figs. 4 and 10). The teeth are strong
and triangular, and there is a thin pedicle foramen. The adductor
muscle impressions can rarely be seen and when they are present,
they are placed more posteriorly than in most other species of *Kje-
rulfina*.

The dorsal interior is rather like that of *Strophomena*. The cardinal
processes are blunt, rounded in cross-section, and the socket plates
are slightly curved outwards. The dorsal adductor impressions are
almost invisible. There is a chilidium with a fold corresponding to the
slit between the cardinal processes.

The shell structure is coarsely pseudopunctate.

Remarks: As mentioned above, this species is very much like
Strophomena. The main difference are the geniculation (instead of
resupination) and the parallel lateral ridges of the ventral muscle
impressions in the young specimens (in *Strophomena* they are curved
even in very young specimens). The development may therefore be
homeomorphic with that of *Strophomena* rather than indicating
that *Strophomena* has developed from *Kjerulfina*. However, the
trend of development towards *Strophomena*-like forms is evident
both in the Scandinavian and British Middle Ordovician (*K.
broeggeri* — *K. limbata* in Norway, *K. trigonalis* — *K. polycyma*
in Shropshire).

K. limbata differs from the contemporaneous *K. foliovalve* in
being of a more regular shape, in the ventral interior being so distinct,
and in having a median bundle of stronger ribs. *K. polycyma* BANCROFT
1929 is still more closely related to it, and differs only in size and in
having *Strophomena*-like ventral muscle impressions even in young
specimens.

Distribution: In zone 4bγ in the Ringerike district. Some speci-
mens which have a similar exterior can also be found in the Oslo—
Asker and Hadeland districts, and they are temporarily referred to
this species.

Kjerulfina broeggeri (HOLTEDAHL 1916).

Textfig. 33A.

1916   *Strophomena brøggeri* sp. n. — HOLTEDAHL, pp. 49—50, 100, pl. 7, figs.
3—5.

Type data: The lectotype is L0095, a dorsal valve showing the interior of the cardinal region. The specimen was figured by HOLTEDAHL (1916, pl. 7, fig. 3) and comes from zone 4bα—β at Bratterud, Ringerike district.

Material: One ventral and two dorsal interiors, all artificial casts, and about 55 valves and complete specimens.

Diagnosis: A large *Kjerulfina* species, with strong concentric rugae, and rounded geniculation with long fringe.

Description: Comparatively large species, the lectotype is 42 mm wide and 30 mm long. Since no material of much importance of exteriors, has been collected since the description by HOLTEDAHL, (1916, p. 49) it is not repeated here.

The only ventral interior known, is from a young specimen, and it only shows the dental plates and a fine pedicle foramen. As usual in young specimens, the teeth are scarcely developed, and the side ridges of the muscle impressions are not developed at all. In another specimen, which was dissolved in acid, they appear to be straight, and comparatively short.

The dorsal interior has long, thin cardinal processes, diverging at about 45°. The socket plates are short, inclined inwards, and diverging at 90°. The adductor impressions are well defined in the lectotype, and are rather small, circular, and placed close together. There is a low chilidium. The shell structure is pseudopunctate, with comparatively large puncta, probably of the same size all over the valves.

Remarks: K. *broeggeri* differs from the Baltic species in the strong sculpture and in the long fringe. The valves are also much thinner in *K. broeggeri*. *K. polycyma* and *K. limbata* have a different shape and dorsal interior, and the ventral muscle impressions are probably not the same either. *K. trigonalis*, the type species, is rather like *K. broeggeri*, but the latter has coarser sculpture, longer fringe and a more distinct dorsal interior. All these differences may be due to changes in ecology, and further studies may show that they ought to be united in one species, which should be named *broeggeri*.

In the material dealt with in this paper, there are some peculiar specimens with «normal» (dorsalwards) geniculation. The specimen which is best preserved was described by HOLTEDAHL (1916, pp. 50, 100) pl. 7, fig. 4), who also mentioned the systematic importance of this discovery. The specimens (four, or possibly five) are like the others as to size, shape and sculpture, and even if no interiors are known, they undoubtedly belong to *K. broeggeri*. The possibility of them being abnormal specimens of *Rafinesquina* (*Hedstroemina*) *holtedahli* sp. n. has been carefully considered, but they differ from that species in many features, and are so like *K. broeggeri* that it is quite evident that specimens with both dorsalwards and ventralwards geniculation occur in this species. The latter are the most numerous, about 90 % of the specimens, or more. The systematic consequences are discussed above.

Distribution: In zone 4bα—β in the Ringerike district, and probably also in zone 4bβ in the Oslo—Asker district.

Kjerulfina lata sp. n.
Pl. 11, figs. 4, 7, textfig. 33I.

Type data: The holotype, PMO 21967, is the cast of a ventral interior from the Coelosphaeridium beds at Furuberget, in the Hamar —Nes district.

Material: 2 dorsal interiors, 6 ventral ones, and a large number of fragmentary casts and exteriors.

Diagnosis: Small, broad, flat *Kjerulfina* species with coarse, well differentiated sculpture.

Description: A rather broad species, two specimens from the Oslo —Asker district are 19 and 25 mm wide and 8,5 and 14 mm long. Hemicircular to hemielliptical outline, right cardinal angles. Valves very slightly convex, or completely flat. Areas low. Delthyrium partly closed by the thin pseudodeltidium. The pedicle foramen small, but persistent in all specimens, even gerontic ones. Sculpture consisting of irregular, coarse ribs with 3—6 striae between each at the margin of the valves. The ribs often stop when they reach a prominent growth-line, giving a discontinuous ornamentation.

Ventral interior with side ridges of the ventral muscles at first diverging at about 120°, then parallel, short. Teeth high, and thin.

Dorsal valve with very strong, vertical cardinal processes placed closely together. The socket plates are remarkable in not diverging from the cardinal processes, but the hinge-line, just outside the notothyrium. Muscle impressions weak, and indistinct. One larval valve shows a strong pedicle (?) scar, and no differentiated cardinal processes. The socket plates, however, are high and strong. This larval specimen is 13 mm wide and 8,5 mm long. It differs slightly from the other ones in the sculpture being more regular, and may belong to another species.

Remarks: This species is referred to *Kjerulfina* because of the shape of the ventral muscle impressions, and the cardinal processes. The convexity of the valves is very slight, and often irregular, probably because of the thin shells in this species. It has no geniculation, but probably belongs to *Kjerulfina* because of the similiarity to young, not geniculated specimen of *K. foliovalve.* The parallel sides of the ventral muscle impressions is characteristic for the genus, see BAN-CROFT (1929, pl. 2, fig. 9, 1945, pl. 38, fig. 5) and ÖPIK (1930, pl. 10, figs. 131—132).

Distribution: In the upper part of zone 4bα in the Oslo—Asker district, and in the Coelosphaeridium beds in the Hamar—Nes district.

Kjerulfina (?) sp.
Pl. 11, fig. 8.

Material: Two ventral interiors and a small number of casts of the exterior.

Description: A small species, 10,5 mm wide and 16 mm long. Valves strongly geniculated dorsally, Leptaenoid in shape, with fine concentric rugae in the disc, and indistinct radial ribs (due to the preservation). The ventral interior has very long muscle impressions with parallel sides, just as in *Kjerulfina.* The teeth are strongly developed.

The dorsal interior and the shell structure are unknown.

Remarks: This species belongs to a group with an interior similar to *Kjerulfina*, but with reversed geniculation or convexity. Since at least *K. broeggeri* can have the geniculation in either direction, it seems reasonable to include these species in *Kjerulfina.*

The present species seems to be related to *Mjoesina mjoesensis* as regards convexity, but differs in the shape of the disc, the size and the parallel sides of the ventral muscle impressions, which are converging in *M. mjoesensis*.

Distribution: In the Mastopora zone (?) in the Langesund—Gjerpen district.

Genus *Oslomena* gen. nov.

Diagnosis: Strophomenids with convex ventral valve, flat or slightly concave dorsal valve. If geniculated, dorsally. Ventral muscle impressions small, sometimes bilobed, surrounded by a ridge. Dorsal interior variable from specimens with diverging septa like *Oepikina* to those with strong bilobed muscle impressions like the earliest species of *Leptaena*.

Type species: Oslomena osloensis sp. n.

Oslomena osloensis sp. n.

Pl. 12, figs. 12—13, 15—16, textfigs. 32D—E, 36—37.

1916   *Rafinesquina* cf. *imbrex* (PANDER) parte — HOLTEDAHL, pp. 15—16, pl.1 figs. 10—11, non fig. 8.

1917   *Rafinesquina (Playfairea) deltoidea* (CONR.) parte — REED, p. 886, pl. 11, figs. 21—30.

Type data: The holotype, PMO 67142, is a cast of the interior of both valves, and the exterior of the dorsal valve, and parts of the ventral one, from the upper part of zone 4bα at Billingstad, Asker district.

Material: 14 interiors of both valves, 11 complete, free specimens, a large nnmb of casts of exteriors or interors, and valves and complete specimens in roek

Diagnosis Oslomena species with regular strong convexity of the ventral valve, and with flat dorsal with a rounded geniculation. Well differentiated sculpture.

Description: Specimens of variable size (cf. textfig. 37). The strongly convex ventral valve is geniculated. There is no disc, or only a very small one in the umbonal part of the valve.

The dorsal valve is always roundly geniculated. The specimens are generally broadest along the hinge- line. Several growth-types are

11

found in the material dealt with in this paper (cf. p. 53). The typical form (from Billingstad, Nakholmen and Bratterud) has a rounded triangular outline, is comparatively large, and has a HL/L ratio of 1,25—1,45. Another type is considerably smaller, with a more rounded outline, and HL/L ratio of 0,91—1,05. It is interesting to note that in all localities from which a large material is collected, only one of these types occur, and both types are never found together in one locality. In other localities, where the material is more limited, other types are found, some being very flat, and some having a stronger convexity than the ordinary ones. In some northern localities, there are also some larger specimens (textfig. 37, B).

It does not seem advisable to discriminate species and subspecies on the growth-types referred to here. Transitional forms occur, and there are no differences as to the internal structures, at least none which can be correlated with the growth-types. The geographical distribution is interesting, too. The first type is found along a 50 km long line, running almost E—W, ranging from rather poor fauna in east to a very rich in west. The other one is more local, found in the Asker district only, about the middle of the line of distribution of the first type. The distance between localities with different growth-types is in some cases less than one km. The distribution of the different growth-types must therefore be attributed to ecological variations which do not reflect themselves in the sediments.

Studies on the growth-lines indicate that, in the dorsal valve, the disc was formed first, with HL/L ratio about 1,4, rounded, with right cardinal angles. When the geniculation took place, the lateral growth decreased rapidly, just as in most geniculated species. The areas therefore have rounded ends instead of being triangular (textfig. 36). The ventral area is high with a delthyrium surrounded by a strong, elevated ridge. The apical angle of the delthyrium is about 95—105°. It is covered by a thick massive pseudodeltidium, with lamellar structure. The growth-lamellae are straight, and very prominent in the central part, bending steeply down towards the notothyrium. This feature is generally not preserved in ordinary specimens. When the shell substance is dissolved in hydrochloric acid, the finer details as well as the bends of the lamella can be seen (pl. 12, fig. 16).

In some well preserved specimens, the relations between the cardinal processes and the pseudodeltidium can be observed. The cardi-
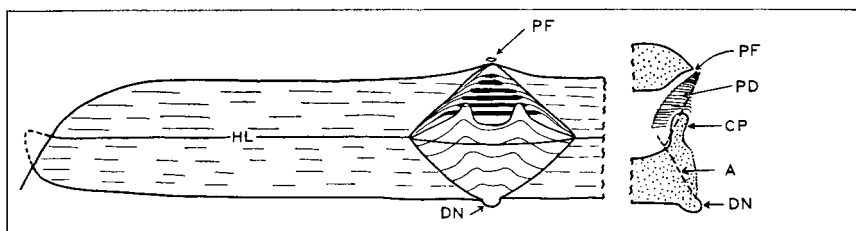
Fig. 36. *Diagramatic figure of the area of Oslomena osloensis sp. n. in frontal and lateral view.* The figure is based on several specimens from two different localities, and show the features of an average, mature specimen. All the specimens are from zone 4ba, in the Asker district.
    Abbreviations: A = Projection of the areas into the lateral, central view. Note that the dorsal area overlap the ventral for some distance. CP = Cardinal process. DN = Dorsal node (Pedicle scar?) HL = Hinge-line, the line of contact of the valves, just below the edge of the dorsal area. PD = Pseudodeltidium. PF = Pedicle foramen.

nal processes in these gerontic specimens are completely surrounded by the pseudodeltidium so that the diductor muscles can not have been attached to the cardinal processes, at least not to their ends. This peculiar feature was observed in two, probably three specimens, the only in which the pseudodeltidium was large anongh. The author is unable to give any satisfactory explanation to this feature. None of the specimens appear to be pathological, and they are definitely not distorted.

In young specimens, the dorsal area is similar to the ventral one, except for being slightly lower. In older specimens, the dorsal area is considerably higher on the sides than in the middle, probably due to differential growth along the hinge-line. The dorsal area is also somewhat longer than the ventral one, due to the ventral valve overlapping the hinge-line (textfig. 36). The notothyrium is parabolic in outline, and completely filled with the chilidium, on which the cardinal processes rest. The growth-lines indicate that the cardinal processes diverged during the growth of the valve. A dorsal node is found below the chilidium. It is very prominent in the young specimens, but as it does not grow, it is less prominent in the adult specimens. In this species, the node is attached to a small shaft, with two small depressions, one on each side. The node is fused to the chilidium. In *Christiania*, a similar node represents the scar of a dorsal foramen.

The sculpture consists of a large number of ribs with 5—8 striae between each. At the apex of the ventral valve there are 3 ribs, while 4—5 are found on the dorsal valve. At the margin, the number of ribs seems to be the same in both valves (about 30). The distance between each rib is from 1 mm to slightly less than 2 mm. The new ribs are formed by intercalation, and a number of them starty contemporaneously at the same strong growth-line.

Dorsal interior: Cardinal processes strong, formed by two slightly diverging plates with subparallel sides and rounded tops. Socket plates diverging at about 120°, ends ancylosed to the base of the cardinal processes. No diaphragm around the disc has been observed. Median septum developed in the central and anterior part of the valve only, resembling the x-plate in the Plectambonitacea. The lateral septa are differently developed. In most specimens the first pair is U-shaped with the open ends converging towards the cardinal processes at about 100°. In some specimens only the posterior branch of the «U» is developed, or it is much stronger than the other one. The second pair of lateral septa converges towards the median septum. In old specimens, the septa are sometimes elevated into strong, vertical nodes. The septa of this species are rounded in cross-section, and differ considerably from the thin, sharp-edged, subparallel ones in *Oepikina.*

Ventral interior: Muscle impressions bounded by a prominent ridge from the rest of the valve. A small number of radial ridges may occur in the muscle impression. The impressions are pointed, or rounded posteriorly (cf. textfig. 34 D—E). The dental plates are strong, diverging at about 100°. Vascular impressions appear as two strong branches from the ends of the muscle impressions. In some specimens traces of large ovarian impressions, covering almost the whole surface of the valves are also found, together with short marginal vascula. A median septum is found in some specimens (pl. 12, fig. 15), generally it is small, and fairly low. The adductor impressions are not clearly distinguished in most specimens. They seem to be placed far posteriorly (textfig. 34 D—E).

Ontogeny: The early development of this species is known from the growthline studies on adult specimens. Only one «larval» valve is found. The larva probably were planconvex, with low triangular areas. The young specimen present is a perfectly flat dorsal valve,

which has a remarkably strong dorsal node. The sculpture and internal structure is the same as in the adult specimens. It is 7 mm wide and 4,5 mm long. The adult specimens from this locality are about 10—11 mm wide and 10—12 mm long.

Shell structure: According to SALMON (1942) an important difference between *Oepikina* and *Rafinesquina* is that the pseudopuncta of *Rafinesquina* are large and placed in radial rows, while the small puncta of *Oepikina* are evenly distributed over the surface of the valves. *Oslomena osloensis* has larger pseudopuncta than the marginal ones in *Oepikina dorsata* (from C 2, Kukruse, Esthonia cf. pl. 13, fig. 2), and of more uniform size (cf. p. 11). The size of the pseudopuncta, however, is not a reliable feature when it comes to discriminating between genera, at least not in Norwegian material.

Remarks: In spite of the rather wide variations found in size, shape and dorsal interior, it does not seem necessary to split this species. The presence of one type in each locality (cf. textfig. 37) and a number of common features indicate that all specimens belong to one, variable species, possibly with a number of local races. It seems to be intermediate between *O. celtica* (HARPER 1952) and *O. girvanensis* (REED 1945). *O. osloensis* is smaller than *O. celtica*, and seems to have more striae between the ribs (5—8 against 3—4). In the larger specimens the outline too is different. *O. girvanensis* is smaller, and the small specimens of *O. osloensis* lack the triangular outline. Within the limits of variation, the dorsal interior of *O. osloensis* shows specimens like both *O. girvanensis* and *O. celtica*. It is also probable that some of the specimens figured by REED (1917, pl. 11, figs. 21—30) could be included in *O. osloensis*. The ventral interior of *O. celtica* has bilobed muscle impressions which is not found in *O. osloensis*, and *O. girvanensis* has a strong median septum, which is seldom developed in *O. osloensis*. It differs from *O. baylei* and *O. multicorrugatella* in having more strongly developed internal structures, larger muscle impressions, and in the external sculpture.

The Russian specimens described by SOKOLSKAJA (1954, pp. 43—46, pl. 2, figs. 14—20) as *Rafinesquina (Playfairea) deltoidea* (CONRAD) may belong to this species. They differ considerably from CONRADS species as defined by SALMON (1942). The subgenus *Playfairea* REED 1917 sensu SOKOLSKAJA 1954 is the same as the new genus *Oslomena*. Since the type of *Playfairea (deltoidea* CONRAD) is a
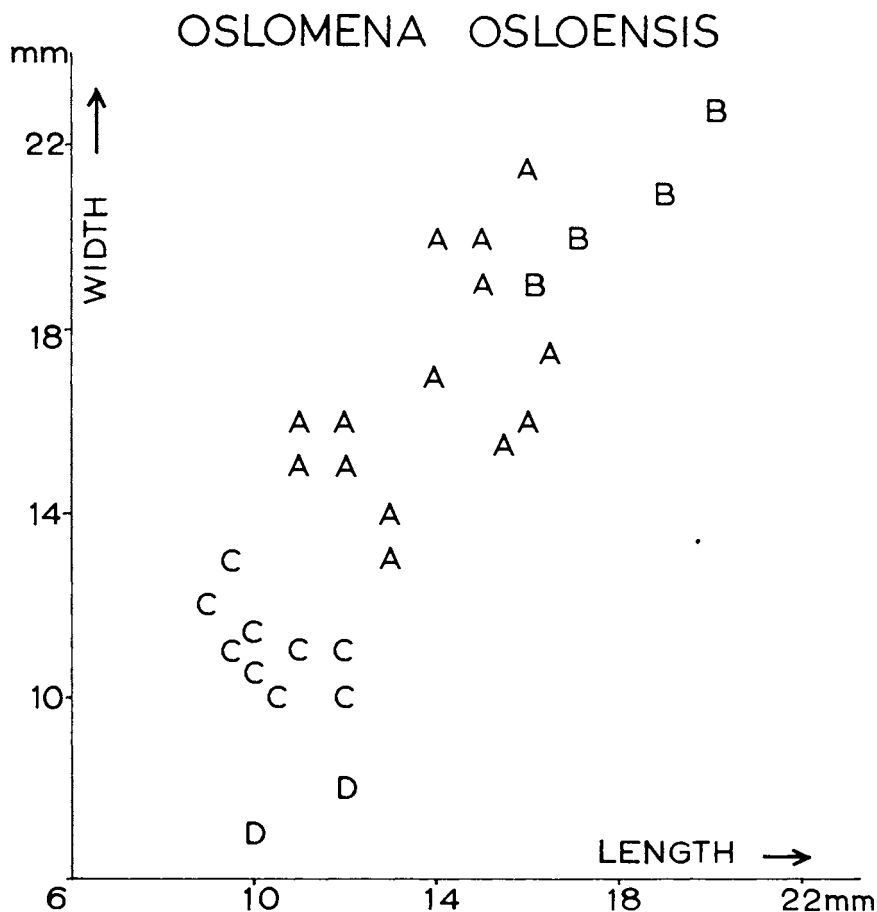
Fig. 37. Diagram showing the variations in size of *Oslomena osloensis* sp. n. from various localities in the Oslo Region. A. indicate typical specimens, populations from Billingstad, Blakstad and Bratterud. B. Indicate the larger specimens from the Toten district. C. indicate the small variety from the populations at Slependen and Gåsøya, Oslo—Asker district. D. are typical specimens of *Oslomena* cf. *girvanensis* (REED 1945), from zone 4bβ, at Gomnes, Ringerike district. Only complete, undamaged specimens are measured.

typical *Rafinesquina*, the name *Playfairea* can not be used instead of *Oslomena*.

Distribution: In the upper part of zone 4bα and probably (large specimens) in the lowest part of zone 4bβ in the Oslo—Asker district,

in zone 4bα—β in the Ringerike district, and in the Coelosphaeridium beds of the Toten district, and possibly also the Hamar—Nes district. In the Langesund—Gjerpen and Ringsaker districts it seems to be replaced by *Oepikina dorsata media*. It is also probably found in the Balclatchie group in the Girvan district, Scotland, in the Chasmops beds in Dalecarlia, Sweden, and in the Baltic region.

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Oslomena aff. *girvanensis* (REED 1945).

Textfig. 37D.
</div>

cf.　1917　*Rafinesquina (Playfairea) deltoidea* (CONRAD) — REED, pl. 11, fig. 23, non figs. 21—22, 24—30.
aff. 1945　*Playfairea girvanensis* sp. n. — REED, p. 311.

Material: One complete specimen, exfoliated to show the dorsal interior. A number of single valves from the same layer and locality are also referred to the same species because of similarity in shape.

Description: A small globose species, longer than broad (cf. text-fig. 37 D). The dorsal interior very much resembles that of *O. girvanensis* (REED 1917, pl. 11, fig. 23). The septa are somewhat obscured by deposition of secondary calcareous tissus, so that they appear to be confluent, forming a triangular area, like that in the dorsal valve of certain *Leptaena*-species. The present species differs from *O. girvanensis* in being smaller, and in the proportions (*O. girvanensis* is wider than long).

Distribution: The specimens referred to this species are all from zone 4bβ at Gomnes—Rud, Ringerike district.

<div align="center">

? *Oslomena celtica* (HARPER 1952).
</div>

1916　*Leptaena* sp. (cf. *unicostata* M & W) — HOLTEDAHL, p. 74, pl. 13, fig. 2.
?1952　*Øpikina celtica* sp. n. — HARPER, pp. 103—104, pl. 5, fig. 7, pl. 6, figs. 10—11.

Material: One specimen, a ventral interior figured by HOLTE—DAHL (l.c.). A number of casts of exteriors from the same locality may belong to this species.

Description: The specimen is 21 mm wide along the hinge-line The projection of the length is 13 mm and the length of the disc is 10 mm. The angle of geniculation is 105—110°. The long and narrow

ventral muscle impressions are bilobed. It resembles the figures given of *O. celtica*, but is somewhat smaller and broader. The muscle impres- sions are also similar. In the Norwegian specimen, the lateral lobes, however, are slightly smaller. *Leptaena unicostata* MEEK & WORTHEN, is described by WINCHELL & SCHUCHERT (1892, p. 412, pl. 32, fig. 8). There are also a number of specimens in the material examined by the author. The disc is larger, and the concentric wrinkles are gene- rally observed in the interior of *L. unicostata*, which also has very strong pseudopuncta. The puncta found in ? *O. celtica* are very small.

Distribution: *O. celtica* is recorded from Grangeeth, County Meath, Eire, in layers probably corresponding to the upper part of zone 4bα in the Oslo region. The Norwegian specimens are from Gravestrand, Frierfjord, in the Langesund—Gjerpen district, and come from the upper part of the Echinosphaerites beds.

Oslomena (?) *papillio* sp. n.
Pl. 9, figs. 13—15.

Type data: The holotype, PMO 38184, is the cast of a small dorsal interior from the Coelosphaeridium (?) beds in the Toten district.

Material: One dorsal and one ventral interior, and a number of casts of the exterior.

Diagnosis: *Oslomena* (?) species with slightly convex ventral valve, flat dorsal, and coarse, undifferentiated sculpture.

Description: A small species with slightly convex ventral valve, and almost flat dorsal. A specimen of average size is 15 mm wide and 12 mm long. The areas are low, and the sculpture is paucicostate, and comparatively coarse. The ventral interior shows strong, posteri- orly inclined teeth, and *Rafinesquina*-like, small muscle impressions with a dividing septum in the anterior end.

The dorsal interior is remarkable, with two diverging septa, and a forked median septum. The cardinal processes are comparatively large, elliptical in cross-section, and a chilidium is present. The in- terior of the valves are smooth, and the shell-structure is unknown.

Remarks: This species can not with certainty be placed in any known genus. It resembles *Holtedahlina* in sculpture, *Rafinesquina* in shape, and *Hedstroemina* in the small muscle impressions. The dorsal interior is similar to that of *Microtrypa* WILSON (1945), and this

type of interior is not known from any other species with similar convexity. Further collecting may give more material, which will show if the species should be included in a new genus.

Distribution: In the Coelosphaeridium (?) beds in the Toten district.

Genus *Oepikina* SALMON 1942.

Oepikina dorsata media (ÖPIK 1930).

Pl. 12, figs. 9—10.

1916 *Rafinesquina imbrex* (PANDER) parte — HOLTEDAHL, p. 15—16, pl. 1, fig. 8, non figs. 10—11.
1930 *Rafinesquina dorsata media* subsp. n. — ÖPIK, pp. 189—190, pl. 14, figs. 161—164.

Material: 6 dorsal interiors 5 ventral and a number of exteriors of single valves. All specimens preserved are casts, and all except one come from altered shale.

Description: The Norwegian specimen seem to be slightly larger than the Baltic ones. (cf. ÖPIK 1930, p. 190). The dimensions of the following four dorsal interiors are characteristic (all measurements are in mm).

Length of disc	Hinge line	Greatest width	Angle of genicula- tion
10	11	14	125°
10	14	16	—
9	11	12	110°
13	12	14	—

The exteriors of this species are badly preserved, and the details of the sculpture can seldom be observed. In the specimens with well preserved surface, ribs and striae are found, just as in the Baltic specimens of this species (cf. ÖPIK 1930, pl. 14, fig. 161). The distance between the ribs might be larger in the Norwegian specimens, and the striae generally better defined. The ventral valve is generally strongly convex, with only slightly marked disc. Diductor muscle impressions very large, expanding over most of the inner surface of the valve. A number of strong, radial ridges are found in the muscle impressions. The adductor impressions are small, narrow. They are placed posteriorly

There is a strong median septum between the two pairs of muscle impressions (cf. textfig. 34 A). A thin pedicle foramen is observed in most specimens.

