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Conodonts from the Ludibundus Limestone (Middle Ordovician) of the Tväreu area (S.E. Sweden)

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With 5 plates and 5 figures in the text

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ABSTRACT

Conodonts have been isolated from erratic limestone boulders originating from the Ludibundus beds of Tväreu. In all, 24 species, three subspecies, and one variety are described. A new genus, *Tvaerenognathus*, is proposed. Two conodont faunas could be distinguished in the material. One of them, found typically developed in crystalline limestone boulders, is characterized by species of, *inter alia*, *Amorphognathus*, *Ambalodus*, *Paracordylodus*, *Tetraprioniodus*, etc. The other fauna, hitherto only found in some boulders of dense limestone, is dominated by *Strachanognathus parva*. A regional comparison with other faunas of a broadly similar age suggests that the Ludibundus limestone of Tväreu corresponds to some part of the upper Trenton in N. America.

The age of the Ludibundus limestone of Tväreu is also discussed on the basis of new finds of graptolites, which indicate the zone of *Diplograptus multidens*. It is stated that if the zone of *Nemagraptus gracilis* corresponds to the lower Ludibundus beds, at least the crystalline limestone boulders of Tväreu, which are of *multidens* age, must be regarded as belonging to a middle part of the Ludibundus beds.

Introduction

So far, very little has been known about conodonts in the Middle Ordovician of Sweden. This may at first seem to be a rather astonishing fact, since the Middle Ordovician strata in this country have been the subject of intense study, particularly during the last decades. However, microfossils, which earlier attracted little attention in Sweden, have only comparatively recently begun to be more thoroughly examined; thus many ostracode species have been shown to be stratigraphically useful. Yet, as is well known, there are still certain difficulties in correlation, particularly between shelly and graptolite-bearing facies in the Middle Ordovician of Scandinavia. This depends first and foremost on the lack of good index fossils common to both types of facies. In consequence we must look for some hitherto neglected group of fossils, which is not restricted to a certain type of facies and which occurs in some quantity. The conodonts fulfil both these requirements. These conditions, and the valuable results achieved by Lindström (cf., *inter alia*, 1955*a*) by investigations in the Lower Ordovician, encouraged a study of the conodonts in the Middle Ordovician of Sweden.

Conodonts from Middle Ordovician strata in Sweden were first reported by Hadding (1913), who described 10 species from the zone of *Climacograptus haddingi* (syn. *Cl. putillus* Hadding, non Hall, cf. Glimberg 1952) of the lower Dicellograptus shale of Scania. Thorslund (1940, pp. 114, 115) mentioned conodonts in boulders from the Tvären area but did not list any species. Nilsson (1952, p. 684) recorded from S.E. Scania some of Hadding's conodonts. From Scania, the occurrence of Middle Ordovician conodonts has also been reported by Hede (1951), Nilsson (1953), and Lindström (1953). Hadding's conodonts were redescribed by Lindström (1955*b*), and Lamont & Lindström (1957) described a new species, *Pygodus anserinus*, based on material from limestones of Llandeilian age, Isle of Öland, and from shales belonging to the zone of *Climacograptus haddingi* at Sularp, Scania. Recently Strachan (1959, p. 49) recorded conodonts from the Ludibundus beds of Tvären and Jemtland.

In this report, the conodont faunas of some erratic limestone boulders from the Tvären area will be treated. As may be gathered from the papers cited above, these faunas are the first extensive ones to be described from the Middle Ordovician of Sweden. The conodonts are unique also in being, to my knowledge, the first ones to be reported from shelly facies with graptolites, which even permit a placing in the standard graptolite succession. The main purpose of this paper is, accordingly, to describe these stratigraphically fairly fixed conodont faunas and, at the same time, to examine their affinities with other faunas of a similar age. In addition, the age of the Ludibundus limestone of the Tvären area is discussed, mainly on the basis of new finds of graptolites.

I am greatly indebted to my teachers, Professor Gerhard Regnéll, Director of the Institute of Paleontology, University of Lund, and Dr. Maurits Lindström of the same Institute, for their great personal kindness, helpful advice and criticism and for the very stimulating interest they have always shown in my work. Without their generous help it would have been impossible for me now to present this report. To Professor Walter C. Sweet, the Ohio State University, Columbus, U.S.A., I wish to convey my sincere thanks for his great kindness in reading the manuscript, for his many suggestions regarding linguistic improvements of it, and for valuable information about N. American conodonts and stratigraphy. I also want to express my gratitude to the authorities of the Paleontological Institute of Uppsala for their

kindness in placing additional material from Tvären at my disposal. To Mr. Ragnar Nilsson, Lund, I wish to direct special thanks for his determination of the graptolite material and for valuable information about the vertical distribution of some graptolites in Scania. I also gratefully acknowledge a grant from the Geological Field Society of Lund (Lunds Geologiska Fältklubb) that made it possible for me to visit the Tvären area in the summer of 1958.

I. The Tvären limestones and their fauna

Occurrence

The area here referred to as the Tvären area is situated about 70 km S.S.E. of Stockholm, on the east coast of Sweden, and includes the bay of Tvären and the archipelago south of it, in which the largest islands are Ringsö, Långö, and Hartsö. The bed-rock in this area consists of Archean rocks (cf. Stolpe 1874), but in 1927 boulders of Cambro-Silurian age were found on the island of Ringsö. Investigations by, in particular, Thorslund (1930, 1940) showed that erratic boulders of Ordovician rocks, mainly fossiliferous limestones, but also sandstones and conglomerates, were distributed over a large part of the archipelago S.S.E. of the bay of Tvären and in places were rather common. According to Asklund (cf. Asklund in Ramsay 1931, p. 372) Tvären is a cauldron, caused by faulting in post-Silurian time. By these dislocations, Cambro-Silurian strata should have been lowered and thus preserved in the deeper parts in the middle of the bay. From these beds, boulders have been transported by glacial drift in the flow direction of the ice, which is indicated as glacial striae (see map in Thorslund 1940, p. 110), and then deposited. The boulders form a "boulder fan" with its apex pointing towards the centre of Tvären, thus clearly indicating the location of the area from which the erratic boulders were derived. The Cambro-Silurian strata of Tvären are thus known only as erratic boulders, but by studies of these it has been possible to reconstruct at least the chief outlines of the sequence.

Lithology, etc.

Among the Cambro-Silurian boulders of the Tvären area, at least three main lithological types may be distinguished, which in all probability originate from the sequence of Tvären, viz.: (1) Limestone; (2) Calcareous sandstone; and (3) Conglomerate.

The sandstone and the conglomerate are very poor in fossils and their age is somewhat uncertain. In any case, however, they are Ordovician. According to Thorslund (1940, p. 119) the sequence of Tvären begins with the conglomerate, which is overlain in turn by the sandstone and limestone. I have dissolved a small sample of the sandstone and the matrix of some conglomerate boulders[1] but have not found any microfossils; therefore these parts of the sequence will not be treated further in this paper.

Whereas the sandstone and conglomerate boulders are very rare, the limestone boulders are rather common to abundant on the islands in the Tvären area, particularly along the shores of the north and west sides of the island of Ringsö, where, locally, up to 50 % of all rubblestones are limestone.

[1] From pebbles of "Orthoceratite" limestone, originating from two big conglomerate boulders at the farm of Kullbo, Island of Ringsö, a well-preserved conodont fauna was dissolved. According to oral communication by Dr. Maurits Lindström the fauna indicates an age, corresponding to the uppermost "Limbata" or lowermost "Asaphus" limestone (Arenigian). The conglomerate should accordingly be younger than lower Arenigian.

As a rule, the limestone is brownish grey, crystalline and medium coarse, sometimes somewhat silicified. It occurs as fragments varying considerably in size, from pebbles and granules to boulders with a diameter of 0.4 m or more.

Another type of limestone is light-grey to yellowish grey, dense, very fine-grained and sometimes somewhat marly. Fragments of this limestone are comparatively rare and all those I have found have been of a small size, the biggest being less than 1.5 dm in diameter.

Fairly often small lenses of fine-grained, grey, marly limestone occur scattered in boulders of brownish crystalline limestone. These lenses, however, generally have crystalline parts and are also in some other respects different from the typical compact limestone. Neither type generally shows any definite bedding-planes, but in a few boulders an alternation between layers of different colour or crystal size has been observed. Very characteristic of the limestones of the Tvären area is a certain content of terrigenous matter, seemingly derived from the Archean rocks in the area. Sometimes, when the rock fragments are numerous, the limestones are almost conglomeratic (cf. picture in Thorslund 1940, p. 113).

Fauna

The limestones are as a rule fairly richly fossiliferous; yet, in the dense light-grey limestones fossils are rather sparse. The fossils are well preserved but often fragmentary. The trilobites have been described by Thorslund (1940). The predominant elements of the fauna are brachipods which are relatively common, and include, *inter alia*, *Hesperorthis inostranzefi* (Wysog.), *Nicolella salme* Öpik, *Platystrophia lynx* (Eichw.), *Leptelloidea musca* Öpik, and *Rafinesquina dorsata* Bekker (cf. Thorslund op. cit.). Trilobites, always in a fragmentary state, are sparse, but *Pharostoma similis* Thorsl. and *Asaphus ludibundus* Törnq. (= *Asaphus nieszkowskii* Fr. Schmidt in Thorslund 1940, cf. Jaanusson 1953, p. 407) are not uncommon. Among other macrofossils found in limestone boulders from Tvären may be mentioned graptolites (see below), gastropods, lamellibranchs, and bryozoans. Microfossils are as a rule numerous in the limestones. Ostracodes are particularly abundant and well preserved in the crystalline boulders. Thorslund (1940) listed 22 species, including nine new ones. Jaanusson (1957) reported in all about 30 ostracode species from Tvären, 19 of them known only from this area in Sweden. Apart from the conodonts found in all boulders examined, the microfauna consists mainly of scolecodonts and spicules of sponges. The occurrence of scolecodonts is somewhat irregular: in certain boulders, particularly the fine-grained types, they are numerous, but in others rather sparse. Spicules are not very common but seem to occur regularly in most boulders; they are represented by monaxon, tetraxon, and hexaxon types.

Age of the limestones

As Thorslund (1930, 1940) has pointed out, the fauna of the limestones from Tvären shows close affinities with those of the Kukruse (C_2) and Idavere (C_3) beds of the Estonian succession, which are regarded as equivalents of the Ludibundus beds in the standard Swedish shelly succession (cf. Jaanusson & Strachan 1954, p. 693). Thorslund (op. cit.) also referred the limestone boulders of Tvären to the Ludibundus beds (= Lower Chasmops limestone in Thorslund; cf. Jaanusson (1951)) without nearer designation of their age. However, Jaanusson & Strachan (1954, p. 687) listed *Dicellograptus divaricatus salopiensis* Elles & Wood from "limestone boulders which according to other fossils belong to the lowermost part of the Ludibundus limestone".

Recently Jaanusson (1957, p. 430) stated that "erratic boulders of the Tvären area are considered as belonging exclusively to the lower part of the Ludibundus beds". In the same publication, the Tvären boulders, from which fossils are described, are with very few exceptions assigned to the lowermost Ludibundus beds. However, no information is given of the means by which this more precise age determination was achieved. As far as I know, among the fossils hitherto listed from Tvären, only *Steusloffia multimarginata* Öpik may possibly indicate that the strata concerned belong to the lowermost Ludibundus beds. However, our knowledge of the stratigraphic distribution of the fossils in the Chasmops series of Sweden is still very imperfect.

In the summer of 1958, I collected some fresh material from limestone boulders in the Tvären area, *inter alia*, some graptolites. All these were found in boulders of more or less crystalline limestone that have as a whole a uniform conodont fauna (cf. p. 14). As mentioned above this type of limestone is completely predominant among the Tvären boulders. Most of the fossils collected in the area have undoubtedly been derived from this crystalline limestone, which is as a rule fairly rich in fossils. The homogeneous conodont fauna in all boulders examined makes it very probable that they represent the same stratigraphic unit. The uniformity of the fauna also indicates that this unit has a rather limited vertical range. Because the conodont fauna is the same, and the same macrofossils are found in all these crystalline limestone boulders, including the graptolite-bearing ones, I do not see any reason to doubt that all boulders belong to the same unit.

