Some Silurian conodont apparatuses and possible conodont dimorphism

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With 5 text-figures and 2 plates

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Conodont apparatuses and many "single element taxa" can be divided into two groups based on morphology and sometimes, the composition of the apparatus. Between these two groups many similarities connect the apparatuses in pairs, in which each pair consists of one apparatus of each type.

New taxa: *Pelekysgnathus dubius* n. sp., *Ligonodina confluens* n. sp., *Ligonodina excavata novoexcavata* n. ssp., and *L. confluens* n. ssp. New combinations: *Distomodus dubius* (RHODES, 1953), *Ligonodina excavata* (BRANSON & MEHL, 1933), and *Hindeodella steinhornensis* (ZIEGLER, 1956).

Conodonten-Apparate und auf Einzelelemente basierende Taxa können in zwei morphologisch und nach der Zusammensetzung der Apparate definierte Gruppen gegliedert werden. Apparate aus den beiden verschiedenen Gruppen können paarweise miteinander verglichen werden. Es werden folgende Taxa neu aufgestellt: *Pelekysgnathus dubius* n. sp., *Ligonodina confluens* n. sp., *L. excavata novoexcavata* n. ssp. und *L. confluens* n. ssp. Neue Kombinationen: *Distomodus dubius* (RHODES, 1953), *Ligonodina excavata* (BRANSON & MEHL, 1933), *Hindeodella steinhornensis* (ZIEGLER, 1956).

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Introduction

The present paper is part of a project on Silurian conodonts, their taxonomy, ecology, and stratigraphic use. A paper dealing with Upper Silurian conodont biostratigraphy is in a late stage of writing, and hopefully it will be completed for publication late this year; the paper will include a full discussion of the stratigraphic significance of apparatuses described herein and details about their relative frequencies. The present paper concentrates on the taxonomy of the better known apparatuses, and most of the known post-*siluricus* zone apparatuses present in the Silurian of Sweden are described. Some indications are also included that a specific concept, based on apparatuses, may not be the natural taxonomy it was thought to be one year ago but only a great step on the way towards this goal. Few indications are yet known, and it is not expected that it will be possible to drastically increase the number and strenght of them within the foreseeable future, because the number of apparatuses is too small if only Silurian material is studied. So, the evidences are presented here, in order that additional data can be searched for in other stratigraphic intervals.

As the dimorphistic nature of the conodonts is not yet proved, names are given to described apparatuses. When possible, one and the same specific name is given to the two components of a pair, both to stress their possible connection and to make a later union of them easier, if their connection is proved. If disproved, they are so different that they will be placed in different families, and the names will not be homonyms. The synonymy lists are kept short, mainly pending necessary type studies.

The reconstruction of the apparatuses is based on the mutual occurrence of all the characters mentioned in JEPPSSON (1971). The characters were distributed into four groups (similar occurrence, similar frequency variation, similar appearance of details, and similar composition of the apparatus). Some of these characters cannot be used separately, as shown below. Similar distribution in time and similarities in certain details may in that case combine the apparatuses into groups of higher order. Similar composition of the apparatus and similar frequency variation are more reliable. However, the test of the correctness of an apparatus, found to be the most sensitive, is that of corresponding ontogenetic stage. That is, all specimens of the elements of an apparatus in a sample are in the same, more or less restricted, interval in the series from juvenile to gerontic. For example, in one sample, all specimens of *H. excavata* are similar in size ("young but mature"), while those of *H. confluens* occur in all sizes.

Two types of individuals

The term apparatus is used nowadays in a fixed sense in conodont terminology (cf. SWEET & BERGSTRÖM 1969), and it may now be defined as the whole set of types of mineralized, hard tissues within one type of individuals at one time. Based on the denticulation of the elements and on the composition of the apparatus, the apparatuses can be divided into two groups. One of them, which will be referred to as A-type apparatuses (and individuals), includes all apparatuses of *Hindeodella* and *Pelekysgnathus*, discussed here. The other group, which will be referred to as B-type apparatuses (and individuals) includes the *Ligonodina* and *Distomodus* apparatuses.

The A-type apparatuses consist of elements that have comparatively short denticles, which, like the cusps, taper to a point, have lenticular cross sections and well developed, more or less wing-like, anterior and posterior edges. The spaces between the denticles are basally v-shaped. The processes are laterally compressed in cross section. In most cases the processes grew considerably in height during the life of the animal, and the denticles became more or less fused. All well-known Silurian A-type apparatuses studied have sp elements, while this element is absent in the B-type apparatuses. (The nomenclature of the elements used here is defined in JEPPSSON 1971.)

The B-type apparatuses include elements with peg-like denticles or with long denticles with nearly parallel margins, rounded cross sections and tips, and very weakly developed anterior and posterior edges. The spaces between the cusp and denticles are broad and basally u-shaped. The processes grow little in height and have a low, broad cross section. These features are best developed in forms with the denticles either nearly perpendicular to the process or directed away from the cusp. However, in elements where the denticles are crowded and directed toward the cusp, as in some ne elements, the denticles are still separated from each other in most specimens. These descriptions are based on illustrative specimens and most of the described characters may be found in both groups. Therefore the correct alignment must be based on the combination of details and, whenever possible, on the whole apparatus.

These two groups of apparatuses are not limited to the Silurian but can be recognized during most of conodont history. *Cordylodus*, one of the oldest known denticulated conodonts, already had the characters of B-type elements.

Ordovician conodont apparatuses with denticulated elements, described by BERGSTRÖM & SWEET (1966), WEBERS (1966), BERGSTRÖM (1968), SWEET & BERGSTRÖM (1969), and KOHUT & SWEET (1968), can also be divided into these two groups as listed below.

Apparatuses of A-type
- *Amorphognathus* spp.
- *Icriodella superba*
- *Phragmodus undatus*
- *Periodon grandis*
- *Rhodesognathus elegans*
- *Rhipidognathus symmetricus symmetricus*
- *Polyplacognathus ramosus*
- *Bryantodina? stauff eri*
- *Bryantodina? abrupta*

Apparatuses, probably of B-type
- *Plectodina furcata*
- *Plectodina posterocostata*
- *Plectodina aculeata*
- *Oulodus oregonia*

The Devonian apparatuses (LANGE 1968) and the Carboniferous apparatuses, found on shale surfaces (SCHMIDT 1934, SCOTT 1934, 1942, RHODES 1952, and others), also fall into these groups as listed below.

A-type apparatuses
- *"Lewistownella"*
- *"Lochriea"*
- *"Scottognathus"*
- *"Westfalicus"*
- "Conodontophoriden-Gattung: *Prioniodina-Falcodus-Scutula-Palmatolepis-Ozarkodina*"
- "Apparate aus *Neoprioniodus-Hindeodella-Roundya-Spathognathodus-?Ozarkodina*"

B-type apparatuses
- *"Duboisella"*
- "Gruppe mit *Ligonodina – Trichonodella*"

Most of those taxa which as yet include only one type of element and which most likely belong to multi-element apparatuses unreconstructed so far, can be recognized as belonging to one or the other of these groups.

Some Post-Silurian conodonts most likely of A-type
- *Angulodus*
- *Avignathus*
- *Arcugnathus*
- *Centrognathus*
- *Cervicornoides*
- *Elictognathus*
- *Geniculatus*
- *Falcodus*
- *Hindeodina*
- *Lambdagnathus*
- *Nodognathus*
- *Palmatodella*
- *Pandorinellina*
- *Polygnathellus*
- *Pinacognathus*
- *Scutula*
- *Subbryantodus*
- *Apatognathus*
- *Bactrognathus*
- *Metaprioniodus*
- *Synprioniodina*

Some Post-Silurian form genera, most likely of B-type
- *Diplododella*
- *Eoprioniodina*
- *Loxognathus*
- *Neoprioniodus*
- *Prioniodina*
- *Tripodellus*
- *Hibbardella*
- *Lonchodina*
- *Lonchodus*
- *Metalonchodina*

None of the platform genera are listed. There are two reasons for this. First, they are principally all of A-type. Second, some of them belonged to "single element apparatuses" (SWEET 1970), and it is as yet impossible to say, whether they originated by reduction from the "multi-element apparatuses" or formed a separate group.

The concept of some genera (e.g. *Neoprioniodus*) is so broad that both types of apparatuses are included. In these cases I have tried to list the genera after their type species.

A few examples of Triassic conodonts are given to show that the two groups can be identified among the Mesozoic conodonts too. *"Hindeodella" uniforma* MOSHER, 1968 and *Chirodella erecta* MOSHER, 1968 are of A-type. *Oncodella idiodentica* MOSHER, 1968, and *Prioniodina petraeviridis* (HUCKRIEDE, 1958) are of B-type. Among the apparatuses described by SWEET (1970) are *Ellisonia robusta* probably of B-type, and *E. delicatula* probably of A-type.

Consequently, these two groups were already established in the Ordovician and existed until the disappearance of the conodonts in Late Triassic times.

Problems

One logical implication of the relation noted above would be that the two groups formed two taxa of high rank. However, this interpretation is absent in all supragenetic classifications proposed so far, and there are many facts that make it difficult to accept such an interpretation.

For instance, each denticle in the elements of *Distomodus dubius* and *Pelekysgnathus dubius* has its own basal cavity tip, while in *Ligonodina* and *Hindeodella* only the cusp has a basal cavity tip. It seems probable that in *Distomodus* and *Pelekysgnathus* each denticle was separately initiated and later incorporated into the base of the cusp. The denticles in *Ligonodina* and *Hindeodella* originate as outgrowths from the oral or distal side of the bar tip. That is, both varieties occur in both groups. One of these growth series may be the original one and the other one the result of an independent and parallel evolution.

A difference in the colour of the hyaline matter is of great taxonomic importance, if variation, depending on preservation, and the stage of growth can be identified. All unaltered elements of the same growth stage of an apparatus in a sample have a distinct colour, which can be used to separate them from those of related apparatuses (BERGSTRÖM & SWEET 1966, JEPPSSON 1969, and others). However, both in *Hindeodella* and *Ligonodina* there are light yellow and dark brown apparatuses.

The central part of the long process of the ne element can form an angle with the cusp of roughly 90 degrees, as it does in *H. excavata* and *L. excavata*, or it can be much larger, about 135 degrees, as it is in *H. confluens*, *H. steinhornensis* s. l., *L. confluens*, and *L. elegans*. That is, both types occur in both genera (cf. Text-fig. 1).

The tr element does not have a posterior process in the apparatuses of *Hindeodella* and *Ligonodina*, which are discussed, but many Devonian and younger tr elements of both genera have well developed posterior processes.

The ne, hi, and tr elements of *Hindeodella excavata* and *L. excavata excavata* are so similar that commonly they cannot be separated.

Pairs

The details listed above, and many similar ones, can only be explained by the current species concept (each species consisting of one apparatus) if there repeatedly occurred parallels and reversals in the course of evolution, not only affecting different details in the same way but also resulting in the same combination of these details. Such distinct details, as the colour of the hyaline matter and the angle between the cusp and the long process of the ne element are combined in the same way in all studied apparatuses of *Hindeodella* and *Ligonodina*. A detailed study shows that similarities are not randomly spread among the different apparatuses of the two groups but are distributed in such a way that the apparatuses are connected as pairs. Each pair consists of one apparatus of each type. Within the pairs, the corresponding elements of unspecialized apparatuses can be so similar that in many cases it is difficult or impossible to separate them in spite of the fact that the apparatuses as a whole are so different that they must be placed in different superfamilies in the taxonomy based on apparatuses (LINDSTRÖM 1970). One example is the *Hindeodella excavata* and *Ligonodina excavata* apparatuses, in which many specimens of the ne and hi elements cannot be separated with certainty, and in which the tr elements were formerly brought together in the same form species.