Dorsal valve abruptly geniculated, with subpentagonal, slightly concave disc with a strong boundary ridge. Short, forked cardinal processes. Socket plates fused to the boundary ridges. Development of branchial septa variable. In some cases the median septum is very small (resembling *Dactylogonia*) and in others, the central pair of septa is almost lacking (resembling *Oepikinella*). In some specimens a thin connection ridge is found between the lateral septa on each side, uniting them into what resembles a branchial loop (cf. textfig. 28 A). The latter feature is clearly seen on the Norwegian material only, while the development of the septa is studied on a large material of *Oepikina* species from Esthonia.

Remarks: This species is evidently a member of the *Oepikina dorsata*-group. In the dorsal interior it is in all details like *O. dorsata media* (ÖPIK). The Norwegian specimens appear to be slightly larger than the Baltic ones.

Distribution: In the Langesund and Ringsaker districts. The few specimens from the Ringsaker district are from the Coelosphaeridium beds, and the more numerous ones from the Langesund—Gjerpen district are from the Echinosphaerites — Bryozoan zones along the shores of Frierfjord. They seem to occur in a thin band only, probably in the lower part of the Bryozoan zone. In Esthonia (ÖPIK 1930, p. 190) it is common in zones C_2 and C_3a.

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Oepikina (? or *Rafinesquina*) sp.

Pl. 12, fig. 11.

</div>

Material: One fragmentary cast of a ventral interior.

Description: The specimen is 19 mm wide, and 17 mm long. It is strongly convex, slightly angular in outline and evidently belonging to an adult specimen. The teeth are strong, and the muscle impressions large, narrow anteriorly, badly defined posteriorly, and have strong radial septa. The shell structure and sculpture are unknown.

Remarks: The specimen must be referred to *Oepikina* or *Rafinesquina* (*Rafinesquina*) because of the muscle impressions. The speci-

men differs both in shape and size from the Norwegian species of
Oepikina. The ventral muscle impression is also smaller than is usual
in that genus. As there is no dorsal interior present, it is impossible
to decide if the specimen belongs to *Oepikina* or *Rafinesquina* (*Rafinesquina*).

Distribution: Judging from the other fossils found together with
this specimen, the horizon is the uppermost part of 4aβ or the transitional beds between 4aβ and 4bα. The locality is Vesleseter in the
Sjåstad district.

Genus *Leptaena* DALMAN 1828.

Type species: Leptaena rugosa DALMAN 1828 (non HISINGER 1827),
selected by KING 1846.

Diagnosis: Strophomenids with strong, slightly differentiated
sculpture, more or less pronounced concentric wrinkles, and generally a very strong geniculation, in connection with a ridge around the
disc. Ventral interior with strong teeth, muscle impressions of variable size and shape, flabellate or with evenly curved or parallel sides.
Adductor impressions small, in the middle of the diductors, and often
surrounded by them. Dorsal interior with strong cardinal processes,
rounded, often perfectly circular muscle impressions, and occasionally
with a complex median septum. Shell substance coarsely pseudopunctate.

History of the generic name: Several types of species were included
in *Leptaena* by DALMAN, and this has led to some confusion. DAVIDSON (1856) and McCOY (1852) based their diagnosis of the genus on
transversalis (= *Plectodonta*). The selection of *L. rugosa* as the type
species by KING (1846), however, is definite, and was apparently
repeated independantly by DALL (1877, pp. 34, 41) and HALL &
CLARKE (1892, p. 276). The type species has generally been placed
in synonymy with *Conchites rhomboidalis* WILCKENS (1769), a badly
known species, which has been recorded from the Lower Ordovician
into the Carboniferous. It has, however, to be mentioned that this
author did not apply binominal nomenclature, his name of the species
was *Chonchitas Rhomboidales anomios inaequilateros* (l.c. p. 79). The
specific name *rhomboidalis* in connection with *Leptaena* should therefore be attributed to WAHLENBERG (1821, p. 65).

POULSEN (1943) redefined this species, and although it is not absolutely certain that the species figured by POULSEN is identical with that of WAHLENBERG, *L. rhomboidalis* is used in this paper as it was defined by POULSEN. On the basis of material from the Silurian of Gotland, this author also redefined *L. depressa* (SOW.), another species which has generally been included in *L. rhomboidalis* sp. coll.

A restudy of the type material of DALMAN (preserved in the Paleozool. avd., Riksmuseet, Stockholm, Sweden), showed that the type of *L. rugosa* were not from the Silurian of Gotland, such as supposed by most authors. They were from the Upper Ordovician Dalmanitina layers in Västergötland, Sweden. As early as in 1908 SCHMIDT suspected this, and in fact it was quite evident from the original description (DALMAN 1828, p. 106 «observatu dignum videatur in schisto superiore montium Vestrogothiae hujus speciei exemplaria numerosa esse obvia, — — —». All other specimens of *Leptaena* in his collection differ in shape, size and proportions from those figured by DALMAN (1828, pl. 1, fig. 1).

Besides SCHMIDT (1908), SOKOLSKAJA (1954, pp. 56—57, pl. 3, figs. 3—9) seem to be the only author who has recognized *L. rugosa* as an Ordovician species. None of the specimens described by the latter author seem, however, to belong to *L. rugosa*. The specimens figured on pl. 3, fig. 3a—b and possibly fig. 7 might be *Hedstroeminas*, because of the prominent bundle of median ribs. The specimen on fig. 6 recall *Kiaeromena juvenilis* (ÖPIK 1930), and that on fig. 8 is quite like *L. (?) indigena* sp. n.

L. rugosa is generally referred to HISINGER (1827). *L. rugosa* (HIS.), however, is a nomen nudum, and the species must therefore be referred to DALMAN (1828).

A number of genera have been made for species of the *Leptaena*-group. Most of them (*Leptagonia* McCOY = *Leptaenella* SOKOLSKAJA 1952, and *Pseudoleptaena* MILRADOVICH 1947, sensu SOKOLSKAJA 1952) are probaly only subgenera of *Leptaena* if they can be given such rank.

The author has not seen *Notoleptaena* GILL. It appears to be a good genus, closely related to *Leptaena*.

In this paper a new genus *Kiaeromena*, type species *Leptaena kjerulfi* HOLTEDAHL 1916, is described. It differs from *Leptaena* in the cardinal processes, and in the shape of the valves.

Leptaena rugosa has, like most Ordovician Leptaenas, flabellate ventral muscle impressions, whereas the Silurian species generally have narrow impressions, with gently curved, or parallel sides. It might therefore be advicable to use *Leptagonia* McCoy (= *Leptaenella* SOKOLSKAJA) as a subgeneric term for the Silurian and younger species.

The stratigraphical range of *Leptaena* (*Leptaena*) is, in this case, restricted to the Middle and Upper Ordovician, and possibly the basal Silurian.

Leptaena rugosa DALMAN 1828.

Pl. 7, figs. 1—2, 4, textfigs. 38G, 39A.

Type data: The lectotype, here chosen, is specimen nr. Br. 10435 (Riksmuseet, Stockholm), a cast of the exterior of a ventral valve from the Upper Ordovician Dalmanitina beds of Få dalaberg, Västergötland, Sweden. DALMANS figure of *L. rugosa* (1828, pl. 1, fig. 1) was evidently based on this specimen and nr. Br. 10446, the cast of the exterior of a dorsal valve from the same horizon at Besstorp, Mösseberg, Västergötland. Both specimens were, according to the labels, collected by DALMAN in 1827. They have both the dimensions given by Dalman for this species (Width 44 mm, length 24 mm).

Description: Moderately large species with about 7—11 strong. evenly concentric rugae, and a sharply elevated ridge around the disc, The radial sculpture is fine, and undifferentiated. The convexity of the disc is strong near the apex, and flattens out posteriorly. The geniculated fringe is long, almost as long as half the disc, and with an angle of geniculation about 120° or more. The cardinal angle is very sharp, and the areas are rather low.

Ventral interior (pl. 7, figs. 1—2) with flabellate muscle impressions with several radial ridges. Adductor muscle impressions small, placed anteriorly. Pedicle foramen wide. Teeth strong, pseudodeltidium unknown. The concentric rugae can also be seen on the inner surface of the valves.

Dorsal interior badly known. The cardinal processes seem to be elongate and diverging, and the chilidium is unknown. The muscle impressions are weak, and rather small. It has not been possible to determine if they are circular, as in the younger species, or if they were elongate bilobed as in some older species.

The shell-structure is coarsely pseudopunctate, the puncta, how-ever, are not so large as in *L. depressa* and many other *Leptaena* species.

Remarks: *L. rugosa* differs from most Silurian Leptaenas in the shape of the ventral muscle impressions, and from most of the Ordo-vician ones in the strong concentric rugae, the high geniculated ridge around the disc, and in the blunt angle between the geniculated fringe and the disc. Its nearest relatives seem to be some species described by BANCROFT MS (1949) from the British Llandovery. None of these species seem to be strictly synonymous with *rugosa*. They all have elongate muscle impressions which are well defined laterally.

Distribution: *L. rugosa* is found only in the uppermost Ordovician of Scandinavia. Some specimens which might be referred to it, or a very similar species are found in the Upper Ordovician in Belgium.

Leptaena (?) indigena sp. n.
Pl. 10, figs. 10—11, textfigs. 38A, 39 G.

Type data: The holotype, PMO 67013, is the cast of a ventral interior from the Coelosphaeridium beds at Brattberg, Ringsaker district.

Material: 6 ventral interiors, one fragmentary dorsal one, and a number of casts of the exterior.

Diagnosis: Large *Leptaena* species, with long hinge-line and sharp cardinal angles, clearly bounded ventral muscle impressions, and *Kiaeromena*-like dorsal interior.

Description: A rather large species, the holotype is 44 mm wide and 23 mm long, which is slightly less than the average size. The valves are abruptly geniculated, the ventral disc is flat, with fine, irregular concentric rugae. The moderately convex geniculated fringe is long, generally just as long as the disc, or even longer. The lateral flanks of the valves are long, and flat. The radial sculpture is comparatively fine, and distinctly differentiated.

The ventral interior show strong teeth, large muscle impressions, which are distinctly bordered, and bluntly pointed posteriorly. The adductors are badly defined. The vascular system can not be seen.
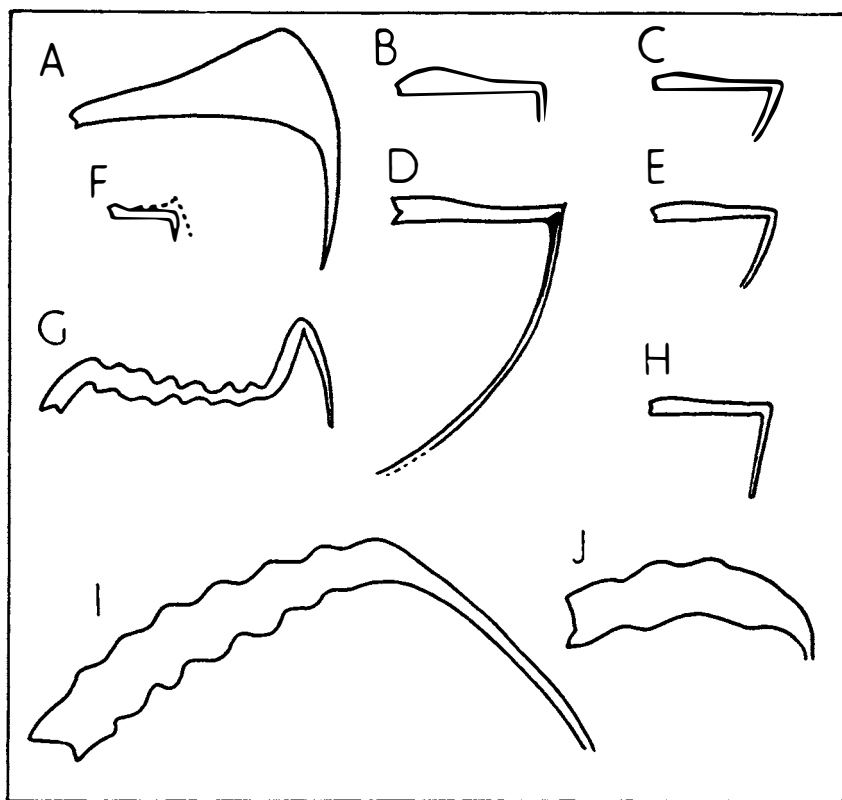
Fig. 38. *Cross-sections of species of Leptaena* and *Kiaeromena*. 9/10th of natural size. A. *L.* (?) *indigena* sp. n. from the Coelosphaeridium Beds in the Ringsaker district. B, D, E, *L. strandi* sp. n. B. A typical and D. a highly gerontic specimen with very long fringe, and high areas. both from the Cyclocrinus (?) Beds of the Hadeland district. E. is a typical specimen from zone 4bγ, just north of Hvalstad in the Asker district. C. *L. veldrensis* sp. n. from the Coelosphaeridium Beds of the Ringsaker district. F. *L. minuta* (Kiær 1926) from the Sphaeronid Shale in the Hadeland district. The dotted line show a section through the raised edge of the median sulcus. G. *L. rugosa* Dalman, from the Dalmanitina zone of Vestergötland, Sweden, to show the difference between this species and the Norwegian, Middle Ordovician ones. H. *L. ennessbe* sp. n. from zone 4bα at Billingstad, Asker district. I. *Kiaeromena kjerulfi* (Holtedahl 1916) from zone 4bβ at Lindøya, Oslo district. *J. Kiaeromena* cf. *juvenilis* (Öpik 1930) from the Coelosphaeridium Beds at Brattberg, Ringsaker district.

The dorsal interior shows two strong parallel cardinal processes, circular, well defined adductor muscle impressions, and three septa posterior to the muscle impressions.

The shell-structure is unknown, but it is supposed to be coarsely pseudopunctate as in the other Leptaenas because of the strong pustules found in the interiors.

This species differs from all other Ordovician Leptaenas in the dorsal interior, which is similar to that of *Kiaeromena*. It differs from that genus in sculpture and geniculation. *L. indigena* seems to be intermediate between *Leptaena* and *Kiaeromena*. It resembles the latter genus also in the differentiated sculpture.

Distribution: *L. indigena* is found in the Coelosphaeridium beds in the Ringsaker district only. Some fragmentary casts from the same horizon in the Toten district may also belong to the same species.

Leptaena strandi sp. n.
Pl. 10, figs. 4—5, textfigs, 38BDE, 39D.

Type data: The holotype, PMO 67019, is the cast of a ventral interior from zone 4bγ at Billingstad, Asker district.

Material: 14 ventral and 2 fragmentary dorsal interiors, and a large number of complete specimens and valves.

Diagnosis: *Leptaena* species with abrupt geniculation with no elevated ridge around the disc. Angle between the fringe and disc about 90°, or slightly less. Ventral muscle impressions broad, short, radially striated and well defined.

Description: Species of moderate size, the holotype, which is rather small, is 20 mm wide and 9 mm long. The discs are almost parallel, and with no elevated ridge, except in very large, gerontic specimens. The geniculated fringe is curved, the angle between it and the disc is 90°, or less, in some gerontic specimens the fringe is longer than the disc, and in one specimen (textfig. 38 D) the marginal part of the fringe is almost parallel to the disc. It is an interesting, but unsolved problem how the animal managed to open and close shells with this structure. The sculpture is undifferentiated, with a few, irregular concentric wrinkles. The areas are comparatively high.

The ventral interior shows strongly defined, broad, short muscle

impressions bordered by a somewhat irregular ridge, and with a badly defined, short median septum. The adductors are small, and well defined, bordered by thin ridges. The diductors are radially striated. A distinct ovarian impression is found in most old specimens. The teeth are strong, and so are the dental plates, which diverge at about 120°. The pedicle foramen was very small, and the pseudodeltidium has not been seen.

The dorsal interiors are badly known, the cardinal processes are unknown, and the muscle impressions appear to be bilobed.

Some specimens from older horizons, especially zone 4bα at Gomnes—Rud, Ringerike district may also belong to this species. The ventral muscle impressions are smaller, and less defined than in the typical specimens, the teeth are also smaller. Because of the limited material, it is impossible to decide if these specimens, which resembles young ones of *L. strandi*, belong to this species. They are widely different from the contemporaneous *L. ennessbe*.

The shell structure is coarsely pseudopunctate, with puncta of uniform size all over the valves. The puncta seem to be smaller in the older specimens than in the younger ones.

Remarks: This species differs from the other members of *Leptaena* in the shape of the ventral muscle impressions, and the angle of geniculation. The muscle impressions, and possibly the dorsal interior is similar to that of *L. rugosa*, which, however, has a different geniculation (textfig. 38 B, C, D, G).

Distribution: In zone 4bγ in the Oslo—Asker, district and the Cyclocrinus beds in the northern part of the Hadeland district. Specimens which can not be distinguished from this species exteriorly, occur abundantly in the Mastopora beds in the Langesund—Gjerpen district. As mentioned above, there are some specimens from zone 4bα in the Ringerike district, which also might belong to this species.

<div align="center">

Leptaena ennessbe sp. n.

Pl. 10, fig. 9, textfig. 38 H.

</div>

Type data: The holotype, PMO 67016, is the cast of a ventral interior from the upper part of zone 4bα at Billingstad, Asker district.

Material: 6 ventral interiors and a number of valves and casts of valves.
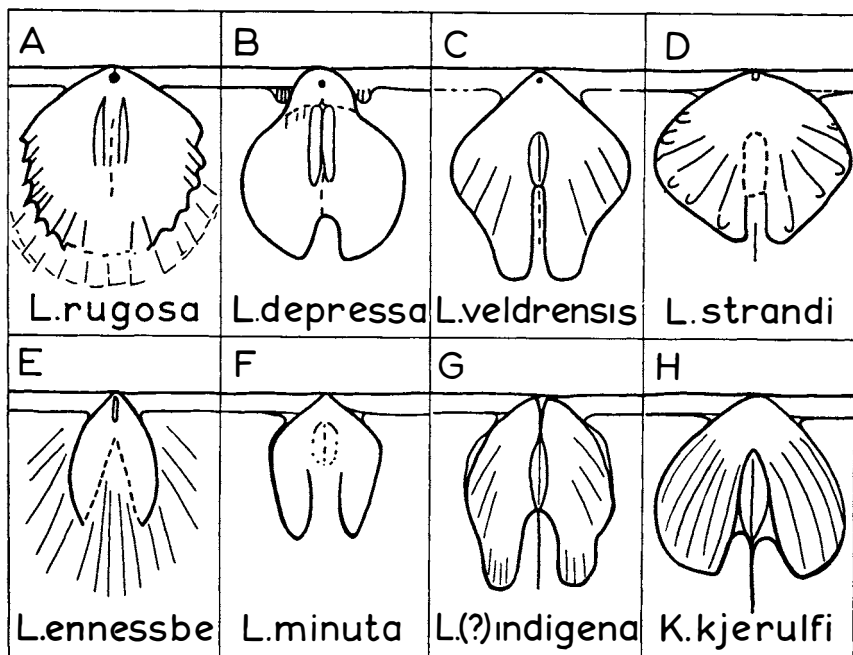
Fig. 39. Ventral interior of species of *Leptaena*. A. *L. rugosa* DALMAN, from the
Dalmanitina zone at Mösseberg, Vestergötland, Sweden. B. *L. depressa*,
(SOWERBY, em. POULSEN 1943) from the Mulde Marl (Upper Wenlock) at Fröjel,
Gotland, Sweden. C. *L. veldrensis* sp. n., from the Coelosphaeridium Beds of
the Ringsaker district. D. *L. strandi* sp. n., from the Cyclocrinus beds (?) of
the Hadeland district. E. *L. ennessbe* sp. n. from zone 4bα, at Billingstad,
Asker district. F. *L. minuta* KIÆR 1926, from the Sphaeronid Shale, Tønnerud-
odden, Hadeland district. G. *L.* (?) *indigena* sp. n. from the Coelosphaeridium
Beds of the Ringsaker district. H. *Kiaeromena kjerulfi* (HOLTEDAHL 1916),
from zone 4bβ, in the Oslo—Asker distriot. The figures are drawn to show the
same size of the disc, and the relative size of the muscle impressions.

Diagnosis: *Leptaena*-species with abrupt geniculation with no
elevated ridge around the disc. Angle between the disc and the fringe
less than 90°. Ventral muscle impressions small, badly defined, with
low, straigth lateral ridges. Large pedicle foramen, with pedicle almost
parallel to the disc. Strong ventral umbonal convexity, otherwise
flat discs.

Description: Comparatively small species, the holotype is 20 mm
wide, and 11 mm long. Sculpture coarse, undifferentiated. There are

usually a few broad, irregular concentric rugae. The discs are flat except for a strong ventral umbonal convexity, which is connected with the pedicle foramen, directed almost parallel to the disc. The geniculation is abrupt, the angle is less than 90°, and the usually long fringe is curved.

The ventral interior shows small teeth, high, thin dental plates, small, badly defined ventral muscle impressions, bounded by low, converging straight lateral ridges. No adductor impressions are defined, the opening between the posterior ends of the diductors is coarsely striated, just as the rest of the interior. The pedicle foramen and pedicle furrow is long and prominent.

The dorsal interior is unknown, and the shell-structure is coarsely pseudopunctate.

Remarks: This species differs from the younger members of the genus in the weakly developed ventral interior, which must be regarded as a primitive feature. The strongly developed pedicle and the direction of the pedicle is peculiar for this species.

Distribution: In zone 4bα in the Oslo—Asker district, and in the lower part of the Coelosphaeridium beds in the Ringsaker district. The presence in the latter district, might indicate that the species is an ecological type of *L. veldrensis*. The specimens of *L. ennessbe* occur in the same sediment (dark mudstones) in both districts, whereas *L. veldrensis* is restricted to siltstones and muddy siltstones.

Leptaena veldrensis sp. n.

Pl. 10, figs. 6—8, textfigs. 38C, 39C.

Type data: The holotype, PMO 67017, is the cast of a ventral valve from the Coelosphaeridium beds at Bratberg, Ringsaker district.

Material: 5 ventral and 4 dorsal interiors, and a number of casts of exteriors.

Diagnosis: Leptaena species with abrupt geniculation, with elevated ridge around the disc in old specimens only. The ventral muscle impressions are prolonged posteriorly, and the valves are much wider than long.

Description: A wide, narrow species, the holotype is 26 mm wide and 10 mm long. There is no elevated ridge in the ventral valve, but a low, rounded one in the dorsal. The fringe is generally shorter than

the disc. The areas are low, and meet at about 90° in adult specimens.
The sculpture consists of comparatively fine, undifferentiated ribs,
and there are only a few, indistinct concentric rugae.

The ventral interior shows the long diductor impressions, short,
well defined adductors, placed far back, and a very high and prominent median septum. The teeth are strong, and the dental plates short.
The vascula are deeply impressed around the ovaria, which are not
divided by the median vascula in the present specimens.

The dorsal interior shows small, diverging cardinal processes,
a smooth chilidium with a median fold, and strong socket plates. The
muscle impressions are strong, bilobed, just as in the *Oslomena*. There
is also a median septum. In the youngest dorsal interior present, Pl.
10, fig. 8, the muscle impressions are not well defined, and the socket
plates are thinner. The ridge around the dorsal disc, which generally
is prominent in this species, is also absent in the young specimen.

The shell structure is pseudopunctate, with the puncta decreasing
slightly in size towards the margin.

Remarks: This species differs from the other Middle Ordovician
Leptaenas in the long ventral diductor impressions, and in the proportions of the valves. The young specimens, and the specimens from
the Langesund—Gjerpen district differ from *Hedstroemina* chiefly in
the elevated ridge around the dorsal disc.

Distribution: In the Coelosphaeridium beds in the Ringsaker
district, and in the Mastopora beds and the upper part of the Bryozoan
beds in the Langesund—Gjerpen district. In the latter district, the
specimens resemble the young specimens in the Ringsaker district,
probably due to different ecology (supply of lime).

Leptaena minuta KIÆR 1926.

Pl. 7, figs. 6—8, textfigs. 38 F, 39 F.

1926   *Leptana minuta* sp. n. — KIÆR, pp. 9—10, textfig 3a—b.

Type data: The lectotype is PMO 34716, a ventral valve showing
the exterior, from the Upper Cyclocrinus beds at Tønnerudodden,
no thern part of the Hadeland district. The lectotype is the specimen
figured by KIÆR (1926, textfig. 3a—b) and in this paper, pl. 7, fig. 7.

Material: 4 dorsal and 6 ventral interiors, and a moderate number (about 20) valves and casts of valves.

Description: A very small species, the lectotype is 10 mm wide and 5,5 mm long. The areas a e moderately high, and almost in the same plane. the discs are flat, with distinct umbonal swellings, largest in the ventral. The geniculation is abrupt, at about 100°, and the fringe is not curved longitudinally. There is a strong sinus, with vertical axis. In the ventral valve, the edges of the disc are raised on both sides of the sinus. In the rest of the ventral valve, and in the dorsal, there is no elevated edges around the disc. The sculpture consists of comparatively strong equal-sized ribs, and no or very few and weak rugae.

The ventral interior shows small teeth, well defined muscle impressions bordered by widely diverging (120°) dental plates, and long, slightly converging lateral ridges. A short, broad median septum is found between the posterior ends of the muscle impressions. The adductors are comparatively large, and placed in the middle of the diductors. The pedicle foramen which is small, has not been seen in all specimens. In a gerontic specimen (pl. 7, fig. 6), the lateral ridges and the dental plates are not connected, and a vascular ridge is developed around the ovaria. The vascular system itself is not well developed. It appears to be the same as of the other Leptaenas.

The dorsal interior shows extremely small cardinal processes, which are placed far anteriorly, and thin, short socket plates, In some specimens the muscle impressions are developed, and there is a median septum, just as in species of *Rafinesquina.*

The shell structure is densely pseudopunctate, with large puncta near the muscle impressions, and smaller ones towards the margin.

The cardinal processes are placed in a depression, which is reflected on the exterior of the valve.

Remarks: This species is easily distinguished from all other Leptaenas because of the sinus, and the dorsal interior. The latter is rather like that of *Rafinesquina*, which, however, lacks the depression, and also generally has pseudopuncta of nearly equal size all over the valve. The straight converging lateral ridges in the ventral interior reminds one of the genus *Mjoesina*, which differs considerably in shape. Several other species of *Leptaena* have a similar structure of the ventral muscle impressions.

Distribution: L. *minuta* is known only from the type locality, where it seems to occur abundantly.

Leptaena cf. *minuta* KIÆR

Material: Two casts of the ventral interior, and a few casts of the exterior.

Description: The specimens are small, and have an abrupt geniculation, with no sinus, or a weak one. The sculpture is similar to that of the typical *L. minuta*.

The ventral interiors, which are badly preserved, seem to correspond to those of *L. minuta* in all details. The dorsal interior and the shell structure is not known.

Remarks: From what is known of it, this species only differs from *L. minuta* in the absence of the sinus. Some specimens have a slight indication of a sinus, and it is possible that the presence of this feature is a function of the ecology, which is different in the localities in which the two types are found. In any case, the material present is too fragmentary to allow a description of a new species. It must be mentioned that the specimens referred to here are from somewhat older beds than the typical *L. minuta*.