Among the new graptolite material from Tvären some species are stratigraphically significant, viz. *Dicellograptus sextans exilis* Elles & Wood, *Orthograptus truncatus intermedius* Elles & Wood and *O. truncatus pauperatus* Elles & Wood. *Dicellograptus sextans exilis* indicates the zone of *Nemagraptus gracilis* or a somewhat lower level (cf., for example, Elles & Wood 1913, tab. A; Hadding 1915*a*, p. 377), whereas *Orthograptus truncatus intermedius* previously had been found to be restricted to higher stratigraphic levels, viz. in Scotland the zone of *Climacograptus wilsoni* and even higher (cf. Elles & Wood 1913), and the zone of *Diplograptus multidens* and higher in Wales (cf. Dean 1958). In Sweden *Orthograptus truncatus intermedius* is listed by Thorslund (1940, pp. 88, 95) from Jemtland, together with, *inter alia*, *Dicranograptus clingani* Carr., *Climacograptus bicornis* Hall, and *Amplexograptus vasae* (Tullb.) Thus *Orthograptus truncatus intermedius* clearly indicates a stratigraphic level above the zone of *Nemagraptus gracilis*. According to Elles & Wood (1913) *Orthograptus truncatus pauperatus* is as well restricted to levels above the zone of *Nemagraptus gracilis*, viz. the zone of *Diplograptus multidens* and higher. *O. truncatus pauperatus* is recorded by Hadding (1915*b*) from as high a horizon as the zone of *Climacograptus styloideus* on Bornholm, and Henningsmoen (1948) reported it from the Black Tretaspis Shale of the Kullatorp bore-core. This species definitely indicates a level above the zone of *Nemagraptus gracilis*. Thus the two last-mentioned graptolites from Tvären give clear evidence of an age younger than that of the zone of *Nemagraptus gracilis*. On the other hand, the finding of *Dicellograptus sextans exilis* and the macrofossils other than graptolites make it rather improbable that the Tvären sequence ranges as high as into the zone of *Dicranograptus clingani*. Accordingly, it is most likely that the crystalline limestones occupy a stratigraphic position between the zones of *Nemagraptus gracilis* and *Dicranograptus clingani*. Now, as is well known, the graptolite succession between these zones is at present not safely established in Scandinavia. The status of Hadding's zones of *Climacograptus rugosus* (= *Diplograptus molestus* according to Thorslund (1948)) and *Amplexograptus vasae* (Hadding

1913, 1915*a*, 1915*b*, 1958) is not settled for a number of reasons (cf. Jaanusson & Strachan 1954). However, Mr. Ragnar Nilsson (oral communication) has recently found a graptolite fauna, including, *inter alia*, *Climacograptus antiquus* Lapw., *Diplograptus molestus* Thorsl., *Orthograptus truncatus* cf. *intermedius* E. & W., *O. vulgatus* (Lapw.), *Diplograptus multidens* E. & W., *D. multidens compactus* E. & W., and *Dicellograptus divaricatus salopiensis* E. & W. This fauna corresponds to that in the zone of *Diplograptus multidens* in Wales. The fauna was found in the core of the Koängen boring 1954 in the classical Fågelsång area in Scania. Interesting in this connexion is the occurrence of *Orthograptus truncatus* cf. *intermedius*, which is not found below the *multidens* zone in the core, and *Dicellograptus sextans exilis*, which ranges into this zone but not higher. *Dicellograptus divaricatus salopiensis*, reported by Jaanusson & Strachan (1954) from the Tvären area, occurs also in the *multidens* zone as mentioned above. Therefore, I think there are good reasons to regard these boulders from Tvären as belonging to the zone of *Diplograptus multidens*, maybe to the lower part of it. However, taking the correlation between shelly and graptolite-bearing facies in Scandinavia proposed by Jaanusson & Strachan (op. cit.; also cf. Jaanusson 1958, p. 233) for granted, one cannot regard the crystalline limestone boulders of Tvären as belonging to the lowermost or Lower Ludibundus beds, but must suppose that they represent a somewhat higher stratigraphic level, probably at least a middle part of the Ludibundus beds. Recently Hadding (1958, p. 184) and Sweet (1958, tab. 1) have published correlation charts, including, *inter alia*, the Ludibundus beds (= limestone). Hadding regarded the Ludibundus beds as equivalent to the zone of *Nemagraptus gracilis*, and the "zone of *Diplograptus molestus*" as contemporaneous with the lowermost Macrourus beds. Sweet correlated the lower part of the Ludibundus beds with the zone of *Nemagraptus gracilis* and the upper part of the same beds with the "zone of *Diplograptus molestus*". The new graptolite material from Tvären tends to support Sweet's correlation, at least in its principal parts.

To sum up, the following conclusions can reasonably be made. The crystalline limestone boulders in the Tvären area belong to the Ludibundus beds. Graptolite evidence indicates that this part of the Tvären sequence most likely is contemporaneous with the zone of *Diplograptus multidens*, possibly the lower part of it. On the other hand, many elements in the fauna show that these strata of the Tvären sequence are equivalent to the Estonian Kukruse (C_2) and, possibly, Idavere (C_3) stages (cf. Thorslund 1940, p. 114). On the supposition that the lowermost Ludibundus beds correspond to the zone of *Nemagraptus gracilis*, the zone of *Diplograptus multidens* must be correlated with a higher part of the Ludibundus beds, probably the middle of it, or possibly even higher.

II. Methods of conodont study

Reference boulder collection and samples

In order to get a representative collection of conodonts from the Ludibundus limestone of the Tvären area a number of the erractic boulders was examined. Some of these were collected in 1954 on the island of Ringsö by Prof. P. Thorslund, Dr. T. Tjernvik, and Dr. V. Jaanusson and were kindly placed at my disposal by Prof. Thorslund. Most of the boulders[1] examined were gathered by me during a stay

[1] The designation "boulder" is here used collectively for all limestones gathered, despite that some of them should more correctly be named pebbles and cobbles.

at the island of Ringsö in the summer of 1958. In collecting the boulders I was anxious not only to get good examples of limestones of the different lithological varieties occurring in the Tvären area, but also, if possible, to choose boulders containing stratigraphically useful fossils, particularly graptolites. Unfortunately graptolites are rare and sporadic in the boulders, and those found occurred almost without exception in pieces too small to yield an adequate number of specimens for a systematic examination of condodont species. Thus most of the conodonts described below do not originate from graptolite-bearing boulders; however, it should be emphasized that samples from all the graptolite-bearing limestone boulders have been searched for conodonts, and all conodonts met with in these were of exactly the same type as the other conodonts. Without any doubt they belong to the fauna represented in all examined crystalline limestone boulders of the Tvären area. The boulders in the collection were numbered and a sample, which was given the same number, was taken from each and examined for conodonts. As will be seen below, the samples are of a somewhat varying size, from c. 0.3 kg to more than 3 kg, depending mainly on the different sizes of the boulders in the collection.

The following samples were dissolved and searched for conodonts:

SAMPLE 1.—Weight: 607 g. Coll. P. Thorslund, Ringsö, 1954. Light-grey to somewhat brownish grey, dense limestone with sparse impurities, mainly scattered grains of Archean rocks. Weathered surfaces light-yellow, and under these a yellowish grey zone of about 2 cm thickness, distinctly limited from the light-grey inner parts of the boulder. Grains of quartz and biotite flakes rather common, pyrite very sparse. Macrofossils very rare, only fragments of a graptolite (indeterminable) and a trilobite cheek found. Spicules and scolecodonts rather abundant.

SAMPLE 2.—Weight: 699 g. Coll. S. M. Bergström, Ringsö, 1958. Same type as sample 1. No macrofossils found. Scolecodonts and spicules rather common.

SAMPLE 3.—Weight: 495 g. Coll. S. M. Bergström, Ringsö, 1958. Light-grey, fine-grained, somewhat marly limestone with sparse grains of Archean rocks. Weathered surfaces brownish grey. Biotite sparse, quartz still more uncommon. No macrofossils found. Ostracodes not rare, *inter alia*, *Oepikella tvaerensis* Thorsl., *Sigmobolbina variolaris* (Bonnema), and *Platybolbina* cf. *inflata* Jaanusson. Sponge spicules and scolecodonts.

SAMPLE 4.—Weight: 291 g. Coll. S. M. Bergström, Ringsö, 1958. Brownish to greenish grey, fine-grained limestone, seemingly without fragments of Archean rocks. Weathered surfaces somewhat reddish yellow. Some quartz grains. Macrofossils not uncommon but very badly preserved. *Pharostoma similis* Thorsl., brachiopod fragments. *Oepikella tvaerensis* Thorsl., scolecodonts and spicules.

SAMPLE 5.—Weight: 400 g. Coll. S. M. Bergström, Ringsö, 1958. Greenish grey, fine-grained, somewhat marly limestone without distinct bedding-planes. Weathered surfaces light brownish grey. Some pyrite grains. No determinable macrofossils found. *Tvaerenella carinata* (Thorsl.), *Oepikella tvaerensis* Thorsl., spicules and scolecodonts rather common.

SAMPLE 6.—Weight: 650 g. Coll. S. M. Bergström, Ringsö, 1958. Greenish grey to grey, very fine-grained limestone with scattered grains of Archean rocks. A distinct alternation between grey and greenish grey layers of varying thickness (most of them however thin) shows the plane of sedimentation. Pyrite rather sparse. A pygidium and some other very fragmentary parts of trilobites, and several graptolite fragments. Ostracodes abundant, *inter alia*, *Oepikella tvaerensis* Thorsl., and *Laccochilina decumana* (Bonnema). Scolecodonts and spicules.

SAMPLE 7.—Weight: 1988 g. Coll. S. M. Bergström, Ringsö, 1958. Brownish grey, medium coarse, somewhat bituminous, crystalline limestone, with irregular lenses of fine-grained, light-grey, marly limestone. Some scattered fragments of Archean rocks. No distinct bedding-plane visible. Macrofossils sparse, fragmentary. Ostracodes abundant, *inter alia, Laccochilina decumana* (Bonnema), *Oepikella tvaerensis* Thorsl., and *Sigmobolbina pentagona* Jaanuss. Some scolecodonts and spicules.

SAMPLE 8.—Weight: 1144 g. Coll. P. Thorslund, Ringsö, 1954. Brownish grey, medium coarse, crystalline limestone without distinct bedding-planes and with lenses of light-grey, fine-grained, marly limestone. In the boulder some straight, 2–3 mm wide veins of calcite were also observed but no fragments of Archean rocks. *Pharostoma* sp. and some other trilobite fragments, crinoid stems and a few poorly preserved brachiopods. Ostracodes common, e.g. *Laccochilina decumana* (Bonnema) and *Oepikella tvaerensis* Thorsl. Scolecodonts rather common, spicules rare.

SAMPLE 9.—Weight: 450 g. Coll. P. Thorslund, Ringsö, 1954. Similar to sample 8, but with a few fragments of Archean rocks. *Pharostoma similis* Thorsl. (part of a cranidium), *Asaphus ludibundus* Törnq., brachiopod fragments, crinoid stems, *Oepikella tvaerensis* Thorsl.

SAMPLE 10.—Weight: 1523 g. Coll. S. M. Bergström, Ringsö, 1958. Dark brownish grey, bituminous, crystalline limestone. Some inclusions of fine-grained, somewhat marly, light-grey limestone and several smaller fragments of Archean rocks. Scattered biotite flakes and quartz grains; pyrite aggregates rather common. A fragmentary pygidium, probably belonging to *Pharostoma similis* Thorsl., *Platystrophia* sp., *Oepikella tvaerensis* Thorsl. and several undeterminable fossil fragments.

SAMPLE 11.—Weight: 3250 g. Coll. S. M. Bergström, Ringsö, 1958. Like sample 10 but somewhat more coarse-crystalline. *Pharostoma similis* Thorsl., *Oepikella tvaerensis* Thorsl., scolecodonts and spicules.

SAMPLE 12.—Weight: 744 g. Coll. P. Thorslund, Ringsö, 1954. Light brownish grey, rather coarse-crystalline limestone with scattered fragments of Archean rocks and inclusions of almost white, marly limestone. Big calcite crystals. Biotite rather common, pyrite not found. The boulder is richly fossiliferous but the fossils are as a rule very fragmentary. *Pharostoma similis* Thorsl. (pygidium), crinoid stems, brachiopod fragments (*Sowerbyella* sp.), *Oepikella tvaerensis* Thorsl., *Laccochilina decumana* (Bonnema), *Orthograptus truncatus* cf. *intermedius* E. & W. and some other graptolite fragments.

Extraction of conodonts

The samples were crushed with a hammer to pieces of about 1 cc size, which were dissolved in 10–15 % commercial acetic acid. As a rule, the Tväre limestones, having a high $CaCO_3$ percentage, were disintegrated almost completely in 2–4 days, but in order to keep the activity of the reaction at a high level, it was necessary to change the acid 1–3 times during this period. Use of monochloracetic acid (Beckmann 1952) was tried, but the somewhat better results obtained by this method do not outweigh the much higher cost of the acid and the inconvenience caused by its poisonous nature. When the reaction had finished the residue was washed in a 0.25 mm screen under running water and then dried at about 80°C. It was found by repeated tests that all the conodont species of the Tväre boulders passed through a 1.03 mm sieve. In most samples with big residues, only the fraction that passed through this sieve was searched for conodonts. A few of the crystalline limestones were somewhat silicified and left a large residue in which conodonts were not very common. In these

cases the conodonts were separated from the matrix by bromoform. The conodonts were picked out with a marten hair brush under a binocular microscope. After this, all the residues, even the fraction above 1.03 mm, were again separated in bromoform and the residues after this treatment searched again for conodonts that might have been overlooked previously. As a rule, rather few specimens were found on this second examination.

During all stages in the extraction of the conodonts all samples were as carefully kept apart as later the conodonts were in order to make it possible to examine whether more than one fauna was represented in the material. Also, by this method it would be possible to see if the conodonts were influenced by different lithological variations of the limestones.

III. The Conodonts

Occurrence, etc.

All examined boulders of the Ludibundus limestone of the Tvären area have been found to contain conodonts, however in a somewhat varying frequency. On an average, about 10 specimens could be identified per 100 g sample, which made it necessary to work with fairly large samples, at least for Swedish conditions. In comparison with the conodont frequency in limestones from the Lower Ordovician of Sweden (Lindström 1955*a*) the frequency in the Tvären boulders is rather low. It is relatively high, however, compared with, for example, that of British Middle Ordovician strata (Rhodes 1953, p. 268). In all, more than 1300 conodonts were identified from the samples, representing 16 genera with 24 species, three subspecies and one (questionable) variety (Table 1). To this sum may be added at least 200 smaller fragments which could be fairly accurately determined as to species but which are excluded from Table 1, because of the difficulty in estimating the original number of complete specimens they represent. Further, a rather great number of specimens have been identified from graptolite-bearing boulders and from smaller samples from other boulders, collected in the Tvären area. In total, more than 1600 conodont specimens have been studied.

The conodonts are light-brown or ivory-coloured, occasionally light-grey, and as a rule lustrous. In general they are excellently preserved; however they are often somewhat broken, particularly the more fragile ones. Probably most fractures arose before extraction from the sediment; this is indicated by the fact that several fragmentary specimens were found in incompletely dissolved pieces of limestone.