When the apparatuses and their elements are more specialized, the apparatuses can be so different that the only remaining similarities are colour, details in growth, distribution in time, and a closely connected evolution. Four pairs are discussed below.

Some of the first reconstructed connections between discrete conodont elements may also be of the pair type instead of the apparatus type. The earliest published groups (HUCKRIEDE 1958) include more types of elements than later reconstructed apparatuses, and among these elements both of those types of elements described here are included. The Conodonten-Apparate E and G, described by WALLISER (1964), contains both *Kockelella* and elements with the general appearance of B-type elements. Several hundred elements of the latter type, from about the same stratigraphic levels, and in part closely similar to the material from Cellon, were extracted from the Hemse Beds on Gotland, but no *Kockelella* specimens were found. To this can be added that all apparatuses of *Ligonodina* yet studied have no sp elements. However, the close connection in the occurrence of *Kockelella* and the other elements as demonstrated by WALLISER (1964) suggests a connection on the pair level between *Kockelella* and some of the other elements.

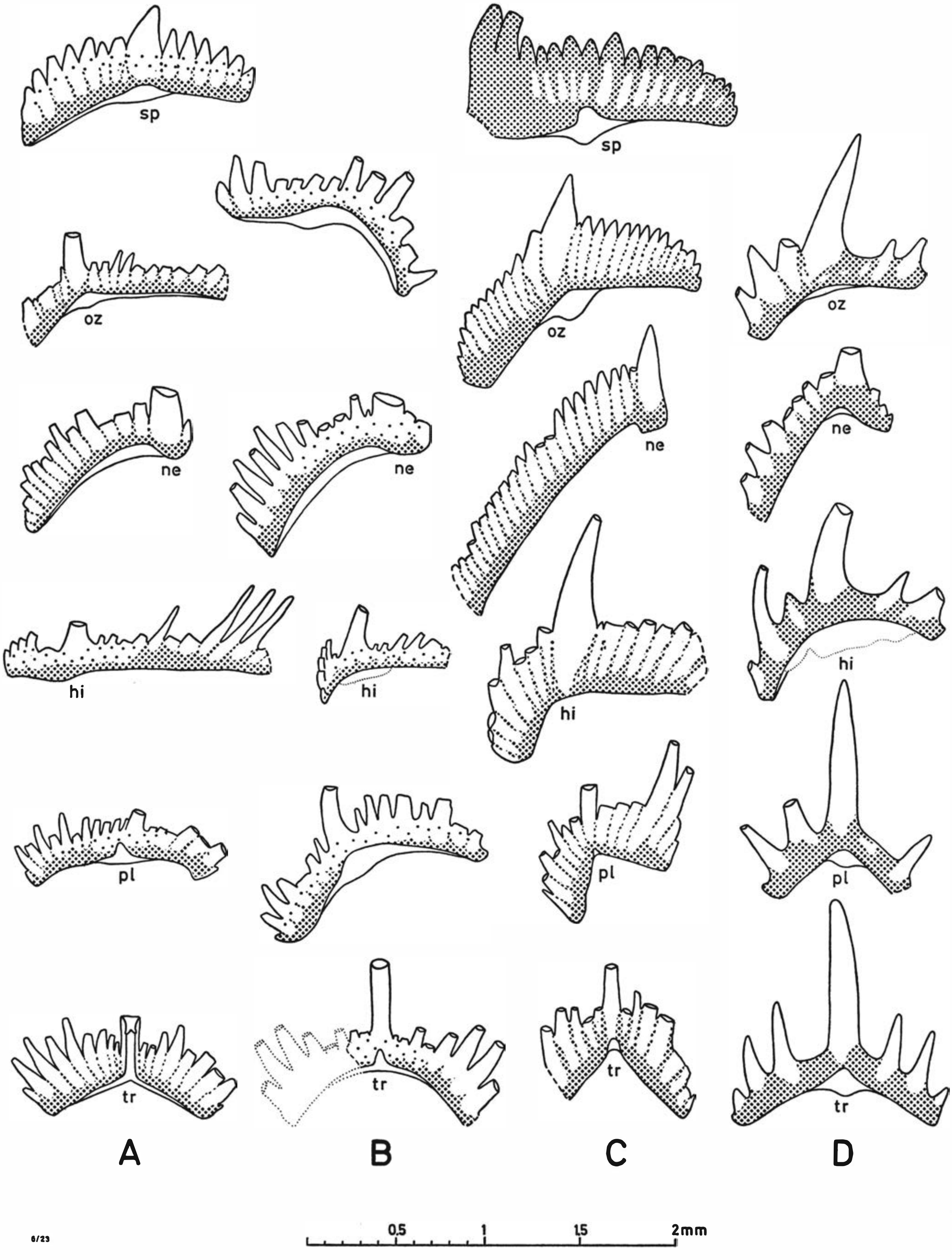
The relations between *Rhipidognathus symmetrica discreta* and *R. s. symmetrica*, as described by KOHUT & SWEET (1968) are in some aspects very similar to those between *Hindeodella excavata* and *Ligonodina excavata*, but whether they really form a pair can only be established by examining large material of these two apparatuses.

Hindeodella excavata and *Ligonodina excavata*

Hindeodella excavata and *Ligonodina excavata excavata* occur together in the *siluricus* zone. *L. excavata* probably extends further down, parallel with the occurrence of *H. excavata* in older zones. Nothing is known about *L. excavata* above the *siluricus* zone (except possibly in the lowest *latialatus* zone) until *L. e. novoexcavata* n. ssp. appears in the lower *eosteinhornensis* zone. *H. excavata* is well represented in the *latialatus* zone, but it disappears in Scania and Gotland at the end of the next lowest (local?) subzone of the *eosteinhornensis* zone (JEPPSSON in manuscript). When the apparatus reappears, it is slightly different, but the known differences are not enough to justify a different subspecific name. Both apparatuses occur in Lower Devonian Beds.

The hyaline matter of all the elements has the same light colour (which separates them from all elements in other apparatuses studied) but there is no difference in this detail between the *H. excavata* and *L. excavata* apparatuses. The denticle roots of white matter with very thin sheets of hyaline matter between them are closly similar or often indistinguishable from one another.

The ne elements of *H. excavata* and *L. e. excavata* are so closely similar that in many cases they cannot be separated. Only mature, well preserved specimens can be placed in either apparatus with certainty. The tr elements of the two apparatuses were assigned to one and the same form species in the past but can be separated now even though they are closely similar. The hi elements are so similar that broken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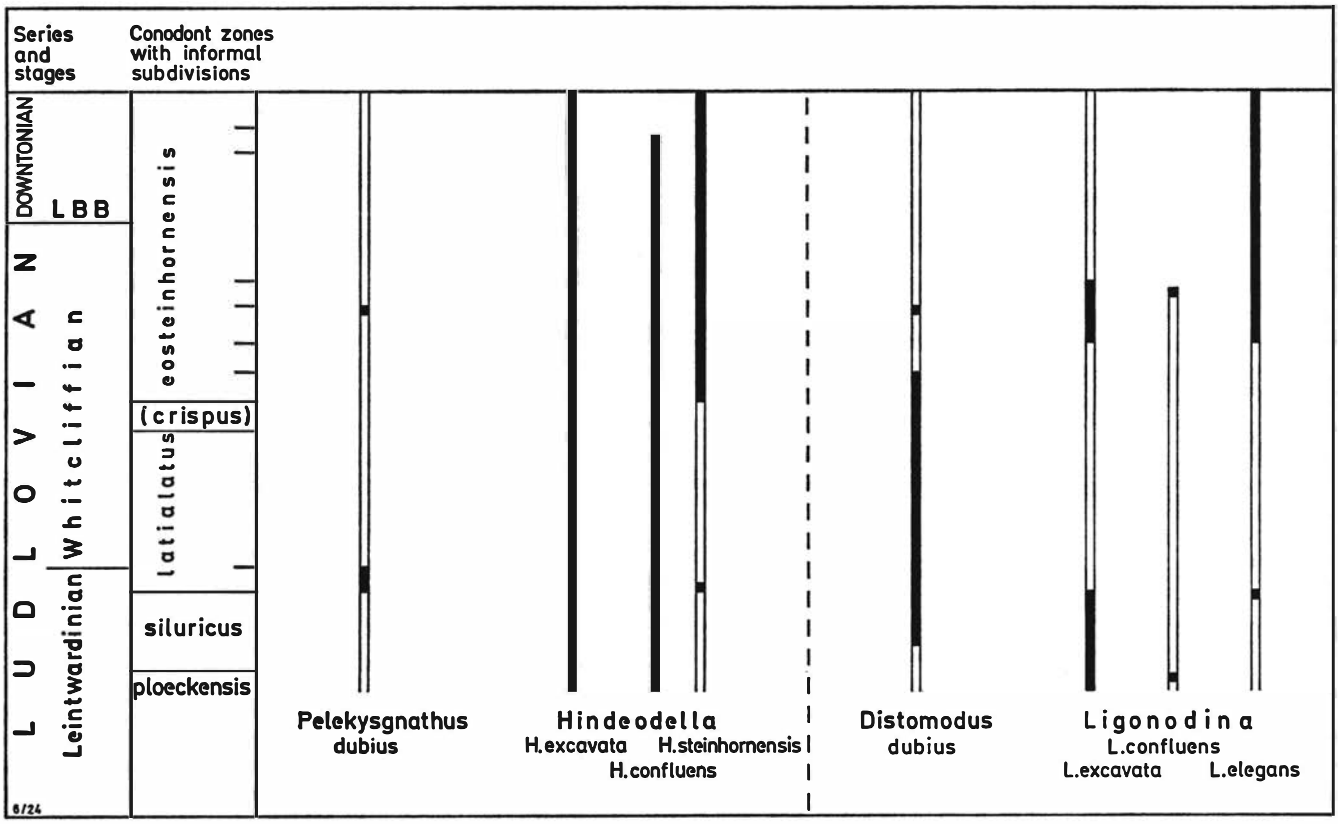

Fig. 2: The known occurrence and absence in time of the discussed apparatuses in northern Europe. The lateral distance between the bars indicates the presumed degree of relationship. Many occurrences are known only from separate samples and specimens, e.g. the mark for the last known occurrence of *H. confluens* is based on two specimens out of several thousand discrete specimens derived from the upper part of the *eosteinhornensis* zone.

specimens are difficult to separate in most cases. The obvious differences between the two apparatuses exist at the apparatus level, because the *Ligonodina* apparatus does not have an sp element and has closely similar oz and pl elements that are very different from those of *H. excavata*.

The elements of *L. excavata novoexcavata* and *H. excavata* from the *eosteinhornensis* zone above the subzone in which *H. excavata* is absent, can be separated without difficulty in most cases, as the *L. e. novoexcavata* elements have a very deep basal cavity. However, some of the elements of *H. excavata* are more similar in this respect to those of *L. excavata excavata* than to stratigraphically older specimens.

The tr element of *L. e. novoexcavata* has a less well developed posterior branch of the basal cavity than that of *L. e. excavata*, and many specimens of the tr element of *H. excavata* from the *eosteinhornensis* zone also have a smaller branch than their predecessors.