Distribution: In the Echinosphaerites and the lower part of the Bryozoan beds in the Langesund—Gjerpen district.

Leptaena sp.
Pl. 7, fig. 13.

Two deviating dorsal interiors of an imperfectly known *Leptaena* species have been found. The first one (pl. 7, fig. 13) is an excellently preserved cast from the lower part of the Coelosphaeridium beds in the Ringsaker district, and the other, fragmentary specimen comes from zone 4bα at Stubdal, Ringerike district. The valves are rectangular, 17 mm wide and 10,5 mm long, with a short geniculation at about 90° to the disc, which is surrounded by a rounded edge. The area is high, and the cardinal processes are large, almost parallel plates. The rather strong socket plates diverge at about 100°. The large muscle impressions are bilobed, just as in *Oslomena*, and there is also a thin median septum. The chilidium is not observed. The vascular system is well defined marginally, and seems to be of the same type as that of *Oepikina* rather than that of *Leptaena*.

The cardinal processes are asymmetrical in both specimens, but this might be accidental.

Remarks: The present species differs from the other Middle Ordovician Leptaenas in the rectangular shape, which is found in a number of Silurian species. The muscle impressions are like those of *Oepikina* and *Oslomena*, from which the present species differs in the cardinal processes, and in having an elevated ridge around the disc. It is remarkable that the species is among the oldest ones recorded, only *L. ennessbe* is contemporaneous.

Kiaeromena gen. nov.

Type species: Leptaena kjerulfi HOLTEDAHL 1916, pp. 72—73, pl. 13, figs. 9—11.

Diagnosis: Strophomeninid genus with large, dorsally deflected valves, generally without distinct geniculation. Broad, flabellate, well defined ventral muscle impressions, with the adductors in the same place as in *Leptaena*. The dorsal muscle impressions are generally well defined, circular or slightly bilobed. The cardinal processes are strong, with characteristic muscle attachments. The pseudodeltidium is large and massive, and the chilidium is thin.

Description: The interior of this genus reminds one of *Leptaena*, especially its Silurian species. It is more highly developed than most contemporaneous Leptaenas. It differs from that genus in the exterior, which is not abruptly geniculated, and very coarsely rugated. The pseudodeltidium is also much larger than in *Leptaena*.

Besides the type species, *Kiaeromena* includes the following species: *K. juvenilis* (ÖPIK 1930), *K. esthonensis* (BEKKER 1921)[1], and *K. richmondensis* (FOERSTE 1909). The latter species together with *L. indigena* sp. n. and *L. luhi* SOKOLSKAJA 1954 form a gradual transition between *Kiaeromena* and *Leptaena*.

Distribution: Middle Ordovician, and probably lower part of Upper Ordovician.

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[1]) This species has been referred to as *Leptaena trigonalis* SCHMIDT 1908 (p. 726 ÖPIK (1930) and SOKOLSKAJA (1954)). *Leptaena trigonalis*, is, however, a nomen nudum, and BEKKERS name has to be used. The reference to «pl. XIII, figs. 150—153» in the list of synonymy given by SOKOLSKAJA (1954, p. 54.) does not refer to SCHMITH 1908, it is taken from ÖPIK 1930, and does therefore not validate the name *trigonalis*.
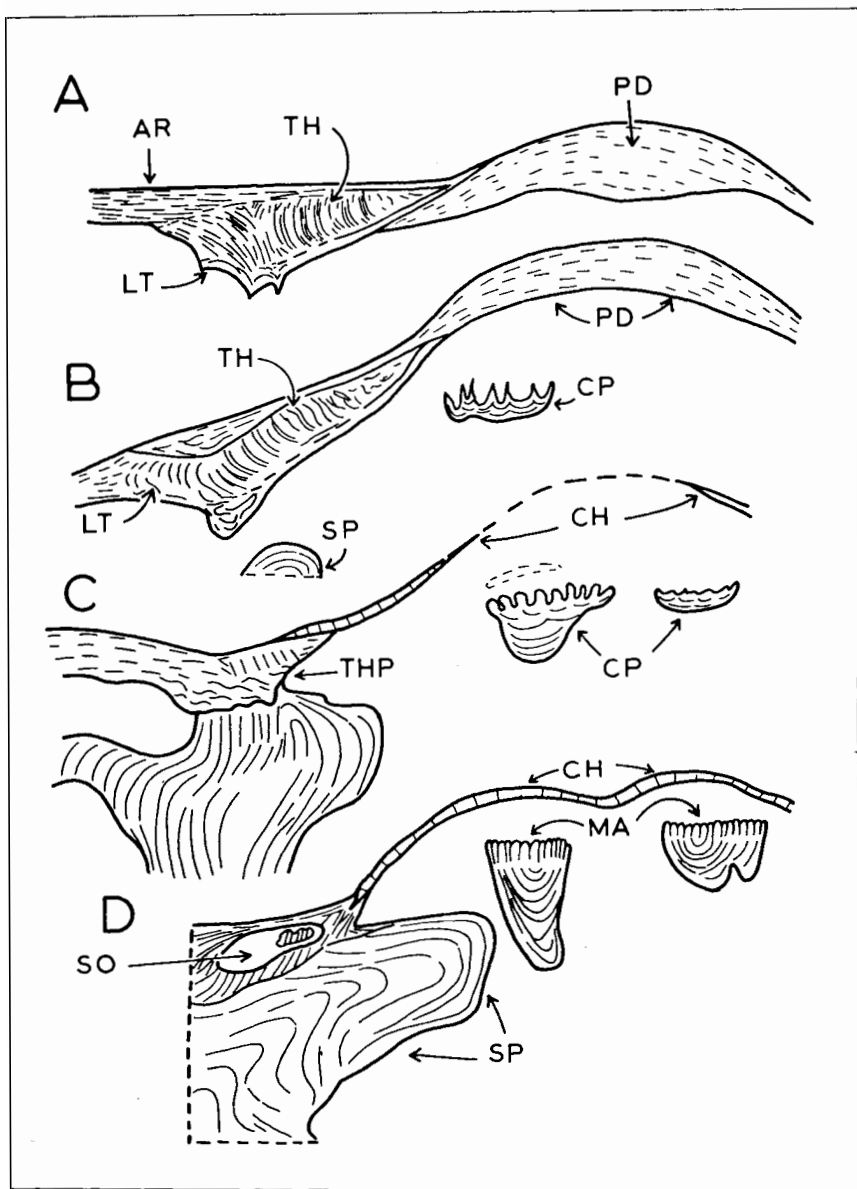
Fig. 40. *Kiaeromena kjerulfi* (HOLTEDAHL 1916). Four horizontal parallel section through a specimen from zone 4bβ at Langåra. Asker district. In C. the border between the tooth and the dorsal valve is obscured due to recrystalliza-

Kiaeromena kjerulfi (HOLTEDAHL 1916).

Pl. 7, figs. 14, 16, pl. 10, figs. 1—3, pl. 14, figs. 2, 9, textfigs. 6C, 38I, 39H, 40—41.
1916 *Leptaena kjerulfi* sp. n. — HOLTEDAHL, pp. 72-73, pl. 13, figs. 9-11.

Type data: The lectotype is PMO L128, a specimen showing the greater part of the dorsal interior, from zone 4bβ at Gåsøya, Oslo— Asker district. The specimen is figured by HOLTEDAHL 1916, pl. 13, fig. 9.

Material: 6 dorsal and 14 ventral interiors, and a large number of valves and complete specimens.

Description: A large species, the lectotype is 70 mm wide and 39 mm long, being a specimen of average size, or slightly larger. The convexity is variable, from specimens with flat disc, and a gently rounded geniculation to specimens which are more evenly convex, with barely visible geniculation. The sculpture consists of coarse, regular and prominent concentric rugae, 9—14 on ordinary specimens. The radial sculpture consists of ribs with 6—8 striae between each. The difference between the ribs and the striae is small, but easily distinguishable. There are very fine growth-lines, similar to those in *Strophomena norvegica.* Irregularities in the sculpture indicating healed fractures are common, in spite of the thick valves (pl. 7, fig. 16, z).

The areas are high, especially the ventral one, and they meet at about 90—120° in ordinary adult specimens. Both the pseudodeltidium, which is very thick and massive, and the thin chilidium, are strongly arched, and almost completely cover the delthyrium and the notothyrium.

The ventral interior shows the well defined muscle impressions, which are broad, with curved sides, and a distinct, low median septum, with the diductor impressions on the anterior end. The teeth are thin, merely thickenings of the strong dental plates. In thin section (text-fig. 40 A—B, TH) they are built up of parallel lamellae of fibrous tissue,

tion. Sections A and B are almost completely in the ventral valve, whereas C and D are through the dorsal valve.

Abbreviations: AR — Area. CH — Chilidium. CP — Cardinal processes. LT — Lateral extention of teeth. MA — Muscle attachment on the cardinal processes (cf. textfig. 6). PD — Pseudodeltidium. SO — Sockets. SP — Socket plate. TH — Teeth. THP — Teeth-plate, with diffuse border against the dorsal valve. Magnification: about 8x.
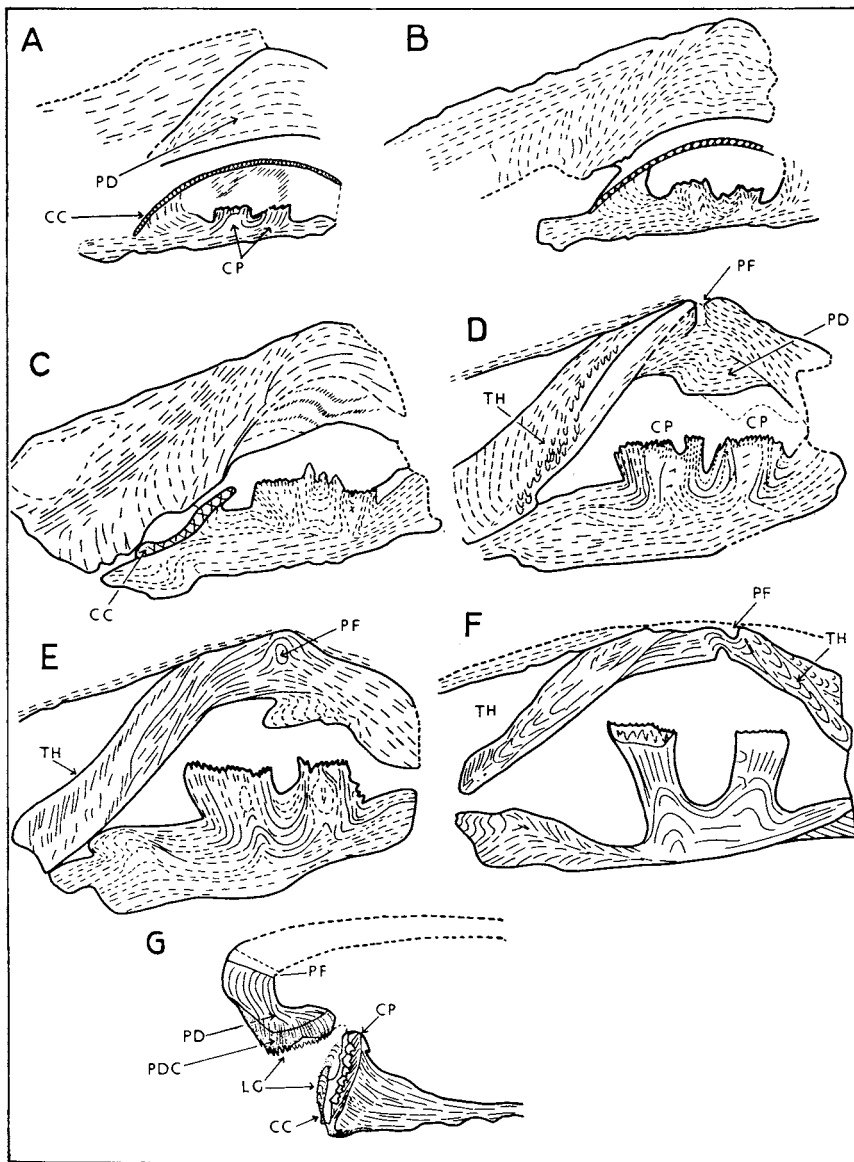
Fig. 41. *Kiaeromena kjerulfi* (HOLTEDAHL). A—F. 6 paralell sections of the central portion of a specimen. G. longitudinal section (incomplete) of another, smaller specimen. Dotted lines indicate reconstructed areas, dotted areas indicate areas colored yellowish-brown. Both specimens are from the middle-upper

which are well differentiated from the rest of the valves. There is always a pedicle foramen, but it is small for a so large species, generally it is less than ½ mm in diameter.

The dorsal interior shows the strongly bounded circular muscle impressions, which seem to have some minor muscle (?) impressions on the posterior end. This might be the other branch of the adductors, found in *Oslomena* and the oldest *Leptaena* species.

In front of the muscle impressions, there are three parallel septa, probably intervascular ones. The socket plates are strong, and the sockets narrow and elongate, corresponding to the shape of the teeth. The cardinal processes are high, vertical, and curved posteriorly. The anterior side is straight, and furrowed by a large number of deep cavities, which are widest near the bottom. These cavities are also found on the upper surface of the processes, and probably served as muscle attachments. No similar structure has been described from other strophomenids. It is only known from this species, and possibly from the other *Kiaeromena* species.

The concentric rugae can be seen also on the interior surface of both valves in spite of their thickness.

The shell structure is comparatively finely pseudopunctate. The structure of the cardinal processes and teeth are described above. The pseudodeltidium and the chilidium have been studied in both vertical and horizontal serial sections (textfigs. 40—41). The latter is a relatively thin plate which in vertical sections (textfig. 41G), and on artificial casts of the exterior show distinct lamellae with the edges turned towards the pseudodeltidium. The tissue of both the latter and the chilidium is yellow-coloured, fibrous and sharply distinguished from the rest of the valve. The pseudodeltidium is a massive block, built up of growth (?) lamellae with edges turned towards the chilidium. Because of these structures, the author believes that this species, as well as others with the same structures, had a ligament, which opened the valves.

part of zone 4bβ, that shown in A—F is from Steilene, Oslo—Asker district, and that shown in fig. G. is from the SE side of Langåra, Asker distrikt.

Abbreviations: CC = Chilidium. CP = Cardinal process. LG = Supposed attachments for ligament. PD = Pseudodeltidium. PDC = Frontal part of pseudodeltidium, coloured by organic material. PF = Pedicle foramen. TH = Teeth.

Remarks: K. kjerulfi differs from all other species of *Kiaeromena* in size and sculpture. It also differs from *K. richmondensis* (and *Leptaena indigena* and *luhi*) in the absence of a strong geniculation, and from *K. juvenilis* in the dorsal muscle impressions. Because of the large, generally well preserved material, this species is much better known than the other species of *Kiaeromena* and *Leptaena*, especially as regards the histological structure. The reason for these features being mentioned here, is that some of them may possibly be used in the systematics when more species have been studied in detail.

Distribution: This species is the guide-fossil for zone 4bβ in the Oslo—Asker district. It is confined to that zone, and is very common in many localities. Outside the Oslo—Asker district, only one specimen has been found at Bilid, Toten district, mentioned by HOLTEDAHL (1916, p. 73). There is no doubt that the specimen belongs to *K. kjerulfi*, but the preservation and lithology does not resemble that which usually is found in the Toten district. A similar species, *K.* cf. *juvenilis*, is, however, found in contemporaneous layers in the Ringsaker district.

Kiaeromena cf. *juvenilis* (ÖPIK 1930).
Pl. 7, figs. 10—12, textfig. 38 J.

Material: Two complete specimens, one showing only the exterior, and one showing both the interiors and exteriors of both valves.

Description: The specimens are comparatively large, the figured one is 26 mm wide and 18 mm long. The valves are roundly geniculated, and have a sculpture consisting of badly differentiated ribs and striae, and a number of broad, concentric rugae, 5 in one specimen and 8 in the other. The distance between the discs (the body-volume) is considerably smaller in the specimen with many rugae (from Asker) than in that from the Ringsaker district.

The ventral interior, which is known only in the specimen from Ringsaker, shows small, well limited muscle impressions, resembling those of *K. kjerulfi* in shape. The adductor muscle impressions are not well defined. The dental plates are strong, but the teeth are thin.

The dorsal interior shows strong cardinal processes, of the same type as in *K. kjerulfi*, and short, high socket plates. The muscle impressions are badly defined, and a transition between septa (branchial) ? and muscle impressions seems to occur, just as in *Oslomena osloensis*,

and in *K. juvenilis* from the Baltic region. The vascular septa are only faintly indicated. The shell substance is coarsely pseudopunctate.

Remarks: The two specimens indoubtly represent intermediate forms between *K. kjerulfi* and *K. juvenilis*. They are larger than most specimens of *K. juvenilis*, and resemble *K. kjerulfi* in the rounded geniculation and the short fringe. The interiors are more like *K. juvenilis*, which also have the bilobed, septate muscle impressions.

Distribution: One specimen (exterior only) is from the upper part of zone 4bα at Arnestadtangen, Asker district, and the other (both interiors and exteriors) is from the Coelosphaeridium beds at Brattberg, Ringsaker district.

Family S t r o p h e o d o n t i d a e CASTER 1939 em. WILLIAMS 1953.

Two species undoubtedly belonging to this family are found in the Middle Ordovician of the Oslo region. These are the oldest representatives of the family, and at least one of them is a very primitive one. The possibility of the family being polyphyletic, and the importance of these species in the discussion of that problem, see p. 22.

The present material of these two species is rather limited. More well preserved specimens will probably be found, and then a more detailed description can be given.

Genus *Stropheodonta* HALL 1952.
Subgenus *Eostropheodonta* WILLIAMS 1951.
Stropheodonta (Eostropheodonta) williamsi sp. n.
Pl. 12, figs. 2—5, textfig. 32A.

Type data: The holotype is PMO 38164, the cast of a dorsal interior from the Cyclocrinus Shale at Furuberget in the Hamar—Nes district.

Material: 5 ventral and 4 dorsal interiors, and a number of casts of the exteriors.

Diagnosis: *Eostropheodonta* species with strong umbonal convexity in both valves, concentric rugae, small dental plates, Socket plates with 5—7 grooves in adults, diverging at about 90°. Dorsal muscle impressions subcircular.

Description: A comparatively large species, the holotype is 33 mm wide and about 23 mm long. The umbonal part is swollen in both valves, so that the specimens have a characteristic longitudinal cross-

section (textfig. 32A). The convexity is greatest near the hinge-line, the rest of the valves are flat, or very slightly convex, and with a rounded marginal geniculation. On both sides of the umbo, the valves are relatively flat. The cardinal angles are sharp. The sculpture consists of numerous (8—11) strong and generally continuous rugae, crossed by irregularly differentiated ribs and striae. There is a narrow bundle of stronger median ribs, generally slightly assymmetrical. The areas are low.

The ventral interior shows well defined, comparatively small muscle impressions, which are radially striated up to the apex of the valve, (cf. *S. (E.) siluriana* (DAV) in WILLIAMS 1951, textfig. 22). The dental plates are strong, short, and with 5—7 prominent, elongate crenulations. The teeth are only slightly developed, the corners between the dental plates and the hinge-line is not elevated, and with practically no deposition of secondary tissue. No pedicle foramen can be seen, and it must have been very small if present at all. There is a pseudodeltidium.

The dorsal interior shows long, blade-like cardinal processes in young specimens, and shorter, thicker ones in older specimens. There is a high chilidium, with a fold corresponding to the slit between the cardinal processes. The muscle impressions in the old specimens are like those in *Rafinesquina*, with an anchor-shaped platform. The sockets are wide, the plates diverging at about 90°, and with grooves, corresponding to the crenulations of the teeth. Because of the preservation of the specimens, these grooves are rarely completely preserved, usually they are found only on one side, and in some cases they were destroyed during preparation. This is the case with the holotype, where the grooves disappeared when a latex cast was made of the specimen. The grooves are visible on the cast, but the soft rock adhered to the latex so that they are no longer clearly visible on the specimen itself, In the young specimens, the crenulations and grooves are not, or only slightly developed.

The rugae can be seen both on the dorsal and ventral interior. Shellstructure unknown.

Remarks: As mentioned above (p. 20) a large number of Strohomenida show more or less vertical striation of the teeth. The specimens present are not more denticulated than many Strophomenas (cf. textfig. 3). This species is included in *Eostropheodonta* because of the cardinalia. WILLIAMS (1951, p. 123) outlined the early development of the Stropheodontids in the following way: «As the stock

evolved, so the dental plates migrated towards the hinge-line to lie parallel with it and finally to lose their identity by fusion with the teeth-plates». The cardinal processes are first bladlike, later more disjunct (cf. WILLIAMS 1953, textfig. 2). In *S. (E.) williamsi* the cardinal processes are longer and more blade-like than in any other Stropheodontid, and the angle of the socket plates (corresponding to that of the dental plates) is about 90°. In the other species of *Eostropheodonta* this angle is 120—150°, and in most other Stropheodontids it is 180° (parallel to the hinge-line). It seems as if *S. (E.) williamsi* represents an earlier stage in the development of the Stropheodontids, where the migration of the dental (and socket) plates towards the hinge-line has just started. The presence of concentric rugations, geniculation, and the comparatively strong development of the muscle attachments and the median septum distinguishes S. (E.) *williamsi* from its congeners (except *S. (E.) helgoeyensis*), and makes it appear higher developed than them. This stronger development of calcareous tissue might, however, as well be due to ecological differences. The two species described here might, therefore either be specialized, blind offshots of the early Stropheodontids, or they might have given rise to the Upper Ordovician- Early Silurian forms, which look less developed in some features because they lived in a different environment (smaller supply of lime and less favorable condition of living).

If not the crenulations were known, this species would most probably have been referred to *Rafinesquina (Hedstroemina)*, indicating that it was derived from that subgenus.

Distribution: This species is found in the Coelosphaeridium beds in the Ringsaker district, (localities Bratberg and Fangberget) and in the Upper Cyclocrinus beds in the Hamar—Nes district (locality Furuberget). One can expect to find the species in the Coelosphaeridium beds in the Hamar—Nes district, and in the Cyclocrinus beds in the Ringsaker district, when more material has been collected from these horizons. There is no great difference in the age of the layers in which this species is found.

<center>

Stropheodonta (Eostropheodonta) helgoeyensis sp. n.

Pl. 12, Fig. 6.

</center>

Type data: The holotype, PMO 38647, is the cast of a dorsal valve from the upper part of the Mjøsa Limestone at Bergsviken, Helgøya, Hamar—Nes district.

Material: The holotype and a fragmentary cast of a ventral interior, and some fragments of the exterior.

Diagnosis: Well calcified *Eostropheodonta* species with short cardinal processes, socket plates diverging at 120°. The dorsal valve is slightly convex, with a distinct, sharp geniculation, and three intervascular (?) septa.

Description: Sculpture differentiated, 3—5 striae between each rib (the fragments of the exterior, found together with the holotype, might belong to another species). Dorsal valve of moderate size, 24 mm wide and 18 mm long. The cardinal angles are right, and the geniculation is sharp, but irregular. Three subparallel septa (intervascular ?) are found in front of the indistinct, uniformly rounded muscle impressions. Traces of vascular impressions are found along the margin of the valve. Cardinal processes high, short, thin parallel plates united with the strongly diverging socket plates (about 120°). 6—7 grooves on each of them. The area is not completely preserved in the holotype.

The ventral valve is very fragmentary, and the cardinal part is badly preserved, so that the specimen might belong to another species.

Remarks: In the development of the cardinalia, this species is like some Llandoverian species of *Eostropheodonta*, such as *E.* cf. *mullochensis* (WILLIAMS 1951, pl. 8, fig. 3) and *S. (E.) davidsoni* (HOLTEDAHL 1916, pl. 7, fig. 6, non WILLIAMS 1951). *S. (E.) helgoeyensis* differs from all congeners in having septa, and a geniculation. Altogether, the species, like *S. (E.) williamsi* is better calcified than the other members of the subgenus. It differs from the latter species in the greater angle of the socket plates, and in having no concentric rugae.

Distribution: All the specimens are found on the same slab, which comes from the upper part of the Mjøsa Limestone (bed e). It is probably considerably younger than *S. (E.) williamsi.*

Indet. Strophomenid nr. 1
Pl. 9, Fig. 7.

Material: One dorsal interior and three casts of the exterior.

Description: Exterior resembling *R. (H.) undata,* but with reversed genicuation. The disc is corrugated by a number of strong rugae, and the radial sculpture is well differentated. The valves appear to be almost parallel. The areas have not been observed.

The dorsal interior, which include only a fragment of the disc, shows small, diverging cardinal processes, an thin chilidum, straight diverging socket plates, and a prominent median septum, thickened posteriorly. The muscle impressions are well defined, and of moderate size. They are cut by a pair of diverging, sharp septa, and the lateral ridges of the muscle impressions are replaced by rows of blunt spines.

Remarks: This species differs from most genera and species known, and the peculiar rows of spines are not known from other Strophomenids.   It differs from *Kjerulfina* in the dorsal interior, and from *Strophomena* in the straight socket plates. It differs from *Rafinesquina* in the orientation of the valves.

Distribution: The exact horizon is unknown, it is supposed to be Middle Ordovician. The specimens come from the highly contact metamorphic sediments near Lauervann in the Sandsvær—Eiker district.

Indet. Strophomenid nr. 2.

Material: One fragmentary cast of a ventral (?) exterior from 15,90 m above the lower phosphate bed at Moldekleiv, Langesund—Gjerpen district. (cf. STØRMER 1953, pp. 71—72).

Description: The present specimen is a disc with a slight umbonal convexity, with 6—7 regular, strong concentric rugae. The traces of radial sculpture are weak, but there seems to have been a strong median rib. If a geniculated fringe was present, it has been broken off.

Remarks: This specimen is of course indeterminable as to species and genus. It is mentioned because it occurs at a very low stratigraphical level (zone of *Did. bifidus* or lower part of *Did. geminus*). Very few Strophomenacea are known from this level, and none of them resemble the present specimen. The size, sculpture, and especially the strong submedian rib reminds one of the genus *Inversella* ÖPIK 1933, which occur abundantly in the slightly older beds (zone 3cβ-γ) in the Oslo—Asker district.

Indet. Strophomenid nr. 3.
Pl. 1, Fig. 17.

Material: 4 exteriors and a fragmentary cast of a ventral interior.

Description: The figured specimen, of average size, is 9,5 mm wide and 4.5 mm long. The cardinal angles are right, and the con-

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vexity moderate. There is a slight umbonal swelling in the ventral valve. The sculpture consists of 3—5 strong radial ribs with a large number of very fine striae between each, and 7—12 concentric rugae, which are strongest near the hinge-line.

The ventral interior, which is an artificial cast, only shows a small, badly defined muscle impression, the main radial ribs of the external sculpture, and a not denticulated hinge-line.