Basal filling

A filling in the basal cavity of conodonts is reported by many authors (cf., for example, Rhodes 1953; Lindström 1955*a*; Müller 1956*a*; Stewart & Sweet 1956; Bischoff & Ziegler 1957), but the first detailed examination of these structures was made by Gross (1957). As previously mentioned, the Tvären conodonts are in an excellent state of preservation. A basal filling is in some species a rather characteristic and regularly occurring structure. Although a closer examination of this is beyond the scope of the present study, some short remarks may have certain interest. Gross, in his important paper of 1957, described two types of basal fillings, viz.:

(1) In conodonts from the Upper Ludlow (Beyrichienkalk) there was a filling in the basal cavity, consisting of a cone-like, excavated plug, situated between the processes with its apex in the basal cavity. The walls of this structure, which I here

Table 1.

	Sample no.											
	1	2	3	4	5	6	7	8	9	10	11	12
Ambalodus triangularis erraticus n.ssp.	—	7	2	2	—	4	44	30	4	12	14	26
Ambalodus triangularis suecicus n.ssp.	—	3	4	—	2	2	41	64	18	17	35	20
Amorphognathus elongata n.sp.	—	—	—	1	—	3	—	—	—	—	—	—
Amorphognathus ordovicica simplicior n.ssp.	—	—	—	1	—	—	3	12	—	2	—	2
Amorphognathus ordovicica simplicior var.?	—	—	—	—	—	—	—	—	—	2	—	—
Amorphognathus tvaerensis n.sp.	?2	—	?1	—	—	?1	27	11	4	8	6	10
Dichognathus typica	—	—	—	—	—	?1	—	—	—	3	—	—
Distacodus? falcatus	—	—	—	1	—	1	1	—	—	—	4	—
Drepanodus homocurvatus	—	1	—	3	3	—	21	2	—	3	4	4
Drepanodus suberectus	—	—	—	—	1	—	4	—	—	—	—	—
Falodus n.sp.	—	—	1	—	—	—	—	—	—	—	—	—
Ligonodina elongata	—	—	1	—	—	—	1	—	1	2	1	5
Oistodus excelsus	—	—	—	—	—	?1	—	—	—	1	2	—
Oistodus sp. aff. *O. inclinatus*	—	—	—	—	—	2	3	—	—	—	—	—
Oistodus robustus n.sp.	—	—	—	—	—	—	6	8	3	5	8	6
Oistodus cf. *venustus*	?1	—	1	—	—	2	1	1	—	—	—	—
Paltodus n.sp.	—	2	—	—	—	—	—	—	—	—	2	—
Panderodus acostatus	—	—	2	—	—	—	—	—	—	—	—	—
Panderodus sp.aff. *P. unicostatus*	—	3	—	—	—	—	1	1	—	2	13	8
Paracordylodus lindstroemi n.sp.	—	—	—	—	—	—	2	8	1	10	5	5
Prioniodus variabilis n.sp.	—	—	—	—	?1	?1	14	9	3	7	10	17
Roundya inclinata	—	3	8	1	—	1	3	1	1	3	—	17
Roundya sp.	—	—	—	—	—	—	—	4	—	—	—	—
Strachanognathus parva	40	115	34	77	118	132	4	9	3	14	12	7
Tetraprioniodus asymmetricus n.sp.	—	—	—	—	—	—	4	6	—	7	9	17
Tvaerenognathus ordovicica n.gen. et sp.	1	—	2	—	—	—	1	1	1	—	1	3
Total	44	134	56	86	125	151	181	167	39	98	126	147

call "basal funnel" (designation in German according to Gross: *Basistrichter*) are, according to Gross, made up of fine lamellae, parallel with the walls of the basal cavity. In the material examined by Gross these lamellae were distinguished from the other lamellae of the conodont by their brownish colour. The cavity in the basal funnel, the "funnel cavity" (German: *Trichtergrube*) could be more or less filled with a "funnel filling" (German: *Trichterfüllung*) that was not transparent and consisted of thicker, less distinct lamellae.

In a number of specimens, representing the species *Paracordylodus lindstroemi* n.sp., *Ligonodina elongata* Rhodes, *Panderodus* sp. aff. *P. unicostatus* (Branson & Mehl), and also *Prioniodus variabilis* n.sp., *Roundya inclinata* Rhodes, and *Tetraprioniodus asymmetricus* n.sp., I have found a structure at the base, which agrees closely with the above description and thus seems to be identical with that examined by Gross. In this connexion it may be mentioned that Lindström (1955*c*) has schematically figured and briefly described the same structure in specimens from Llandeilian shales

at Fågelsång, Scania. In the Tvären material a basal funnel is found in only about half the number of specimens available of the species mentioned above, whereas the other specimens lack such a structure. It must be emphasized that there is no doubt that the latter specimens do belong to the same species as the former; they are quite identical in all details except the development of a basal funnel, and it seems to me very probable that a basal funnel was originally developed in all specimens of these species. Being comparatively weakly attached to the base of the conodont, the basal funnel has subsequently become loose and dropped off. Because the presence or absence of a basal funnel thus seems to depend primarily only on the state of preservation, there is no reason to assign specimens with or without this structure to different species.

Gross stressed that in his material there was a difference in colour between the basal funnel and the rest of the conodont. This is not very conspicuous in many of the Tvären specimens. In part at least this might be a result of the fact that the Tvären conodonts as a rule are brownish while Gross' specimens seem to have been transparent or white; thus, there is generally no sharp contrast like that described by Gross between the brown funnel walls and the rest of the conodont in the Tvären conodonts. Yet, a difference in colour may sometimes be seen. Thus the basal funnel is blackish brown or almost black in some specimens, whereas the other parts of the conodont are light-brown. In other cases the whole conodont is uniformly coloured. In the former case the walls of the basal funnel are thick and have a more or less amorphous appearance. On the other hand, in the latter case, the funnel walls have almost exactly the same general appearance as the other parts of conodont, are thin and seem to consist only of laminae which connect the processes in compound conodonts. It is interesting to note that there is also a difference in the chemical composition between these types of a basal funnel. The darkish brown, amorphous type is not dissolved in diluted hydrochloric acid like the other parts of the conodont, but the other type of a basal funnel is easily dissolved. Between these types of basal funnels there is a series of transitions. I think there are good reasons to suppose that the different composition of the funnel walls may be referred to different stages in the post-mortem mineralization and fossilization process. It may be noted in this connexion that similar structures were also found by Lindström (1955*a*) in Lower Ordovician conodonts.

(2) The other type of a basal filling, described by Gross, was originally found in some specimens of, *inter alia*, *Scolopodus* cf. *striatus* Pander and *Drepanodus* sp. (=*Oistodus* sp. in Gross) from the Upper Devonian of Latvia. According to Gross this type of filling is dark reddish brown and occupies the whole or greater part of the basal cavity and is built up of large, flat lamellae parallel with the base. It is not differentiated into a basal funnel and a funnel filling.

This type of filling is common in the material from Tvären. I have found it in a great number of specimens belonging to *Amorphognathus ordovicica simplicior* n.ssp., *Am. tvaerensis* n.sp., *Ambalodus triangularis erraticus* n.ssp. and *A. triangularis suecicus* n.ssp., *Oistodus robustus* n.sp., and probably also in *Distaccdus? falcatus* Stauffer. Like the basal funnel, the filling does not occur in all specimens referred to these species. However, it occurs comparatively more commonly than the basal funnel, and the majority of the specimens have at least remains of it in the basal cavity. This filling is particularly well developed in species of *Amorphognathus*. In the rather wide and deep basal cavity of these platform conodonts, it is possible even at a low magnification to distinguish the large, flat lamellae of the basal filling. The

outer such lamellae are often developed outside the basal cavity itself; thus, they range over the margins of the cavity and form a sometimes rather thick plate which covers the whole aboral side of the conodont. In several cases an outer lamella does not completely cover the next inner one, the margins of the lamellae, when this is repeated, thus being arranged in a concentric pattern. The outer surface of the filling is in typical cases rather smooth, but has in some specimens a thin coating of pyrite. Yet, in many specimens it has a somewhat different appearance with outer lamellae white, porous and, particularly in the centre, more or less excavated, obviously partly dissolved. Undoubtedly this is a post-mortem phenomenom. All stages in the decomposition of the basal filling are represented in the material: from specimens with only the central parts of the outermost lamella destroyed, to others in which only small remains of the inner lamellae are left in the deepest parts of the basal cavity. In quite a large number of specimens, parts of, or the whole of, the basal filling are lacking, without any signs of dissolution phenomena in the remaining parts. The most probable explanation of these phenomena is that the basal filling in these specimens was but loosely attached to the walls of the basal cavity and fell away at the time of deposition or during the extraction process.

Glenister (1957, p. 722) mentioned the occurrence of an "aboral plate" in specimens of *Amorphognathus* from the Maquoketa formation. From her description it is not possible to judge whether this structure is quite identical with the basal filling described above, but it seems to me probable that this is the case.

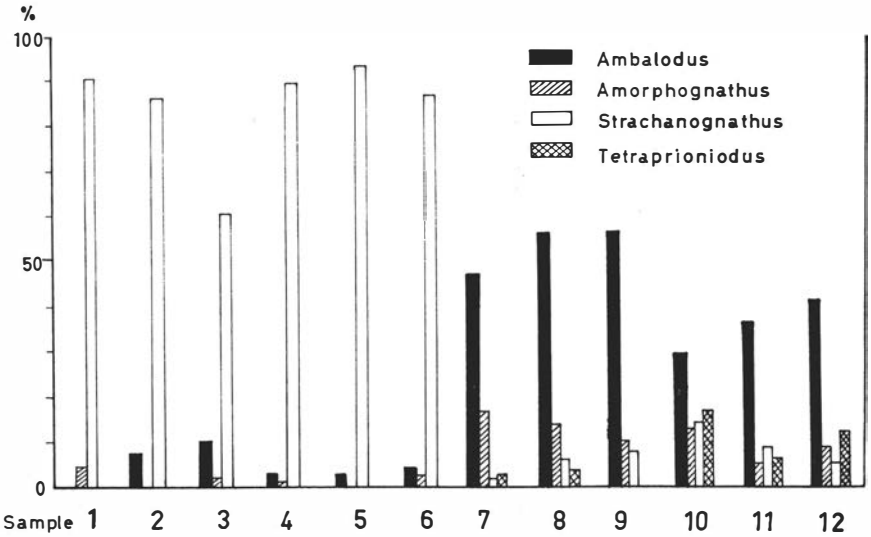
Müller (1956*a*) has discussed the occurrence in *Palmatolepis* of a basal filling apparently of a similar type to that described above. He found that it was not confined to certain stages of size but may occur in "young" as well as in "old" specimens. As a whole this applies also to the Tvären specimens. Even in small conodonts a well-developed basal filling may sometimes be seen, but in general it is more common in larger specimens. Of interest in this connexion is the finding of what seems to be an "old" specimen, judging from the very well-developed sculpture on the oral side, which had the basal filling replaced by a thin, darkish, chitinous coat, covering the inner walls of the basal cavity.

The basal fillings of *Ambalodus* and *Oistodus robustus* seem to be of the same general type as that described above in *Amorphognathus*. Also *Distacodus? falcatus* has a filling in the basal cavity and probably also belongs here; however, the basal cavity of this species is very narrow and the filling occupies only the inner part of it. A close histologic examination (including sectioning) is therefore necessary to determine the structure of the filling. Yet, a protruding basal funnel is not found in this species, so it is not probable that the filling is of the type described under (1) above.

Some aspects of the composition of the conodont faunas of Tvären

The frequency of the several species and subspecies found in the samples is given in Table 1. Samples 1–6 are taken from grey, fine-grained or dense limestones whereas 7–12 come from darker, as a rule more or less brownish grey, crystalline limestones (cf. pp. 7–8).

A study of Table 1 shows several striking features not only with regard to the distribution of conodont species but also with regard to their respective frequency in the different samples. As a whole, samples 1–6 agree fairly well to species, and this applies also to samples 7–12. As already mentioned these two groups of samples may be said to represent the two main lithological types of the Ludibundus limestone of Tvären, viz. the grey, dense or fine-grained, and the brownish grey, crystalline varie-



Text-fig. 1. Diagram showing the frequencies of some important conodont genera in the samples 1–12. The % values refer to the percentage of all conodonts in the sample that belong to a certain genus.

ties. Undoubtedly the composition of the conodont fauna of the samples 1–6 and that of samples 7–12 are so diverse that I think one is fully justified in speaking about two different conodont faunas. The first of these is characterized especially by *Strachanognathus parva* Rhodes, which completely dominates the fauna with only sporadic occurrences of other species, *inter alia*, *Amorphognathus elongata* n.sp., which is, however, found only in samples 4 and 6. Both *Ambalodus* and *Amorphognathus* are rare. On the contrary, species of *Ambalodus* and *Amorphognathus* are quite abundant in the other fauna, making up to 50 % of all specimens found. In addition, *Oistodus robustus* n.sp., *Prioniodus variabilis* n.sp., and *Tetraprioniodus asymmetricus* n.sp. are characteristic, and are found only in this fauna. *Strachanognathus parva* also occurs in samples 7–12 but only in a relatively small number.