Hindeodella confluens and *Ligonodina confluens* n. sp.

Hindeodella confluens and *Ligonodina confluens* n. sp. show a higher degree of specialization than *H. excavata* and *L. excavata*. This is evident in the larger difference between the elements within the apparatus. All well preserved elements of these two apparatuses have the same dark brown colour and very deep denticle roots. The angles between the processes and cusps of the corresponding elements are closely similar. *H. confluens* is well known and occurs from at least the

Fig. 1: A. *Hindeodella excavata* (BRANSON & MEHL, 1933). The sp element is from sample Bj 67–30, the oz element from a sample from Gogs, parish of Lau, Gotland, the ne, hi, and pl elements from sample Bj 67–36, and the tr element from sample ES 137 (coll. A. Martinsson). The tr element is also pictured on Pl. 1, fig. 30. LO 4383–4388. B. *Ligonodina excavata excavata* (BRANSON & MEHL, 1933). The same specimens as pictured on Pl. 1, figs. 25–29. The cristagalliform element is drawn in the space for the oz element and the walliseriform element in the space for the pl. element. C. *Hindeodella confluens* BRANSON & MEHL, 1933. The sp element is from sample Bj 67–30, the oz and ne elements from Bj 67–44, the hi element from Bj 67–30 and the pl and tr elements from Bj 67–36. LO 4389–4394. D. *Ligonodina confluens* n. sp. The same specimens as pictured in Pl. 2, figs. 1, 3, 6, 7, and 9. The samples Bj 67– are derived from beds belonging to the *latialatus* zone, exposed in the ditch at Bjärsjölagård. The samples Gogs and ES 137 are from the *siluricus* zone. Preserved parts of the basal filling are outlined with a dotted line, as is the reconstructed process of the tr element of *L. excavata*.
◄
Areas with secondary white matter are dotted. In a taxonomy based on apparatuses the closest relationship between the apparatuses may be expressed in the following way (A, C) and (B, D), i.e. *Hindeodella* and *Ligonodina*, respectively. However, many similarities connect them in another way (A, B) and (C, D); dimorphism is suggested as a possible explanation.

Wenlockian throughout the Ludlovian, except it is not found in samples from the second lowest subzone in the *eosteinhornensis* zone. *L. confluens* on the other hand is very rare, and it is only found at two localities. The first locality probably belongs to the upper *ploeckensis* zone (only a few scattered samples from lower levels were studied), and the second locality is from a high level in the lower *eosteinhornensis* zone.

Hindeodella steinhornensis s. l. and *Ligonodina elegans*

That *Hindeodella steinhornensis* s. l. and *Ligonodina elegans* are even more specialized than *H. confluens* and *L. confluens* is apparent from the appearance of the elements of the apparatuses. The similarities between the apparatuses are also smaller than in the two earlier described pairs. The colour and a few details in the direction of the processes are the only obvious connecting links, except a detail in the evolution and the distribution in time. The evolution of alternating denticles can be followed within the *H. steinhornensis* s. l. lineage in the Silurian. After the initiation of one small denticle between the large ones on the hi and pl elements in the Late Whitcliffian, the evolution included, step by step, both a spreading of this feature to most of the other elements in the apparatus and an increase in the number of small denticles. In the uppermost Pre-Gedinnian, the hi and pl elements of the *Ligonodina elegans* s. l. apparatus with alternating denticles appear abruptly (Text-fig. 4).
The oldest known occurrence of these two apparatuses is near the border between the *siluricus* and *latialatus* zones, where a few specimens of both types of apparatuses occur in my samples from Scania and Gotland. There are still too few specimens to base any taxonomic conclusions on, but the *Ligonodina* specimens are so different from *L. elegans* that they probably belonged to a taxon which should be separated at the species level from *L. elegans*. The next appearance of them is near the border between the *crispus* and *eosteinhornensis* zones, where WALLISER (1964) reports *L. elegans* from Spain, while *H. steinhornensis* s. l. provides the zone fossils in the *eosteinhornensis* zone.

Pelekysgnathus dubius and *Distomodus dubius*

Pelekysgnathus dubius and *Distomodus dubius* are very different. Except that each denticle has its own basal cavity tip (Text-fig. 5), there are few details in common on normally developed specimens. However, some aberrant specimens are intermediate between the apparatuses and cannot be identified with certainty. In those elements of the *Distomodus dubius* apparatus, which only occasionally has denticles, the denticles are in many cases closely similar to those of the *Pelekysgnathus dubius* apparatus. Both apparatuses have the same distribution in time, even if the *Distomodus* apparatus is much more common and the *Pelekysgnathus* apparatus only occasionally appears. The oldest known occurrence of both of them is near the *siluricus-latialatus* boundary. *P. dubius* is not known above the lowest part of the *latialatus* zone, except that it does occur in material from Diddlebury (i.e. a rather high level in the lower *eosteinhornensis* zone), while *D. dubius* has a more continous occurrence in Scania extending into the lowest *eosteinhornensis* zone.

Descriptions of apparatuses

Distomodus BRANSON & BRANSON, 1947

The description of *Distomodus* was based on material from the Lower Silurian. Different elements of the type species were also included under the names *Trichonodella brassfieldensis* and *Drepanodus simplex*. These elements, together with other elements undescribed by BRANSON & BRANSON (1947), form an apparatus similar to that of the Ludlovian species. The genus probably existed in the Ordovician; however, it cannot yet be identified from pictures of single elements but only from the characters of the whole apparatus. Older synonyms to the name *Distomodus* (described from the Ordovician) may exist but no such name is known.

Distomodus dubius (RHODES, 1953)
Pl. 1, figs. 1–13

1953 *Cordylodus ? dubius* n. sp. – RHODES, p. 299; Pl. 23, figs. 221–224.
1953 *Distomodus suberectus* n. sp. – RHODES, p. 290; Pl. 23, figs. 207, 208, 210, 211.
1953 *Distomodus curvatus* n. sp. – RHODES, p. 290; Pl. 23, figs. 209, 226–228.
1953 *Distomodus curvatus* var. *dentatus* n. var. – RHODES, p. 291; Pl. 23, figs. 217, 218, 229, 230.

M a t e r i a l : 958 specimens from Scania and a few hundred from Gotland.
D e s c r i p t i o n : The dark brown colour of the hyaline matter is common to the different elements. The white matter of the cusp starts at the basal cavity tip, which is situated near the anterior margin of the cusp. It does not fill the whole cross section of the cusp until high up in it, and so, in side view, there is a triangular area of hyaline matter basally on the cusp. This is best visible on elements with a laterally compressed cusp. Otherwise, the white matter is well developed, both in the cusps and denticles. Even the very small denticles generally have white matter. The denticles are discrete, and each one has its own basal cavity tip.
N e e l e m e n t : The ne element was described by RHODES (1953) as *Distomodus suberectus*. To his description can only be added that commonly the cusp is slightly curved backward and inward throughout its lenght, and that it is strongly compressed (sword-like) on mature specimens like the ne element of *Ligonodina elegans*. Often the inner lateral edge basally carries one or rarely two compressed denticles. The material studied is abundant enough to conclude that this is a variation within the species without any systematic value, as is the case in the other elements.
H i e l e m e n t : The hi element was described by RHODES (1953) as *Cordylodus? dubius*. To his description only a few details can be added. There can be at least four denticles on the posterior edge. Each one of the denticles has its own basal cavity tip (best visible from the outside). In large specimens, the innermost denticles can be completely overgrown, and their former presence can only be deduced from the existence of their basal cavity tips. The anterior edge also carries denticles, but the distance between the tip of the basal cavity and the first denticle is about 200 μ or more; the first denticle on the posterior edge occurs about 60–90 μ (occasionally only 25 μ) from the tip. Therefore, since the parts of the base, which are more than 200–300 μ from the tip of the basal cavity, are often absent, and the innermost denticles are often

reduced or broken, these denticles are not too often seen. They are short, strongly compressed and often broken below the white matter.

As on the oz and pl elements, the base of the conodont proper (as distinct from basal filling) of the hi element is thickest along the edges. The anterior-lateral edge forms a long peninsula, which, however, in most cases is broken. It is impossible to say whether originally there was a thin sheet connecting it with the rest of the conodont proper, or if it originally was protruding as on the oz and pl elements.

Oz and pl elements: These elements were described by RHODES (1953) as *Distomodus curvatus* and *D. c.* var. *dentatus*. The specimens included here are more variable than those belonging to the other elements, and in the future it may be possible to separate the oz and pl elements.

The base is triangular in outline with one outer posterior-lateral and two anterior corners and ridges. The outer anterior-lateral ridge is more or less weakly developed and can be missing. If it is missing, the outline of the base is a rounded square with two well developed corners (those with ridges) and two weakly developed corners (one outer anterior-lateral, and one inner posterior-lateral). The two well developed ridges form the edges of the cusp, while the third fades out a short distance above the base. The cusp is twisted, so that the posterior-lateral ridge edge towards its tip has a nearly posterior position. Basally the two well developed ridges generally have denticles, while denticles do not occur as commonly on the third ridge.

At least the outer denticles seem to be formed on the basal filling, independent of the conodont proper of the main part of the element, and they are not fused to the main part until a later growth stage. In cross section the denticles have a rounded lens-shape with sharp edges on the central and distal sides.

Along all three corners the conodont proper continues far down on the basal filling (generally as far down as this is preserved). On the outer and anterior sides, between the ridges, deep broad notches can occur in the conodont proper. However, the aboral part of the conodont proper and the basal filling are generally destroyed.

Tr element: The tr element is similar to the hi element, but it has two anterior-lateral edges, a more rounded base, and well developed denticles on the lateral edges. This element, like many other tr elements, is not perfectly symmetrical. One of the lateral edges has more and larger denticles than the other one. On this edge the first denticle is closer to the basal cavity tip (of the cusp) than the first denticle on the other edge. The anterior edge of the cusp is formed by the edge of the side with less denticles, while the other edge fades away at about the middle of the cusp. In a few cases this edge can be traced higher up on the cusp, and it comes very close to the other ridge. The posterior edge of the base continues upward and forms the posterior edge of the cusp. In mature specimens there are generally two denticles on one lateral process, three denticles on the other, and one denticle on the posterior process. There is a v-shaped notch in the conodont proper on the anterior side.

Simple cone element: An element also belongs to *Distomodus dubius*, which so far is not shown to be homologous with any of those of *Hindeodella*. Its cusp has one anterior and one posterior edge, which maintain their relation down on the base. The basal cavity is very shallow, and the sides of it are out-flexed. In cross section the cusp is rounded lens-shaped. The inside of the shallow basal cavity often has an anterior-posterior furrow. Denticles of the other elements, which were not fused to the rest of the conodont proper and which are found as separate units together with juvenile specimens of some of the other elements, cannot be separated from juvenile specimens of these elements. Thus, the counted number of these elements often is higher than expected.

In some samples there also are a few aberrant specimens, which cannot be identified with any of these elements described here. They combine details from both the elements of this apparatus and from those of *Pelekysgnathus dubius* and intergrade between these two apparatuses.

Remarks: The name *dubius* is here selected as the name of this taxon, because the holotype of *dubius* is the only pictured holotype of the three available names, and because it is based on a specimen of the element most readily identified (it can be identified without any doubt!). The homologies of the elements of this species with those of *Hindeodella* are somewhat uncertain, but the one proposed here is probably correct.