Remarks: The species most probably belongs to the Plectambonitacea, but it is very difficult to determine the genus. The sculpture reminds one of *Plectambonites* and *Athiella.* The weakly developed interior, and the smooth hinge-line also indicates a relationship with the latter genus. The species referred to *Athiella,* however, are generally more convex, and have a different sculpture.

Distribution: The specimens are found in zone $4a\alpha_1$, the beds just above the Orthoceros Limestone ($3c\gamma$) at Hamar, Hamar—Nes district.

Trends of evolution in the Strophomenacea.

It is difficult to follow trends of evolution in the Strophomenacea, because of the large number of forms known, and because of the ecological variation of diagnostic features at least in some groups. Probably the Strophomenacea developed from the geologically older Plectambonitacea. It is, however, difficult to trace the subgroup within this superfamily which gave rise to the Strophomenacea. There is also a possibility of the latter superfamily being polyphyletic.

A study of the oldest known Strophomenacea indicates that two lines of development can be traced. The first one, the origin of which is unknown, started with *Kjaerina-Hedstroemina,* and gave rise to the younger Rafinesquinas and most of the Stropheodontids. This line started with species with thin shells, and long, blade-like cardinal processes, and straight, narrowly diverging socket plates (i.a. «*Rafinesquina*» *llandeiloensis*).

The other line of development started with *Oepikina* and gave rise to *Oslomena, Leptaena* and other genera. The early forms had t ick valves, branchial septa, bilobed dorsal adductor muscles, and short, often bifurcated cardinal processes.

A number of genera can not at present be placed in any of these lines of development. *Strophomena* possibly belongs to the *Oepikina-*

line, but this has not been proved. It is very difficult to place genera like *Kjerulfina* and *Holtedahlina*.

The *Oepikina*-line is evidently linked with *Christiania* in the development of the branchial septa, even if *Oepikina* is less specialized. Both the cardinal processes of *Christiania oblonga*, and the ontogeny of *C. holtedahli* (described above, p. 117, 124) indicate that the Christianiadae are related to the Leptestids. In *Oepikina* the cardinal processes are related to that of the Sowerbyellinids (textfig. 2 C).

At present it is impossible to divide the family Strophomenidae into two or more subfamilies based on the lines of development referred to here. Only a very careful study on the ontogeny and relative geological age of the oldest members of the family may throw some light on this problem. Until this is done, the author prefers to use the classification of WILLIAMS (1953), with the Leptaenoidina separated as a subfamily.

The relations of the Stropheodontids is not quite clear. WILLIAMS (1950, 1953) believed that the family developed from some primitive Strophomenidae in the end of the Upper Ordovician, and that it was a monophyletic family. He did not mention which primitive Strophomenids he thought was the ancestors, but it is evident from this descriptions that they must have been closely related to *Kjaerina* and *Hedstroemina*, with their long, slender cardinal processes, and more or less widely diverging socket plates.

SCHMIDT (1951) suggested that the family Stropheodontidae was highly polyphyletic. This was, however, partly due to the broad interpretation of the denticulation of the hinge-line advocated by this author. The development of the different types of denticles, and the structure of the teeth, which seem to have formed the base for the development of the Stropheodontid denticulations are described above (p. 20).

The author's observations indicate that the Stropheodontids developed from *Hedstroemina*-like forms, such as suggested by WILLIAMS, but as early as in the Middle Ordovician. Here it must be mentioned that the important diagnostic feature in the family Stropheodontidae are not the crenulated teeth, which are found in a large number of unrelated Strophomenid genera. It is the coalecense of the teeth with the hinge-line which characterises the Stropheodontidae. The value of the crenulated teeth for the articulation of the valves

was probably very small, and in any case inferior to that of the cardinal processes, which developed parallel to the teeth, and probably took over their functions as well.

The fact that the histological structure which formed the base for the development of the crenulations is found in the majority of the Strophomenid genera, and the presence of crenulations in gerontic specimens in a large number of different species indicates that the family Stropheodontidae might be polyphyletic. This has, however, not been proved, and the distinct trend of evolution of the teeth in that family is not found in other groups. It therefore seems safe to keep that family distinct from the other Strophomenacea, even if some minor groups, like *Strophonella* might have developed independantly (cf. HOLTEDAHL 1916).

In this paper the family Christianidae WILLIAMS 1953 in included in the Plectambonitacea as a separate family, related to the Sowerbyellinidae. Further studies may show that it should be removed to the Strophomenidae as a subfamily (including the *Oepikina*-group). The family evidently is intermediate between the two superfamilies, and closely related both to the Leptestinids and the *Oepikina*-group of the Strophomenidae. It might also be convenient to restrict the Plectambonitacea to forms with an Orthoid cardinal process, and to include the Sowerbyellidae and the Christianidae either in the Strophomenacea, or in a new superfamily.

Faunal assemblages and correlation.

As mentioned by STØRMER (1953), several different faunal provinces can be discriminated within the Oslo region, and this also applies to the Strophomenidae. The details of the distribution are shown in the tables (p. 200—205). The most prominent faunal provinces are:
1) The Oslo—Asker district, where the Strophomenids show distinct British affinities. Baltic elements in the fauna are few, and occur only in special horizons. The British areas which resemble the Oslo—Asker district, are Northern England, North Wales and Central Eire.
2) The Ringerike—Hadeland districts, with a largely indigenous fauna, with some affinities to Great Britain, especially Shropshire.
3) The Langesund—Gjerpen district, with a definitely Baltic fauna, in spite of the western position of the district.

4) The Hamar—Nes district, with a mixed fauna, with both Baltic, British and indigenous forms.
5) The Ringsaker district, with a mixed Baltic—American fauna.

In the Toten district, and in the Northern part of the Hadeland district the fauna seems to be rather like that found in the two other northern districts, even if the number of common species is small. In the northern districts of the Oslo region, the specimens of Strophomenids seem to be larger than in the other districts, and this applies also to the Toten district. Even species which occur both in southern and northern districts, are generally much larger in the northern ones (cf. p. 54). This might be due to the more littoral character of the northern deposits, and the better supply of oxygen in connection with the rich algal flora.

The other areas in the Oslo region, the Eiker—Sandsvær, Modum and Sjåstad districts seem to be intermediate between the Oslo— Asker and the Langesund—Gjerpen districts. The fauna of the two latter districts is not well known, and that of the Eiker—Sandsvær district have a number of local species, especially Plectambonitacea from the oldest beds.

Because of the striking differences in fauna in the provinces, it is very difficult to correlate the zones of the different districts only with the aid of the Strophomenids. In some cases it is easier to correlate the faunas with more distant ones.

The Baltic elements, which occur especially in the Langesund— Gjerpen and the Mjøsa districts, indicate a correlation of the Coelospaeridium beds and the Echinosphaerites and Bryozoan beds with the Kukruse stage (C 2) in Esthonia. This correlation is also well documented in other animal groups. These beds probably correspond to zones 4bα—β in the Oslo—Asker and Ringerike districts.

The American elements, which are few, and found only in the Ringsaker district, are at least at present of no stratigraphical value.

The british elements, mainly in the Oslo—Asker and Ringerike districts indicate a correlation between the zones with *Bancroftina typa* and *Dalmanella wattsi* and the upper part of zone 4bα (above the bentonite beds, cf. HAGEMANN & SPJELDNÆS 1955). This correlation is supported by a number of common species. (*Eoplectodonta acuminata, Chonetoidea alpha, Sampo oepiki* and others). The correlation between the zone of *Onniella reuschi* and 4bγ is not yet so well documented.

It is difficult to place the zones of the Oslo region in the standard graptolite sequence, especially the zones 4aβ—4bγ. This problem has recently been discussed by JAANUSSON & STRACHAN (1954) and HA-GEMANN & SPJELDNÆS (1955). NILSSON (1953) made the important discovery of a mixed graptolite fauna consiting of guide fossil for the zones of *Nemagraptus gracilis* and *Dicranograptus clingani*. This might indicate that the *Nemagraptus gracilis* fauna extends vertically through the *peltifer* and *wilsoni* zones. At present it is therefore diffi-cult to use graptolites in the correlation of this part of the Middle Ordovician, until the graptolite sequence has been revised in detail.

It is also evident that a new stratigraphy could not be based on the Strophomenids only, and since several stratigraphically important groups have not been described from the Oslo region (trilobites, Dalma-nellids and bryozoans), no detailed correlations are made in this paper.

The vertical distribution of the faunas is studied especially in the Oslo—Asker district, and the following notes mainly apply to that district.

In zones $4a\alpha_{1-4}$, the Strophomenid fauna is small, consisting only of Plectambonitids. Both in this zone and in $4a\beta$, all the species seem to be local ones which are not useful for correlation.

In the lower part of zone 4bα, there are few Strophomenida, only Plectambonitids, and only local species. Among the characteristic fossils are *Salopia* spp. and other Orthids. The fauna in the middle part of the zone is not well known, and appears to be poor.

In the upper part of the zone, between and above the bentonite beds, a new and very rich fauna is found. The typical fossils are: *Eoplectodonta acuminata*, *Oslomena osloensis*, *Ptychoglyptus valdari*, *Christiania holtedahli*, and *Nicolella* sp., *Glyptorthis* sp. *Kullervo* sp. and a number of others. This fauna is wide-spread in Great Britain, Eire and Scandinavia. Generally it is found in the top of, or just above the volcanic beds indicating the maximal volcanic activity in the Middle Ordovician (cf. VOGT 1947). A considerable break in the se-quence is often found above this fauna (Cf. BANCROFT 1933, HAGEMANN & SPJELDNÆS 1955 and HARPER 1952, who described a graptolite fauna of the *Dicranograptus cligani*-zone just above the fauna mentio-ned here). The Derfel Limestone fauna, described by WHITTINGTON & WILLIAMS (1955) is rather like this 4bα-fauna, even if no species seem to be common, the fauna is definitely of the same type. The

Derfel Limestone, is, however, succeeded by a graptolite fauna of the *Nemagraptus gracilis* zone. Even if the age of the *Nemagraptus gracilis*-fauna is regarded to be uncertain, it seems as if the Derfel Limestone is older than the upper part of 4bα, which have several species in common with the Balclatchie of the Girvan district, and the zones of *Bancroftina typa* and *Dalmanella wattsi* in N. Wales and Shropshire. A possible explanation of this problem is that during the period of maximal volcanic activity, the fauna was destroyed over large areas, especially by ash-falls. The empty space after the destroyed fauna was filled partly with immigration from areas less affected by the volcanism (the Baltic region, the Scottish-American region) and partly by rapid expansion of faunas already accustomed to the «volcanic habiat» (possibly the Derfel Limestone fauna). This might explain the peculiar mixed fauna found in zone 4bα, but there is at present no definite proves for this hypotesis.

In zone 4bβ, a characteristic fauna is found in the Oslo—Asker district consisting of large, generally indigenous forms. The significant ones are *Kiaeromena kjerulfi*, *Eoplectodonta* (?) *percedens*, *Porambonites kjerulfi* n.sp. Outside the Oslo—Asker district, this zone is. not well defined in the fauna or lithology.

In zone 4bγ there are two faunizones, a lower one with a transition to 4bβ, and *Kjerulfina foliovalve*, *Chonetoidea gamma* and *Sowerbyella sericea askerensis* as index fossils. In the Ringerike and Hadeland districts the first and last of these species are represented by nearly related ones. (*Kjerulfina limbata* and *Sowerbyella sericea hadelandica*).

The upper part of the zone has the same Strophomenid fauna as the next younger zone, 4bδ., with *Sampo indentata* and *Kjaerina lepta*. In the lower part of zone 4bδ, *Strophomena* (*Gunnarella*) *delta* and *Eoplectodonta* (?) *rhombica* is added to this fauna.

The uppermost part of zone 4bδ is almost devoid of brachiopods in the Oslo—Asker district. In the Ringerike district, this subzone (4bδ$_2$, of *Tretaspis kiaeri*) yields *Strophomena* (*Gunnarella*) cf. *rigida* and other fossils which are typical for the overlying Tretaspis Shale (zone 4cα).

The faunizones, of the Strophomenida of the Oslo—Asker district do therefore not in all cases correspond to the stratigraphical units used at present, which are mainly based on the lithology of the beds.
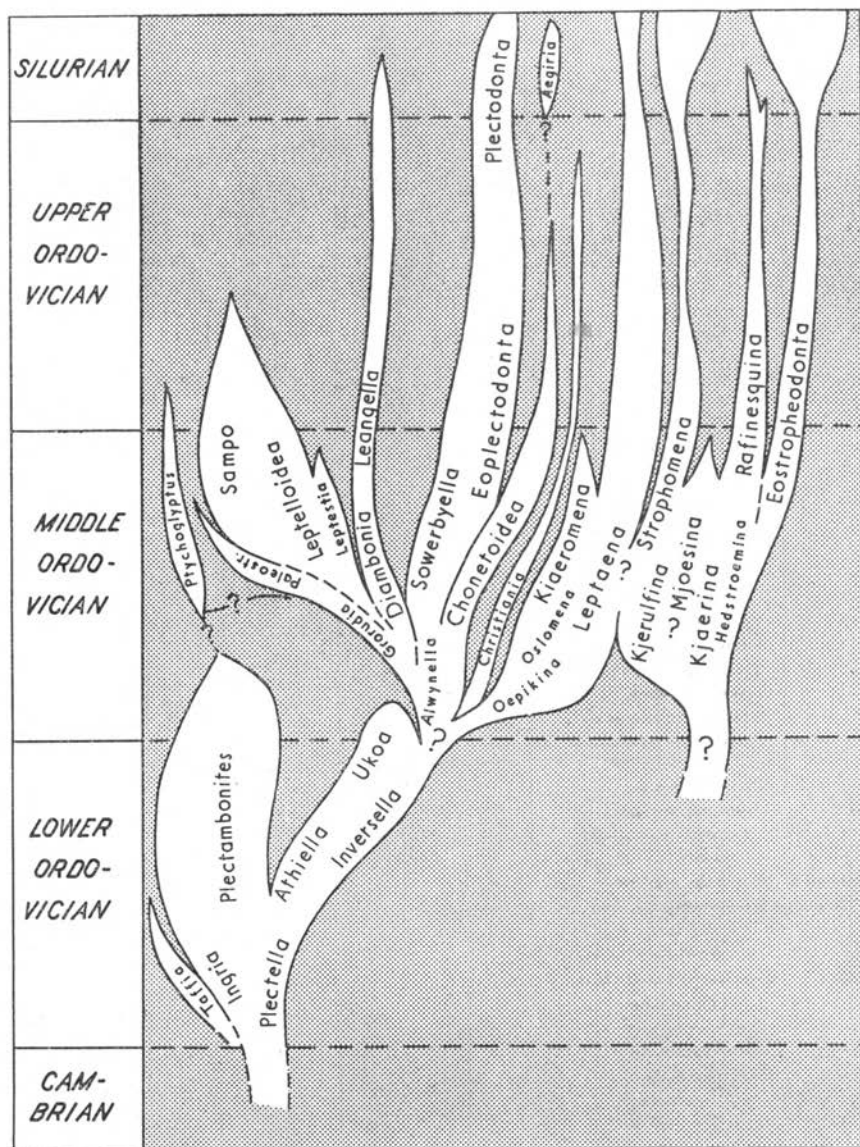
Fig. 42. A diagram illustrating the authors hypothesis of the development of the Strophomenida. Note that the border between the Lower and Middle Ordovician is placed at the base of the *bifidus*-zone, and that between the Middle and Upper Ordovician at the base of the zone with *Pleurograptus linearis*. *Ptychoglyptus* should be firmly united with Paleostr. (= *Paleostropomena*).

SPECIES	aα	aβ	bα	bβ	bγ	bδ	Oslo—Asker	Gj.—Langesund	Fiker—Sandsv.	Ringerike	Hadeland	Toten	Hamar—Nes	Kingsaker	
1) *Ptychoglyptus valdari*	—	—	1	—	—	—	1	—	—	?	?	—	—	—	
2) *Gvorudia grorudi*	—	2	—	—	—	—	2	—	—	—	—	—	—	—	
3) *Gvorudia* (?) *glabrata*	—	3	3	—	—	—	3	—	—	—	—	.	—	—	
4) *Paleostrophomena* (?) *majori*	—	—	—	—	—	—	—	4	—	—	—	—	—	—	ec–bz
5) *Leptestia* aff. *jukesi*	—	—	—	—	—	—	—	5	—	—	—	—	—	—	bz
Sampo															
6) *S.* (*S.*) *indentata*	—	—	—	—	6	6	6	—	—	?	—	—	—	—	
7) *S.* (*Leptellina*) *oepiki*	—	—	7	—	—	—	7	—	—	?	7	—	—	—	
8) *S.* (*Leptellina*) *elevata*	—	—	8	—	—	—	?	—	—	8	—	—	—	—	.
Leptelloidea															
9) *L.* (*Benignites*) *heintzi*	9[3]	—	—	—	—	—	—	—	9	—	—	—	—	—	
10) *L.* (s.l.) *rosendahli*	—	—	—	—	—	—	—	—	—	—	—	—	—	10	cø
11) *L.* (s.l.) *sp.*	11[4]	11	—	—	—	—	—	—	11	—	—	—	—	—	
12) *Diambonia* (?) *leifi*	—	—	—	—	—	—	—	12	—	—	—	—	—	—	bz–ma
13) *Diambonia anatoli*	—	—	13	—	—	—	13	—	—	—	—	—	—	—	
14) *Leangella hamari*	—	—	—	—	—	—	—	—	—	—	—	—	14	—	cy
Alwynella															
15) *A. osloensis*	—	15	—	—	—	—	15	?	—	15	?	—	—	—	
16) *A. intermedia*	16[4]	16	—	—	—	—	16	—	—	—	—	—	—	—	
17) *A. ildjernensis*	17[2-4]	—	—	—	—	—	—	17	—	17	—	—	—	—	
Sowerbyella															
18) *S. sericea soudleyensis*	—	—	—	—	—	—	—	—	—	—	18	18	18	—	cy

Column group headers: **ZONES** (aα, aβ, bα, bβ, bγ, bδ) — **DISTRICTS** (Oslo—Asker, Gj.—Langesund, Fiker—Sandsv., Ringerike, Hadeland, Toten, Hamar—Nes, Kingsaker)

19)	S. sericea askerensis	—	—	19	—	19	—	—	—	—	
20)	S. sericea hadelandica	?	—	—	—	—	—	—	—	—	Lcy
21)	S. ringsakerensis	—	—	—	—	—	?	—	—	21	cø, en
22)	S. (?) sp.	—	22	—	22	—	—	22	—	—	
	Eoplectodonta										
23)	E. acuminata	23	—	23	?	23	—	—	—	—	
24)	E. karina	24	—	24	?	24	—	—	—	—	
25)	E. (?) percedens	25	25	25	25	25	25	—	—	—	
26)	E. (?) rhombica	—	—	26	26	26	—	26	—	—	
	Chonetoidea										
27)	C. gamma	—	—	27	—	27	—	27	—	—	
28)	C. alpha	28	—	28	—	28	—	—	—	—	
29)	C. stoermeri	29³	—	—	—	29	—	—	—	—	
	Christiania										
30)	C. holtedahli	30	—	30	30	30	30	30	30	30	cø
31)	C. cf. holtedahli	31	—	31	31	—	—	—	—	—	
32)	C. oblonga	32¹⁻²	—	—	32	32	—	—	—	—	
33)	C. cf. oblonga	—	33	—	—	33	—	—	—	—	
34)	C. elongata	34⁴	34	34	34	34	34	—	—	—	
	Rafinesquina										
35)	R. (Rafinesquina) sp.	—	—	—	—	—	—	—	35	35	cø
36)	R. (Kjaerina) lepta	—	36	36	—	36	?	—	—	—	
37)	R. (Hedstroemina) holtedahli ..	37	37	—	37	—	—	—	—	—	
38)	R. (Hedstroemina) ungula	38	38	—	38	—	—	?	—	—	cy?
39)	R. (Hedstroemina) cf. robusta..	—	—	—	—	—	—	—	39	39	cø
40)	R. (Hedstroemina) aff. robusta.	—	—	—	—	—	—	—	40	40	cø
41)	R. (Hedstroemina) muensteri ..	41	41	—	41	—	—	—	—	—	
42)	R. (Hedstroemina) muensteri ..	42	42	—	42	—	—	—	—	—	
42)	«R». ringerikensis	—	—	—	—	—	—	—	—	—	
	Mjoesina										
43)	M. mjoesensis	—	—	—	—	—	43	—	43	—	cy-mk
44)	M. cf. mjoesensis	—	—	—	—	—	—	—	44	44	cø

SPECIES	ZONES						DISTRICTS									
	aα	aβ	ba	bβ	bγ	bδ	Oslo—Asker	Gj.—Langesund	Eiker—Sandsv.	Ringerike	Hadeland	Toten	Hamar—Nes	Kingsaker		
45) M. gregaria	—	—	—	—	—	—	—	—	—	—	—	45	?	—	co	45
Strophomena																
46) S. norvegica	—	—	46	46	—	—	46	—	—	46	46	—	—	—	cy?	46
47) S. hirsuta	—	—	—	—	—	—	—	—	—	—	—	—	—	47	co	47
48) S. keilhaui	—	—	—	—	—	—	—	—	—	—	—	—	48	—	cy	48
49) S. steinari	—	—	—	—	—	—	—	—	—	—	—	—	—	49	co	49
50) S. sp.	—	—	—	—	—	50²	—	—	—	50	—	—	—	—		50
51) S. (Gunnarella) delta	—	—	—	—	—	51	51	—	—	—	—	—	—	—		51
52) S. (Gunnarella) beta	—	—	—	52	—	—	—	—	—	52	52	—	—	—		52
53) S. (Gunnarella) alpha	—	—	53	—	—	—	53	53	—	—	53	—	—	—	ec, cy	53
54) S. (Gunnarella) cf. rigida	—	—	—	—	—	54²	—	—	—	54	—	—	—	—		54
Kjerulfina																
55) K. foliovalve	—	—	—	—	55	—	55	—	—	—	?	—	—	—		55
56) K. limbata	—	—	—	—	56	—	?	—	—	56	?	—	—	—		56
57) K. broeggeri	—	—	57	57	—	—	?	—	—	57	—	—	—	—		57
58) K. lata	—	—	58	—	—	—	58	—	—	—	—	—	—	—		58
59) K. (?) sp.	—	—	—	—	—	—	—	59	—	—	—	—	—	—	bz	59
Oslomena																
60) O. osloensis	—	—	60	60	—	—	60	—	—	60	?	60	—	—	co	60
61) O. celtica (?)	—	—	—	—	—	—	—	61	—	—	—	—	—	—	ec	61
62) O. aff. girvanensis	—	—	—	62	—	—	—	—	—	62	—	—	—	—		62

#	Species	1	2	3	4	5	6	7	8	(last col.)	aα
63)	O. (?) papilio	—	—	—	—	—	—	—	63	cy?	63
	Oepikina										
64)	O. dorsata media	—	—	—	—	64	64	64	64	cø, bz, ms	64
65)	O. (? or Rafinesquina) sp.	65	65	65s	—	—	—	—	—		65
	Leptaena										
66)	L. (?) indigena	—	—	—	—	—	?	66	66	cø	66
67)	L. strandi	—	67	67	67	67	67	67	—	ma, cy	67
68)	L. ennessbe	—	68	68	—	—	—	68	68	cø	68
69)	L. veldrensis	—	—	—	—	69	—	69	69	bz, cø, ms	69
70)	L. minuta	—	—	—	—	—	70	—	—	Ucy	70
71)	L. cf. minuta	—	—	—	71	—	—	—	—	ec-bz	71
72)	L. sp.	—	72	72	72	—	—	72	72	cø	72
	Kiaeromena										
73)	K. kjerulfi	—	—	73	73	73	73	—	—		73
74)	K. cf. juvenilis	—	74	74	74	—	—	74	74	cø	74
	Stropheodonta										
75)	S. (Eostropheod.) williamsi	—	—	—	—	—	—	75	75	cø-cy	75
76)	S. (Eostropheod.) helgoeyensis	—	—	—	—	—	—	76	76	mk	76
77)	Indet. Strophomenid nr. 1	—	—	—	77	—	—	—	—	hor.?	77
78)	Indet. Strophomenid nr. 2	78^{1-2}	—	78	—	—	—	—	—		78
79)	Indet. Strophomenid nr. 3	79^1	—	—	—	79	—	79	—		79

Abbreviations: In the aα-column, the upper figures (i.a. 9^3) indicate the subzone (-s) in which the species occur. In the bδ-column, n^2 indicates that the species is found in subzone $4b\delta_2$ of *Tretaspis kiaeri*. For the districts where the ordinary stratigraphical symbols are not in use, the last column in the table shows the stratigraphical distribution of the species. cø = Coelosphaeridium beds, cy = Cyclocrinus beds (L = lower, U = upper part), mk = Mjøsa Limestone, ec = Echinosphaerites beds, bz = Bryozoan beds, ma = Mastopora beds, ek = Encrinite Limestone. A n^s in the Oslo—Asker column indicate that the species is found in the Sjåstad district only. (for stratigraphical terms and boundaries of the districts, see STØRMER 1953).

LIST OF REFERENCES

ANGELIN, N. P. & LINDSTRÖM, G. 1880. Fragmenta Silurica e dona Caroli Henrici Wegelin. pp. 1—60, 20 pls. Holmia (Stockholm).

ARBER, M. A. 1939 The Nature and Significance of the Pedicleforamen in *Leptaena* DALMAN. Geol. Mag. *76*, pp. 82—92 Hertford.

— 1940. The relation of the Valves to the Pedicle in the Strophomenid Brachiopods. ibid. *77*, pp. 161—174. Hertford.

— 1942. The Pseudodeltidium of the Strophomenid Brachiopods. ibid. *79*, pp. 179—187. Hertford.

BANCROFT, B. B. 1929. Some New Genera and Species of Strophomenacea from the Upper Ordovician of Shropshire. Mem. Proc. Manchester Liter. Philos. Soc. *73*, pp. 33—65, 2 pls. Manchester.

— 1933. Correlation Tables of the Stages Costonian-Onnian in England and Wales. Privately published by the author.

— 1945. (†) The Brachiopod Zonal Indices of the Stages Costonian to Onnian in Britain. Journ. Paleont. *19*, pp. 181—252, 17 pls. Menasha, Wis.

— (MS) 1949 (†). Welsh Valentian Brachiopods and The Strophomena antiquata Group of Fossil Brachiopods. (Edited by A. Lamont) Preprint from the «Quarry Managers Journal»[1].

BASSLER, R. S. 1932. The Stratigraphy of the Central Basin of Tennessee. State of Tennessee. Dept. of Education. Div. of Geology. Bull. *38*, pp. 1—183 + i—x, 49 pls. Nashville, Tenn.

BEECHER, C. E. 1891. Development of the Brachiopoda. Part I, Introduction. American Journ. Sci. *41*. New Haven.

— 1891a. Development of Bilobites. ibid. *42*. New Haven.

— 1892. Development of the Brachiopoda. Part II. Classification of the Stages of Growth and Decline. ibid. *44*, pp. 132—155. 1 pl. New Haven.