In text-fig. 1 a comparison is given between the frequencies in samples 1–12 of *Ambalodus*, *Amorphognathus*, *Strachanognathus*, and *Tetraprioniodus*, the most common elements in these faunas. Specimens belonging to these genera are easily recognizable even in a fragmentary state; accordingly in the sums given in Table 1 even incomplete specimens have been included. As regards *Amorphognathus* only fragments comprising at least the greater part of the "platform" have been counted as one specimen, in order to avoid over-representing this genus. Even very small fragments of *Amorphognathus* can be identified readily and taking all these as representing one specimen would give a false picture of the frequency of that genus in the samples. As may be seen in the text-figure, there is a very striking difference in the frequency of these genera between samples 1–6 on one hand, and 7–12 on the other, whereas within each of these two groups, the frequency of a genus is rather constant. This figure shows clearly some of the characteristics of the two conodont faunas. At this point the question arises whether these faunas represent different stratigraphic units,

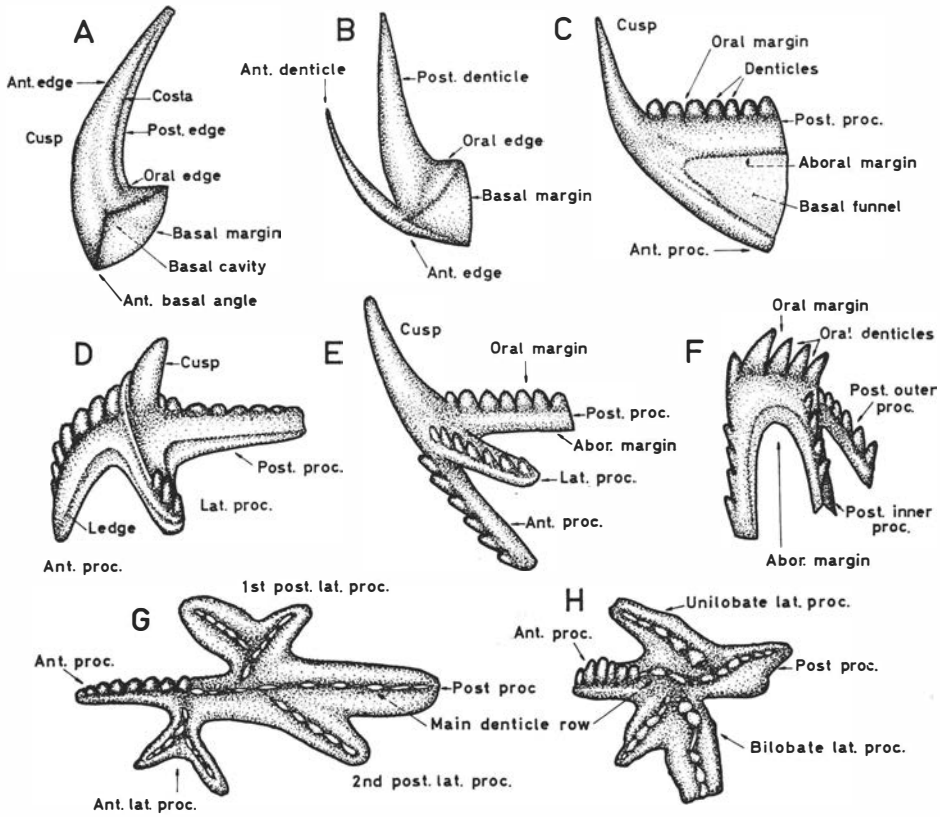
or whether the divergent composition of the faunas should be ascribed to other factors. About this problem the following may be said at present:

Although a number of samples, besides those from the boulder collection, have been examined with regard to the composition of the conodont fauna, no one among crystalline limestones has been found to contain a fauna quite similar to that of samples 1–6, in the following called the "*Strachanognathus* fauna" after its predominating element.[1] On the other hand, all dense or fine-grained limestones of the Tvären area do not carry this *Strachanognathus* fauna. In dense, grey limestones, very poor in macrofossils, it seems to occur fairly regularly, but in yellowish, sometimes somewhat marly varieties, the other fauna, here designated the "*Ambalodus* fauna" is often met with. This *Ambalodus* fauna characterizes all crystalline limestone boulders examined, the graptolite-bearing ones included.[2] The fact that the *Strachanognathus* fauna thus seems to be restricted to a certain lithological type of limestone may appear to corroborate the hypothesis that the different composition of the two faunas would depend on ecological factors. However, as is well known, the "conodont-bearing animal" seems to have been ecologically indifferent, and identical conodont faunas occur in isochronous marine strata of quite diverse types (cf., for example, Rhodes 1954, pp. 431–433; Rexroad 1958).

Thus I think there is no reason to accept this hypothesis as the only possible or most probable explanation of the problem of the two faunas. A secondary transport and deposition of *Strachanognathus* as well as an eventual "selective destruction" of other elements in the fauna of the dense limestones does not seem likely, particularly in view of the fragile nature of *Strachanognathus*. Keeping these facts in mind I think one cannot dismiss the possibility that the two conodont faunas of the Tvären limestones represent two different conodont zones and, consequently, that the crystalline limestones and the more fine-grained and dense limestones, which bear the *Strachanognathus* fauna, do not belong to exactly the same stratigraphical unit. As it has been noticed above (p. 4) the crystalline limestones are rather richly fossiliferous, and it has been demonstrated above that they in all probability correspond to the zone of *Diplograptus multidens* and possibly to the lower part of it; thus, the *Ambalodus* fauna is of *multidens* age. As for the *Strachanognathus* fauna, I am not able at present to fix its age. As mentioned, the limestones bearing these conodonts are very poorly fossiliferous and the fossils found occur also in the crystalline limestones, so that they give little help in the determination of the relative age of the limestones. Nor have I found any determinable graptolites in boulders with *Strachanognathus* fauna. Thorslund (1940, pp. 112, 114), however, listed some graptolites from "one boulder of grey, compact, but little marly limestone" which, judging from the description, probably bears the *Strachanognathus* fauna. The species mentioned by Thorslund have little stratigraphical value but Strachan (1959) added *Dicellograptus divaricatus salopiensis* E. & W., probably from the same boulder (cf. Jaanusson & Strachan 1954, pp. 687–688). This species indicates an age corre-

[1] It must be pointed out that also in crystalline limestone boulders *Strachanognathus* occasionally may occur in rather high frequencies (30–40 %). But the general character of the fauna shows that also in those cases the fauna is the *Ambalodus* fauna.

[2] Cf. sample 12. As a further example may be mentioned that from a sample with *Orthograptus truncatus pauperatus* E. & W. was dissolved a fauna, consisting of *Ambalodus* spp. (4 spms.), *Amorphognathus* spp. (7 spms.), *Oistodus robustus* n.sp. (1 spms.), *Paracordylodus lindstroemi* n.sp. (3 spms.), *Prioniodus variabilis* n.sp. (8 spms.), *Strachanognathus* (7 spms.), and *Tvaerenognathus ordovicica* n.gen. et sp. (2 spms.) thus a rather typical *Ambalodus* fauna.



Text-fig. 2. Terminology and orientation in some conodont genera. Terms used in this paper illustrated. Abor. = aboral; ant. = anterior; lat. = lateral; post. = posterior; proc. = process. A, *Acontiodus*. B, *Strachanognathus*. C, *Paracordylodus*. D, *Ambalodus*. E, *Prioniodus*. F, *Tvaerenognathus*. G, *Amorphognathus* (form similar to *A. tvaerensis* n.sp.; in other species the 2nd post. lat. proc. may be missing). H, *Amorphognathus* (transition form to *Polyplacognathus*. After specimen from lowermost Middle Ordovician strata, Isle of Öland, coll. M. Lindström).

sponding to that of the zone of *Nemagraptus gracilis* or slightly younger (cf. above p. 6).

As mentioned above Strachan (op. cit.) noticed conodonts from graptolite-bearing limestone boulders from the Tvären area. Through the courtesy of Dr. Strachan I have had the opportunity to examine his conodonts. *Strachanognathus parva* is the dominating species in the material, which in all probability belongs to the *Strachanognathus* fauna.

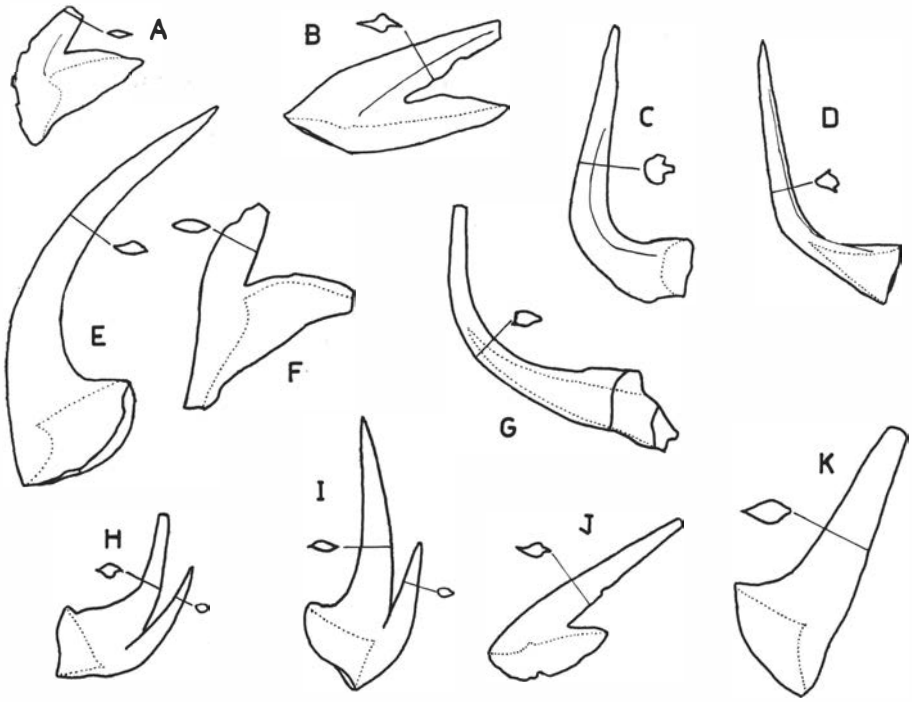
Because the vertical distribution of the conodont species which occur in the faunas now discussed is as yet almost unknown in Sweden it is impossible to arrive at safe conclusions regarding the mutual position of the faunas only on the basis of their components. The occurrence of *Oistodus robustus* and *Tetraprioniodus asymmetricus*, both having closely related forms (undescribed) in lower strata, suggests that the *Ambalodus* fauna is the older of the two faunas. On the other hand, *Amorphognathus elongata* is related to forms from the Llandeilian of Sweden (cf. text-fig. 2 H) which

might indicate that the *Strachanognathus* fauna is the older of the two. However, until more material from other localities becomes available, I think it hazardous to try to guess which of the two conodont faunas is the older; the fact that they show as a whole rather great affinities to each other, gives clear indication that the eventual difference in age cannot be great.

From a zoological point of view the *Strachanognathus* fauna has special interest. The conspicuous dominance of *Strachanognathus parva*, which sometimes totals more than 90 % of all specimens in the fauna, is quite remarkable. Mass occurrences of a single (in this case somewhat variable) species are to my knowledge very seldom reported. Lindström (1957, p. 164, Table 1) found almost half the number of specimens in a fauna from the Lower Ordovician of Sweden to belong to *Oistodus triangularis* Lindström. Bischoff & Ziegler (1957, p. 19) noticed that *Polygnathus webbi* Stauffer makes up about 50 % of the conodont fauna of the *Amplexus*-Kalk (Upper Middle Devonian, Germany). In this connexion it may be mentioned that Sannemann (1955*a*, p. 123) reported an Upper Devonian fauna with 90 % of all specimens belonging to the genus *Palmatolepis*. Now, in a natural conodont assemblage, the proportions between the different specimens which constitute the assemblage seem to be rather constant. A conodont fauna is composed of many such assemblages, probably from more than one species of conodont-bearing animals and therefore of somewhat varying composition. Yet the fact that the relative number of specimens in every assemblage seems to be constant should have the effect that in an extensive material the proportions between different conodont species will also tend to be constant, obviously even after the original assemblages have been disintegrated and their constituents mixed. That this is really so may be seen in text-fig. 1; it is true that here the frequencies of only four species are given, but I think the general tendency is clear. The predominance of *Strachanognathus* in the fauna thus indicates not only that this species was a very common element in the assemblages constituting the fauna, but also gives some support to the hypothesis that some types of these assemblages originally may have been composed exclusively of *Strachanognathus*. If this is true the name *Strachanognathus* would in fact designate a species even in a true zoological sense, viz. the conodont-bearing animal. Be this as it may, the fact remains that the conodont assemblages, which constitute this *Strachanognathus* fauna, must have been rather unique, with an appearance entirely different from the hitherto described natural assemblages (cf. Schmidt 1934; Scott 1934, 1942; DuBois 1943; C. L. Cooper 1945; Rhodes 1952), which as a rule contain 4–5 species and 10–12 specimens. As far as I know, no Middle Ordovician conodont assemblage has yet been described. Unfortunately, a reconstruction of the assemblages that constitute the faunas concerned here seems to be impossible.

IV. Significance of the conodonts

Particularly during the last decades conodonts have been proved to be very useful as guide fossils in many parts of the world. A large number of species has so far been found to be common to N. America and Europe (cf., *inter alia*, Rhodes 1953; Sannemann 1955*a*; Bischoff & Ziegler 1957), and correlations over long distances by means of conodonts have been possible in several cases (cf. Lindström 1955*a*; Lamont & Lindström 1957; Rhodes 1953, 1955; Sannemann 1955*b*). However, because only comparatively few conodont faunas have hitherto been described from the Ordovician our knowledge of the distribution and stratigraphic range of conodont



Text-fig. 3. General outlines, cross-sections, and basal cavities (dotted lines) of some specimens of simple conodonts from the Ludibundus limestone of Tvären. Half diagrammatic. Average magnification: A, B, F, H, I × 50; C, D, E, G, J, K × 40. A, *Falodus* n.sp., specimen LO 4057 t. B, *Oistodus cf. venustus* Stauffer, specimen LO 4061 t. C, *Distacodus? falcatus* Stauffer, specimen LO 4026 t. D, *Paltodus* n.sp., specimen LO 4022 t. E, *Drepanodus homocurvatus* Lindström, specimen 4068 t. F, *Oistodus robustus* n.sp., specimen LO 4043 T. G, *Panderodus* sp. aff. *P. unicostatus* (Branson & Mehl), specimen LO 4023 t. H, *Strachanognathus parva* Rhodes, specimen LO 4042 t. I, same species, specimen from sample 1. J, *Oistodus* sp. aff. *O. inclinatus* Branson & Mehl, specimen LO 4027 t. K, *Drepanodus suberectus* (Branson & Mehl), specimen LO 4059 t.

species in this portion of the stratigraphic column is still especially imperfect. This is accentuated by the fact that some important faunas, particularly among the oldest described, have been hard to place exactly stratigraphically. The possibilities of making correlations by means of conodont species are thus at present restricted to a certain degree. Most authors have correlated formations only on the basis of common genera and a general resemblance of the faunas. Indubitably such comparisons may in many cases be of great value, but I think that close correlations can be made only by means of common conodont species with known vertical ranges. However, much work remains until a "conodont chronology" of the Palaeozoic is established. Recently, extremely promising results especially for the Devonian have been reported by, *inter alia*, Bischoff & Ziegler (1957). As yet certain parts of the Palaeozoic, among those the Middle Ordovician, are not very well known as regards the conodonts. Until more material has been described I would not find it advisable to base too definite stratigraphical conclusions on the known ranges of conodont genera; in many instances new finds have materially extended the known vertical ranges of

many genera previously thought to be restricted to a certain part of the geological column. Similar discoveries may certainly be expected in the future as well.