The denticles of all elements have their own small basal cavity tips. This may be explained by the assumption that they were formed around separate papillae and later fused to the cusp part of the element. If this was the case it would also explain some details which occur in this species and in *Pelekysgnathus dubius*. No case of the outermost denticle(s) in a stage of forming is known. This is contrasting to the relation in *Hindeodella* and *Ligonodina* where this feature is the rule. In some faunas with the elements of *Distomodus* of medium-size, a large amount of small simple cones have been found. These units are closely related to *Distomodus dubius* as is evident both from their appearance and occurrence and are closely similar to the denticles of the elements of this species. They are best interpreted as denticles, which were not fused to the main part of the element at the time of death of the animal. There are also known some specimens which ought to be interpreted as being in a stage of fusion (cf. WALLISER 1964, Pl. 10, figs. 1–7, 10–12; and Pl. 1, figs. 2, 7–13 in this paper).

Autecology: *Distomodus dubius* is among the species in the material studied with the largest frequency difference between Gotland and Scania. This cannot be interpreted as if only those horizons in which it is common in Scania and the ones in which it is rare on Gotland were sampled because its frequency on the whole is consistent from its first to its last occurrence in Scania. On Gotland, it is common only in the extremely rich faunas from the *siluricus* zone, while it is practically absent in younger beds. In most cases its frequency is opposite to that of *Panderodus unicostatus*, which is one of the few species occurring in restricted environments and which probably is most abundant in shallow water sediments. The sequence in Scania is mainly shaly, while on Gotland the studied part of the Hemse and higher beds consists mainly of near-reef limestone and algal rich sediments. The species evidently disappeared from Scania, when the sediments indicate deposition in more shallow water (e.g. the algae-rich Bjärsjölagård Limestone).

The specimens of *D. dubius* are generally large and well developed in the beds from Scania, while those from Gotland are much smaller. The material from Gotland does not look stunted but seems to be juvenile. This may indicate that the juvenile individuals lived in a more shallow environment than the mature ones of this species.

Occurrence: In Scania *Distomodus dubius* is abundant from the *siluricus* zone into the lowest local subzone of the *eosteinhornensis* zone. It is not seen in younger beds. On Gotland the species is common in several samples from the *siluricus* zone.

This species, or a very nearly related one, also occurs in upper Gedinnian beds. Different elements have been described by CARLS & GANDL (1969) under the names *Rotundacodina* *dubia* (RHODES 1953), *Acodina aragonica* CARLS & GANDL, 1969, and probably also under the names *Drepanodus curvatus* (RHODES 1953) and *Rotundacodina elegans* CARLS & GANDL, 1969.

Ligonodina excavata (BRANSON & MEHL, 1933)

1933 *Trichognathus excavata* BRANSON and MEHL, n. sp. — BRANSON & MEHL, p. 51, Pl. 3, fig. 36.

Remarks: As noted in the description of *Hindeodella*, it is now evident that the lecto-type of *Trichognathus excavata* is distinct from most other specimens described under that name. Already in 1957, WALLISER noted that the type was extreme, compared with the bulk of the material described under this name. JEPPSSON (1969) noted the existence of a *Ligonodina* apparatus with a tr element closely similar to but distinct from that of *H. excavata*, and some morphologic differences were given to distinguish them. However, direct comparison of the type specimen of *T. excavata* with material from a sample of the same conodont zone as the type specimen but from Gotland (containing tr elements of both the *H. excavata* and *Ligonodina* apparatuses) showed that the type specimen is distinct from the tr element of *H. excavata* and that it agrees with that of the *Ligonodina* apparatus in every studied detail. Therefore, the name of this apparatus is based on *Trichognathus excavata*.

The ne element of this apparatus has either been incorrectly assigned to *H. excavata* or possibly "*Neoprioniodus multiformis*". Specimens of the hi element have been assigned to *H. excavata*, while larger specimens are known as *Ligonodina salopia* (it is yet impossible to say, if the type of *L. salopia* belongs here).

L. excavata also occurs in the Lower Devonian, where different elements were described by ZIEGLER (1960) as *Lonchodina cristagalli*, *Lonchodina walliseri*, *Ligonodina* n. sp. WALLISER 1960, *Trichonodella inconstans*, and *Prioniodina excavata*. This apparatus is closely similar to the nominal one and should at most be separated at only the subspecific level. The two elements, described as *L. cristagalli* and *L. walliseri* are the pl and oz elements, but their correct homologies are not yet known, even though it seems probable that the cristagalliform element is the oz element and the walliseriform one is the pl element.

Description: The hyaline matter of all elements is light yellow to light yellowish brown. The denticles are long and slender, rounded in cross section and, for a *Ligonodina* apparatus, closely spaced. Differences between the material from the *siluricus* zone and that from the *eosteinhornensis* zone are small but consistent, so it is appropriate to treat them as different subspecies.

Ligonodina excavata excavata
(BRANSON & MEHL, 1933)
Pl. 1, figs. 25–29; text-fig. 1 B

Material: More than 100 specimens.

Diagnosis: The typical subspecies of *Ligonodina excavata* has a broad and long third branch of the basal cavity on the tr element. All the elements have shallow basal cavities.

Description: The roots of the denticles are well developed. In small specimens there is only a narrow sheet of hyaline matter between the white matter of the denticle roots, while in larger specimens this thin separation, if still existent, becomes invisible when the whole process is filled by white matter, except the edges of the basal cavity. The shape of the denticle roots, the colour of the hyaline matter, and the shape of the elements (except the oz and pl elements) are so similar to those of *H. excavata* that fragments of medium-sized or small specimens cannot be separated from fragments of *H. excavata* specimens.

Ne element: The ne element is closely similar to that of *H. excavata*, and it is impossible to sort less well preserved or small to medium-sized specimens. Normally, compared to *H. excavata*, the cross section of the cusp and denticles is more rounded in *L. e. excavata*; the edges are less well developed; the basal cavity is much broader, the short process is slightly more outwardly directed, and often this process has two well developed denticles. The downwardly directed inner lip is very obvious on the ne element of *Hindeodella excavata*, in which it is broadly triangular and obliquely downwardly directed. In inner lateral view it normally covers the central part of the basal cavity. This lip is much less conspicous in *L. excavata*, in which it is short and very broadly rounded and inwardly-downwardly directed. The basal cavity in *L. e. excavata* is more shallow and grows much wider than in *H. excavata*, and often parts of the basal filling are preserved in *L. e. excavata*. Like the other elements of this apparatus, the ne element of *L. e. excavata* grows much larger and coarser than that of *H. excavata*.

Hi element: The hi element is closely similar to that of the *H. excavata* apparatus. It is difficult or impossible to sort small specimens. There are many suppressed denticles around the cusp as on the hi element of *H. excavata*, but on large specimens these denticles are completely overgrown (resorbed?), and there is a rather broad, rounded notch between the cusp and the first denticle. The cusp and the denticles are rounded in cross section and have very weakly developed edges. Often the oral margin of *L. excavata* is more arched, especially on the anterior-lateral process, and the posterior process is less outwardly bowed than on the hi element of *H. excavata*.

Oz and pl elements: The oz and pl elements vary from nearly straight specimens to very strongly arched, bowed and twisted specimens. Generally, the posterior process is arched and outwardly bowed, except the very end, which is straight or slightly inwardly bowed. The anterior process is arched and inwardly bowed. Most specimens have a long well developed cusp, which basally is backwardly and inwardly curved. Distally it is straight. On some specimens the size of the cusp is nearly the same as that of the denticles. The basal cavity is shallow and broadly inwardly expanded below the cusp. It narrows evenly below the posterior process. Under the anterior process (anterior of the expansion below the cusp) the basal cavity is comparatively narrow, and distally it decreases in width to a narrow furrow.

Tr element: The tr element is the second easiest to separate from that of *H. excavata*. The processes are arched. The cross section of the cusp and denticles is more or less rounded, and the notch between them is rounded, at least on smaller specimens. On the posterior side of the cusp, the third branch of the basal cavity is normally shorter and broader than it is on *H. excavata*. The tip of this branch is also rounded instead of pointed. For more details see WALLISER (1957), JEPPSSON (1969) and page 52 and Pl. 1, fig. 29 in this paper.

Occurrence: The *Ligonodina excavata excavata* apparatus is known from the Hemse Beds at Millklint and from Grogarnshuvud, both Gotland. The type specimen is from the Bainbridge Formation at Lithium, Missouri. The occurrences at Millklint and at Lithium are from the *siluricus* zone (Late Leintwardinian in age, JEPPSSON in manuscript). The occurrence at Grogarnshuvud is slightly older (upper *ploeckensis* zone?). "*Lonchodina walliseri*" occurs in the upper *ploeckensis* zone and in the *siluricus* zone in Cellon (WALLISER 1964), and most likely it is the same subspecies described here.

Ligonodina excavata novoexcavata n. ssp.

Pl. 1, figs. 21–24; text-fig. 3

Material: 45 specimens from the Burgsvik, Hamra and Sundre Beds on Gotland.
Derivation of name: This subspecies is younger than the typical subspecies.
Holotype: The specimen of a hi element figured in Pl. 1, fig. 21 and in text-fig. 3.
Type stratum and area: The cliff section at Juves, parish of Sundre, southern Gotland, described by MUNTHE (1921). Sample G 69–47, 0.90–1.05 m below the top of the Hamra Beds, as defined by MUNTHE (op. cit.). In modern usage, this boundary is placed at a lower level in this section, and the type stratum is assigned to the Sundre Beds (Late Whitcliffian, Ludlovian, and Silurian in age). High level in the lower part of the *eosteinhornensis* zone.
Diagnosis: A subspecies of *Ligonodina excavata* with deep basal cavity, the tip of which often penetrates more than half of the process.
Description: The directions of the processes and their general shape are the same as those of *L. excavata excavata* elements. All specimens at hand are of small to medium size and much smaller than those of the nominal subspecies. They are also much more gracile than those of the nominal subspecies. These characters of the specimens from Gotland are probably significant, because they are common to all studied specimens which are derived from rather different lithologies and many different localities from the Burgsvik, Hamra and Sundre Beds. The different elements are better separated from those of *H. excavata* than those of the typical subspecies, and it is easy to separate them.
The colour is light yellow. The cusps and denticles are rounded in cross section. No basal fillings are preserved in the material studied.

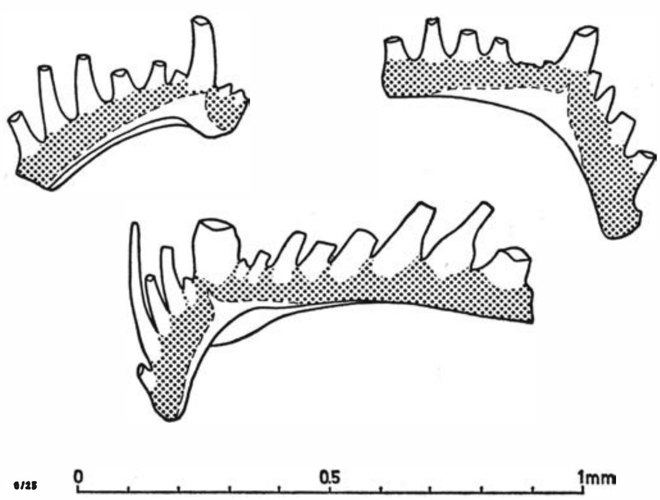

Fig. 3: *Ligonodina excavata novoexcavata* n. ssp. The same specimens as pictured on Pl. 1, figs. 21–23. The shape of the basal cavity is outlined with a dashed line.