— & CLARKE, J. M. 1889. The Development of some Silurian Brachiopoda. Mem. N.Y. State Museum *1*, nr. 1, pp. 1—95, 8 pl. Albany.

[1] Subsequent authors (i. a. WILLIAMS 1951, p. 86) have regarded this paper invalid because it is not legally published according to the rulings of the International Commision on Zoological Nomenclature (Bull. Zool. Nomencl. *4*, p. 146, case 19b). This rule, however, did not attain legal force until May 25th 1950, when it was published (cf. Bull. Zool. Nomencl. *4*, p. 57, case 8, and pp. vii—viii) Since the disputed paper was published in May 1949, the present rules cannot be applied to it, and it must be invalidated according to the rulings legal at the time of publication.

BEKKER, H. 1921. The Kuckers stage of the Ordovician Rocks of NE Esthonia. Acta et Comm. Universitatis Dorpatensis *A 2*, nr. 1, pp. 1—92, 12 pls. Tartu.

— 1922. A new Brachiopod (*Leptestia*) from the Kuckers Stage in Esthonia. Geol. Mag. *59*, pp. 361—365. Hertford.

BRØGGER, W. C. 1887. Geologisk kart over øene ved Kristiania. Nyt Mag. f. Naturvid. *31*. Kristiania/Oslo.

CARPENTER, 1853. On the Intimate Structure of the Shells of the Brachiopoda. In DAVIDSON: British Fossil Brachiopods, Vol. I, part II, pp. 23—40, pls. 4—5. Paleontographical Soc. London.

COOPER, G. A. & KINDLE, C. H. 1936. New Brachiopods and Trilobites from the Upper Ordovician of Percé, Quebec. Journ. Paleont. *10*, pp. 348—372. pls. 51—53. Menasha, Wis.

— & WILLIAMS, A. 1952. Significance of the Stratigraphic Distribution of Brachiopods. Journ. Paleont. *28*, pp. 326—337, Menasha, Wis.

CUMINGS, E. R. 1903. The Morphogenesis of Platystrophia. A study of the Evolution of a Paleozoic Brachiopod. Amer. Journ. Sci. ser. 4, *15*, pp. 1—48, 121—136. New Haven.

— & GALLOWAY, J. J. 1915. Studies of the Morphology and Histology of the Trepostomata or Monticuliporids. Bull. Geol. Soc. Amer. *26*, pp. 349 —374, pls. 10—15. New York.

DALL, W. H. 1877. Index to the Names which have been applied to the Subdivisions of the Class Brachiopoda. U. S. Nat. Mus. Bull. *8*, pp. 88. Washington, D.C.

DAVIDSON, T. 1851—1886. A Monograph of the British Fossil Brachiopoda. Vols. *1—6*. Paleontographical Soc. London.

— 1886—1888. A Monograph of the Recent Brachiopoda. Trans. Linn. Soc. London. ser. 2, *4*, zool. London.

DESLONGCHAMPS, E. E. 1862. Note sur le developpement du deltidium chez les brachiopodes articules. Bull. Soc. Geol. France (2) *19*, pp. 409—413, pl. 9. Paris.

— 1864. Recherches sur L'Organisation du Manteau chez les Brachiopodes Articules et Principialement sur les Spicules calcaires contenus dans son Interieur. Mem. Soc. Linn. Normandie. *14*, 35 pp., 3 pls. Paris/Caen.

DALMAN, J. W. 1828. Uppställning och Beskrivning af de i Sverige funne Terebratuliter. Kongl. Vet. Akad. Handl. *1827*, pp. 85—155, pls. 1—6. Stockholm.

FOERSTE, A. J. 1912. Strophomena and other Fossils from Cincinnatian and Mohawkian Horizons, chiefly in Ohio, Indiana and Kentucky. Bull. Sci. Lab. Denison Univ. *17*, pp. 17—174, pls. 1—18.

— 1924. Upper Ordovician Faunas of Ontario and Quebec. Geol. Surv. Canada. Mem. *138*, pp. 1—255, 44 pls. Ottawa.

GAERTNER, H.-R. v. 1930. Silurische und tiefunterdevonische Trilobiten und Brachiopoden aus den Zentralkarnischen Alpen. Jahrb. Preuss. Geol. Landesanst. *51*, 1 pp. 188—252, pls. 24—26, Berlin.

HAGEMANN, F. & SPJELDNÆS, N. 1955. The Middle Ordovician of the Oslo
    Region, Norway. 6. Notes on bentonites (K-Bentonites) from the Oslo—
    Asker district. Norsk. Geol. Tidsskr. 35, pp. 29—52. Bergen.
HALL, J. 1847. Paleontology of New York 1. 338 pp., 98 pls. Albany.
— 1852. ibid. II, Albany.
— & CLARKE, J. M. 1892—94. Paleontology of New York 8. Parts 1—2.
    760 pp. 108 pls. Albany. (In the text, this paper is referred to as H.
    & C. 1892, because part 1, to which all references apply, was issued this
    year).
HARPER, J. C. 1952. The Ordovician Rocks between Collon (Co. Louth) and
    Grangegeeth (Co. Meath). Scient. Proc. Roy. Dublin Soc. (N.S.) 28, pp.
    85—112, pls. 5—7. Dublin.
HAVLIČEK, V. 1952. O ordovických zàstupcich čeledi Plectambonitidae (Brachi-
    opoda). (Summary in english and russian). Sbornik Ustreniho Ustavu
    Geologickeho. od. pal. 19, pp. 397—428, pls. 13—15 Praha.
HENNINGSMOEN, G. 1953. The Middle Ordovician of the Oslo Region, Norway. 4.
    Ostracoda. Norsk Geol. Tidsskr. 32, pp. 35—56, 5 pls. Bergen.
HISINGER, W. 1827. Gottland, Geognostiskt beskrifvit. Kongl. Vet. Akad.
    Handl. 1826, pp. 3 11—337, pls. 7—8. Stockholm.
— 1837. Lethæa Svecica seu Petrificata Sveciæ, iconibus et characteribus
    illustrata. 124 pp., 39 pls. Holmia (Stockholm).
HOLTEDAHL, O. 1916. The Strophomenidae of the Kristiania Region. Vidensk.
    Selsk. Skrifter. I. Mat.-Naturvidensk. Kl. 1915, no. 12, pp. 1—117, 16
    pls. Kristiania (Oslo).
HUXLEY, J. 1942. Evolution, the Modern Synthesis. 645 pp. (George Allen &
    Unwin Ltd.) London.
JAANUSSON, V. & STRACHAN, I. 1954. Correlation of the Scandinavian Middle
    Ordovician with the Graptolite Succession. Geol. Fören. Forhandl. 76,
    pp. 684—696. Stockholm.
JONES, ●. T. 1928. Plectambonites and Some Allied Genera. Mem. Geol. Surv.
    Great Britain 1, part 5. pp. 367—527, pls. 21—25. London.
KING, W. 1846. Remarks on certain genera belonging to the class Pallio-
    branchiata. Ann. Mag. Nat. Hist. 18, pp. 26—42, 83—94. London.
KIÆR, J. 1926. Sphaernoidkalken paa Hadeland. (Summary in english). Norsk
    Geol. Tidsskr. 9, pl. 1—22, pl. 1, Oslo.
KJERULF, T. 1865. Veiviser ved Geologiske excursioner i Christiania Omegn.
    Universitetsprogram. Christiania/Oslo.
KOZLOWSKI, R. 1929. Les Brachiopodes Gotlandiennes de la Podolie Polonaise.
    Palaeontologica Polonica. 1. Warszawa.
LAMONT, A. 1934. Lower Palæozoic Brachiopoda of the Girvan District: Sug-
    gestions on Morphology in relation to Environment Ann. Mag. Nat.
    Hist. (10) 14, pp, 161—184. London.
LINDSTRÖM, M. 1953. On the Lower Chasmops Beds in the Fågelsång District
    (Scania). Geol. Fören. Forhandl. 75, pp. 125—148, 1 pl. Stockholm.
McCOY, F. 1846. Synopsis of the Silurian Fossils of Ireland. Dublin.

McCoy, F. 1852. in Sedgwick, A. & McCoy, F.: Synopsis of the Classification of the British Paleozoic Rocks. London.

Murchison, R. I. 1839. The Silurian System. 768 pp. 37 pls. London.

— , Verneuil, E. de & Keyserling, A. 1845 de. Geologie de la Russie D'Europe et des Montagnes de L'Oural. 2 Paleontologie. 512 pp. 50 pls. Londres & Paris.

Nilsson, R. 1953. Några iakttagelser rörande undre och mellersta dicello-graptusskiffern i västra Skåne. Geol. Fören. Forhandl. 75, pp. 43—48. Stockholm.

Pander, C. H. 1830. Beiträge zur Geognosie des Russichen Reiches. pp. 1—165. 31 pls. St. Petersburg (Leningrad).

Percival, E. 1944. A contribution to the Life History of the brachiopod Terebratella inconspicua Sowerby. Trans. Roy. Soc. New. Zealand 71, pp. 1—23. Wellington.

Portlock, J. E. 1843. Report on the Geology of the county of Londonderry and parts of Tyrone and Fermanagh. 784 pp. 38 + 9 pls. Dublin.

Poulsen, C. 1943. The Silurian Faunas of North Greenland II. Medd. Grøn-land 2. avd. 72, nr. 3. 60 pp. 6 pls. København.

Reed, F. R. C. 1905. New Fossils from the Haverfordwest District. Geol. Mag. dec. 5 2, pp. 444—454, pl. 23. London.

— 1917. The Ordovician and Silurian Brachiopoda of the Girvan District. Trans. Roy. Soc. Edinburgh 51, pp. 795—998, 24 pls. Edinburgh.

— 1932. Report on the Brachiopods from the Trondheim Area. In «The Hovin Group in the Trondheim Area» by J. Kiær. Skrifter Vidensk. Akad. Oslo, I, Mat.-Naturvidensk. Klasse 1932, nr. 4, pp. 115—146, pls. 18—22. Oslo.

— 1941. A new Genus of Trilobites and other Fossils from Girvan. Geol. Mag. 78, pp. 268—278, pl. 5. Hertford.

— 1944. Notes on some new Ordovician Brachiopods from Girvan. Ann. Mag. Hist. (11) 11, pp. 215—222. London.

— 1952. (†). Revision of Certain Ordovician Fossils from County Tyrone. Proc. Roy. Irish. Acad. 55, sect. B. nr. 3. pp. 29—136, 5 pls. Dublin.

Salmon, E. S. 1942. Mohawkian Rafinesquininae. Journ. Paleont. 16, pp. 564—603, pls. 85—87. Menasha, Wis.

Schmidt, F. 1908. Beitrag zur Kentniss der Ostbaltischen, Vorzüglich Unter-silurischen Brachiopoden der Gattungen Plectambonites Pand., Leptaena, Dalm. und Strophomena Blainv. Bull. Acad. Imp. Sci. St. Petersbourg. 1908, pp. 717—726. St. Petersburg. (Leningrad).

Schmidt, H. 1951. Das Stropheodonte Schloss der Brachiopoden. Abh. Sencken-bergischen Naturforschenden Gesellsch. 485, pp. 103—120, pls. 50—51. Frankfurt am Main.

Schuchert, C. 1896. Brachiopoda, in Zittel/Eastman: Text-book of Paleon-tology.

— & LeVene, C. M. 1929. Brachiopoda in Pompeckj: Fossilium Catalogus I: Animalia 42, 139 pp. Berlin.

Schuchert, C. & Cooper, G. A. 1930. Stratigraphy and Paleontology of Percé, Quebeck. Amer. Journ. Sci. (5) *20*, pp. 161—176, 265—288, 365—392, 5 pls. New Haven.

— 1932. Brachiopod Genera of the Suborders Orthoidea and Pentameroidea. Mem. Peabody Mus. Nat. Hist. *4* part 1. New Haven.

Størmer, L. 1953. The Middle Ordovician of the Oslo Region, Norway. 1. Introduction to Stratigraphy. Norsk Geol. Tidsskr. *31*, pp. 37—141, 6 pls. Bergen.

Termier, H. & Termier, G. 1948. La respiration et la circulation chez les Brachiopodes: leur repercussions sur la coquille. Bull. Soc. Hist. Nat. Afrique Nord. *39*, pp. 57—69. Alger.

Thompson, J. A. 1927. Brachiopod morphology and genera (Recent and Tertiary) N. Zealand Board Sci. and Art. Manual 7 338 pp. Wellington.

Ulrich, E. O. & Cooper, G. A. 1942. New Genera of Ordovician Brachiopods. Journ. Paleont. *16*, pp. 620—626, pl. 90. Menasha, Wis.

Verneuil, E. de 1845 = Murchison, R. I., Verneuil, E. de & Keyserling, A. de. 1845.

Vogt, T. 1947. Vulkanismens faser i Trondheimsfeltet. Det kongelige Videnskabers Selskabs Forhandl. *19*, pp. 42—70. Trondheim.

Wahlenberg, G. 1821. Petrificata Telluris Svecanae. Acta Soc. Reg. Sci. *8*. pp. 1—116, pls. 1—4 and 7 (parte). Vpsaliæ (Uppsala).

Walcott, C. D. 1912. Cambrian Brachiopoda. Monogr. U. S. Geol. Surv. *51*, pp. 1—872, 104 pls. with 363 pp. explanation. Washington D. C.

Wang, Y. 1949. Maquoketa Brachiopoda of Iowa. Mem. Geol. Soc. America. *42*, 55 pp. 11 pls. New York.

Whittington, H. B. 1938. New Caradocian Brachiopods from the Berwyn Hills, North Wales. Ann. Mag. Nat. Hist. (11) *2*, pp. 241—259, pls. 10—11. London.

— & Williams, A. 1955. The Fauna of the Derfel Limestone of the Arenig District, North Wales. Phil. Trans. Roy. Soc. ser. B *238*, no. 658. pp. 397—430, pls. 38—40. London.

Wilckens, C. F. 1769. Nachricht von seltenen Versteinerungen vornemlich des Thier-Reiches welche bisher noch nicht genau genug beschrieben und erklärt worden — — — —. 82 pp. 8 pls. Berlin/Stralsund. (Does not apply binominal nomenclature).

Willard, B. 1928. The Brachiopods of the Ottosee and Holston Formations of Tennessee and Virginia. Bull. Mus. Comp. Zool. *68*, pp. 255—292. 3 pls. Cambridge, Mass.

Williams, A. 1949. New Lower Ordovician Brachiopods from the Llandeilo-Llangadock District. Geol. Mag. *86*, pp. 161—174, 226—238. 2 pl. Hertford.

— 1951. Llandovery Brachiopods from Wales with special reference to the Llandovery District. Quart. Journ. Geol. Soc. *108*, pp. 85—136, pls. 3—8. London.

— 1953. The Classification of the Strophomenid Brachiopods. Journ. Washington Acad. Sci. *43*, pp. 1—13. Washington D. C.

WILLIAMS, A. 1953a. North American and European Stropheodontids: Their Morphology and Systematics. Mem. Geol. Soc. America. *56*, 67 pp. 12 pls. New York.

— & KING, W. B. R. 1948. On the Lower Part of the Ashgillian Series in the North of England. Geol. Mag. *85*, pp. 205—212, pl. 16. Hertford.

WILSON, A. 1932. (not seen). Trans. Roy. Soc. Canada, ser. 3 *26*, sect. 4,

— 1944. *Rafinesquina* and its Homomorphs *Opikina* and *Opikinella:* From the Ottawa Limestone of the Ottawa-St. Lawrence Lowlands. ibid. *38*, pp. 145—203, 2 pls. Ottawa.

— 1945. *Strophomena* and its homomorphs *Trigrammaria* and *Microtrypa:* From the Ottawa Limestone of the Ottawa-St. Lawrence Lowlands. ibid. *39*, pp. 121—147, 2 pls. Ottawa.

WINCHELL, N. H. & SCHUCHERT, C. 1895. The Lower Silurian Brachiopoda of Minnesota. Chapter 5 in: Geology of Minnesota, *3*, part 1, pp. 333—474, pls. 29—34. Minneapolis.

ÖPIK, A. 1930. Brachiopoda Protremata des Estländischen Ordovizischen Kukruse-Stufe. Acta et Comm. Universitatis Dorpatensis *A 17*, 1, 261 pp. 22 pls. Tartu.

— 1932. Über die Plectellinen. ibid. *A 23*, 3, 85 pp. 12 pls. Tartu.

— 1933. Über Plectamboniten. ibid. *A 24*, 7, 79 pp. 12 pls. Tartu.

— 1934. Über Klitambonitinen. ibid. *A 26*, 5, 238 pp. 48 pls. Tartu.

— 1939. Brachiopoden und Ostracoden aus dem Expansusschiefer Norwegens. Norsk Geol. Tidsskr. *19*, pp. 117—142, 6 pls. Oslo.

ИВАНОВА, Е. А. 1949. Онтогенез некоторых каменноугольных брахиопод. Тр. Палеонт. Инст. АН СССР т. XX. стр. 243—267. табл. 1—3.

САРЫЧЕВА, Т. Г. 1948. К вопросу о возрастных изменениях раковины продуктид. Известия АН СССР Сер. биол. 1948. стр. 235—259.

— 1949. Морфология, экология и эволюция подмосковных каменноугольных продуктид (роды Dictyoclostens, Pugilis и Antiquatonia). Тр. Палеонт. Инст. АН СССР т. XVIII, стр. 1—306. табл. 1—36.

САРЫЧЕВА, Т. Г. и СОКОЛЬСКАЯ, А. Н. 1952. Определитель палеозойских брахиопод подмосковной котловины. Тр. Палеонт. Инст. АН СССР. т. XXXVIII. стр. 1—307 табл. 1—71.

СОКОЛЬСКАЯ, А. Н. 1949. Возрастные изменения хонетид и их таксономическое значение. Тр. Палеонт. Инст. АН СССР т. XX. стр. 268—279.

— 1950. Chonetidae Русской платформы. Тр. Палеонт. Инст. АН СССР т. XXVII. стр. 1—108. табл. 1—12.

— 1954. Строфонениды русской платформы Тр. Палеонт. Инст. АН СССР т. LI. стр. 1—190. табл. 1—18.

ADDENDUM

Since this paper was submitted to printing, three important papers have arrived, which have to be mentioned here because they have some influence on the results given by the author.

1) ОРАСПЫЛЬД, А.. Л1956. Новые брахиопоы йыхвиского, кейлаского и вазалеммаского горизонтов. Тр. Инст. Геол. АН Зст. ССР т. I сТр. 41 — 67 табл. I—IV.

Some of the species described in that paper are nearly related to some of those found in this paper. *Leptaena taxilla* is probably identical with *L. indigena*, *L. rugosoides* is related to *L. veldrensis*. *L. fluviatilis* might be a *Hedstroemina*, related to one of the species described in this paper. *Actinomena occidens* resemble *Strophomena steinari* both in shape and size, but a closer examination is necessary to determine if they are synonyms. *Holtedahlina sakuensis* and *rakverensis* belong to the same group of species as *Oslomena* (?) *papilio*, and they all definitely belong to *Holtedahlina*.

The relationships mentioned here show that the baltic affinities of the Middle Ordovician Strophomenids of the Mjøsa districts were even stronger than supposed when this paper was written.

2) WILLIAMS, A. 1956: The Calcareous Shell of the Brachiopoda and its Importance to their Classification. Biol.Reviews *31*, pp. 243—287. Cambridge.

This is a very important paper, which describes the anatomical base of the features used in the classification of fossil brachiopods, together with a detailed and instructive comparison between living and fossil forms. The taxonomic value of the different morphological features are critically discussed, and even if most of his conclutions are negative, this paper will probably form the base of future discussions of the taxonomy and phylogeny of fossil brachiopods, and will also induce new studies on anatomical subjects.

As mentioned by WILLIAMS, the author has expressed deviating views on some points (p. 251, structure of the pseudopuncta = taleolae, and p. 281, affinities of *Christiania*). The arguments for the author's views are found above (pp. 9—13 and 37,195). In the description of the vascular system, WILLIAMS uses a different terminology, and material from many more groups than the author. Except for this the main difference between his opinion and that of WILLIAMS seem to be that the author attempts to follow the development of the ventral vascular system of the Orthacea back to more primitive stages than that of *Billingsella*.

Through comparison with modern forms WILLIAMS arrives to the conclusion that a periostracal pad united the valves, and acted as a ligament in many fossil brachiopods. The author arrived to the same conclusion by the study of the muscle impressions, and the growth-lines on the pseudodeltidium and the areas. The presence of a supra-apical foramen in connection with a pseudodeltidium might have something to do with this. The pseudodeltidium was generally found in connection with a strong periostracal pad, and in Strophomenids with a large functional pedicle, which increased in diameter as the animal

growed, the pedicle foramen increased in diameter by resorption of shell tissue. This resorption (observed i. a. in *Leptaena rhomboidalis*) was not radial, but eccentric, moving the centre of the foramen further into the ventral valve. This was probably due to the presence of the periostracal pad, which made growth in the opposite direction impossible or at least difficult. In these species the adult pedicle foramen also include the apical part of the delthyrium, and from the adult specimens alone, it is impossible to conclude if the foramen originally was supra-apical or apical. It is therefore possible that the supra-apical foramen in some groups is a secondary feature formed by directed resorption away from the delthyrium because of the presence of a strong periostracal pad. This might explain the presence of the supraapical foramen in the Nisusids, and perhaps other groups.

Even if the author disagees with WILLIAMS in some anatomical and taxonomic details, he wholeheatedly subscribe to the conclusions given by him, both as regards the anatomical interpretation of the morphological features, and their taxonomic importance.

3) COOPER, G. A. 1956: Chazyan and related Brachiopods. Smithsonian Misc. Coll. vol. *147*, pp. 1—1245, 269 pls. Washington.

This monumental work on the Middle Ordovician brachiopods of North America has immensely increased our knowledge of the Ordovician faunas. Because of its excellent figures, clear diagnoses of genera and species, complete stratigraphic data, and well arranged indexes it is also handy and easy to use in spite of its size.

A large number of new genera are named, and some of the species described by the author belong to them. *Diambonia* (?) *leifi* and *Leptelloidea* (s.l.) *rosendahli* belong to *Bilobia*, and *Eoplectodonta* (?) *karina* to *Anisopleurella*. It is possible that *Strophomena* (*Gunnarella*) *beta* and *delta* belong to *Bellimurina* and that *Leptaena minuta* KIÆR and *Leptaena* sp. (cf. pl. 7 fig. 13) belong to *Cyphomena*.

The number of genera which are common to the Middle Ordovician of North America and the Oslo Region is rather high, they are: *Paleostrophomena*, *Ptychoglyptus*, *Eoplectodonta*, *Leptellina*, *Bilobia*, *Anisopleurella*, *Sowerbyella*, *Christiania*, *Chonetoidea*, *Leptaena*, *Oepikina*, *Strophomena*, *Rafinesquina*, and possibly *Bellimurina* and *Cyphomena*.

Some of the species described by COOPER might be identical with some in this paper, or at least very nearly related to them. They are: *Bilobia hemisphaerica* COOPER (p. 760, pl. 193 D) is very like *B. rosendahli*, *Leptaena ordovicica* COOPER (p. 820, pl. 228 B) is very like *L. strandi*. *Eoplectodonta* (?) *dubia* COOPER (p. 810, pl. 209 C) is quite like *E. acuminata*, and *Christiania platys* COOPER (p. 861, pl. 210 D, 215 B, G) is quite like *C. holtedahli*. Further studies might also show identical or nearly related species in *Sowerbyella* and *Leptellina*.

The resemblance between the Norwegian and the North American strophomenid faunas is striking, and when the rest of the brachiopods are described, the number of common genera and species will certainly increase.

It is difficult to try a correlation based on one animal group only, and the

author will therefore only point out two remarkable features in the distribution of the strophomenids. The fauna in zone 4bα seem to correspond asthonishingly well to that found in the lower part of the Portersfield stage in the Appalachians, especially the Boutetort, Arline and Efna formations. The fauna found in the Coelosphaeridium beds in the Ringsaker district (and only here) seem to correspond to that found in the upper part of and just above the Wilderness stage, the Oranda, Rodman and Martinsburg formations.

Generally it is supposed that zone 4bα and the Coelosphaeridium beds are not very different in age (cf. STØRMER 1953, p. 113), and this problem has to be investigated.

The classification used by COOPER deviates sligthly from that used in this paper, especially in the higher units within the Plectambonitacea, but some of COOPERS new subfamilies have very brief diagnosis, and this classification has to be studied more in detail.

EXPLANATION TO PLATES

All photographs are unretouched. The specimens with preserved calcareous valves are marked *calc*. The casts are marked *cast*, and the artificial impressions, made of latex or plasteline are marked *impr*. If the casts are made by dissolving the valves in hydrochloric acid. *HCl* is added to *cast*.

If possible the name of the collector is given, according to the labels. The following abbreviations are used: *Hz*= professor A. Heintz, *Hm* = Dr. G. Henningsmoen, Sk = State Geologist S. Skjeseth, Sp = the author, St. = professor L. Størmer. These abbreviations are also used in STØRMER (1953, p. 40). Other abbreviations are: OH = professor O. Holtedahl, J K = professor J. Kiær, TS = Professor T. Strand.

PLATE 1.

Fig. 1. *Ptychoglyptus valdari.* sp. n. 66933. Ventral interior, impr. Railway section W. of Billingstad st., Asker district. zone 4ba. Coll. Sp. 1,3 5x.

Fig. 2. *Ptychoglyptus valdari* sp. n. 18853 HOLOTYPE. Dorsal interior, impr. Road section at Slependen, Asker district. zone 4ba, Coll. Hz. 1,45x

Fig. 3. *Ptychoglyptus valdari* sp. n. 56080. Exterior of dorsal valve, impr. Loc., Hor. and Coll. as fig. 2. 2,45x.

Fig. 4. *Grorudia* (?) *glabrata* sp. n. 66930, ventral interior, impr. Sentralinstituttet, Blindern, Oslo. Zone 4aβ—4ba (transition) Coll. Sp. 2,6x.

Fig. 5. *Alwynella osloensis* sp. n. 66940 HOLOTYPE. Dorsal interior and exterior, impr. E. of Tåsen st., Oslo. zone 4aβ. Coll. Sp. 4,1x

Fig. 6. *Alwynella ildjernensis* sp. n. 66928, HOLOTYPE, dorsal interior and exterior, impr. Northern side of Ildjernet, Nesodden, Oslo—Asker district. Zone 4aα_4. Coll. Sp. 3,8x.

Fig. 7. *Grorudia grorudi* sp. n. 66938, ventral interior, cast HCl. Vassholmen, near Snarøya, Bærum district, Zone 4aβ. Coll. Sp. 3,3x.

Fig. 8. *Grorudia* (?) *glabrata* sp. n. 66929 HOLOTYPE. Dorsal interior, impr. Sentralinstituttet, Blindern, Oslo. Zone 4aβ—4ba (transition) Coll. Sp. 2,1x.

Fig. 9. *Alwynella osloensis* sp. n. 69931, dorsal interior, impr. E. of Tåsen st. Oslo. Zone 4aβ. Coll. Sp. 3,8x.