In the material from Tvären the following species have been described previously:

Ambalodus triangularis Branson & Mehl was originally described from the Thebes sandstone, Missouri, according to Sweet (1959 *in litt.*) probably of a Maysvillian age. Later it has been reported from the following formations: The Maravillas fm. of the Marathon Basin, Texas (Graves & Ellison 1941), which is regarded as belonging to the Richmondian (Twenhofel *et al.* 1954; also cf. King 1937, p. 36); the phosphatic member of the Maquoketa fm. of Iowa (probably pre-Richmondian in age according to Glenister 1957); the Bighorn Dolomite of Wyoming (Richmondian or slightly older, cf. Stone & Furnish 1959); the Galena fm. of Iowa and Minnesota (Middle and Upper Ordovician, cf. Ethington 1959); and the Eden formation of Ohio and Kentucky (Upper Ordovician, cf. Sweet, Turco, Warner, & Wilkie 1959). In Europe this species has hitherto been recorded only from Great Britain, viz. the Gelli-grin and Pen-y-garnedd limestones (Upper Caradocian, cf. Rhodes 1953), the Keisley limestone (? Upper Ordovician, cf. Rhodes 1955, and below p. 21), and recently the Crûg limestone (Caradocian, cf. Lindström 1959). As will be demonstrated below (p. 26), this species is represented in the Tvären material by two types, which differ only slightly from the main species; in this paper they will be referred to as subspecies. One of these new subspecies is found also in the Crûg limestone. The occurrence of *A. triangularis* in the Middle Ordovician strata of Tvären is the earliest so far published. While the main species according to recent researches seems to occur through the Middle and Upper Ordovician, it is possible that at least *A. triangularis suecicus* n.ssp., described from the Tvären material, has a more limited stratigraphical range.

Amorphognathus ordovicica Branson & Mehl was also first described from the Thebes sandstone (Branson & Mehl 1933) and its stratigraphical range seems to agree closely with that of *Ambalodus triangularis*. The Tvären type is not quite identical with the American species and is described as a new subspecies. As in the case of the preceding species, the Tvären occurrence is the oldest hitherto reported.

Dichognathus typica Branson & Mehl has been found in several Middle and Upper Ordovician formations of N. America. Stauffer (1935*a*) reported it from the Glenwood beds, and similar forms are described from the Maquoketa fm. of Iowa. According to Sweet (1959 *in litt.*) the species ranges up through the Eden and the Maysville.

Distacodus? falcatus Stauffer has hitherto been described only from the Glenwood beds (Stauffer 1935*a*) and the basal part of the Decorah shale (Stauffer 1935*b*). Recently Ethington (1959) reported similar forms from the Galena fm. Probably the species is restricted to Middle and, possibly, early Upper Ordovician strata.

Drepanodus suberectus (Branson & Mehl) and *Drepanodus* spp. of "*homocurvatus*"-type seem to have a wide vertical distribution. As pointed out below, there may be differences between specimens from Lower and Middle Ordovician which are perhaps stratigraphically significant. However, before more material has been described, nothing definite can be said on this question.

Ligonodina elongata Rhodes was originally described from the Gelli-grin and Pen-y-garnedd limestones (Rhodes 1953) and has later been found also in the Keisley limestone (Rhodes 1955) and the Crûg limestone (Lindström 1959). In N. America Ethington (1959) listed it from the Galena fm., and recently Sweet, Turco, Warner, & Wilkie recorded two specimens of this species from the lower part of the Eden formation. Because Rhodes (1953) did not find it in the Llandeilo limestone, it seems possible that the species is restricted to post-Llandeilian strata.

Oistodus excelsus Stauffer was first recovered from the lower part of the Decorah shale (Stauffer 1935*b*). Recently it has also been found in the Bighorn of Wyoming (Stone & Furnish 1959) and the Galena fm. (Ethington 1959). Thus it seems to range at least through the Middle Ordovician.

Oistodus inclinatus Branson & Mehl is not represented by typical specimens in the Tvären material, but some specimens are closely related to that species. In Europe similar forms were found in Arenigian and Llanvirnian-Llandeilian strata by Sannemann (1955*b*); in N. America *O. inclinatus* has a wide vertical range from Lower Ordovician (Prairie Du Chien beds, Furnish 1938) to Upper Ordovician (Maquoketa fm. of Iowa, Glenister 1957). Probably the name *O. inclinatus* as used by different authors covers more than one species.

Typical *Oistodus venustus* Stauffer has not been found in the Tvären material. However, specimens probably identical with Llandeilo limestone material referred to this species by Rhodes (1953) are met with. Very similar specimens are described from the zone of *Climacograptus wilsoni* at Morroch Bay, S.W. Scotland (Lindström 1957) and from the Galena fm. (Ethington 1959).

Panderodus acostatus (Branson & Branson) was first met with in the Brassfield fm., Kentucky (Lower Silurian, cf. Branson & Branson 1947). Later it was reported from the Upper Ordovician (Maquoketa fm. of Iowa, Glenister 1957). In Europe similar forms are listed from the Middle Ordovician (Llandeilo limestone, Rhodes 1953) to the Upper Silurian (Lower Ludlow, Aymestry limestone, Rhodes op. cit.). Obviously this very simple type has a wide vertical range, and has little value as an index fossil.

Panderodus sp. aff. *P. unicostatus* (Branson & Mehl) is apparently identical with specimens referred to *P. unicostatus* by several authors, but in my opinion there is reason to doubt that it is quite identical with Branson & Mehl's original from the Bainbridge fm., Missouri (Upper Middle Silurian, cf. Flint & Ball 1926). Forms referred to *P. unicostatus* are recorded in Europe from the Middle Ordovician (Llandeilo limestone, Rhodes 1953) to the Upper Silurian (Upper Ludlow, Walliser 1957).

Roundya inclinata (Rhodes) was originally described from the Llandeilo limestone (Rhodes 1953). From N. America it is recorded from the Maquoketa fm. of Iowa (Glenister 1957) and the Galena fm. (Ethington 1959).

Strachanognathus parva Rhodes has previously been found only in the type strata, the Keisley limestone, Great Britain (Rhodes 1955). Its occurrence in the Middle Ordovician of Sweden is very remarkable and will be discussed in some detail below (cf. p. 23).

The above list includes some species, viz. *Drepanodus suberectus, D. homocurvatus, Oistodus inclinatus, Panderodus acostatus,* and *P.* sp. aff. *P. unicostatus,* which according to our present knowledge have a wide stratigraphic range. This circumstance reduces essentially their usefulness as guide fossils, particularly in age correlations between formations. However, the remaining species bear out at typically Middle Ordovician character of the Tvären faunas. *Ambalodus triangularis, Amorphognathus ordovicica, Dichognathus typica, Distacodus? falcatus, Ligonodina elongata, Oistodus excelsus, O.* cf. *venustus, Roundya inclinata,* and *Strachanognathus parva* have hitherto not been listed from strata older than Middle Ordovician. Of these species *Roundya inclinata,* along with the forms of *Panderodus* and *Oistodus venustus,* was recovered by Rhodes (1953) from the Llandeilo limestone. Yet, *Ligonodina elongata* was not found in these strata. It was however met with in the Gelli-grin and Pen-y-garnedd limestones, which is also true of forms of *Amorphognathus ordovicica* (Rhodes op. cit.). These facts make it clear that the Tvären faunas are of a post-Llandeilian age.

Among the species previously not reported from Europe, *Dichognathus typica* and *Distacodus? falcatus* have their oldest known occurrences in the Glenwood beds (cf. Stauffer 1935*a*). *Oistodus excelsus* is described from the lower part of the Decorah shale, and *O. venustus* from the Glenwood beds. (The last-mentioned species has not been encountered in its typical form in the Tvären material, however.) This shows that the Tvären faunas in all probability are not older than these strata. On the other hand, the occurrences of *Ambalodus triangularis*, typical *Amorphognathus*, *Ligonodina elongata*, and *Roundya inclinata* definitely indicate a somewhat younger age. At this point of the discussion it can be stated that the age of the Ludibundus limestone of Tvären, as based on the conodonts, is definitely post-Llandeilian, and apparently, post-Chazyan.

As for the problem of determining the uppermost possible stratigraphic position as well as fixing more precisely the age of the strata concerned, direct comparisons with some other conodont faunas of a broadly similar age are helpful. It should be remarked that, in the following, the Tvären faunas are treated collectively under the assumption that they differ only slightly in age.

Starting with Sweden, the only Middle Ordovician conodont fauna that is known to some extent, is that of the Upper Llandeilian, redescribed by Lindström (1955*b*). In spite of the fact that only a fraction of the conodonts in that fauna has hitherto been described, it is possible to comment on its relation to the Tvären faunas. *Pygodus anserinus* Lamont & Lindström,[1] *"Arabellites" serra* Hadding, *Cordylodus spinatus* (Hadding), and *C. ramosus* Hadding, which are very characteristic elements of the Llandeilian fauna, are entirely lacking in the Tvären material. As far as our present knowledge goes, the zones of *Climacograptus haddingi* and *Diplograptus multidens* in Sweden thus contain clearly distinct conodont faunas. It is of interest to note in this connexion that recent investigations (Lindström, and the author) have led to the result that the zone of *Nemagraptus gracilis*, as represented by the lowermost Ludibundus beds at Böda harbour, Isle of Öland,[2] also contains a conodont fauna, which in several respects differs from those of Tvären.

In Germany no true Middle Ordovician conodont fauna has hitherto been described. Sannemann (1955*b*), however, has listed several species from Arenigian-Llandeilian strata, but those faunas do not conform with the Tvären faunas; as a whole, the former faunas have an older character.

The Middle Ordovician conodont faunas of Great Britain are better known. After a pioneer research by J. Smith (1907), modern descriptions of conodonts from these strata have been published by, in particular, Rhodes (1953, 1955) and Lindström (1957, 1959), but also by Lamont & Lindström (1957).

Rhodes (1953) has described the fauna of the Llandeilo limestone, which has a superficial resemblance to the Tvären faunas. Elements common to both faunas are *Drepanodus suberectus*, *Panderodus acostatus*, *Oistodus* cf. *venustus* (= *O. venustus* in Rhodes), *Roundya inclinata*, and possibly *Drepanodus homocurvatus* (? = *Oistodus curvatus* in Rhodes) and *Panderodus* sp. aff. *P. unicostatus* (? = *P. unicostatus* in Rhodes). *Inter alia*, the following species, which are absent in the Tvären material, have been found in the Llandeilo limestone: *Cordylodus flexuosus* (B. & M.) (= *Cyrtiniodus complicatus* in Rhodes), *Ligonodina valma*, *Zygognathus deformis* (Stauffer)

[1] Ethington, Furnish, and Markewicz (1958) reject *Pygodus anserinus* as a conodont without giving any reasons. However, according to my opinion the species is no doubt a typical lamellar conodont, which sometimes even has a basal filling.

[2] Regarding the find of *Nemagraptus gracilis* at this locality, see Regnéll (1948, p. 20).

(= *Gyrognathus elongata* in Rhodes), and *Ozarkodina tenuis*. The reverse is the case with, for example, *Paracordylodus lindstroemi*, *Amorphognathus elongata*, *Ligonodina elongata*, *Strachanognathus parva*, and *Tvaerenognathus ordovicica*. Further *Ambalodus* and *Amorphognathus* are very well represented in the Tvären material but are almost absent in the Llandeilo limestone. A fairly close relationship exists between these faunas; however, the occurrence of *Ligonodina elongata* and forms of *Amorphognathus ordovicia* and *Ambalodus triangularis* indicates a younger age of the Tvären faunas (cf. above).

Lamont & Lindström (1957) have recorded conodonts from several Llandeilian localities in the Southern Uplands of Scotland. The fauna is very similar to that of the zone of *Climacograptus haddingi* of Sweden, a fact which enables long distance correlations. As has been noted this fauna is clearly different from that of Tvären.

A more nearly contemporaneous fauna was described by Lindström (1957) from Morroch Bay, S.W. Scotland, originating from strata belonging to the zone of *Climacograptus wilsoni*. Unfortunately this fauna occurs in black shales which are tectonically affected; this fact, together with the circumstance that most of the specimens are only preserved as moulds, makes the identification of species difficult. However, *Oistodus* cf. *venustus* (*O.* sp. in Lindström) and possibly *Paltodus* n.sp. (= *Acontiodus* n.sp. 3 in Lindström) are shared with the Tvären faunas. Noteworthy in the Morroch Bay material is the occurrence of *Periodon* n.sp. aff. *aculeatus*; no *Periodon* is found in my material. This may perhaps indicate that the Morroch Bay funa is slightly older than the Tvären ones, but until the vertical range of the conodonts concerned is known in more detail, nothing can be said definitely about the mutual position of these faunas.