Ne element: The cusp of the ne element is basally curved inwards and backwards. Distally it is straight. Basally the long process is directed 90–100 degrees from the cusp. Centrally it is arched to 120–135 degrees and bowed. Distally the degree of curvature decreases. The short process normally carries two denticles, and it is directed slightly downward and obliquely outward. In inner lateral view the angle with the long process seems to be nearly as small as 90 degrees. This results from large expansion of the inner side below the cusp. The axis of this expansion coincides with that of the cusp.
Hi element: Basally the cusp of the hi element is curved backward and distally it is straight. The processes are straight. The anterior-lateral process is slightly dowardly directed, and it is often directed almost straight inward. The processes are connected by thin, curved sheets on the sides of the basal cavity.
The posterior process carried at least eight denticles. The oral edge of the anterior-lateral process is directed slightly anteriorly. Basally the five or six denticles are backwardly curved, and distally they are straight. They are nearly parallel with the distal part of the cusp. The tip of the basal cavity forms a slightly curved cone. On the aboral side of the processes the cavity continues in deep and broad furrows which shallow and narrow distally.
Pl and oz elements: As in the typical subspecies the pl and oz elements are so similar that they cannot be separated. Basally the cusp is backwardly curved and slightly compressed but is straight and rounded in cross section distally. It is also slightly twisted. The posterior process is arched, and in the central part it is outwardly bowed. Distally it is straight or bowed inward. Some specimens have the outward curvature just posterior of the cusp, and some have it at midlength, combined with a twisting of the process, so that the oral edge is inwardly directed in the curve. It is possible that these differences separate the oz and pl elements, but complete elements are still too few to permit any conclusions. In the material studied, the posterior process carries four to six denticles, aligned perpendicular to the process or slightly inclined or anteriorly curved. The anterior process is arched, inwardly bowed and more or less twisted so that the oral edge can be directed outward and forward. It carries four or five reclined denticles. The basal cavity is deep and broad and continues in distally narrowing furrows beneath the processes. On specimens with the outward bow of the posterior process close to the cusp the inner side of the process is similarly expanded as on the ne element, while only the basal cavity side is expanded on the other specimens.
Tr element: Basally the cusp of the tr element is curved backward. The processes are arched and bowed and carry about six slightly recurved denticles. The basal cavity is deep and its posterior side is posteriorly and laterally expanded. It continues in narrow furrows below the processes.
Occurrence: This apparatus is known from the Burgsvik, Hamra and Sundre Beds, Gotland. The occurrences of "*Lonchodina walliseri*" in sample 37 and upwards in Cellon are of the same age, and probably it is this subspecies.

Ligonodina confluens n. sp.

Derivation of name: From the shape of the denticles on the oz element and from the supposed relations to the *Hindeodella confluens* apparatus.
Holotype: The pl element figured on Pl. 2, fig. 7 and on text-fig. 1 D.

Type stratum and area: Sample G 69–47, 0.90–1.05 m below the top of the Hamra Beds (as defined by MUNTHE 1921) at Juves. (See also p. 52 under *L. excavata novoexcavata.*) Late Whitcliffian, Ludlovian, Silurian in age.
Diagnosis: An apparatus of *Ligonodina*, with peg-like denticles except on the anterior process of the oz element, where the denticles are basally fused, and on the ne element where they are basally compressed. The hi element has a short posterior process.
Remarks: *Ligonodina confluens* is now known in the Hemse Beds and the topmost Hamra (Sundre?) Beds. The younger material is slightly different from the older, and these two types are assigned here to different subspecific taxa.

Ligonodina confluens n. ssp. 1
Pl. 2, Fig. 12–16

Material: Only five specimens are so well enough preserved to serve as the basis for a description. However, they are very well preserved and all necessary details can be studied. Two of the specimens are oz elements and there is one specimen each of the hi, pl, and tr elements. All of them are from the same sample.
Diagnosis: This subspecies has a very short posterior process on the hi element. The space between the cusp and the first denticle is not larger than the width of the cusp.
Description: The denticles are peg-like, and the space between them is about equal to their diameter. An exception is the anterior process of the oz element, which has compressed, fused denticles. Probably, the ne element is slightly different also. The hyaline matter is dark brown, but as is common in *Ligonodina*, it is almost completely replaced by diffuse white matter in mature specimens.
Oz element: One complete, large specimen and one medium-sized specimen are known. The oz element is slightly but evenly arched and bowed. The cusp is short, pointed and compressed on the medium-sized specimen but rounded on the mature specimen. Centrally the element is very thick. The posterior process is short, inwardly twisted, and it carries one peg-like functioning denticle near the tip and one nearly overgrown denticle between the cusp and the peg-like denticle. The anterior process has increased considerably in height by fusion of the base of the denticles. It carries two laterally compressed, radially directed denticles on the medium-sized specimen and on the large specimen four well developed ones. Outside these denticles are two immature denticles. Basally the distal and central parts of the compressed denticles and cusp are formed by hyaline matter. The basal cavity is shallow and very broad under the thick and basally expanded central part of the element; it narrows toward the process tips.
Ne element: The ne element is unknown, but there is little doubt that it was closely similar to that of *L. c. confluens.*
Hi element: The cusp of the hi element is long, pointed, rounded in cross section and basally recurved but distally straight. The posterior process is short and carries one peg-like denticle near the tip. The anterior-lateral process is arched, laterally directed and carries three peg-like denticles. The basal cavity is expanded below the cusp and the central part of the processes.
Pl element: The pl element is bowed, and the anterior process is arched. The cusp is short, stout, and rounded lenticular in cross section. The posterior process is short, centrally twisted outward, inwardly bowed, and it carries two peg-like denticles. The anterior process has three peg-like denticles which are about perpendicular to the process. The basal cavity is shallow and expanded below the cusp and central part of the processes where two basal cavity lips are formed. The basal cavity narrows below the processes.
Tr element: The cusp of the tr element is stout, slightly recurved basally but straight distally and has a rounded cross section. The processes are about straight, directed obliquely downward and slightly backward; they carry six peg-like denticles each, the third of which is the largest. The denticles are about parallel with the cusp.
Occurrence: Known only from the sample Grogarnshuvud 2 (G 67–33) from just below the waterlevel on the north shore. Hemse Beds.

Ligonodina confluens confluens n. ssp.
Pl. 2, figs. 1–11; text-fig. 1 D

Material: 38 specimens from the section at Juves.
Diagnosis: The nominal subspecies of *L. confluens* is characterized by the fact that many elements have a very large distance between the cusp and the first denticle on one or both of the processes.
Description: The hyaline matter is dark brown, and it is not milky as it is in mature specimens of the older subspecies. The peg-like denticles are slightly more slender and widely spaced than in the older subspecies.
Oz element: The cusp and denticles on the anterior process of the oz element are similar to those of an oz element of a *Hindeodella* apparatus, i.e. triangular in side view, laterally compressed, and basally fused on mature specimens. The straight posterior process carries three peg-like denticles on one small complete specimen, but the inner one of these is absent (resorbed?) on a large complete specimen. The root of white matter reveals its former presence. The anterior process is straight and directed obliquely downward and slightly inward; it carries two or three denticles with lenticular cross sections. The basal cavity is rather broad below the cusp and extends as narrowing furrows below the processes.
Ne element: In general shape, the ne element is very similar to that of *Hindeodella confluens.* It is separated from that of *H. confluens* by its rather long anterior process, by the fact that the processes do not grow considerably in height by fusion of the denticles, and by the rounded cross sections of the denticles above the compressed basal parts. The cusp is slightly curved inward and has a lenticular cross section. The long process is slightly arched, bowed, and directed obliquely downward. On this process, a medium-sized complete specimen carries nine denticles with basally lenticular cross sections and deep roots on the inner ones. The short process is slightly bowed outward, directed downward and carries two or three denticles, similar to those of the long process. The basal cavity is well developed, and the inner side is expanded below the cusp.
Hi element: The cusp of the hi element is long, basally recurved and directed slightly inward; it has a rounded cross section. The posterior process is comparatively short, straight or slightly arched and has one or two functioning peg-like denticles. The innermost denticle is absent (resorbed?), and a large diasthem is developed posterior to the cusp. The former presence of a denticle in this diasthem is revealed by the presence of a root of white matter, while the oral surface of the process is flat or even slightly depressed. The anterior process is straight and directed obliquely inward and downward. It carries two or three, widely spaced, backwardly curved peg-like denticles. The basal cavity is moderately developed.

P l e l e m e n t : As is the case in other *Ligonodina* apparatuses, the pl element is highly variable and occurs in slightly different varieties, which generally are intermediate in shape between the tr and the oz elements. One of these varieties is closely similar to the tr element but asymmetric, as the angles between the cusp and the processes are unequal and between the cusp and the first functioning denticle one of the processes has a large gap (the same type as described above under the hi element). Each process has about two functioning peg-like denticles.

The other type has only one, compressed, large denticle on the very short process, and probably two peg-like denticles on the other process. The distance between the cusp and the first peg-like denticle is normal, and that between the cusp and the compressed denticle is smaller.

T r e l e m e n t : The cusp of the tr element is long, basally curved slightly backward, distally straight and rounded in cross section. The processes are directed obliquely downward, and each one carries three or four peg-like, basally slightly recurved denticles. The distance between the cusp and the centralmost denticle is slightly larger than that on the tr element of the older subspecies, but it is small compared with that of the previously described variety of the pl element. The basal cavity is conical and well developed below the cusp. The posterior side is expanded and has a triangular outline.

O c c u r r e n c e : *Ligonodina confluens confluens* n. ssp. is known from the Sundre Beds exposed at Juves, which are Late Whitcliffian in age. (For details see p. 68.)

Ligonodina elegans

WALLISER, 1964, sensu JEPPSSON, 1969
Text-fig. 4

1964 *Ligonodina elegans* n. sp. – WALLISER, p. 41; Pl. 9, fig. 19; Pl. 32, figs. 16–21.

1969 *Ligonodina elegans* WALLISER, 1964 – JEPPSSON, p. 21; Fig. 4.

M a t e r i a l : The material studied includes more than 1600 discrete specimens.

R e m a r k s : Only a few details can be added to the descriptions and discussions of this species in WALLISER (1964) and JEPPSSON (1969). A discussion with Dr. S. M. BERGSTRÖM and direct comparison with material of *Plectodina* have revealed that the detortiform element may be the oz element (i.e. it corresponds to the zygognathodiform element) and that the ortuformiform element may be the pl element. The detortiform element is the most variable of the elements and includes more or less "detorted" elements. Also, the other elements are variable and it will probably be possible to divide the species into several subspecies.

The material studied covers most of the known range of the apparatus. The differences are small between my oldest material from high levels in the lower *eosteinhornensis* zone and the following levels up to and including those from the next highest level in the Beyrichienkalk (samples with the ostracodes *Nodibeyrichia tuberculata* and *Kloedenia leptosoma*, coll. and det. A. MARTINSSON). However, in a small fauna from the highest level (a sample with the ostracodes *Kloedenia wilkensiana* and *Nodibeyrichia gedanensis*, coll. and det. A. MARTINSSON) there are two hi elements of *L. elegans*, one of which has denticles alternating in size on the posterior process. As long as only this specimen was known, no conclusions about its importance could be drawn. However, a brief study of the material from Spanish Sahara, described by ETHINGTON & FURNISH (1962) showed that samples SHH-60 and SHH-61 contain a fauna which, from the evolutionary level of a few specimens of *H. steinhornensis* s. l., cannot be younger than high levels in the *eosteinhornensis* zone. There is little doubt that the material described by ETHINGTON & FURNISH (1962) as *Hindeodella* sp. is the hi element, *Apathognathus* aff. *A. lipperti* is the detortiform element, and *Neoprioniodus* sp. is the ne element of an apparatus of the *Ligonodina elegans* stock. Specimens, both of hi and pl elements, occur with denticles alternating in size – one small denticles between the normal sized ones – together with specimens with "normal" denticulation (cf. descriptions and figures in ETHINGTON & FURNISH 1962). So far, it is not known if the oz, ne, and tr elements had alternating denticulation. Another yet unanswered question is whether this variety was occasional and short lived, or if it replaced the older variety in higher beds.