Fig. 10. *Grorudia grorudi* sp. n. 66939 HOLOTYPE. Dorsal interior, impr. E. of Tåsen st. Oslo. Zone 4aβ. Coll. Sp. 4,0x.

Fig. 11. *Grorudia grorudi* sp. n. Dorsal interior, impr. Tørtberg, Oslo. Zone 4aβ. Coll. H.-F. Grorud. 4,0x.

Fig. 12. *Grorudia* (?) *glabrata* sp. n. 66941, ventral interior, small specimen, cast. Sentralinstituttet, Blindern, Oslo. Zone 4aβ—4ba (transition). Coll. Sp. 9,2x.

Fig. 13. *Paleostrophomena* (?) *majori* sp. n. 64790 HOLOTYPE, ventral interior, impr. Shore section between Gravestrand and Saltboden, Frierfjord, Langesund—Gjerpen district. Bryozoan beds (99—100 m up in the section). Coll. St and H. Major. 1,7x.

Fig. 14. *Alwynella osloensis* sp. n. 66934, ventral interior, impr. E. of Tåsen, Oslo. Zone 4aβ, Coll. Sp. 2,7x.

Fig. 15. *Alwynella intermedia* sp. n. 66935 HOLOTYPE, fragmentary dorsal valve, calc. North-eastern side of Ildjernet, Nesodden, Oslo—Asker district. Zone 4aβ—4aα_4 (transition). Coll. Sp. 4,2x.

Fig. 16. *Alwynella intermedia* sp. n. 66937, exterior of ventral valve, calc. Loc. Hor. and Coll. as fig. 15. 5,6x.

Fig. 17. Indet Strophomenid, nr. 3 36819, exterior, calc. Railway section just N. of Hamar, Hamar—Nes district. Zone 4aα_1 (just above 3c) Coll. TS, 2.9x.

Fig. 18. *Grorudia* (?) *glabrata* sp. n. 66936, fragment with sculpture, calc. Sentralinstituttet, Blindern, Oslo. Zone 4aβ—4ba (transition) Coll. Sp. 7,8x.
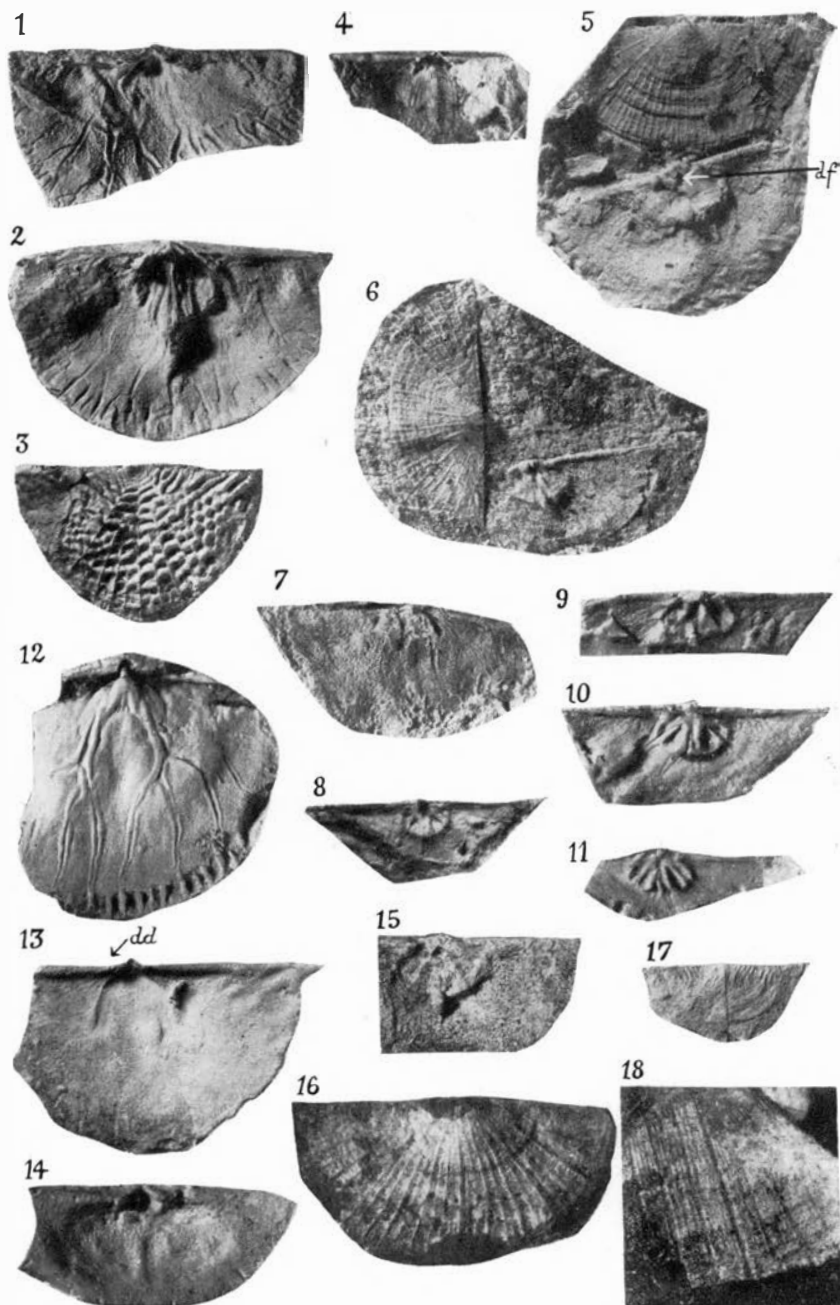
PLATE 1

PLATE 2.

Figs. 1, 2. *Leangella hamari* sp. n. 37879, dorsal and ventral view of HOLOTYPE calc. Slightly etceded with dilute hydrochloric acid to show the interior. Cyclocrinus Shale, Furuberget, Hamar—Nes district. Coll. OH 1907. 4,5x.

Fig. 3. *Leangella hamari* sp. n. 66983 Dorsal interior, cast HCl Hor. Loc. and coll. as above .2,5x.

Figs. 4, 5. *Leptelloidea* (s. l.) *rosendahli* sp. n. 66984 HOLOTYPE Dorsal and ventral wiew of interior cast. Brummundal, Ringsaker district. Coll. H. Rosendahl. 3x.

Fig. 6. *Diambonia anatoli* sp. n. 66985 HOLOTYPE, dorsal interior, cast. Road section just N. of Halsen, Nesøya, Asker district, Zone 4b*a*. Coll. Sp. 3,6x.

Figs. 7, 8. *Diambonia anatoli* sp. n. 66986 and 66987, ventral interiors, casts, showing median septum (ms). Loc. Hor. and Coll. as above. 3,6x.

Figs. 9, 11. *Diambonia* (?) *leifi* sp. n. 64785, dorsal and ventral wiew of complete specimen, impr. 99—100 up in the section between Gravestrand and Skjelbukten, Langesund—Gjerpen District. Coll. H. Major & St. 5,3x.

Fig. 10. *Diambonia* (?) *leifi*, sp. n. 57536. Dorsal interior, cast. HOLOTYPE. Just N. of Stranda, Frierfjord, Langesund—Gjerpen district. Mastopora beds. Coll. St. 5,3x.

Fig. 12. *Chonetoidea gamma* sp. n. 66988 HOLOTYPE, dorsal interior, cast. Blakstad Road Junction, Asker district, zone 4b*γ*, coll. Sp. 4,5x.

Fig. 13. *Chonetoidea gamma* sp. n. 66989 dorsal interior, cast, showing badly defined branchial arcs, and some large spines outside them. Loc., Hor. and coll. as above. 4,5x.

Fig. 14. *Chonetoidea iduna* ÖPIK. 66966, dorsal interior, cast. Billingstad Asker district, zone 4 c*a*. Coll. Sp. 4,5x.

Figs. 15—16. *Sampo* (*Sampo*) *indentata* sp. n. 66990 and 66991. Dorsal interiors, impr. Railway section N. of Hvalstad st., Asker district, zone 4b*γ*, Coll. Sp. 3,1x.

Fig. 17. *Sampo* (*Leptellina*) *oepiki* (WHITTINGTON). 66993. ventral interior, cast. Coelosphaeridium beds, Ringsaker. Coll. Sk, 2,4x.

Fig. 18. *Sampo* (*Leptellina*) *oepiki* (WHITTINGTON), 66992. Dorsal interior, cast, S. end of Nakholmen, beside the large syenite dike. Oslo district. Zone 4b*a*, Coll. Sp. 5,3x.

Fig. 19. *Sampo* (*Leptellina*) *oepiki* (WHITTINGTON) 57733. Dorsal interior, impr. At 5. telephone pole S. of the curve S. of Ruden, Hadeland. Zone 4b*a*-*β*. Coll. TS. 2,2x.

Fig. 20. *Chonetoidea alpha* sp. n. 67027, HOLOTYPE, dorsal interior, cast. Above the second tunnel W of Billingstad st. Asker district. Zone 4b*a*, Coll. Sp. 6,2x.

Figs. 21—22. *Chonetoidea alpha* sp. n. 67028 and 67029. Ventral interiors showing ventral cavities (vc) Loc., Hor. and coll. as above. 6,2x.
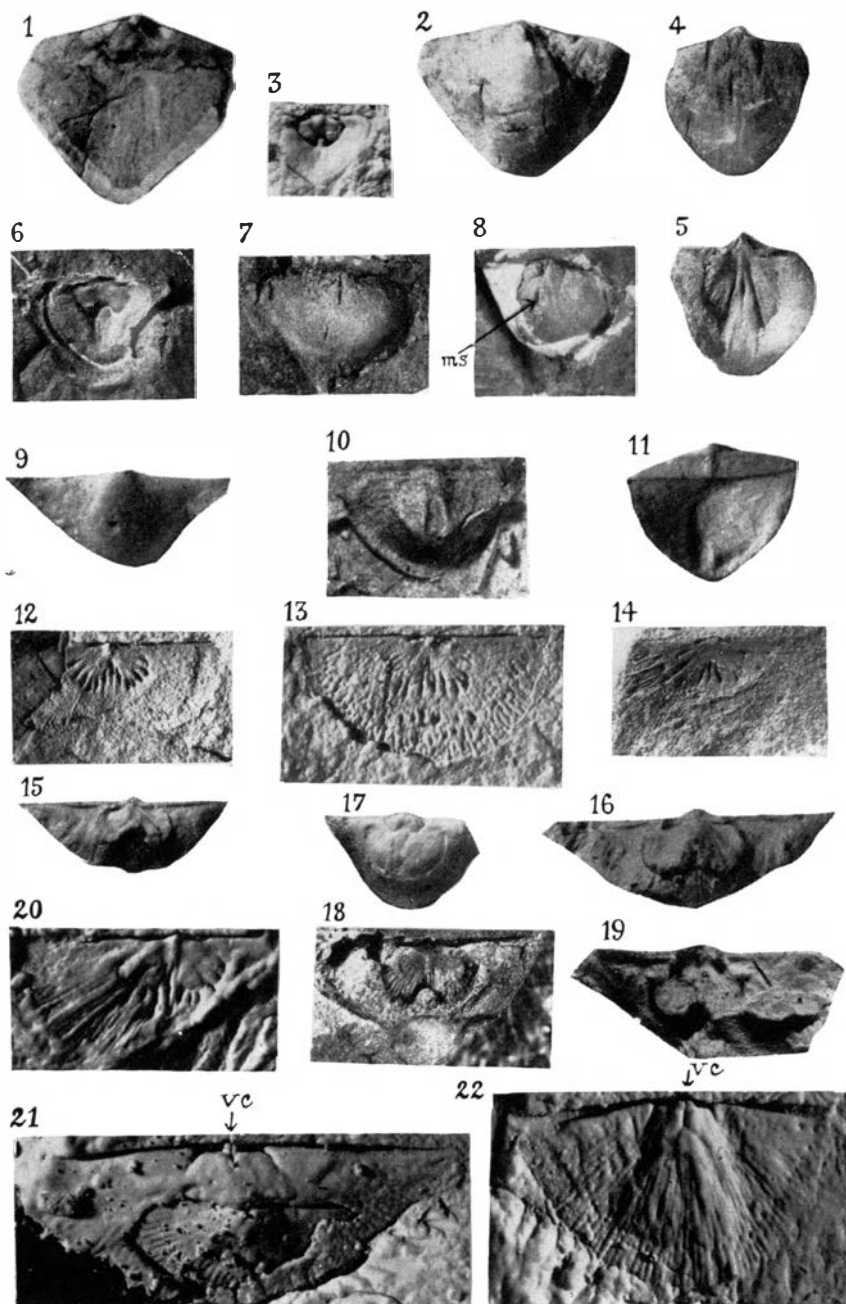
PLATE 2

PLATE 3.

Fig. 1. *Sowerbyella sericea soudleyensis* JONES. L. 85, larval dorsal interior, impr. Bergsvika, Helgøya, Hamar—Nes district, Cyclocrinus beds. Coll. OH. Cf. HOLTEDAHL 1916, pl. XIV, fig. 3. 12x.

Figs. 2—3. *Sowerbyella sericea soudleyensis* JONES, 66977 Ventral interior and exterior of larval valves, impr. Stavsberget, Helgøya, Hamar—Nes, district, Coll. JK 12x.

Fig. 4. *Sowerbyella sericea soudleyensis* JONES. L. 85, dorsal interior of an adult specimen. impr. Hor. Loc. and Coll. as in fig. 1. 2,8x.

Fig. 5. *Eoplectodonta karina* sp. n. 66978 HOLOTYPE. Dorsal interior, calc. SE. end of Nakholmen, Oslo district. Zone 4b*a*, Coll. Sp. 5,5x.

Fig. 6. *Eoplectodonta acuminata* (HOLTEDAHL) 66979, Ventral interior, cast, showing denticulation (d.). Southern end of Nakholmen, Oslo district. Zone 4b*a*, Coll. Sp. 5,5x.

Fig. 7. *Eoplectodonta acuminata* (HOLTEDAHL) 66980. Dorsal interior, impr. Loc., Hor. and Coll. as fig. 6. 2,9x.

Fig. 8. *Eoplectodonta acuminata* (HOLTEDAHL) 66981. Showing corrugations on the exterior of the dorsal valve, and the areas. Loc., Hor. and Coll. as fig. 6. 7x.

Fig. 9. *Eoplectodonta acuminata* (HOLTEDAHL) 66982. Ventral interior, impr. showing ciliar groves (Cg). Vesleseter, Sjåstad district. Zone 4b*a*. Coll. St. 3,5x.

Fig. 10. *Eoplectodonta acuminata* (HOLTEDAHL) 19025, Dorsal interior, impr. Royal Palace, Oslo. Zone 4b*a*. Old collection. 3,5x.

Fig. 11. *Eoplectodonta acuminata* (HOLTEDAHL) 5279, LECTOTYPE. Exterior of dorsal valve and areas. Loc., Hor. and coll. as fig. 10. 3,5x.

Fig. 12. *Eoplectodonta acuminata* (HOLTEDAHL) 5278, Ventral interior, impr. Loc., Hor. and Coll. as in fig. 10. 3,5x.
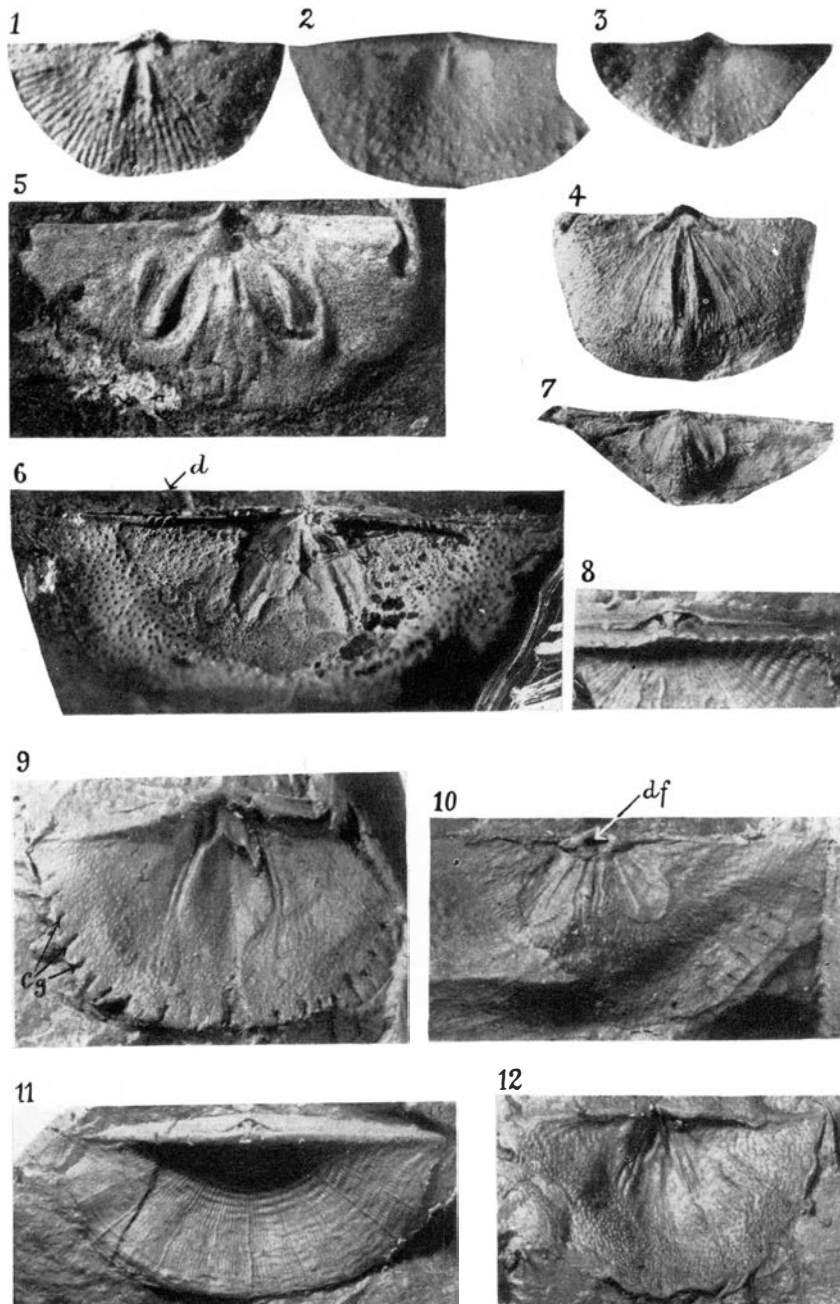
PLATE 3

PLATE 4.

Fig. 1. *Sowerbyella sericea hadelandica* subsp. n. 67138 HOLOTYPE. Ventral exterior calc. From the lower Cyclocrinus beds in a section between Jonsrud and Stensrud in the northern part of Hadeland. Coll. TS. 2,8x.

Figs. 2—3. *Eoplectodonta* (?) *rhombica* (MCCOY) 64371. Two different wievs of a ventral interior, cast HCl, showing the denticulated hinge-line. From zone 4bδ at Vestern—Grindvoll, Hadeland district. Coll. St. & Hm. 1,35x.

Fig. 4. *Leptestia* (?) *jukesi* (DAV.) 8682. Ventral interior, cast, from the Bryozoan zone at Skjælbugten, Langesund—Gjerpen district. Coll. W. C. Brøgger 1881. 1,35x.

Fig. 5. *Leptelloidea* (s. 1.) 66634. Fragmentary dorsal interior (impr.) from the transitional beds between zone 4aα$_4$ and 4aβ at Muggerudkleiva, Eiker—Sandsvær district. Coll. St. Hz. Hm. Sp. 1,9x.

Fig. 6. *Sampo* (*Leptellina*) *oepiki* (WHITTINGTON) 57733, Ventral interior cast, showing the vascular system. From zone 4bα—β at 5. telephone pole S. of the curve S. of Ruden, Hadeland district. Coll. TS. 5,5x.

Fig. 7. *Sowerbyella sericea hadelandica* subsp. n. 67134. Dorsal interior, cast, from the lower Cyclocrinus beds in a section between Jonsrud and Stensrud in the northern part of Hadeland. Coll. TS, 2,8x.

Fig. 8. *Sampo* (*Sampo*) *indentata* sp. n. 67135. HOLOTYPE. Ventral interior, cast, HCl, showing vascular system. From zone 4bγ in a railway section W. of Billingstad, Asker district. Coll. Sp. 5,5x.

Fig. 9. *Eoplectodonta* (?) *percedens* (HOLTEDAHL). 67137. Ventral interior, cast HCl, showing the denticulated hinge-line. From zone 4bβ at Blakstad brygge, Asker district. Coll. Sp. 3,7x.

Fig. 10. *Leptelloidea* (*Benignites*?) *heintzi* sp. n. 66651. HOLOTYPE. Ventral interior, cast, from zone 4aα$_3$ at Ravaldsjøelven, Eiker—Sandsvær district, Coll. St, Hz, Hm, Sp. 2,9x.

Fig. 11. *Leptelloidea* (*Benignites*?) *heintzi* sp. n. 66651. Smaller ventral interior from the same piece of rock as the holotype. 2,8x.
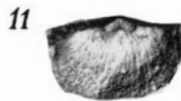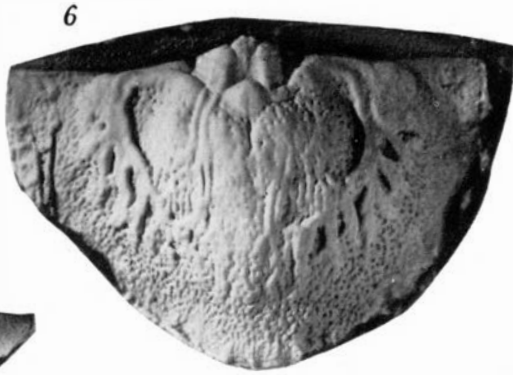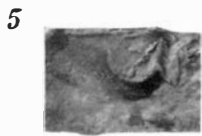
PLATE 4

PLATE 5.

Figs. 1—9. *Christiania holtedahli* sp. n., a series of larval and young valves from zone 4bα at Blakstad Road Junction, Asker district. *1,6* (66942, 66947) Dorsal exteriors, impr. 3,3x. *2,5* (66943, 66946) Dorsal interiors in which the cardinal processes are not differentiated from the socket plates. 3,3x. *3* (66944) ventral interior, 1,8x. *4.* (66945) Dorsal interior with cardinal processes well differentiated. 1,8x. *9* (66950) Dorsal interior of young adult specimen, 1,8x. *7* (66948) Dorsal exterior with growth-lines, cast. 5x. *8* (66949) Smallest dorsal interior 5x. cast. Coll. Sp.

Figs. 10—11. *Christiania holtedahli* sp. n. L144, HOLOTYPE. Two different aspects of the same ventral interior, showing vascular markings and intervascular septa. Bratterud, Ringerike, zone 4bα—β. cast. The specimen was also figured by HOLTEDAHL 1916, pl. XVI, fig. 7. 1,8x. Coll. JK.

Fig. 12. *Christiania elongata* sp. n. 66967 HOLOTYPE Interior of both valves, showing the dorsal side, cast. Sentralinstituttet, Blindern, Oslo district. Zone 4aβ—4bα. 1,8x. Coll. Sp.

Fig. 13. *Christiania* cf. *oblonga* (PANDER) 66968, Specimen with partly exfoliaated ventral valve, showing the dorsal interior. Calc. S. of Vassholmen, Snarøya, Oslo district, zone 4aβ. 1,5x. Coll. Sp.

Fig. 14. *Christiania oblonga* (PANDER), 60368 Fragmentary ventral interior, cast. Muggerudkleiva, Eiker—Sandsvær district. Zone $4a\alpha_{1-2}$. 1,8x. Coll. St.

Fig. 15. *Christiania holtedahli* sp. n. 66969. Dorsal interior, calc. of a large specimen. Arnestadtangen, Asker district. Zone 4bα Coll. Sp. 2,4x.

Fig. 16. *Christiania holtedahli* sp. n. 66970. Ventral interior with distinct pseudopuncta and intervascular septa. cast. Brattberg, Ringsaker, Coelosphaeridium beds. 1,25x. Coll. Sk.

Figs. 17—22. *Christiania oblonga* (PANDER), 66971—66976, a series of dorsal interiors, calc. from Popowka near Leningrad. Probably from zone C1, or slightly lower. *17—18.* Two valves in different views, 6x. *19—22.* Four different types of cardinal processes found in this species. 13x. Those shown in figs. *19, 22* are the common ones.
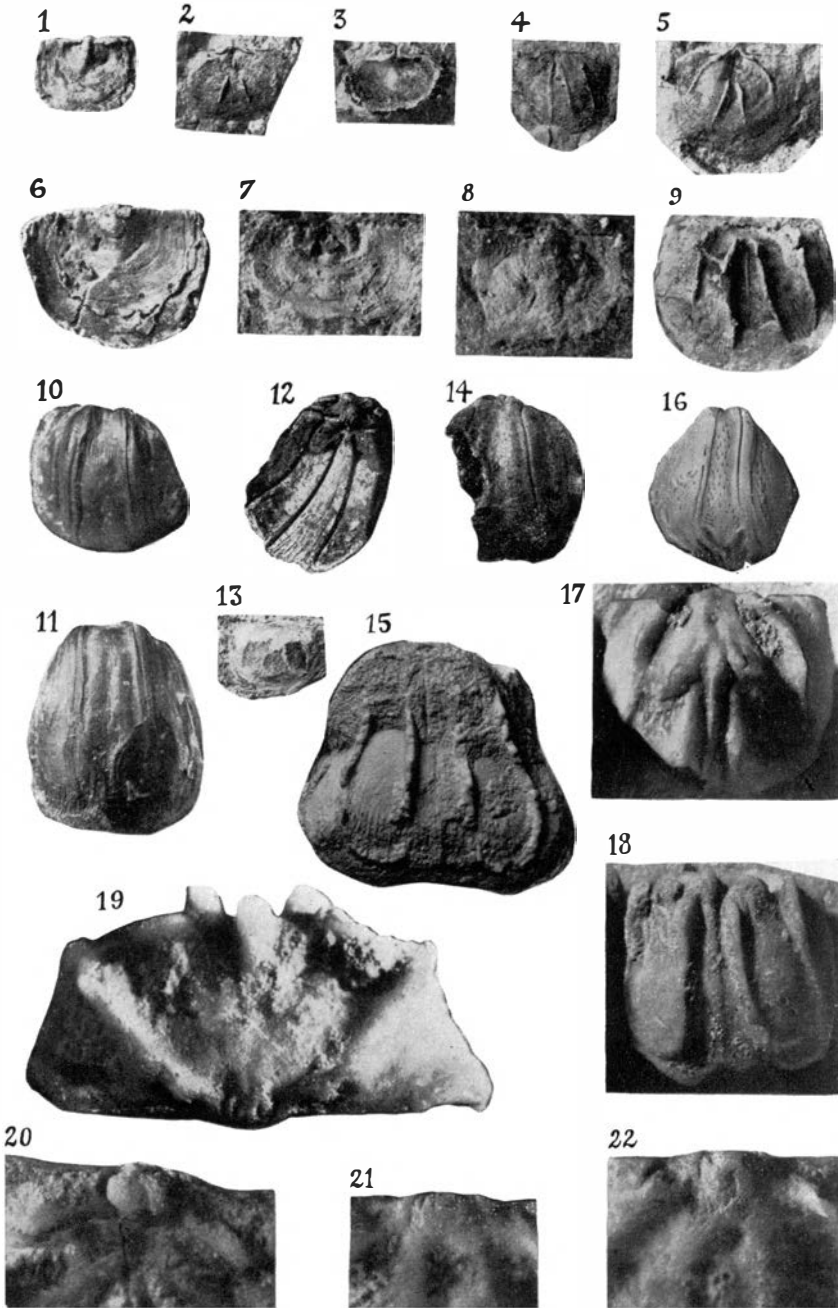
PLATE 5

PLATE 6.