Rhodes (1953) has described the faunas of the Gelli-grin and Pen-y-garnedd limestones, belonging to the Upper Caradocian. The abundant occurrence of *Ambalodus* and *Amorphognathus* recalls the Tvären faunas; however, these Upper Ordovician faunas in North Wales are very clearly distinguished by the presence of, *inter alia*, *Icriodella* spp., *Zygognathus superba*, and *Holodontus superbus*. Another fauna of a similar age, viz. from the Crûg limestone, has recently been described by Lindström (1959). Lindström regards this fauna as slightly younger than those of the Gelli-grin and Pen-y-garnedd limestones. It is not very similar to the older Tvären faunas. Common species to the Crûg and Tvären faunas are *Ambalodus triangularis erraticus*, *Ligonodina elongata*, and *Prioniodus variabilis*, but otherwise the Crûg fauna is characterized by younger elements, such as *Icriodella superba* and *Roundya divaricata*.

Another fauna, which has a certain interest in this connexion is that of the Keisley limestone, Westmorland, described by Rhodes (1955). The age of this limestone is not quite safely established on account of the difficulties in correlating the macrofauna with that of other formations. However, the Keisley limestone has generally been compared with the Boda limestone of Dalarna, Sweden (cf. Reed 1896, 1897; Warburg 1925; Thorslund 1935; Stubblefield 1939), and regarded as probably belonging to the Ashgillian (cf. Rhodes 1955). However, Lindström (1959) has assumed that Caradocian beds may be involved in the supposed "reef" complex of the Keisley limestone. If this holds true, the occurrence of certain old faunal elements in the Keisley limestone would be explained. Conodonts common to the Tvären faunas are *Panderodus acostatus*, *Strachanognathus parva*, and, possibly, *Ligonodina elongata*. Particularly the common occurrence of *Strachanognathus parva* in the Tvären and Keisley limestones is highly puzzling, because this species seems to be rather special-

ized and has never been found in any other faunas described so far. *Strachanognathus parva* has also been found by the present author in a sample from the lower Caradocian of Lockne, Jemtland, Sweden. In addition this species is met with in samples of the Ludibundus limestone from Dalarna and the Isle of Öland. In view of the fact that the Swedish occurrences are well fixed stratigraphically, the occurrence of *Strachanognathus parva* in the Keisley limestone lends a certain support to Lindström's hypothesis.

North American faunas, broadly equivalent in age to the Tvären faunas, include those of the Glenwood beds (Stauffer 1935*a*); Plattin limestone (Branson & Mehl 1933); Decorah shale (Stauffer 1930, 1932, 1935*b*); Fort Peña and Woods Hollow formations of the Marathon Basin (Graves & Ellison 1941); Bromide and Viola limestones (Branson & Mehl 1943); Kimmswick limestone, Missouri (Strothmann in Branson 1944); Harding sandstone (Sweet 1955); and the Galena fm. (Ethington 1959).

The faunas of the Glenwood beds, Harding sandstone, Plattin limestone, and the Bromide limestone are dominated by fibrous conodonts, particularly *Chirognathus* and related genera. Conodonts of this type are completely absent in the Tvären material; thus the faunas concerned have a very different composition. Yet two species seem to be common to the Tvären faunas, viz. *Drepanodus suberectus* and forms of *D. homocurvatus*. Further, *Oistodus venustus* and *Distacodus? falcatus* are listed from the Glenwood beds, and *Dichognathus typica* from the Plattin. It is evident, nevertheless, that on the basis of only these species no correlation can be made. It is worth mentioning that species of *Chirognathus* occur also in Swedish strata; however, hitherto only one species, viz. *Chirognathus alternans* (Hadding), has been described. This species was met with in strata of an Upper Llandeilian age (Lindström 1955*b*). As far as known, the genus is not represented in younger beds in Sweden. In view of the wide occurrence of a *Chirognathus*-"zone" in N. America it is reasonable to suggest that the Swedish strata bearing *Chirognathus* are at least broadly contemporaneous with *Chirognathus*-bearing beds in N. America. If this is so, the Tvären faunas are definitely younger than not only the Swedish but also the N. American faunas just referred to. Sweet (1955) correlated the Harding fm. of Colorado with the Glenwood shale of Minnesota and regarded it to be of a Black River age (=the Wilderness Stage of the Mohawkian Series, cf. Cooper 1956, p. 8). The Bromide and Plattin limestones belong, at least in the greater part, to the Wilderness stage also (cf. Cooper op. cit., chart 1) and consequently, the Tvären faunas appear to be of a Trentonian age, or possibly younger.

The conodont faunas of the Fort Peña and Woods Hollow formations in the Marathon region, Texas, consist mainly of simple forms. This feature relates the faunas concerned rather to older faunas than to those of Tvären. The rich conodont fauna of the Decorah shows certain similarities to the Tvären faunas, *inter alia*, in the occurrence of true platform conodonts (*Amorphognathus* of "*Polyplacognathus*-type"). Stauffer (1935*b*) recognized a total of about 27 genera and 70 species, a number which would probably be somewhat reduced by a revision of the material. In any case, *Distacodus? falcatus*, *Oistodus excelsus*, *Drepanodus suberectus* and, possibly, *Dichognathus typica* are shared with the Tvären material. From the Kimmswick of Missouri several species are figured in Branson (1944; from Freddie Strothmann's master's thesis) without descriptions. A certain similarity to the Tvären faunas offers the common presence of species of *Amorphognathus*, *Drepanodus suberectus*, *Dichognathus typica*, and, possibly, *Drepanodus homocurvatus*. From the Viola limestone only

few conodonts are listed by Branson & Mehl (1943), all from the lower part of the formation. *Dichognathus typica* and possibly *Oistodus inclinatus* are shared with the Tvären faunas. However, Decker (1952, p. 101) reported, *inter alia*, *Nemagraptus gracilis* from the Lower Viola. Accordingly, the listed conodont fauna may be somewhat older than those of Tvären. The Decorah and the Kimmswick are of an age at least broadly similar to the Lower Viola and consequently the Tvären faunas may be regarded as slightly younger than the faunas of these formations.

Recently Ethington (1959) described the conodonts of the Galena fm. of Iowa and Minnesota. Among Ordovician faunas thus far described in N. America these faunas have the greatest similarity to the Tvären material. Thus, among 16 genera found in Tvären, at least 11 also occur in the Galena, and nine of the 24 species met with in the Tvären faunas appear to be common with the Galena. It is true that some of these include long-ranging forms of little stratigraphic value, but, on the other hand, there are several species which according to our present knowledge have a more restricted stratigraphic range. The Galena of Iowa can be divided in three members, viz. in descending order the Dubuque, the Stewartville, and the Prosser. Ethington showed that the lower part of the Prosser contains a conodont fauna closely related to the faunas of the underlying Decorah as well as to those of the lower Viola and Kimmswick. Common elements with the Tvären faunas are, *inter alia*, *Dichognathus typica*, which was found only in the Prosser. The overlying member, the Stewartville, is unfortunately developed mainly in a dolomitic facies, which, like the uppermost Prosser, has yielded only sparse and long-ranging conodonts. Yet, from the uppermost Stewartville and above all from the upper member, the Dubuque, numerous and well preserved conodonts were recovered. From these beds Ethington listed, *inter alia*, forms of *Amorphognathus* and *Ambalodus triangularis*, *Oistodus venustus*, *Ligonodina elongata*, and *Roundya inclinata*, which show a close relationship to the Tvären faunas. The uppermost part of Dubuque contained some species, particularly *Icriodella acuta*, which indicate an Upper Caradocian age.

Looking at the vertical distribution in the Galena of species common to Tvären and the Galena, it is evident that the Tvären faunas in all probability are younger than the lower Prosser and older than the upper Dubuque. The meager conodont fauna of the Stewartville does not permit any closer comparisons, but the occurrence of forms of *Amorphognathus* and *Ambalodus triangularis* together with *Oistodus* cf. *venustus*, *Ligonodina elongata*, and *Roundya inclinata* in the Tvären material makes it rather probable that the Tvären faunas correspond to some part of the lower Stewartville. According to Twenhofel *et al.* (1954, chart 2) this means that the Tvären strata should correspond to the upper Trenton.

In this connexion it must, however, be remarked that the age of the Dubuque and the Stewartville is at present a matter of some dispute. Recently Sweet, Turco, Warner, & Wilkie (1959) described the conodonts of the Eden formation of Ohio and Kentucky. They noted a fairly close similarity between the composition of the conodont faunas of the Eden and those of the Dubuque and Stewartville members of the Galena and correlated the Dubuque and the Stewartville with the lower Eden. The faunas of the Eden and Tvären have some species in common but most of these forms have little stratigraphic significance. The younger age of the Eden fauna in comparison with those of Tvären is indicated by the occurrence of some species, *inter alia*, *Ambalodus elegans*, *Keislognathus gracilis*, and *Sagittodontus dentatus* which are hitherto not recorded with certainty from strata older than Upper Ordovician. As a whole the conodont fauna of the type Eden closely agrees also with those of

the Gelli-grin and Pen-y-garnedd limestones of Wales (cf. also Sweet & Miller 1958).

The age determination of the Tvären strata, achieved by means of the conodonts, is supported to a certain extent by evidence of the graptolites associated with the conodonts in the erratic boulders of Tvären. As demonstrated above, the graptolites indicate the zone of *Diplograptus multidens*. Now, as is well known, *Nemagraptus gracilis* occurs in the Black River, and *Pleurograptus linearis* is found in the Holland Patent shale, belonging to the Utica (cf. Ruedemann 1947, p. 120). This indicates that the zone of *Diplograptus multidens* is of a Trentonian age. In this connexion it may also be mentioned that the Gelli-grin limestone of Wales according to Elles (1937, pp. 488, 492) corresponds to the zone of *Pleurograptus linearis;* the Pen-y-garnedd limestone is generally regarded to be equivalent to the Gelli-grin limestone. These facts make it possible to place the conodont faunas from the limestones concerned as well as those of the Eden and the upper Galena in the standard graptolite succession.

To sum up, the following may be said about the Tvären conodonts. Two conodont faunas have been identified in boulders of Middle Ordovician limestones from the Tvären area. One of these faunas belongs to a middle part of the Ludibundus beds, which according to new graptolite evidence corresponds to the zone of *Diplograptus multidens*. This fauna is characterized, above all, by species of the genera *Ambalodus*, *Amorphognathus*, *Paracordylodus*, and *Tetraprioniodus*, and is found in a number of boulders of crystalline limestone, but also in boulders of other lithological types. The other fauna, distinguished by the predominance of *Strachanognathus parva*, has so far only been met with in boulders of grey, dense to fine-grained limestone. The mutual stratigraphic position of these faunas is not yet settled.

A regional comparison with other conodont faunas of a broadly similar age shows that the Tvären faunas differ in several respects from those of the lower Middle Ordovician as represented by faunas from the zones of *Climacograptus haddingi* and *Nemagraptus gracilis*, as well as from that of the Llandeilo limestone. Further, they differ in several respects from the fauna of the zone of *Pleurograptus linearis* as represented by the Gelli-grin and Pen-y-garnedd limestones of Wales. No European fauna has been described from shelly facies in the intervening strata. A comparison with N. American faunas suggests that the Tvären Ludibundus limestone possibly is equivalent to the upper Trenton, as represented by some lower part of the Stewartville member of the Galena fm. of Iowa. It must be emphasized, however, that our present knowledge of the vertical distribution of conodont species in the Middle Ordovician is only fragmentary. Thus, the above correlation must be regarded as only provisional.

V. Nomenclature, figures, etc.

The terminology of simple conodonts and some compound types used in this paper conforms with that of Lindström (1955*a*), but for some small modifications. Some important terms applied to these types as well as to platform conodonts are illustrated in text-fig. 2. Terms not illustrated, and not in common use in the literature will be explained in the descriptions.

One question which may perhaps seem trifling, but which is in fact important in the description of conodonts, is how the conodonts are oriented. It would mean a

considerable progress if a uniform orientation could be accepted, since this would make it much easier to compare directly descriptions and illustrations from different publications. Recently Müller (1956*b*) proposed a new orientation of conodonts, where, *inter alia*, the commonly used designations "anterior" and "posterior" are substituted by "A" and "B". I still hesitate to accept this new orientation which would make a thorough revision of the conodont systematics necessary. In this paper I use the orientation introduced by Lindström (op. cit.). Thus in both simple and compound conodonts the oral edge is oriented horizontally like the longitudinal axis of platform types.

It is well known that there are considerable difficulties in producing acceptable photographs of conodonts. This fact, and the circumstance that the necessary photographic equipment was not available, led me to follow the precedent of, *inter alia*, Furnish (1938) and Lindström who have achieved beautiful results in drawing conodonts. All figured specimens were drawn, using an Abbe's apparatus at a magnification of about 100 ×, and then reduced. The specimens were not whitened with NH_4Cl before reproduction, and no reconstructions of fragmentary specimens were made.

The catalogue numbers refer to the number in the collections of the Institute of Paleontology, University of Lund, where the originals to the figures are deposited.

VI. Descriptions

Ambalodus Branson & Mehl, 1933

TYPE SPECIES.—*Ambalodus triangularis* Branson & Mehl, 1933.

REMARKS.—There is a varying spelling of the name of this genus in the literature. In their generic description, the description of the genotype, and the explanation to their plates, Branson & Mehl (1933) originally called the genus *Ambalodus*. However, in the "Index of genera and species" in a later part of the same series of papers (Branson, Mehl, & Branson 1934, p. 345) they wrote *Ambolodus*. Huddle (1934) wrote *Amabalodus*, which is probably a misprint. The name *Ambalodus* is later used by Graves & Ellison (1941), Branson (1944), Fay (1952), Glenister (1957), Stone & Furnish (1959), Ethington (1959), Lindström (1959), and Sweet, Turco, Warner, & Wilkie (1959). However, Branson & Mehl (1944) called the genus *Ambolodus*, which was later followed by Ellison (1946), Rhodes (1953, 1955), Lindström (1955*a*, 1957), Rhodes & Wingard (1957), and Fay (1958).