As it is now, this part of the material from sample SHH-60 and SHH-61 is best correlated with the uppermost Beyrichienkalk. This fauna is probably characteristic for the very latest Pre-Gedinnian (cf. MARTINSSON 1965, 1967).

O c c u r r e n c e : The *Ligonodina elegans* apparatus is very common in the upper *eosteinhornensis* zone, but it occurs also in the lower *eosteinhornensis* zone. In Sweden, however, it is rare in the latter unit, and it is known only from high levels of the lower *eosteinhornensis* zone. However, WALLISER (1964) reported *L. elegans* (only the hi element was then included under this name) from a sample with "*Spathognathodus*" *crispus* from Santa Creu at Barcelona, i.e. in the zone below the *eosteinhornensis* zone. Two less well preserved specimens of this stock are also known from the *siluricus* zone, but they are slightly different from the material from the *eosteinhornensis* zone.

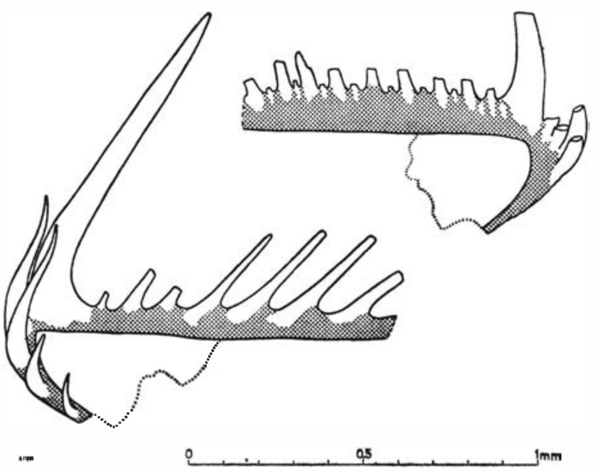

Fig. 4: *Ligonodina elegans* s. l.; two hi elements from sample Geschiebe Jar 8 (with the ostracodes *Nodibeyrichia gedanensis* and *Kloedenia wilckensiana*, coll. and det. Dr. A. MARTINSSON) from Jarosławiec (Jershöft) Pommern (cf. MARTINSSON 1965). Preserved parts of the basal filling outlined with dotted line. LO 4395, 4396.

Hindeodella excavata (BRANSON & MEHL, 1933)

JEPPSSON, 1969
Pl. 1, fig. 30, text-fig. 1 A

1933 *Prioniodus excavatus* BRANSON and MEHL, n. sp. – p. 45; Pl. 3, figs. 7, 8.

1969 *Hindeodella excavata* (BRANSON & MEHL, 1933) – JEPPSSON, p. 18; Figs. 1 G–L, 3.

Material: More than 6000 discrete conodont elements.
Remarks: *Hindeodella excavata* (BRANSON & MEHL, 1933) is now among the best known apparatuses and only a few details can be added. As shown by WALLISER (1957) the type of *Trichognathus excavata* is different from most material assigned to this form species. JEPPSSON (1969) noted that the tr element of *Hindeodella excavata* is very similar to that of a *Ligonodina* apparatus. A study of BRANSON & MEHL's material revealed that the type specimen of *Trichognathus excavata* originated from a *Ligonodina* apparatus and hence, that reference must be excluded from the list of synonyms. The best character to separate the tr element of *H. excavata* from that of *Ligonodina excavata* is that the anterior side of the cusp is basally concave and that two winglike edges form the anterior-lateral corners. That of *L. excavata* is convex with two very weakly developed anterior-lateral edges, which may be situated in a depressed "furrow" on large specimens as is the case on the type specimen. The cusp and denticles are normally compressed, while those of *L. excavata* are more rounded.
Some material from Juves (high level in the lower *eosteinhornensis* zone) is slightly different from that of the *siluricus* zone, but the known differences are not yet sufficient to erect a new subspecies.

Hindeodella confluens BRANSON & MEHL, 1933, sensu JEPPSSON, 1969
Text-fig. 1 C

1933 *Hindeodella confluens* BRANSON and MEHL, n. sp. – BRANSON & MEHL, p. 45; Pl. 3, figs. 21–23.
1969 *Hindeodella confluens* BRANSON & MEHL, 1933 – JEPPSSON, p. 15; Figs. 1 A–F, and 2 (includes synonymous specific names).

Material: The material available includes more than 3000 discrete specimens.
Remarks: As the *Hindeodella confluens* apparatus is well described, the reader is referred to the descriptions cited in JEPPSSON (1969) and the discussion in that paper. A study of the type specimens of the species, described by BRANSON & MEHL (1933) has confirmed their inclusion as younger synonyms as proposed by JEPPSSON (1969).

Hindeodella steinhornensis (ZIEGLER, 1956) s. l.

1956 *Spathognathodus steinhornensis* n. sp. – ZIEGLER, p. 104.
1964 Conodonten-Apparat J. – WALLISER, p. 14.

Remarks: The general appearance of the apparatus of *Hindeodella steinhornensis* is described by WALLISER (1964) as Conodonten-Apparat J, except that "*Plectospathodus*" *alternatus* is the pl element and that "*P. flexuosus*" and "*Ozarkodina typica typica*" must be excluded. It is also now known that *Trichonodella "symmetrica"* s. str. and *Neoprioniodus "bicurvatus"* s. str. belong to *Hindeodella confluens*; this does not affect the bulk of the material included in the apparatus by WALLISER (1964).

Genus *Pelekysgnathus* THOMAS, 1949

Remarks: *Pelekysgnathus* was described from Upper Devonian beds. Subsequent authors have also described representatives from the Lower Devonian (JENTZSCH 1962, CARLS & GANDL 1969). Its stratigraphic occurrence is scattered (e.g. it is only known from the lowermost part of the section studied by CARLS & GANDL, 1969), and the appearance of the genus in the Upper Silurian is by no means unexpected, since no ancestor is known to occur in the Lower Devonian.
The species described here coincides in most details with typical representatives of *Pelekysgnathus*. The differences are mainly found in the shape and number of the denticles. However, more mature specimens from Diddlebury have denticles that are more fused than those in the Swedish material, and *P. serrata* of the Lower Devonian also has better developed denticles than younger species.
Material, described by KOZUR (1968: Pl. 2, fig. 16) as *Gondolella (Celsigondolella) watznaueri praecursor* from Muschelkalk in Germany, is superficially very similar to the species described here.
Pelekysgnathus is closely related to *Icriodus*, as pointed out by different authors. LINDSTRÖM (1964) described the most striking similarity – a second basal cavity tip in the first denticle. It is expected that their apparatuses are similar (cf. CARLS & GANDL 1969: 163). LANGE (1968) reported two very interesting clusters, each with a pair of *Icriodus* elements and a number of *Acodina elements*. CARLS & GANDL (1969) also reported occurrence of *Acodina* together with *Pelekysgnathus* and *Icriodus*. BARNETT (1971) noted that *Icriodus woschmidti* and *Acodina* sp. had a parallel occurrence and nonoccurrence. A relationship between *Pelekysgnathus* and undenticulated elements is also suggested from the material studied by the author. This mutual occurrence may either be caused by the fact that the undenticulated elements were only a growth stage, or they may have been parts of the apparatus together with denticulated ones. The occurrence of basal cavity tips both in the cusp and the denticles may indicate that they originated as separate units, which in a later growth stage fused in the same way as the denticles of *Distomodus dubius* were fused to the cusp.
Ecology: BARNETT (1971) showed that *Icriodus woschmidti* has an ecologically restricted occurrence. The scattered occurrence of the species of *Pelekysgnathus* is evidence of similar restrictions in their occurrence.
The general picture is that these genera were able to expand their ranges into the shelf areas only during brief periods while normally they were restricted to other areas. That these periods of flourishing were not local but a least regional is evident from the appearance of the genera at about the same time in different areas. *P. dubius* appears both in Scania and on Gotland in the same time interval that *Icriodus latialatus* appears in Cellon, and after a brief visit both species disappear again before the end of the *latialatus* zone. This appearance occurs when the extremely rich and diversified *siluricus* zone fauna was transformed into the *latialatus* zone fauna by depauperation. On a larger scale is the worldwide appearance of *Icriodus woschmidti* at about the same time in different areas. However, this appearance is also controlled (modified?) by environmental factors (BARNETT 1971).
This expansion can either have been an expansion into a vacuum as the *siluricus-latialatus* border events can be interpreted, or have had genetic causes as the rich Devonian *Icriodus* diversification may indicate.

Pelekysgnathus dubius n. sp.
Pl. 1, figs. 14–20, text-fig. 5

Material: 40 specimens from Scania, two from Gotland and eight from Britain.
Derivation of name: *Pelekysgnathus dubius* n. sp. differs more from the type species than do most other species.

Another reason for this name is the supposed relations to *Distomodus dubius*.

Holotype: The specimen figured in Pl. 1, fig. 17, originating from sample Lunnarne 1 c, from material excavated about 50 m S of the road bridge at the boundary between the parishes of Gudmundtorp and Bosjökloster, Skåne, Sweden. The age is youngest Leintwardinian (or possibly oldest Whitcliffian), Ludlovian, Silurian.

Diagnosis: A species of *Pelekysgnathus* with denticles that are few in number, have a long free part, and which are similar to the cusp in shape and size.

Orientation: The specimens are orientated in accordance with LINDSTRÖM (1964), i.e. the process is anterior, and the denticle-like structure, the base of which is partly compressed, is the cusp. The side with an obvious fold in the basal cavity is the inside.

Description: The cusp of *Pelekysgnathus dubius* n. sp. is as large as, or larger than, the denticles. Its shape is similar to that of the denticles, which are strongly compressed laterally and in lateral view triangular (between 0.5 and 2 times higher than their width; it is the lowest ratio in mature specimens). On mature specimens the lower parts of the cusp and denticles are fused. As in other species of this genus the process is different from that of the bar elements, in which the cross section is massive with a shallow, basal groove. Instead, the bases of the denticles are connected directly with the expanded basal cavity. The bases of the cusp and the denticles form an arch with the denticles more or less centrifugally directed. As in other species of *Pelekysgnathus* the basal cavity has more than one tip – one in the cusp and at least in some specimens one in each of the following denticles. There are two unbroken specimens, 160 and 300 μ long, with one denticle; three unbroken specimens, 375, 400, and 425 μ long, with two denticles; and some specimens with three denticles. The largest specimen studied has three denticles left; originally it probably had four or more. There are also a few small specimens, which belong to this species and which consist of only a cusp (denticle?).

Fig. 5: *Pelekysgnathus dubius* n. sp. The same specimens as pictured in Pl. 1, figs. 14–16. The shape of the basal cavity is outlined with a dashed line.