Figs. 1—2. *Sowerbyella ringsakerensis* sp. n. 66952 and 66951. Dorsal interiors of young specimens, impr. Bratberg, Ringsaker, Coelosphaeridium zone. 2,7x. Coll. Sk.

Fig. 3. *Sowerbyella ringsakerensis* sp. n. 66951 HOLOTYPE. Dorsal interior, impr. Loc. Hor. and Coll. as figs. 1—2. 2,7x.

Fig. 4. *Sowerbyella ringsakerensis* sp. n. 66953. Ventral interior of highly gerontic specimens, cast. Hor., Loc. and Coll. as fig. 1—2. 4x.

Fig. 5. *Sowerbyella sericea askerensis* subsp. n. 66954 HOLOTYPE. Ventral interior, cast. Railway section N. of Hvalstad st., Asker district. Zone 4bγ. Coll. Sp. 4x.

Fig. 6. *Sowerbyella sericea soudleyensis* JONES, 66977. Detail of ventral interior, impr., showing muscle impressions and ventral cavities (vc). Stavsberget Helgøya, Hamar—Nes district, Cyclocrinus Beds. Coll. JK. 11,5x.

Fig. 7. *Eoplectodonta* (?) *percedens* (HOLTEDAHL), L132, LECTOTYPE. Exterior of ventral valve. calc. Bratterud, Ringerike. Zone 4b (α—β). Coll. JK. impr. 1,85x.

Figs. 8—9. *Christiania* cf. *holtedahli* sp. n. 66955. Ventral interior of pathological (?) specimen. Gomnes—Rud, Ringerike, zone 4ba. Coll. JK. 2,8x.

Fig. 10. *Christiania holtedahli* sp. n. 66956. Dorsal interior (impr.) of large specimen. Vesleseter, Sjåstad district. Zone 4ba. Coll. St. 2,3x.

Figs. 11—12. *Sampo* (*Leptellina*) *elevata* sp. n. 7513, HOLOTYPE. Ventral interior, cast. Gomnes—Rud. Ringerike. Zone 4ba. Coll. JK. 2,8x.

Fig. 13. *Mjoesina* cf. *mjoesensis* (HOLTEDAHL), 66957. Ventral interior, impr. of a specimen which resemble the typical form. Bratberg, Ringsaker, Coelosphaeridium Beds. Coll. Sk. 1,5x.

Fig. 14. *Christiania oblonga* (PANDER), 60368. Exterior and interior of dorsal valves, impr. Muggerudkleiva, Sandsvær—Eiker district. Zone 4a$a_{1\text{-}2}$. Coll. St. 1,8x.

Fig. 15. *Leptaena strandi* sp. n. 57837, HOLOTYPE, Ventral interior, cast. Road section between Jonsrud and Stensrud, Hadeland. Zone 4ba—β. Coll. TS, 2,5x.

PLATE 6

1   2   5

3   4

6   *vc*

8   X

11

9   7   12

10   13

14   15
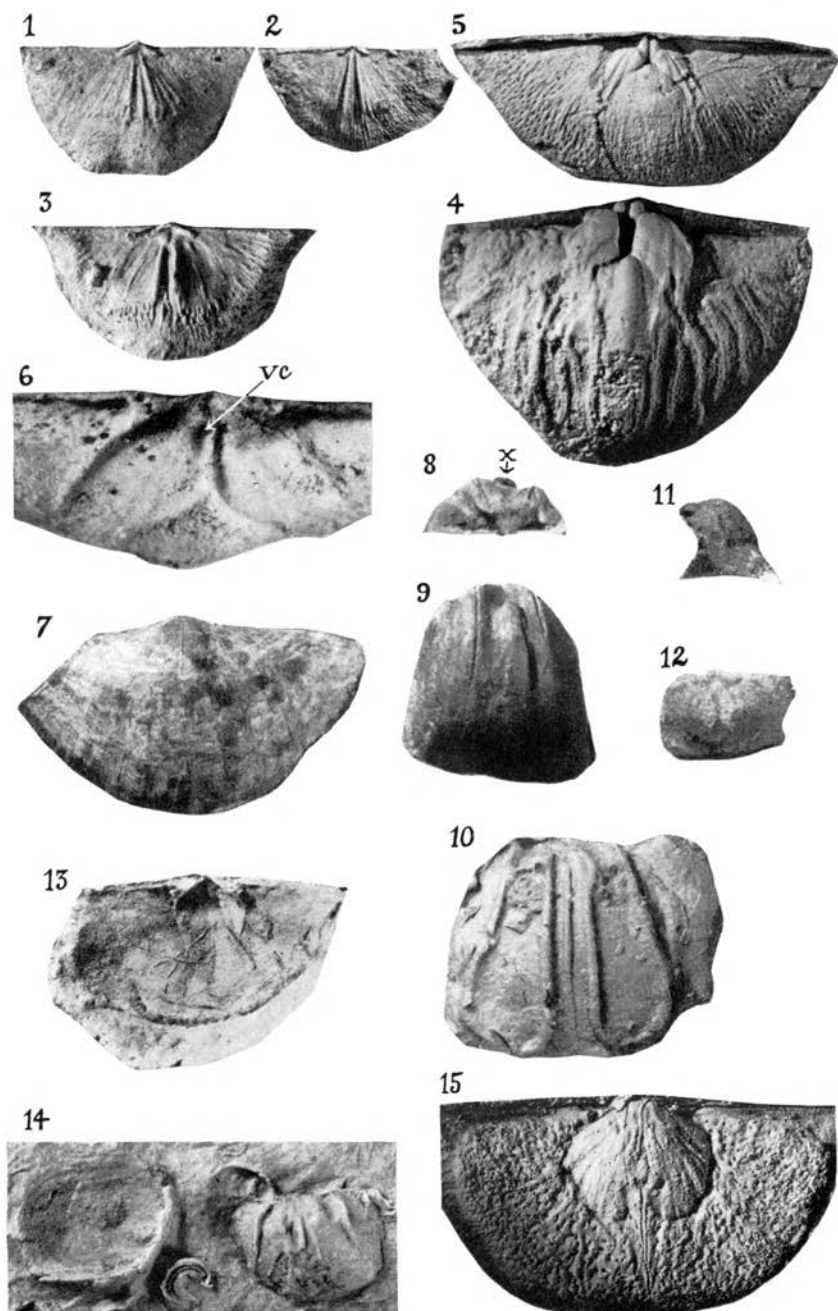
PLATE 7.

Figs. 1—2. *Leptaena rugosa* DALMAN. Br. 10441 and Br. 10420. Ventral interiors, cast. Ålleberg, Vestergötland, Sweden. Dalmanitina-zone. Coll. unknown. 1,1x.

Fig. 3. *Leptaena emarginata* (BARRANDE) Br. 32644. Ventral interior showing pedicle foramen (pf) and outline of muscle impressions (dark). calc. Visby, Gotland, Sweden. Silurian, probably upper Llandovery or lower Wenlock. Coll. unknown. 1,1x.

Fig. 4. *Leptaena rugosa* DALMAN, Br. 10435 LECTOTYPE. Dorsal exterior, cast. Fårdalaberg, Vestergötland, Sweden. Dalmanitina-zone. Coll. Dalman 1827. 1,1x.

Fig. 5. *Kjerulfina foliovalve* sp. n. 66958. Dorsal interior, impr. showing the pedicle (?) groove in a young specimen (pg). Railway section N. of Hvalstad st. Asker district. Zone 4bγ. Coll. Sp. 3,2x.

Figs. 6, 8. *Leptaena minuta* KIÆR. 66959. Dorsal and ventral interiors, cast. Tønnerudodden, Hadeland. Sphaeronid Limestone. Coll. JK. 2,5x.

Fig. 7. *Leptaena minuta* KIÆR. 34716. LECTOTYPE. Exterior of dorsal valve, calc. Tønnerudodden, Hadeland. Sphaeronid Limestone. Coll. JK. 2,5x.

Fig. 9. *Leptaena* sp. Br. 32218. Fragmentary dorsal interior (calc.) showing the details of the muscle impressions. Eksta Djupvik, Gotland, Sweden. Wenlock. Coll. unknown, 1,6x.

Figs. 10—12. *Kiaeromena* cf. *juvenilis* (ÖPIK) 66960 and 66961. Dorsal and ventral interior and ventral exterior of the same specimen (cast HCl). Bratberg, Ringsaker, Coelosphaeridium Beds. Coll. Hm. 1x.

Fig. 13. *Leptaena* sp. 66962. Dorsal interior, impr. Bratberg, Ringsaker, lowest part of Coelosphaeridium beds. Coll. Sk. 1,75x.

Fig. 14. *Kiaeromena kjerulfi* (HOLTEDAHL) 66963, Small, complete specimen, calc. Ildjernet, Nesodden. Oslo district. Zone 4bβ. Coll. Sp. 1x.

Fig. 15. *Leptaena depressa* (SOW.) Br. 32215. Ventral interior (calc.) showing structure of teeth (d) and ventral muscle impressions. Eksta Djupvik, Gotland Sweden. Coll. unknown. 4x.

Fig. 16. *Kiaeromena kjerulfi* (HOLTEDAHL) 66964. Fragment showing healed fracture (z) in the valve (cast). Lindøya, Oslo district. Zone 4bβ. Coll. Sp. 6x.

Fig. 17. *Kiaeromena juvenilis* (ÖPIK) 66965. Dorsal interior (calc.) showing chilidium (ch) with slight fold. Kukruse, Esthonia. Zone C2a. Coll. A. ÖPIK 5x.

The specimens with Br-numbers, belong to the Swedish State Museum of Natural History, Dept. of Paleozoology, Stockholm, Sweden.
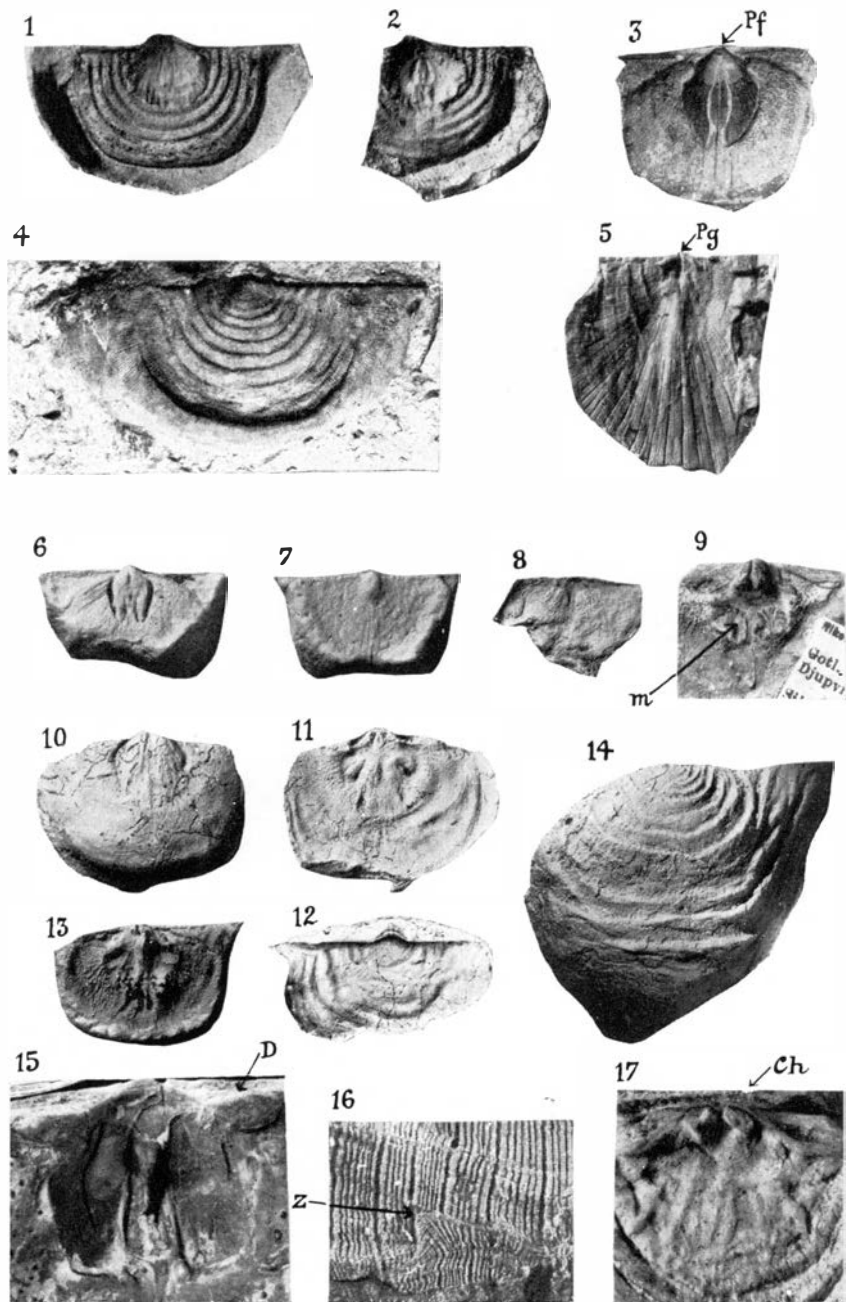
PLATE 7

PLATE 8.

Fig. 1. *Rafinesquina* (*Hedstroemina*) aff. *robusta* (BANCROFT), 66998, Fragmentary dorsal interior (impr.). Brummundal, Ringsaker district. Coelosphaeridium zone. 1,35x. Coll. H. Rosendahl.

Figs. 2—4. *Rafinesquina* (*Hedstroemina*) aff. *robusta* (BANCROFT). 66999. Ventral (2) and dorsal interiors (impr.) Loc., Hor. and Coll. as in fig. 1. 2x.

Fig. 5. *Rafinesquina* (*Hedstroemina*) cf. *robusta* (BANCROFT) 66995, Ventral interior, impr. Bruflaten, Veldre (boulder). Coelosphaeridium zone. Coll. Sp. 1,3x.

Fig. 6. *Mjoesina mjoesensis* (HOLTEDAHL) 67001, Ventral interior, cast. Furuberget, Hamar—Nes district. Cyclocrinus-beds. Coll. OH. 2,4x.

Fig. 7. *Mjoesina* cf. *mjoesensis* (HOLTEDAHL) 67002, Ventral interior, cast. Brattberg, Ringsaker district. Coelosphaeridium-beds. Coll. Sk. 1,8x.

Fig. 8. *Rafinesquina* (*Rafinesquina*) sp. 67003, Ventral interior, cast. Brattberg, Ringsaker district. Coelosphaeridium-beds. Coll. Sk. 1,3x.

Fig. 9. *Rafinesquina* (*Hedstroemina*) *ungula*, 7835, Exterior of ventral valve, calc. Vestbråten, Ringerike, Zone 4bγ, Coll. JK. 1x.

Fig. 10. *Rafinesquina* (*Hedstroemina*) *ungula* sp. n. 7834 HOLOTYPE. Ventral interior, cast. Vestbråten, Ringerike. Zone 4bγ. Coll. JK. 1x.

Fig. 11. *Rafinesquina* (*Hedstroemina*) *ungula* sp. n. 67000 Dorsal interior, cast. Vestbråten, Ringerike. Zone 4bγ. Coll. JK. 1x.

Fig. 12. *Mjoesina gregaria* sp. n. 66994, Dorsal exterior, cast. Sund, Einavatn, Toten. Coelosphaeridium Beds. Coll. N. Heintz & Sk. 1x.

Fig. 13. *Mjoesina gregaria* sp. n. 66996, HOLOTYPE. Ventral interior, cast. Sund, Einavatn, Toten. Coelosphaeridium Beds. Coll. N. Heintz & Sk. 1x.

Fig. 14. *Rafinesquina* (*Hedstroemina*) *holtedahli* sp. n. 66997, HOLOTYPE. Ventral interior. Røyselandet, Ringerike. Zone 4ba-β. Coll. JK. 1,8x.
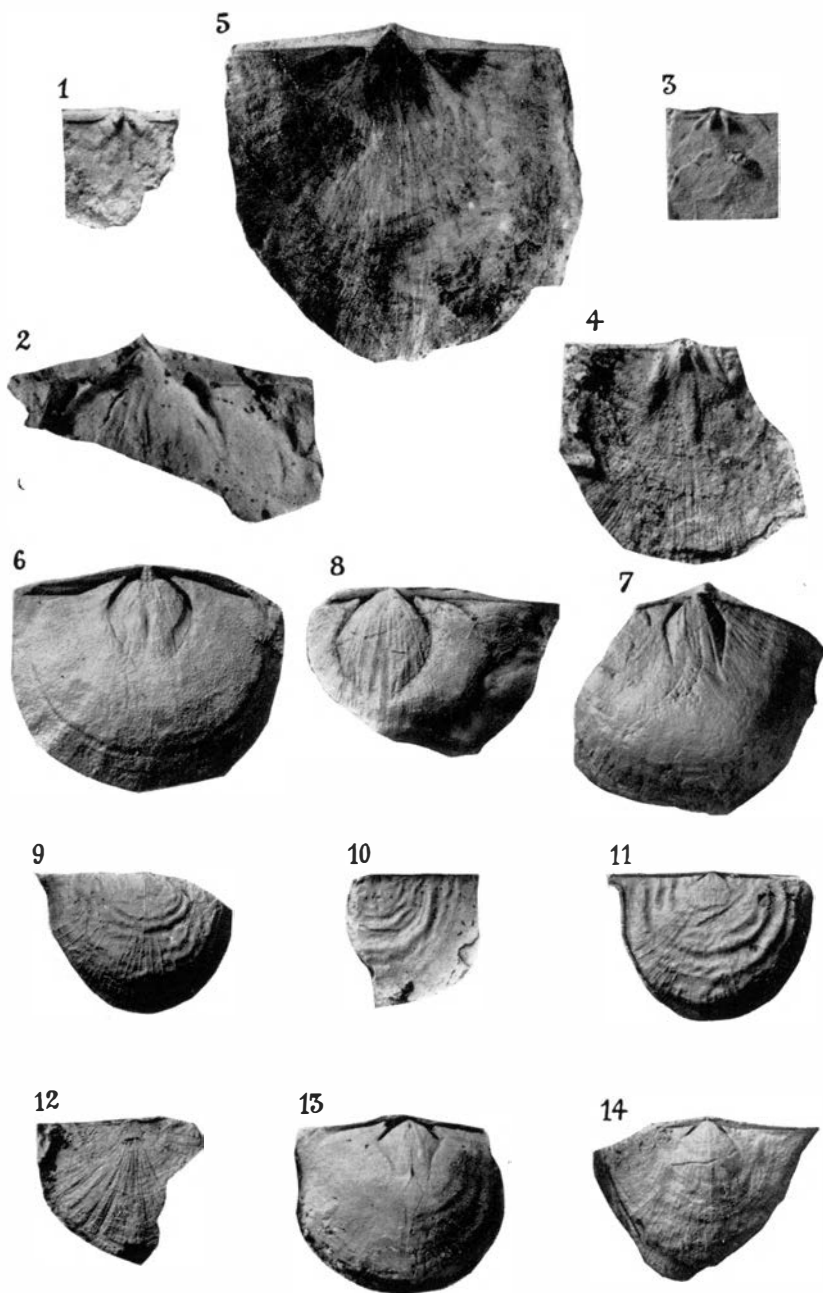
PLATE 8

PLATE 9.

Fig. 1. *Kjerulfina foliovalve* sp. n. 67004, HOLOTYPE. Dorsal interior, impr.
Railway section N. of Hvalstad St., Asker district. Zone 4bγ. Coll. Sp.
1,25x.

Figs. 2—3. *Kjerulfine foliovalve* sp. n. 67005 and 67006. Dorsal interiors, impr.
Loc., Hor. and Coll. as in fig. 1. 1,25x.

Fig. 4. *Kjerulfina limbata* sp. n. 67011, HOLOTYPE. Ventral interior, cast.
Vestbråten, Ringerike. Zone 4bγ. Coll. St. 1,25x.

Fig. 5. *Kjerulfina foliovalve* sp. n. 67007. Dorsal exterior of larval valve.
cast. Loc., Hor. and Coll. as in fig. 1. 8,8x.

Fig. 6. *Kjerulfina orta* (ÖPIK), 67144. Ventral interior. calc. Kukruse, Esthonia.
Zone C2. Coll. A. Öpik. 1,25x.

Fig. 7. Indet Strophomenid nr. 1. 67010. Fragmentary dorsal interior, impr.
Lauervann, Eiker—Sandsvær district. Coll. Hz. 1,6x.

Fig. 8. *Kjerulfina foliovalve* sp. n. 67009. Dorsal interior and exterior, impr.
Loc., Hor. and Coll. as in fig. 1. 1,25x.

Fig. 9. *Kjerulfina limbata* sp. n. 67012. Dorsal interior, impr. Loc., Hor. and
Coll. as in fig. 4. 1,35x.

Fig. 10. *Kjerulfina limbata* sp. n. 67008. Somewhat atypical ventral interior,
impr. Loc., Hor. and Coll. as in fig. 4. 1,35x.

Fig. 11. *Strophomena* sp. 9330. Dorsal exterior, calc. Frognøya, Ringerike.
Zone 4bδ$_2$, zone of *Tretaspis kiaeri*. Coll. JK. 1,7x.

Fig. 12. *Strophomena (Gunnarella) beta* sp. n. 55427. HOLOTYPE. Complete
specimen with partly exfoliated ventral valve, calc. Bratterud, Ringe-
rike. Zone 4bβ. Coll. JK. 0,85x.

Fig. 13. *Oslomena* (?) *papillio* sp. n. 38184. Exterior of ventral valve, impr.
Road between Sund and Eksberget, Toten. Cyclocrinus-beds ?. Coll.
JK. 2,2x.

Fig. 14. *Oslomena* (?) *papilio* sp. n. 38184. HOLOTYPE. Dorsal interior, impr.
Loc., Hor. and Coll. as in fig. 13. 2,2x.

Fig. 15. *Oslomena* (?) *papilio* sp. n. 38138. Ventral interior, impr. Loc., Hor.
and coll. as in fig. 13. 2,2x.

Fig. 16. *Strophomena (Gunnarella)* cf. *rigida* (BARRANDE) 9330. Dorsal (?)
exteriors calc. Loc., Hor. and Coll. as in fig. 11. 1,7x.
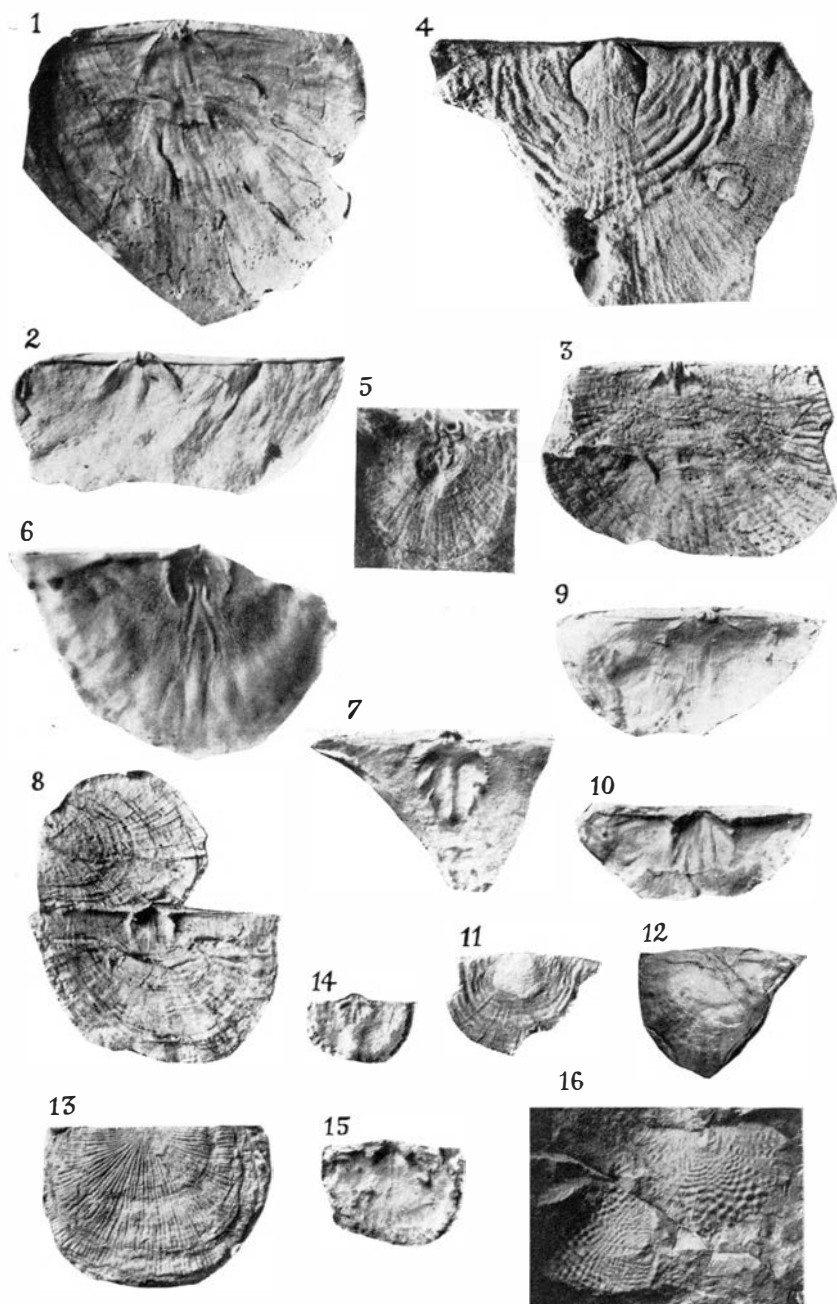
PLATE 9

PLATE 10.

Figs. 1—2. *Kiaeromena kjerulfi* (HOLTEDAHL) 67014. Dorsal and ventral interior, cast. Lindøya, Oslo district. Zone 4bβ. Coll. T. Kjerulf. 1,5x.

Fig. 3. *Kiaeromena kjerulfi* (HOLTEDAHL), 66964. Ventral interior, cast. Loc. and Hor. as in fig. 1—2. Coll. Sp. 0,85x.