Now, as seen above, the original name of the genus was *Ambalodus*. This name is used throughout in Branson & Mehl's paper of 1933. Because no remark was made in this publication that *Ambalodus* was considered a misprint by the authors and should be changed to *Ambolodus*, it is evident that *Ambalodus* has priority over *Ambolodus* (Internat. Rules Zool. Nomenclature, art. 25). Yet, in 1934 Branson & Mehl published a list of errata together with the last part of their "Conodont Studies" and in this list the name of the genus was changed to *Ambolodus*. However, according to the Internat. Rules Zool. Nomenclature, art. 19, such a change of an earlier published generic name is invalid. Since *Ambalodus* is not a homonym, it can thus be stated that the only valid name of the genus is *Ambalodus*.

Ambalodus triangularis Branson & Mehl, 1933

This species is reported from the Upper Ordovician by several authors (cf. Fay 1952). On comparison of the figured specimens, it becomes obvious that in the material referred to this species there is a fairly wide variation. This variability of the species has recently been quite strikingly demonstrated in a fauna from the Crûg limestone, Great Britain (Lindström 1959). In the conodont material from Tvären, specimens belonging to *Ambalodus* play a numerically important rôle, being, next to *Strachanognathus parva*, the most abundant elements in the faunas. The material includes more than 300, on the whole well-preserved specimens, which, however, show fairly small morphological variation; in fact, very soon it became evident that all specimens referred to this species from Tvären could be brought to one of two types, which were easily distinguishable from each other. Yet, neither of these types seems to be quite identical with *Ambalodus triangularis*, at least according to what can be judged from the descriptions and figures of the cotypes of Branson & Mehl. Also, a direct comparison with American specimens, referred to this species, from the Economy Member, Eden fm., Ohio, shows certain differences, even apart from the much better state of preservation of the Tvären specimens. Yet, I am conscious of the fact that these differences, however striking and constant in my material, may be hard to distinguish in less well preserved specimens from other faunas. Therefore, in order to avoid "critical" systematics in this genus, I think it advisable not to erect two new species. However, the types are too dissimilar to be brought together, and, therefore, I have chosen to refer them to two new subspecies under *Ambalodus triangularis*.

The subspecies concept is earlier used in the conodont systematics by, *inter alia*, Ziegler (1956), Flügel & Ziegler (1957), Bischoff (1957), and Bischoff & Ziegler (1957). It seems to me that a moderate use of this lower systematic unit is to be preferred to the founding of new species with relatively small differences from previously described species. Therefore, the Tvären material of *Ambalodus* is here divided into the following two subspecies.

Ambalodus triangularis Branson & Mehl ssp. *erraticus* n.ssp.

Pl. 3, figs. 15–17.

DERIVATION OF NAME.—From Latin *erraticus* = vagrant. The holotype was recovered from an erratic limestone boulder.

HOLOTYPE.—LO 4049 T, pl. 3, figs. 16, 17.

DIAGNOSIS.—An *Ambalodus* with a conspicuous cusp and straight or somewhat bent, rather slender, orally denticulated anterior and posterior processes that make an angle of c. 80–100° with each other. Lateral process short and denticulated. Immediately posterior to the lateral process, a marked, triangle-shaped depression above the basal margin, limited by a more or less distinct ledge. Denticles much lower than the cusp.

DESCRIPTION.—This conodont is composed of a central cusp, from which three orally denticulated processes diverge, viz. a straight, often pointed posterior, a slightly longer, generally somewhat bent anterior, and a short, weak lateral process.

The posterior process is 2–3 times as long as wide, is convex orally and has a somewhat pointed end. Orally, it bears a row of very low, often indistinct and sometimes

irregularly developed denticles, which are fused and laterally somewhat compressed; their apices are as a rule not very pointed.

The anterior process is generally distinctly longer than the posterior, is slender with a pointed distal end, and is directed in a bow downwards and laterally. The angle between the anterior and the posterior processes varies but amounts as a rule to 80–100°; often the inner basal margins of these processes meet at an angle, thus in these cases not forming a curve as in the following subspecies. Along the convex oral surface of the anterior process there is a row of denticles of subequal size, often more than 10 in number. They are rather low, about as high as broad, and generally not reaching one-third of the height of the cusp. The denticles are basally confluent but have free, often somewhat pointed apices. Laterally they are compressed, having moderately convex lateral faces and sharp anterior and posterior edges.

The lateral process originates just below the cusp. It is short, as a rule straight, and strongly compressed laterally. Orally it bears 1–3 discrete, somewhat pointed denticles. From this denticle row, a low costa rises to the denticle immediately in front of the cusp.

The cusp is suberect, rather long and pointed. Its breadth at the base is c. one-half to two-thirds of the height. The outer face is strongly convex, the inner slightly convex or flat and the anterior and the posterior edges fairly sharp. The outer face is very finely longitudinally striated.

On the inner side a conspicuous ledge is developed a little above the basal margins of the processes, and a similar one runs along the outer face of the anterior process to the lateral process. At the posterior process a comparatively weaker ledge may run just above the basal margin at the posterior part of the process; yet sometimes it is not developed at all. Slightly posterior to the cusp the ledge makes a sharp curve upwards and then turns down again and meets the lateral process; thus, there is formed a most characteristic triangle-shaped depression at the outer-lateral face of the anterior part of the posterior process. The basal cavity is deep but not very wide. Very often there is a basal filling in the Tvären specimens.

REMARKS.—As a whole, the above description agrees in most details reasonably with that of *Ambalodus triangularis* given by Branson & Mehl. However, at least from what may be seen by comparison with their figured cotypes, ssp. *erraticus* is distinguished by longer and more slender anterior and posterior processes, which form a smaller angle with each other; furthermore according to what may be gleaned from the published descriptions and figures, American specimens seem to lack the characteristic depression posterior to the lateral process. By courtesy of Dr. Maurits Lindström, I have had the opportunity to examine two specimens of *Ambalodus triangularis* from the Eden fm., Ohio, which also missed this structure. In this connexion it may be mentioned that this characteristic seems to be constantly developed in the material from Tvären referred to ssp. *erraticus*. In fact, transition forms into ssp. *suecicus* are not found among the several hundreds of specimens examined. Yet, in a conodont fauna from the Crûg limestone, recently described by Lindström (1959), there seems to be greater variation in these structures, with transitional and other atypical forms present. However, most specimens in that fauna can be referred to ssp. *erraticus*.

MATERIAL.—More than 145 specimens.

OCCURRENCE.—Common in boulders of Ludibundus limestone from the Tvären area. Crûg limestone (Great Britain) (Lindström 1959).

Ambalodus triangularis Branson & Mehl ssp. *suecicus* n.ssp.

Pl. 3, figs. 11–14.

DERIVATION OF NAME.—After *Suecica*, Latin for Sweden.

HOLOTYPE.—LO 4046 T, pl. 3, fig. 12.

DIAGNOSIS.—An *Ambalodus* with subequally long, orally denticulated anterior and posterior processes that make an angle of c. 100° with each other. Denticles on the anterior process well developed, as a rule almost as high as the cusp; denticulation on the posterior process weak and irregular. Lateral process short, orally with a low number of short denticles; sometimes however indistinctly developed and undenticulated. Basally-laterally a conspicuous ledge running around the processes. Basal cavity rather wide and deep.

DESCRIPTION.—The unit consists of a straight posterior process and an anterior process of about the same length which may be straight or slightly curved. The angle between these processes varies to some degree but amounts in general to c. 100° or somewhat more. At the junction of the processes there is a cusp, from the base of which a short lateral process diverges anteriorly-laterally.

The posterior process is as a rule somewhat weaker than the anterior one, has an obtuse distal end and is orally denticulated. The denticles are low, fused, not sharply pointed and often undistinctly and irregularly developed; the number of easily distinguishable denticles on this process is generally low.

The anterior process is directed somewhat downwards (at an horizontal orientation of the posterior process). In comparison with the posterior process it is more robust, about twice as long as wide, and generally with a somewhat pointed end. Orally it bears a row of 5–10 stout, rather big, on an average c. twice as high as broad denticles, which are basally confluent but have free, not very pointed apices. All denticles are slightly laterally compressed with moderately convex lateral faces and sharp anterior and posterior edges; their size increases posteriorly to the biggest denticle which is often No. 2 or 3 from the cusp. All denticles are somewhat proclined.

The cusp is suberect, stout and rather short; as a rule, it is not much higher than the denticles in front of it. Being a little laterally compressed it has convex lateral faces and sharp anterior and posterior edges. The lateral faces of the cusp are finely striated longitudinally. The apex of the cusp is as a rule not sharply pointed.

From a point below the base of the cusp the short lateral process diverges. Sometimes, particularly where weakly developed, it is almost straight but generally it is bent in a curve anteriorly-laterally and directed a little downwards. Orally there is a sharp ridge on which there may be 1–4 low, often discrete, pointed denticles; however, not infrequently the process is quite short and bears no denticles. From the lateral process a low but conspicuous costa runs up on the denticle immediately in front of the cusp.

The inner margins of the anterior and posterior processes meet generally in a curve. A little above the basal margin a very conspicuous ledge runs round the processes; on the outer side it bends from the lateral process to the ends of the anterior and posterior processes.

The basal cavity is rather wide and deep at the anterior and posterior processes; into the lateral process it extends as a narrow but deep furrow. As a rule, in the Tvären specimens, it is more or less filled with a basal filling.

REMARKS.—This subspecies of *Ambalodus triangularis* is easily distinguished from ssp. *erraticus*, *inter alia*, by its shorter cusp, the longer denticles on the anterior pro-

cess, and the generally more robust appearance. Moreover, it lacks the triangle-shaped depression posterior to the lateral process, characteristic of ssp. *erraticus*. It has a certain resemblance to *Ambalodus robustus* Rhodes but seems to differ in its generally denticulated lateral process, the comparatively shorter size of the anterior and posterior processes, and the fact that the denticles of the anterior process are not parallel with the cusp. However, the characteristics of *Ambalodus robustus*, given by Rhodes (1953), in particular the undenticulated lateral process, seem to me insufficient to distinguish it from such near related species as *Ambalodus triangularis* and *A. elegans* Rhodes. From experience of several hundred well preserved specimens of *Ambalodus*, I am of the opinion that the denticulation of the lateral process varies greatly, even in specimens which in other details are quite similar. Thus, it seems that this character has little systematic value, at least on the species level.

MATERIAL.—More than 206 specimens.

OCCURRENCE.—Very common in boulders of Ludibundus limestone from the Tvären area, especially the crystalline ones.

Amorphognathus Branson & Mehl, 1933

TYPE SPECIES.—*Amorphognathus ordovicica* Branson & Mehl, 1933.

BRANSON & MEHL'S GENERIC DEFINITION (Branson & Mehl 1933, p. 126).— "Irregularly branched asymmetrical dental plates with rays or branches of varying size and extending in varied directions within a common basal plane that is arched or flat. The rays are more or less lanceolate, usually with a raised margin on the oral surface and a conspicuous longitudinal median crest on the oral side that is crenulate, nodose, or is constructed of more or less fused denticles."

REMARKS.—Branson & Mehl (op. cit., p. 127) noticed that their material, on which the generic description was based, was throughout fragmentary. This is also the case with the holotype of *Am. ordovicica*, the type species of the genus; according to what may be judged from Branson & Mehl's picture of the holotype, it lacks at least the anterior process. On more complete specimens from Great Britain Rhodes (1953, p. 283) gave a description of an *Amorphognathus*, referred to *Am. ordovicica*. He added nothing to the original description of the genus but published the first figure of a complete *Amorphognathus*. Later Sweet (1955), Glenister (1957), Ethington (1959), and Lindström (1959) have given descriptions of *Amorphognathus*.

In spite of its fragmentary state, Branson & Mehl's genotype shows several important morphological characters characteristic of the genus. The specimen concerned is an antero-posteriorly extended unit, which is composed of a posterior and an anterior process, the latter evidently partly missing in this specimen. Along the middle of this unit there is an antero-posterior row of denticles, here called the "main denticle row". From the posterior part of the anterior process is developed a bilobate, rather short lateral process. On the opposite side, and a short distanc posteriorly, another bigger, bilobate, lateral process departs from the anterior part of the posterior process. Orally the lateral processes bear a median row of denticles that at the junction with the main denticle row are lower than those of the latter row.

Most of the later described species referred to *Amorphognathus* have a very similar branching plane and show also in other characters close affinities to this specimen. These species include *A. complicata* Rhodes, *A. inaequalis* Rhodes, *A. duftona* Rhodes,

and *A. tvaerensis* n.sp.[1] Together with *A. ordovicica* they constitute a uniform group of platform conodonts which could be described as follows.

REDEFINITION.—Compound, asymmetrical, lamellar platform conodonts, branched in a horizontal plane, and consisting of an antero-posteriorly directed central unit that is composed of a slender, often blade-like, anterior process, and a broad, flat posterior process. From the anterior process is developed a branched or unbranched lateral process at one side, and posterior to this a similar lateral process departs from the other side, on the posterior process; sometimes more than one lateral process may diverge from the posterior process, but there is always a distance between the points where the denticle rows of the lateral processes meet the main denticle row. Orally the processes bear a conspicuous and, as a rule, denticulated, median crest. Aboral surface deeply excavated over almost the whole area, this excavation forming a rather wide and deep basal cavity.

As seen above, Branson & Mehl's generic definition is rather broad and some types of platform conodonts, rather different from the genotype, have been brought to this genus. Particularly remarkable among these forms is the one on which Stauffer (1935*b*) founded the genus *Polyplacognathus*, viz. *P. ramosa*. This genus was regarded as a junior synonym of *Amorphognathus* by Branson & Mehl (1944) and Ellison (1946) and subsequent authors have accepted their opinion.