The basal cavity is strongly expanded to an elongated dome-shaped structure and extends below the whole element, except the posterior part of the cusp. The aboral parts of the conodont proper are broken, but the edges of the remaining parts are very thin; they probably covered the whole oral surface of the basal filling, which is large and brittle. Nothing of its margins or aboral surface is preserved, but the remaining parts fill the whole basal cavity, to which it is strongly fixed. The volume of the basal filling is much larger than that of the conodont proper. The basal cavity is constricted beneath the posterior end of the cusp, but the expansion starts below about the middle of the cusp and reaches on the inner side nearly 90 degrees below the anterior part of the cusp. Just anterior of this point there is a fold in the wall of the basal cavity, and behind this fold the basal cavity slowly decreases in width.

The specimens consisting of only a cusp (?) differ from this description in that most of the sides of the basal cavity are absent.

Also, two rather small specimens differ from this description. The first one has one denticle on the oral side of the inner expansion of the basal cavity. The second one also has an extra denticle on the oral side of the basal cavity, but behind the cusp the denticle row, consisting of two denticles, is strongly curved inward. On the inner side of the cusp, both specimens have a thin ridge, which continues to the extra denticle and over it. The second specimen also has such a ridge on the inside of the second denticle. The other specimens have normally developed, thin ridges reaching from the anterior to the posterior end and continuing into the edges of the cusp and denticles.

Occurrence: *Pelekysgnathus dubius* occurs in the following samples. Scania: Bj 1 a and Bj 67–44 from Bjärsjölagård, Kl 69–9 from Klinta and Lunnarne 1 a, 1 b, 1 c, and II. These samples are from the lower *latialatus* zone. A single uncertain specimen also occurs in Tulesbo I from the lowermost *eosteinhornensis* zone. Gotland: G 67–54 from Gogs and G 69–47, both from the uppermost Hemse Beds, the first sample probably from the very top of the *siluricus* zone and the second one from the lower *latialatus* zone. In the Welsh Borderland this apparatus occurs in a sample from Diddlebury from the lower *eosteinhornensis* zone in Late Whitcliffian.

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References

BARNETT, Stockton G. (1971): Biometric determination of the evolution of *Spathognathodus remscheidensis*: A method for precise intrabasinal time correlations in the Northern Appalachian. — J. Paleontol. **45**: 274–300, Tulsa.

BERGSTRÖM, Stig M. (1968): Biostratigraphy of the Lower Ordovician sequencee at Skattungsbyn, Dalarna (Abstract). — Geol. Fören. Stockholm Förhandl. 90: 454, Stockholm.

BERGSTRÖM, Stig M. & SWEET, Walter C. (1966): Conodonts from the Lexington Limestone (Middle Ordovician) of Kentucky, and its lateral equivalents in Ohio and Indiana. — Bull. Am. Paleont. 50: 229, 269–441, Ithaca.

BRANSON, E. B. & BRANSON, C. C. (1947): Lower Silurian conodonts from Kentucky. — J. Paleontol. **21**: 549–556, Tulsa.

BRANSON, E. B. & MEHL, M. G. (1933): Conodont studies number 1. — Univ. Missouri Studies., **8**: 1–72, Columbia, Missouri.

CARLS, Peter & GANDL, Josef (1969): Stratigraphie und Conodonten des Unter-Devons der Östlichen Iberischen Ketten (NE Spanien). — N. Jb. Geol. Paläont. Abh., **132**: 155–218, Stuttgart.

ETHINGTON, R. L. & FURNISH, William M. (1962): Silurian and Devonian conodonts from Spanish Sahara. — J. Paleontol., **36**: 1253–1290, Tulsa.

HUCKRIEDE, Reinhold (1958): Die Conodonten der mediterranen Trias und ihr stratigraphischer Wert. — Paläont. Z., **32**: 141–175, Stuttgart.

JENTZSCH, Ingrid (1962): Conodonten aus dem Tentaculiten-Knollenkalk (Unterdevon) in Thüringen. — Geologie, **11**: 961–985, Berlin.

JEPPSSON, Lennart (1969): Notes on some Upper Silurian multielement conodonts. — Geol. Fören. Stockholm Förhandl., **91**: 12–24, Stockholm.

— (1971): Element arrangement in conodont apparatuses of *Hindeodella* type and in similar forms. — Lethaia, **4**: 101–123, Oslo.

— (Manuscript): Upper Silurian conodonts of Southern Sweden.

KOHUT, J. J. & SWEET, W. C. (1968): The American Upper Ordovician standard. X. Upper Maysville and Richmond conodonts from the Cincinnati Region of Ohio, Indiana and Kentucky. — J. Paleontol., **42**: 1456–1477, Tulsa.

KOZUR, Heinz (1968): Conodonten aus dem Muschelkalk des germanischen Binnenbeckens und ihr stratigraphischer Wert. Teil 1. Conodonten vom Plattformtyp und stratigraphische Bedeutung der Conodonten aus Oberen Muschelkalk. — Geologie, **17**: 930–946, Berlin.

LANGE, Friedrich-Georg (1968): Conodonten-Gruppenfunde aus Kalken des tieferen Oberdevon. — Geologica et Palaeontologica, **2**: 37–57, Marburg.

LINDSTRÖM, Maurits (1964): Conodonts. — 196 p., Amsterdam, London, New York (Elsevier).

— (1970): A suprageneric taxonomy of the conodonts. — Lethaia, **3**: 427–445, Oslo.

MARTINSSON, Anders (1965): The Siluro-Devonian genus *Nodibeyrichia* and faunally associated kloedeniines. — Geol. Fören. Stockholm Förhandl., **87**: 109–138, Stockholm.

— (1967): The succession and correlation of ostracode faunas in the Silurian of Gotland. — Geol. Fören. Stockholm Förhandl., **89**: 350–386, Stockholm.

MOSHER, J. Cameron (1968): Triassic conodonts from western North America and Europe and their correlation. — J. Paleontol., **42**: 895–946, Tulsa.

MUNTHE, Henrik (1921): Beskrivning till kartbladet Burgsvik jämte Hoburgen och Ytterholmen. — Sveriges Geologiska Undersökning, Ser Aa, **152**: 172 p., Stockholm.

RHODES, F. H. T. (1952): A classification of Pennsylvanian conodont assemblages. — J. Paleontol., **20**: 886–901, Tulsa.

— (1953): Some British Lower Palaeozoic conodont faunas. — Phil. Trans. Roy. Soc. London, Ser B., **237**: 261–334, London.

SCHMIDT, H. (1934): Conodonten-Funde in ursprünglichem Zusammenhang. — Paläont. Z., **16**: 76–85, Stuttgart.

SCOTT, H. W. (1934): The zoological relationships of the conodonts. — J. Paleontol., **8**: 448–455, Tulsa.

— (1942): Conodont assemblages from the Heath formation, Montana. — J. Paleontol., **16**: 293–300, Tulsa.

SWEET, Walter C. (1970): Uppermost Permian and Lower Triassic conodonts of the Salt Range and Trans-Indus Ranges, West Pakistan. — *In* Stratigraphic boundary problems: the Permian and Triassic of West Pakistan, Kansas Univ. Dept. Geol., Spec. Publ., **4**: 207–275, Lawrence.

— & BERGSTRÖM, Stig M. (1969): The generic concept in Conodont Taxonomy. — Proceedings of the North American Paleontological Convention, Part C: 157–173.

THOMAS, Leo (1949): Devonian – Mississippian formations of southeast Iowa. — Bull. Geol. Soc. Am., **60**: 403–438, New York.

WALLISER, Otto H. (1957): Conodonten aus dem oberen Gotlandium Deutschlands und der Karnischen Alpen. — Notizbl. Hess. Landesamtes Bodenforsch., **85**: 28–52, Wiesbaden.

— (1964): Conodonten des Silurs. — Abh. Hess. Landesamtes Bodenforsch., **41**: 106 p., Wiesbaden.

WEBERS, Gerald F. (1966): The Middle and Upper Ordovician conodont faunas from Minnesota. — Minn. Geol. Surv., SP **4**: 123 p., Minneapolis.

ZIEGLER, Willi (1956): Unterdevonische Conodonten, insbesondere aus dem Schönauer- und dem Zorgensis-Kalk. — Notizblatt Hess. Landesamtes Bodenforsch., **84**: 93–106, Wiesbaden.

— (1960): Conodonten aus dem Rheinischen Unterdevon (Gedinnium) des Remscheider Sattels (Rheinisches Schiefergebirge). — Paläontol. Z., **34**: 169–201, Stuttgart.

Plate 1

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Figs. 1–13: *Distomodus dubius* (RHODES, 1953). All samples are from Skåne, Sweden. Samples Bj 67– are from the ditch at Bjärsjölagård, samples Lunnarne 1 b and 1 c are from material excavated in the ditch, described in the explanation to fig. 14, and sample Kl 67–17 is from a section measured at Klinta, parish of Bosjökloster.

Fig. 1: Ne element. Sample Bj 67–44. LO 4397.
Figs. 2–3: Hi element. Sample Bj 67–36. LO 4398, 4399.
Fig. 4: Hi element. Sample Bj 67–44. LO 4400.
Fig. 5: Tr element. Sample Bj 67–44. LO 4401.
Fig. 6: Tr element. Sample Lunnarne 1 b. LO 4402.
Fig. 7: Pl or oz element. Sample 67–38. LO 4403.
Fig. 8: Pl or oz element. Sample 67–36. LO 4404.
Fig. 9: Pl or oz element. Sample Lunnarne 1 b. LO 4405.
Fig. 10: Sample Bj 70–1. LO 4406.
Figs.11–12: Sample Bj 67–27. LO 4407, 4408.
Fig. 13: Sample Kl 67–17. LO 4409.

Figs.14–17: *Pelekysgnathus dubius n. sp.* All specimens are from the lower part of the *latialatus* zone and either latest Leintwardinian or earliest Whitcliffian, Ludlovian, Silurian in age.

Fig. 14: Sample Lunnarne 1 b from material excavated in the ditch about 50 m S of the road bridge at the boundary between the parishes of Gudmundtorp and Bosjökloster, Skåne, Sweden. LO 4410.
Fig. 15: Sample Kl 69–9 from a section measured in the cliff 300 m ESE of Vrangelsborg, parish of Bosjökloster, Skåne, Sweden. LO 4411.
Fig. 16: Sample Bj 67–44 from the ditch at Bjärsjölagård, Skåne, Sweden. LO 4412.
Fig. 17: Holotype. Sample Lunnarne 1 c. The same locality as the specimen on fig. 14. LO 4413.

Figs.18–20: *Pelekysgnathus dubius* n. sp. The specimens are derived from material in the collections in Lund labelled "Bjärsjölagård lag 1 a". At Bjärsjölagård "lag 1 a" includes beds from the lowermost *latialatus* into the lower *eosteinhornensis* zone, but from the conodont fauna, it is probable that the sample originates from the same level as the specimens in figs. 14–17.

Fig. 18: Specimen with two denticles in oral view. LO 4414.
Figs.19–20: Two abberant specimens. LO 4415, 4416.

Figs.21–24: *Ligonodina excavata novoexcavata* n. ssp. The same specimens as in Text fig. 3. All four specimens are from sample G 69–47. For further details see legend to Pl. 2, figs. 1–11.

Fig. 21: Hi element. Holotype. LO 4417.
Fig. 22: Ne element. LO 4418.
Fig. 23: Oz or pl element. LO 4419.
Fig. 24: Tr element. LO 4420.