Fig. 4. *Leptaena strandi* sp. n. 67018. Ventral interior, cast. Gomnes—Rud, Ringerike district. 2,8x. Zone 4ba, upper part. Coll. JK.

Fig. 5. *Leptaena strandi* sp. n. 67019. HOLOTYPE. Ventral interior, cast. Railway section W. of Billingstad st. Asker district. Zone 4bγ. Coll. Sp. 2,2x.

Fig. 6. *Leptaena veldrensis* sp, n. 67017. HOLOTYPE. Ventral interior, cast. Brattberg, Ringerike district. Coelosphaeridium beds. Coll. Sk. 3 ⋎.

Figs. 7—8. *Leptaena veldrensis* sp. n. 67015. Dorsal interiors, impr. Loc., Hor. and Coll. as in fig. 6. 1,75x.

Fig. 9. *Leptaena ennessbe* sp. n. 67016. HOLOTYPE. Ventral interior, cast. Railway section W. of Billingstad st. Asker district. Zone 4ba. Coll. Sp. 2,7x.

Fig. 10. *Leptaena* (?) *indigena* sp. n. 37455. Dorsal interior, impr. Fangberget, Ringsaker district. Coelosphaeridium-beds. Coll. Braastad. 1,1x.

Fig. 11. *Leptaena* (?) *indigena* sp. n. 67013. HOLOTYPE. Ventral interior, impr. Brattberg, Ringsaker district. Coelosphaeridium-beds. Coll. Hm. 1,1x.
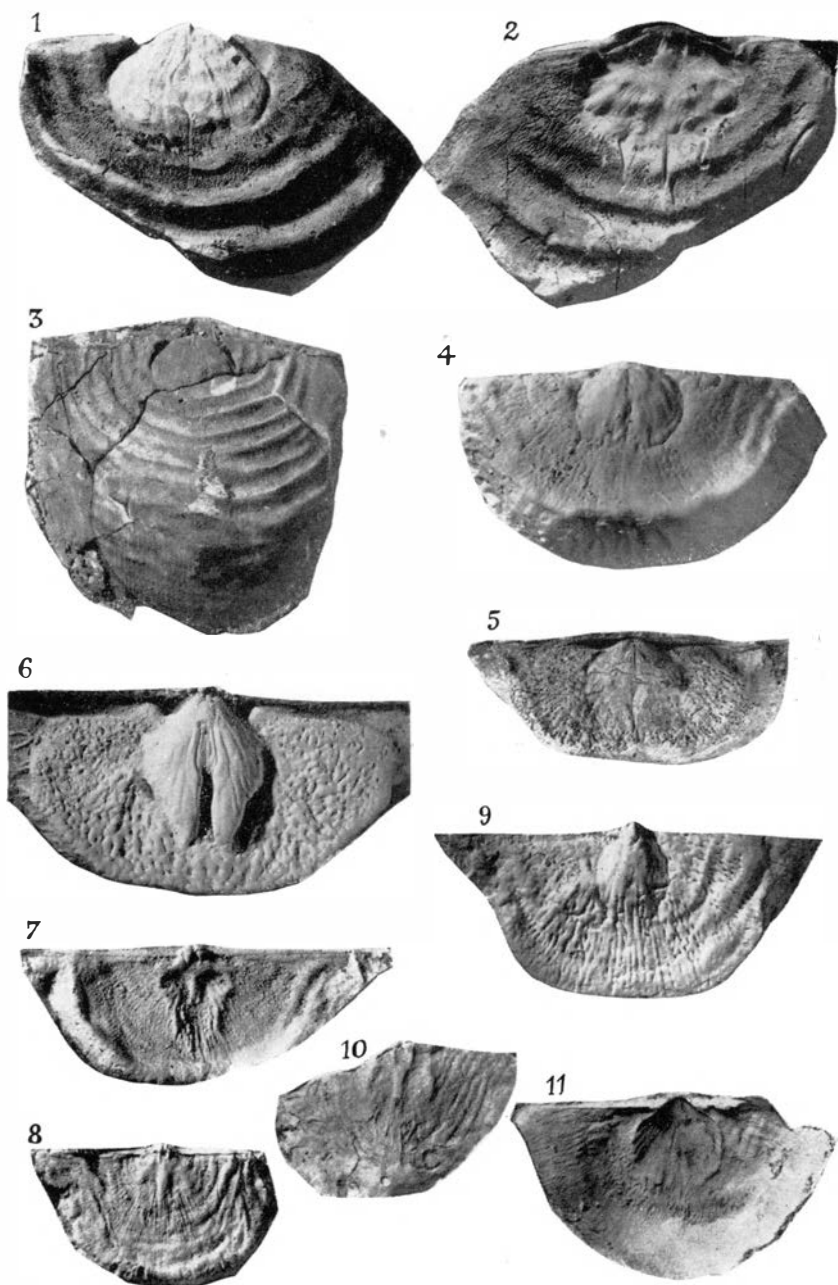
PLATE 10

PLATE 11.

Fig. 1. *Strophomena norvegica* sp. n. 7117, HOLOTYPE. Dorsal interior, impr. W. side of Røysetangen, Ringerike district. Zone 4ba. Coll. J.K. 1,8x.

Fig. 2—3. *Strophomena norvegica* sp. n. 7117 and 67020. Ventral interiors, and exterior of areas impr. Loc., Hor. and Coll. as in fig. 1. 1,8x.

Fig. 4. *Kjerulfina lata* sp. n. 21965. Exterior of ventral valve, impr. Furu-berget, Hamar—Nes district. Coelosphaeridium-beds. Coll. OH. 2x.

Fig. 5. *Strophomena (Gunnarella ?) alpha* sp. n. 67021. HOLOTYPE. Ventral interior, impr. Railway section W. of Billingstad st. Asker district. Zone 4ba. Coll. Sp. 1,5x.

Fig. 6. *Strophomena (Gunnarella ?) alpha* sp. n. 67023. Ventral exterior, impr. Loc., Hor. and Coll. as in fig. 5, 1,5x.

Fig. 7. *Kjerulfina lata* sp. n. 21967. HOLOTYPE. Ventral interior, impr. Loc., Hor. and Coll. as in fig. 4. 2x.

Fig. 8. *Kjerulfina* sp. 67024. Ventral interior, impr. 99—100 m in the section between Gravestrand and Skjælbugten, Frierfjord, Langesund —Gjer-pen district. Mastopora zone. Coll. Major & St. 1,5x.

Fig. 9. *Strophomena hirsuta* ? sp. n. 38040. Dorsal interior, impr. possibly belonging to this species, or a young specimen of *S. steinari*. Fang-berget, Ringsaker district. Coelosphaeridium-beds. Coll. OH. 1,1x.

Fig. 10. *Strophomena hirsuta* sp. n. 67022, Ventral interior, cast. Fangberget, Ringsaker district. Coelosphaeridium-beds. Coll. OH. 0,95x.

Fig. 11. *Strophomena steinari* sp. n. 67026. HOLOTYPE. Ventral interior, impr. Brattberg, Ringsaker district. Coelosphaeridium-beds. Coll. Sk. 0,8x.

Fig. 12. *Strophomena steinari* sp. n. 67025. Dorsal interior, impr. Loc. and Hor. as in fig. 11, Coll. Hm. 0.8x.
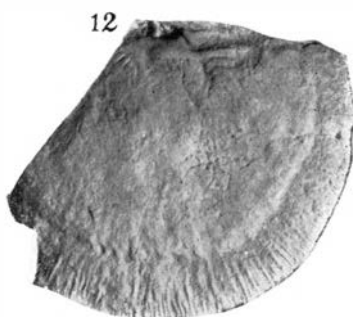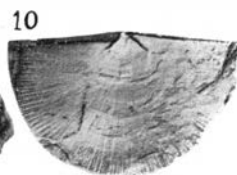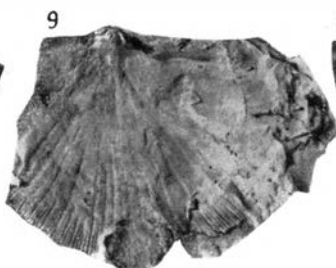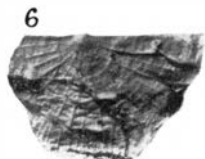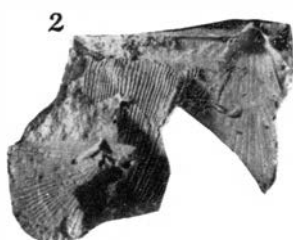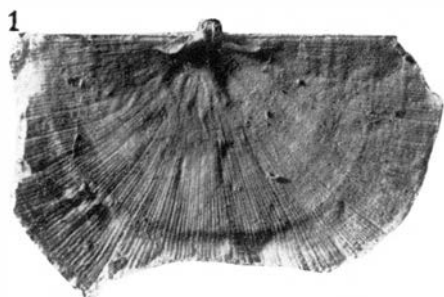
PLATE 11

PLATE 12

Fig. 1. *Strophomena (Gunnarella) delta* sp. n. 67145. HOLOTYPE. Dorsal interior, calc. from zone 4bδ at the SW-ern end of Borøya, Bærum, Oslo —Asker district. Coll. Sp. 1,9x.

Fig. 2. *Stropheodonta (Eostropheodonta) williamsi* sp. n. 67140. Ventral interior, impr. from the Coelosphaeridium beds at Brattberg, Ringsaker district. Coll. Sk. 1x.

Fig. 3. *Strophoedonta (Eostropheodonta) williamsi* sp. n. 36164, HOLOTYPE. Dorsal interior, impr. of a gerontic specimen from the Cyclocrinus beds at Furuberget, Hamar—Nes district. Coll. JK. 1,1x.

Figs. 4—5. *Stropheodonta (Eostropheodonta) williamsi* sp. n. 37380, two different views of a dorsal interior, impr. From the Coelosphaeridium beds at Fangberget, Ringsaker district. Coll. OH. 2x.

Fig. 6. *Stropheodonta (Eostropheodonta) helgoeyensis* sp. n. 38647, HOLOTYPE. Dorsal interior, impr. From the upper part of the Mjøsa Limestone at Bergvika, Helgøya, Hamar—Nes district. Coll. exc. 2,5x.

Fig. 7. *Strophonella* sp. Br. 35731. The area of a ventral valve, calc. showing the denticules (*d*) and denticules partly covered by growth of the area (*dg*). From the Mulde Marl (upper Wenlock) at Tegelbruket, Frøyel, Gotland, Sweden. 1,5x.

Fig. 8. *Strophomena neglecta* (JAMES) 67141. Area of ventral valve, calc., showing denticulated teeth (*d*). From the Richmondian (Maynesville) of Blanchester, Ohio, U.S.A. 1,5x.

Fig. 9. *Oepikina dorsata media* (ÖPIK) 64756. Ventral interior, impr. from the bryozoan zone at Gravestranden, Frierfjord, Langesund—Gjerpen district. Coll. St. & H. Major. 1,9x.

Fig. 10. *Oepikina dorsata media* (ÖPIK) 67143. Dorsal interior, impr. showing a specimen resembling *Oslomena* in the development of the branchial septa. From the Bryozoan zone at Gravestranden, Frierfjord, Langesund—Gjerpen district. Coll. W. C. Brøgger. 1,9x.

Fig. 11. *Rafinesquina* or *Oepikina* sp. 67136. Fragmentary ventral interior, impr. from 150 m S. of Vesleseter, Sjåstad district. Coll. St. & Hm. 1,9x.

Figs. 12—13. *Oslomena osloensis* sp. n. Dorsal and ventral wiews of a complete specimen cast HCl. From zone 4ba, railway section W. of Billingstad, Asker district. Coll. Sp. 2,3x.

Fig. 14. *Rafinesquina (Kjaerina) lepta* sp. n. 67133. HOLOTYPE. Dorsal interior, calc. from the lower part of zone 4bδ at Rauskjær, Oslo—Asker district. Coll. Sp. 3,4x.

Fig. 15. *Oslomena osloensis* sp. n. 67142. HOLOTYPE. Ventral interior, cast HCl, from zone 4ba at Arnestad, S. Vollen i Asker, Oslo—Asker district. Coll. Sp. 3,7x.

Fig. 16. *Oslomena osloensis* sp. n. 67139. Ventral area, cast HCl, showing structure of pseudodeltidium (*Pd*) and the cardinal processes (*dent*). From zone 4ba at Arnestad, S. of Vollen i Asker, Oslo—Asker district. Coll. Sp. 10x.
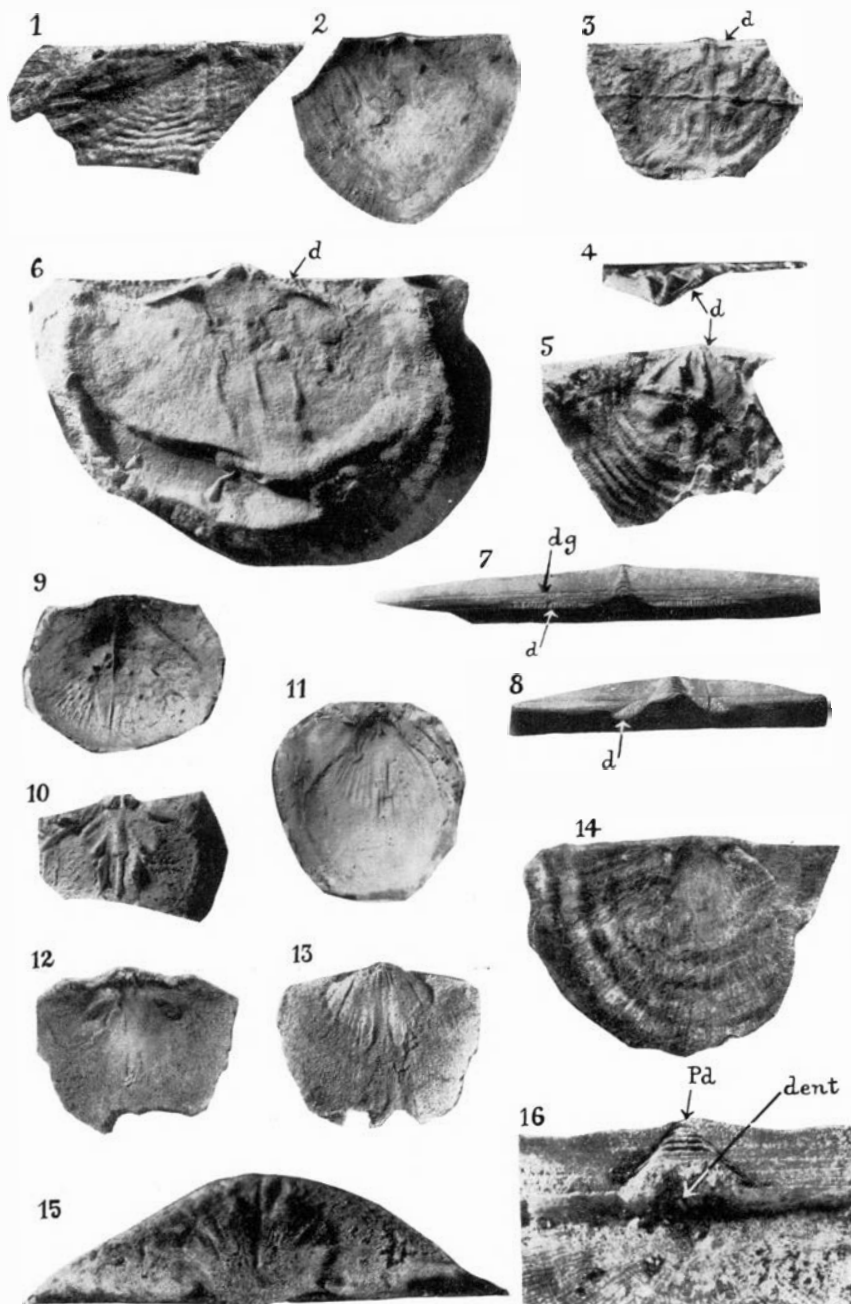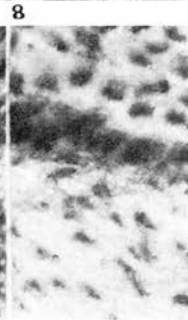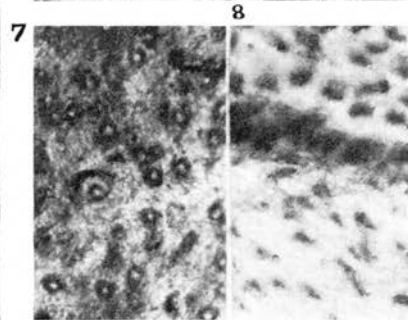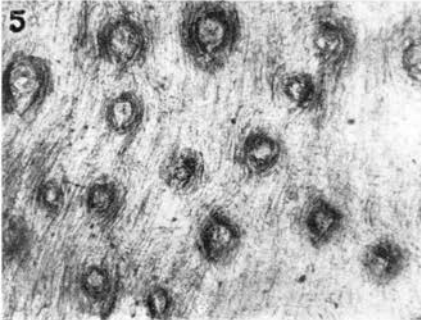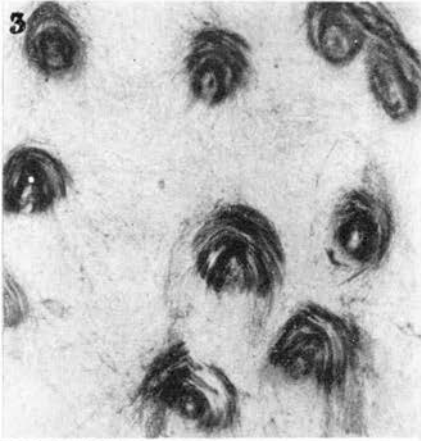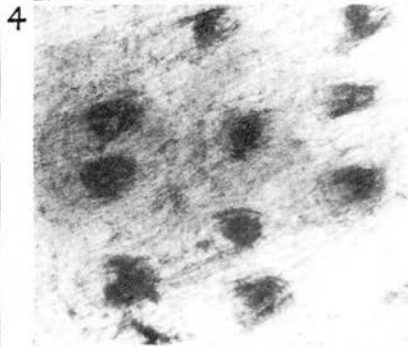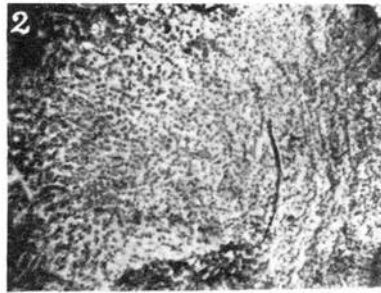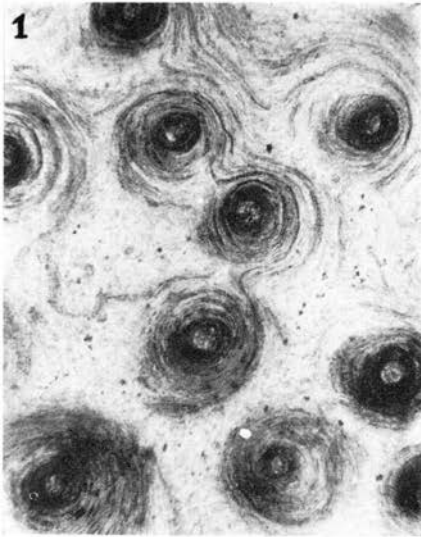
PLATE 12

PLATE 13

All figures are about 50x. except fig. 2, which is about 25x.

Fig. 1. *Leptaena depressa* (SOW.) dry peel of the dorsal valve of a specimen from the Mulde Marl, Frøyel, Gotland, Sweden, showing pseudopuncta.

Fig. 2. *Oslomena osloensis* sp. n. Dry peel of ventral valve of specimen from zone 4bα at Billingstad, Oslo—Asker district, showing small puncta.

Fig. 3. *Leptaena depressa* (SOW.) Thin section, showing the pseudopuncta in the dorsal valve of a specimen from the same horizon and locality as that in fig. 1.

Fig. 4. *Inversella* sp. Dry peel showing pseudopuncta in a specimen from zone B3 in the Leningrad district.

Fig. 5. *Sampo (Sampo) indentata* sp. n. Thin section showing pseudopuncta from the ventral valve of a specimen from zone 4bγ, north of Hvalstad st. Asker district.

Figs. 6—7. *Ptychoglyptus valdari* sp. n. Thin sections showing puncta and nonpunctate radial rib (*R*) in a specimen from zone 4bα at Billingstad, Asker district.

Fig. 8. *Strophomena neglecta* (JAMES) thin section showing pseudopuncta partly obscured by recrystallisiation. Richmondian, Ohio, U.S.A.
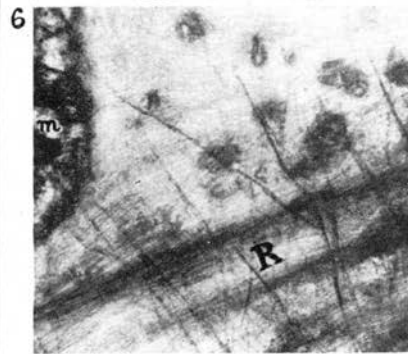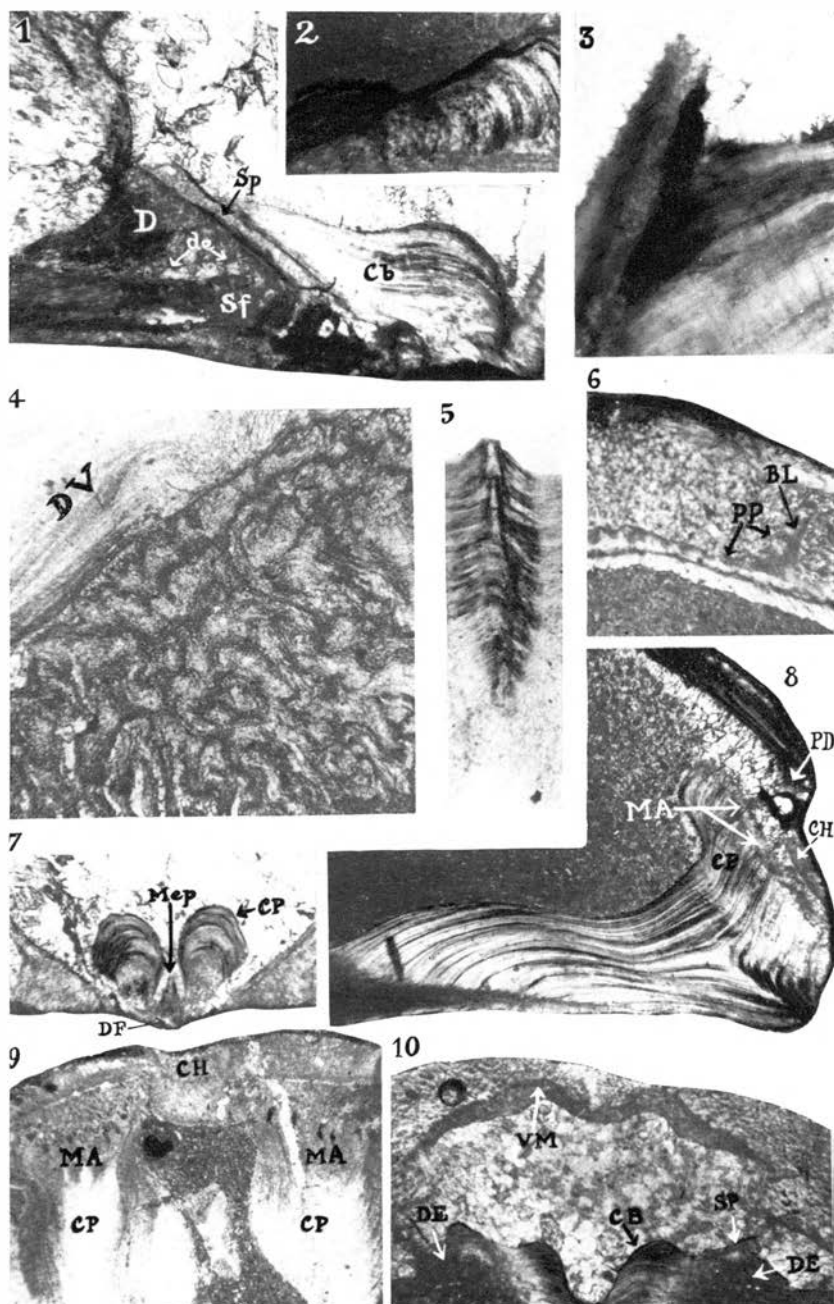
PLATE 13

PLATE 14

Photomicrographs showing the structure of the shell.

Figs. 3—4 are about 50x, fig. 5 is about 40x, and the rest are about 17x.

Fig. 1. *Strophomena planumbona* HALL (Ordovician, U.S.A.). Section just behind the cardinal processes, showing the supporting tissue of the latter (*Cb*), the socket plates (*Sp*), the teeth (*D*) the semidenticles of the teeth (*de*) and the irregular, pseudopunctate tissue in the sockets (*Sf*). Dry peel. Cf. textfig. 3E.

Fig. 2. *Kiaeromena kjerulfi* (HOLTEDAHL) from zone 4bβ at Langåra, Oslo— Asker district. Dry peel, showing the teeth, cf. textfig. 40A.

Fig. 3. *Leptaena depressa* (SOW.) from Frøyel, Gotland, Sweden. Thin section showing a pseudopunctum with open aperture, and filled with a yellowish substance differing from the clear calcite in the rest of the specimen (cf. p. 10).

Fig. 4. *Leptaena depressa* (SOW.) from Frøyel, Gotland, Sweden. Dry peel showing the structure of a tooth, with the irregular, semidenticulated border towards the dorsal valve (*DV*).

Fig. 5. *Leptaena depressa* (SOW.) from Frøyel, Gotland, Sweden. Thin section showing a pseudopunctum in longitudinal section.

Fig. 6. *Sampo* (*Sampo*) *indentata* sp. n. from zone 4bγ, Billingstad, Asker district, showing the structure of the branchial lamellae (BL), being formed by horizontal pseudopunctae (*PP*).

Fig. 7. *Oepikina dorsata* (BEKKER), from zone C2, Kukruse, Esthonia, showing the cardinal processes (*CP*), the rudimentary median cardinal process (*Mcp*) and the dorsal foramen (*DF*) cf. textfig. 2C.

Fig. 8. *Leptaena depressa* (SOW.) from Frøyel, Gotland, Sweden, showing a longitudinal section through the deltidium and notothyrium. *CP* = Cardinal processes, *MA* = Muscle impressions, *CH* = Chilidium, *PD* = Pseudodeltidium.

Fig. 9. *Kiaeromena kjerulfi* (HOLTEDAHL) from zone 4bβ at Langåra, Oslo —Asker district, showing the thick chilidium with median fold (*CH*) cardinal processes (*CP*) with characteristic muscle attachments (*MA*). Cf. textfig. 40D.

Fig. 10. *Oepikina dorsata* (BEKKER) from zone C2, Kukruse, Esthonia, showing semidenticulated teeth (*DE*), socket plates (*SP*), bases of the cardinal processes (*CB*) and the tissue coating the ventral muscle impressions (*VM*). Cf. textfig. 2E.

PLATE 14

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