Figs.25–29: *Ligonodina excavata excavata* (BRANSON & MEHL, 1933). The same specimens as in Text fig. 1 B. All five specimens are from sample ES 137 (coll. Dr. A. Martinsson) from Millklint, parish of Gammelgarn, Gotland. The sample is from the Millklint Limestone, Hemse Beds. It is Leintwardinian, Ludlovian and Silurian in age and belongs to the *siluricus* zone.

Fig. 25: Hi element. LO 4421.
Fig. 26: Ne element. LO 4422.
Fig. 27: Oz or pl element. Cristagalliform element. LO 4423.
Fig. 28: Oz or pl element. Walliseriform element. LO 4424.
Fig. 29 a and b: Tr element. Anterior and posterior view, respectively. LO 4425.
Fig. 30: *Hindeodella excavata* (BRANSON & MEHL, 1933). Tr element. Anterior view. Sample ES 137 (coll. A. Martinsson). For details, see figs. 25–29. LO 4388.

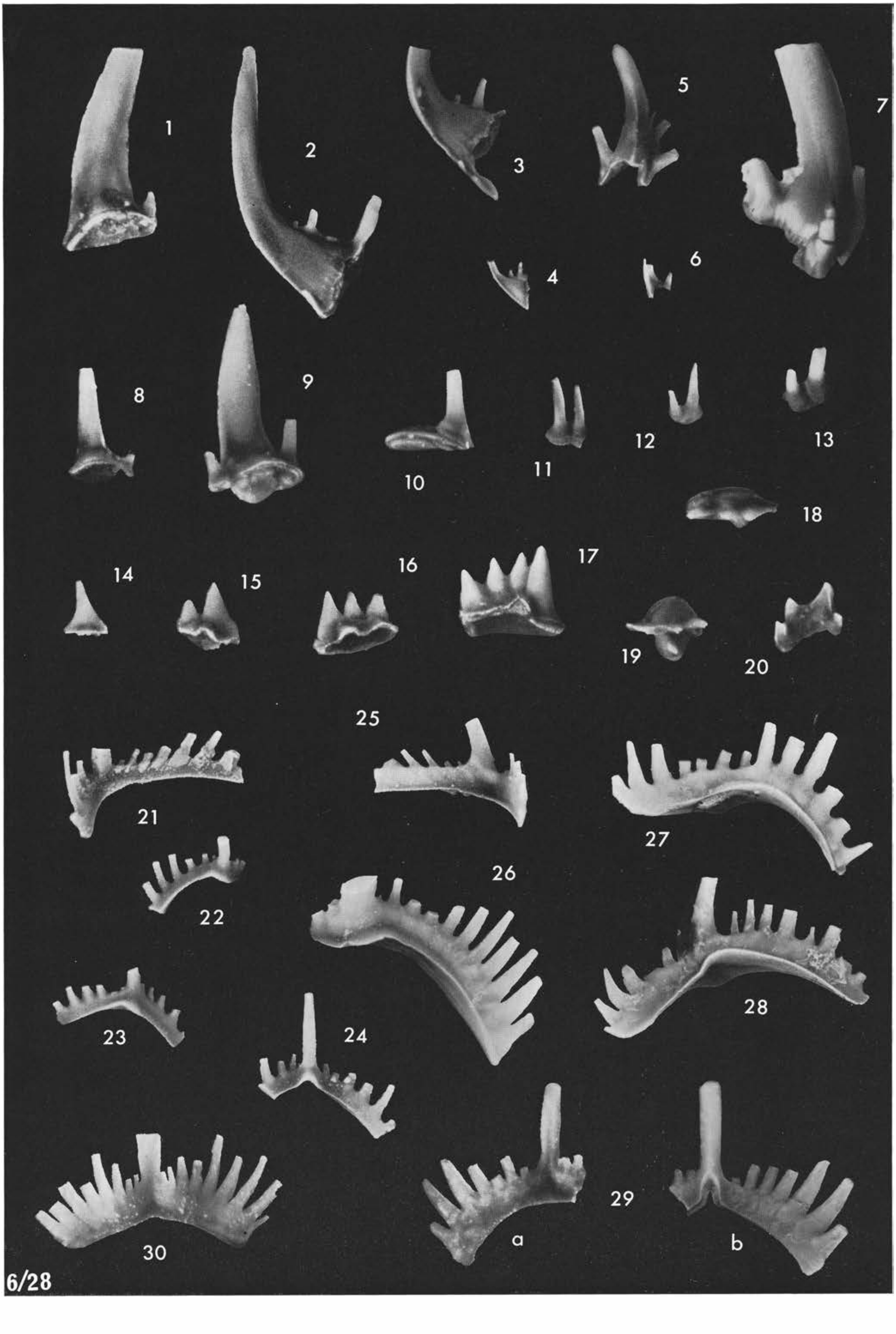
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Plate 2

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Figs. 1–11: *Ligonodina confluens confluens* n. sp. All the specimens are derived from three samples collected from the cliff section at Juves, parish of Sundre, Gotland, Sweden. Sample G 69–49 was collected 0.0–0.1 m below the boundary between the Sundre and Hamra beds as defined by MUNTHE (1921), sample G 69–48 from 0.9–1.05 m below this boundary and G 66–108 (coll. Dr. Sven Laufeld) 1.15 m below this boundary. In modern literature (e.g. Martinsson 1967) this boundary is drawn at a lower level in this section and the sampled interval is placed in the Sundre Beds. The sampled interval is Late Whitcliffian, Ludlovian, and Silurian in age. High level in the lower part of the *eosteinhornensis* zone.

Fig. 1: Oz element. The same specimen as in Text fig. 1 D. Sample G 69–49. LO 4426.

Fig. 2: Oz element. Small specimen with the inner denticle on the posterior process still functional. Sample G 69–49. LO 4427.

Fig. 3: Ne element. The tip of the long process is broken. The same specimen as in Text fig. 1 D. Sample G 69–47. LO 4428.

Fig. 4: Ne element. This specimen is in an earlier ontogenetic stage than that in fig. 3. Parts of the basal filling are preserved. Sample G 69–47. LO 4429.

Fig. 5: Hi element. Small specimen with only one functional denticle on the posterior process. The tip of the anterior lateral process is broken. Sample G 66–108. LO 4430.

Fig. 6: Hi element. Parts of the basal filling are preserved. The same specimen as in Text fig. 1 D. Sample G 69–49. LO 4431.

Fig. 7: Pl element. Holotype. The same specimen as in Text fig. 1 D. Sample G 69–47. LO 4432.

Fig. 8: Pl element. Small specimen. Sample G 69–47. LO 4433.

Fig. 9: Pl element. The process to the right in the figure is broken. Sample G 69–49. LO 4434.

Fig. 10: Pl element. Sample G 69–47. LO 4435.

Fig. 11: Tr element. Large specimen. The same specimen as in Text fig. 1 D. LO 4436.

Figs.12–16: *Ligonodina confluens* n. ssp. All specimens are from sample Grogarnshuvud 2 (G 67–33) from just below the waterlevel on the north shore of Grogarnshuvud, parish of Östergarn, Gotland, Sweden. The sampled interval belongs to the Hemse Beds and is Leintwardinian or possibly Bringewoodian, Ludlovian, and Silurian in age and belongs either to the upper *ploeckensis* zone or, less probable, to the lower *siluricus* zone.

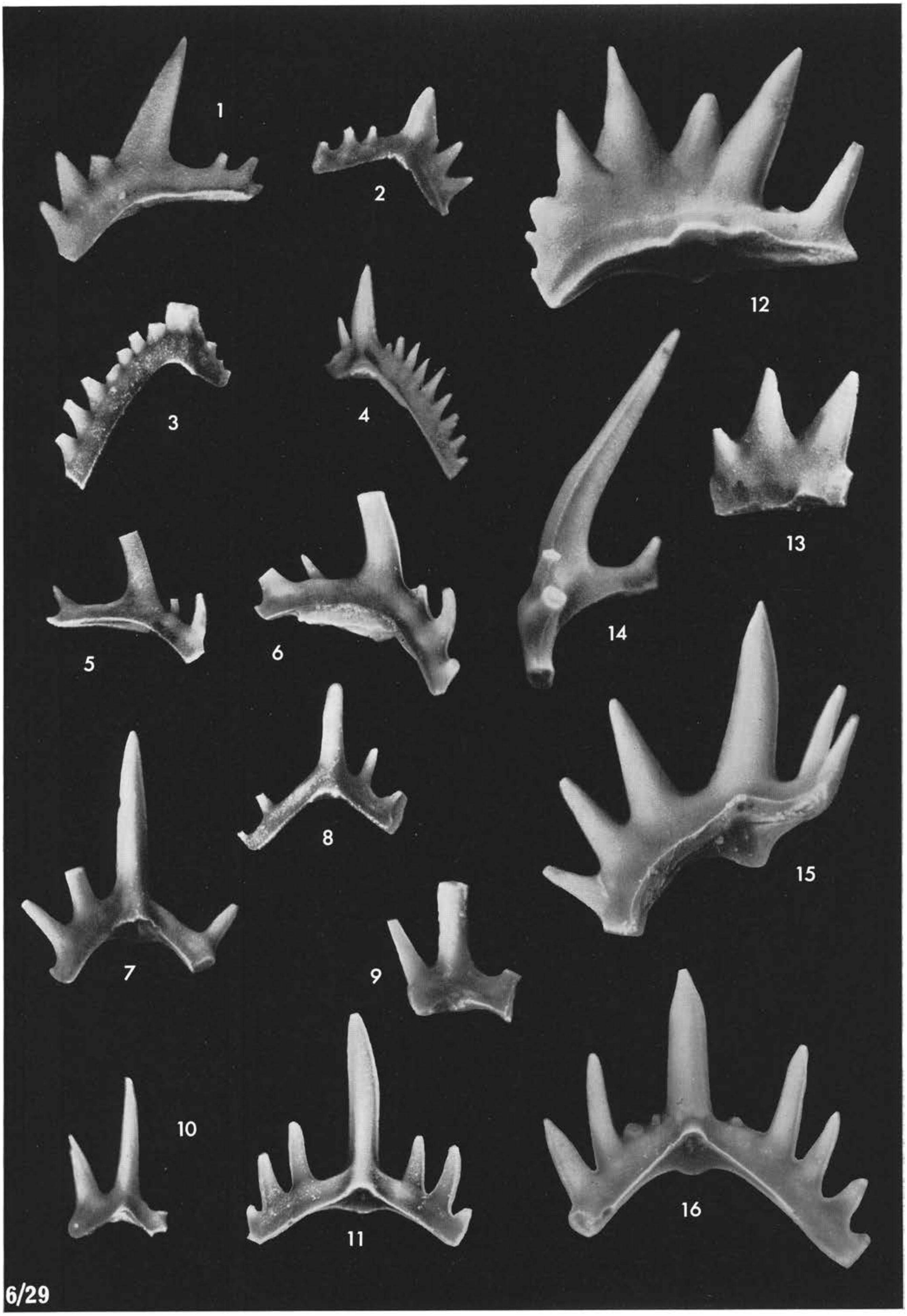
Fig. 12: Oz element. LO 4437.

Fig. 13: Oz element. Small specimen with the posterior process broken. LO 4438.

Fig. 14: Hi element. The tip of the anterior lateral process is broken. LO 4439.

Fig. 15: Pl element. LO 4440.

Fig. 16: Tr element. The tip of the right process is broken. LO 4441.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