In the material of platform conodonts from Tvären some specimens represent a new species, seemingly close to the forms that were brought to *Polyplacognathus* by Stauffer. From Stauffer's definition of the genus and figures of the genotype, *P. ramosa*, it appears that the general organization in *Polyplacognathus* is similar to that in *Amorphognathus* with the exception that in the genotype all processes meet at a common junction in the middle of the conodont unit. Further, the appearance of the aboral side is distinguished from that of the species of *Amorphognathus* mentioned above; the latter have the whole aboral side more or less excavated, whereas *Polyplacognathus*, as seen on Stauffer's illustration (op. cit. pl. 75, fig. 23), is characterized by a very narrow basal cavity with somewhat raised margins. Often these margins are closed together and united to a simple central ridge which rises from the aboral surface which otherwise is smooth. This shape of the aboral side is rather typical and occurs in some younger conodont genera. The oral denticulation of Stauffer's species is also different from the type occurring in *Amorphognathus*; it is noticed that except for the median rows of denticles there may occur series or groups of denticles scattered over the whole oral surface. However, it must be mentioned in this connexion, that recently Lindström (1959) found that a similar type of denticulation may indeed occur also in otherwise typical specimens of *Amorphognathus* but it is however a rare structure.

From the above it is clear that the genus *Polyplacognathus* in some respects is distinguished from *Amorphognathus*, as represented by the genotype. At present it is, however, uncertain whether these differences should motivate a separation of *Polyplacognathus* from *Amorphognathus*. To this uncertainty may also be contributed the fact that according to oral communication from Dr. M. Lindström, in the uppermost Lower Ordovician and lowermost Middle Ordovician of Sweden species of "*Polyplacognathus*-type" develop from forms belonging to *Amorphognathus*; in those strata the genera concerned are not clearly distinguished. Before corresponding forms have

[1] According to Ethington (1959) *A. tridigitata* Glenister and *A. adunca* Glenister probably only represent fragmentary specimens of *A. complicata* Rhodes.

been subjected to examination in the Middle Ordovician, I therefore, with a certain hesitation, still regard *Polyplacognathus* as a junior synonym of *Amorphognathus*. Perhaps it will become clear in the future that the two genera concerned are well distinguished in the Middle Ordovician.

TERMINOLOGY AND ORIENTATION AT *Amorphognathus*.—Some important terms are illustrated in text-figs. 2 G–H. The specimens are oriented with the main denticle row horizontally.

Amorphognatus elongata n.sp.

Pl. 5, figs. 1–3.

DERIVATION OF NAME.—The posterior lobe of the bilobate process is elongated.

HOLOTYPE.—LO 4056 T, pl. 5, figs. 1–3.

DIAGNOSIS.—An *Amorphognathus* with five processes, viz. one anterior, one posterior, one unilobate lateral, and one bilobate lateral process. The anterior process, the unilobate process and the anterior lobe of the bilobate process are all of about the same length, and pointed distally. The posterior process is c. 1.5 times and the posterior lobe of the bilobate process c. 3 times longer than the anterior process. This posterior lobe is very slender, blade-like, and has orally well developed denticles. All processes carry central, simple denticle rows orally.

DESCRIPTION.—The platform-like unit consists of five processes that diverge in a common horizontal plane. All processes are orally denticulated, and the denticles are placed in a simple, central row at every process.

The anterior lobe of the bilobate process and the unilobate process are as long as the anterior process, and all these processes are rather slender, distally pointed, straight, and rather short. The angle between the anterior and the unilobate lateral processes is c. 75°, and that between the anterior process and the anterior lobe of the bilobate process c. 90°. These processes carry a low number (less than 10) of small, fused denticles. The denticle row of the unilobate process does not reach the main denticle row.

The posterior process is straight, about 1.5 times as long as the anterior process, broader than the other processes and has a somewhat rounded distal end. Its median ridge carries about 10 low, fused denticles which form an angular main denticle row with the denticles of the anterior process; its anterior and posterior parts make an angle of c. 130°–140° with each other.

The posterior lobe of the bilobate lateral process is c. 3 times as long as the anterior process and makes an angle of more than 150° with that process. This lobe is very slender, as a whole blade-like, distally somewhat twisted, and has a pointed end. At the lateral faces near the basal margin a distinct ledge runs along the whole process. A similar but weaker ledge runs also round the other processes. On the conspicuous median ridge of the process dealt with there is a series of sharply pointed, laterally compressed denticles, discrete at the distal part of the process but proximally confluent. The denticles are highest at the distal end of the process and become continuously lower proximally, and more rounded apically. The denticle rows of this and the anterior lobe meet the main denticle row at the same point.

The aboral surface has a median, narrow basal cavity which is limited by raised margins, which sometimes are joined to a central ridge. The rest of the aboral surface is smooth.

REMARKS.—The species is found only in a very limited number in samples from the boulders Nos. 4 and 6. However, the holotype is complete and rather well preserved and because this conodont is of a type not described previously, I think I am justified in erecting a new species in spite of the scanty material.

In somewhat older strata in Sweden there occur species that are closely related to *Am. elongata* (according to oral communication from Dr. Maurits Lindström) and one of these is figured at text-fig. 2 H. These forms constitute a group of platform conodonts that in the general organization plan differ from that represented in *Am. ordovicica* and allied species. The processes diverge from the middle of the conodont unit, often from almost the same point at the main denticle row. Also, the lateral processes are often more or less blade-like with comparatively high denticles. These characteristics together with the appearance of the basal cavity remind one very much of the genus *Polyplacognathus* Stauffer, 1935. As stated, this genus is, however, generally regarded now as a junior synonym of *Amorphognathus*.

MATERIAL.—Four specimens.

OCCURRENCE.—Hitherto found only in boulders Nos. 4 and 6 of Ludibundus limestone from the Tvären area.

Amorphognathus ordovicica Branson & Mehl, 1933

1933. *Amorphognathus ordovicica* Branson & Mehl, p. 127, pl. 10, fig. 38.
1941. *Amorphognathus ordovicica* Branson & Mehl–Graves & Ellison, pp. 5, 7, pl. 3, figs. 32, 36–38.
1944. *Amorphognathus ordovicica* Branson & Mehl–Branson, p. 95.
1952. *Amorphognathus ordovicica* Branson & Mehl–Fay, p. 63.
cf. 1953. *Amorphognathus ordovicicus* Branson & Mehl–Rhodes, p. 283, pl. 20, figs. 47–49.
1955. *Amorphognathus ordovicicus* Branson & Mehl–Rhodes, p. 123, pl. 9, fig. 4.
1959. *Amorphognathus ordovicica* Branson & Mehl–Stone & Furnish, p. 220, pl. 32, fig. 12.
? 1959. *Amorphognathus* aff. *A. duftona* Rhodes–Ethington, p. 270, pl. 40, fig. 11.
cf. 1959. *Amorphognathus* cf. *ordovicica* Branson & Mehl–Lindström, p. 436, pl. 2, figs. 12–17.

REMARKS.—As mentioned above (p. 29) Branson & Mehl based the species on fragmentary material. On the basis of more complete specimens from the Gelligrin limestone RHODES (1953) gave a redescription of *A. ordovicica*. However, a comparison between Rhodes's figured specimens and Branson & Mehl's holotype (Branson & Mehl 1933, pl. 10, fig. 38) shows some differences, the most obvious being the different lengths of the posterior lobe of the posterior lateral process. In the holotype this lobe is much shorter than the posterior process, whereas in the specimens from the Gelli-grin limestone it is distinctly longer, evidently sometimes as long as the posterior process or even longer. This difference might perhaps seem trivial, but the fact is that the mutual lengths together with the number, location and orientation of the processes must be regarded as fundamental characters in distinguishing species of *Amorphognathus*. That the difference in question is constant for the Welsh specimens appears likely from a remark by Rhodes in the description of *Amorphognathus ordovicica* (Rhodes 1953, p. 283): "Specimens exhibit a remarkable similarity to one another, there being no appreciable variation in form." Thus this form does not seem to represent a mere development stage of a form, identical with the American type. However, direct comparisons between specimens from Great Britain and the holotype will be necessary, before it is possible to come to a definite conclusion with regard to the systematic position of this form.

In this connexion, some remarks concerning the genus *Balognathus* Rhodes, 1953, may perhaps have a certain interest. At an early stage of the examination of the material treated here, some conodont fragments were found indubitably belonging to *Amorphognathus* but very similar to a species of *Balognathus*. This led me to examine the characters of the latter genus. It must be emphasized that I have not seen the holotype of *Balognathus expansa* Rhodes, the genotype; the following discussion is based entirely on the description and figures given by Rhodes (1953, pp. 284–285).

The following is a short synthesis of the diagnosis and remarks on *Balognathus*, given by Rhodes.

The genus includes platform conodonts, consisting of a slender anterior part and a flat, broad posterior platform. On the anterior part (process) and the platform there are rows of denticles; anteriorly there is a simple row, but on the platform a lateral denticle row diverges at a sharp angle from the former row. At the anterior process one denticle is higher than the other, forming a cusp, from the base of which a lateral process is developed. The aboral surface is deeply excavated.

According to Rhodes, *Balognathus* differs from *Amorphognathus* in:

(1) "The stronger development of the median cusp, which is always conspicuous";

(2) "the anterior bar (process), which is strongly denticulated";

(3) "the platform development is confined to a lateral extension of the posterior 'bar' of the unit" (cf. op. cit., p. 284).

About these points the following may be said. In fact, there are species of *Amorphognathus* with one of the denticles of the anterior process bigger than the others, thus forming a cusp (Lindström 1959). A strong denticulation of the anterior process does not constitute a valid difference from *Amorphognathus*; in this paper forms of *Amorphognathus* are described that have very large denticles in the anterior process. The third point, the platform development confined to a lateral extension of the posterior process, may at first seem rather characteristic. However, a closer study of the figures of the holotype of *Balognathus expansa* (cf. Rhodes op. cit., pl. 20, figs. 50, 52, 57; also fig. 3, p. 284) shows that this specimen in all probability is fragmentary; its posterior part is missing and in the anterior inner margin of the 'platform' there seems to be a fracture. In fact, one might hazard a guess that this fracture is what remains of an antero-laterally directed process that has been broken off. Further, it seems rather probable to me that the denticle rows on the posterior "platform" extended out on to two processes, the bases of which are broken in this specimen. This would be homologous with similar structures in other genera. However, if this reconstruction hypothesis is correct, the genotype of *Balognathus* would actually be a good specimen of the Welsh form of *Amorphognathus ordovicica*. Consequently, in that case *Balognathus* should be regarded as a junior subjective synonym of *Amorphognathus*. However, because I have not seen the specimen in question, I do not want to omit the possibility that Rhodes' original interpretation of the organization of *Balognathus* may be correct. In all events, a re-examination of the holotype and supplementary material is needed before the genus *Balognathus* may be accepted.

After this was written, I learned that Dr. M. Lindström during his work with the conodont fauna of the Crûg limestone has come to a very similar opinion regarding the status of *Balognathus* (cf. Lindström 1959).

In the material from Tväre which is comparatively rich in specimens of *Amorphognathus* there are forms which in their general organization plan and length of the processes are closely related to *Am. ordovicica*. It is true that the Swedish and

American specimens do not agree perfectly, but on the other hand, the differences do not seem significant enough to justify the erecting of a new species. I will therefore tentatively refer the Tvären specimens to a new subspecies of *Am. ordovicica*; perhaps in the future when more material is accessible, it will be possible to promote this subspecies to the rank of species.

Amorphognathus ordovicica Branson & Mehl ssp. *simplicior* n.ssp.

Pl. 4, figs. 2, 5, 6.

DERIVATION OF NAME.—Latin *simplicior* = comparative of *simplex*, simple. The posterior lobe of the posterior lateral process is absent or only weakly developed.

HOLOTYPE.—LO 4051 T, pl. 4, figs. 2, 5.

DIAGNOSIS.—An *Amorphognathus* with a usually bilobate anterior lateral process, and a posterior lateral process with an undistinctly or weakly developed posterior lobe. In lateral view, the anterior process is gently arched. Main denticle row almost straight or somewhat sigmoidal.

DESCRIPTION.—The central unit, formed by the anterior and the posterior processes, is straight or almost so. From the anterior process diverges a rather short, anterior lateral process that may be bilobate, but is generally broken off, and from the posterior process diverges another lateral process; thus, there is a definite distance between the points, where the lateral processes originate.

The anterior process, which constitutes the anterior part of the central unit, is of about the same length as the posterior process or shorter, straight, very slender and has a pointed distal end. On the lateral faces of it, a low but conspicuous ledge runs above the aboral margin, which forms a curve in lateral view, the posterior part of the anterior process being arched. The process is quite strongly compressed from the sides, and its relatively thin oral margin bears 6–15 denticles, which form the anterior part of the main denticle row. These denticles are stout, 1–2 times as high as wide, basally confluent but apically free, and not very pointed. Being somewhat laterally compressed, the denticles have convex lateral faces and sharp anterior and posterior edges. The highest denticle is located a little posterior to the middle of the process, and from there the heights of the denticles decrease continually anteriorly, the most distal denticles being very small.

The anterior lateral process diverges from the anterior process at a point near the highest denticle. As a rule this process is broken off, but it has been possible to study it on the undamaged specimens found. It seems to be generally bilobate but it is possible that in specimens of an early development stage the process may be unilobate. At all events it is lower and much weaker than the anterior process, with the lobes, when they are both developed, making an angle of 70–90° with each other. Orally the lobes are denticulated, but sometimes denticles may be missing in the posterior one. The denticles are low, confluent, and often more or less irregularly and indistinctly developed.

The posterior process that forms the posterior part of the central unit is broad, with the general outline bulbous and platform-like in oral view, as a rule with a somewhat pointed distal end. In the middle of it the main denticle row runs orally on a low ridge that may be almost straight but sometimes winds a little. The denticles are low, stubby, as a rule more or less confluent, and with sharp anterior and posterior edges; often the highest denticles of the posterior process are situated somewhat

posterior to the middle of the process. Anteriorly and posteriorly the denticulation of this process is irregular, and denticles often are missing on the central ridge of the anterior part of the posterior process.

A posterior lateral process originates from the anterior part of the posterior process. In most specimens, it is, strictly speaking, bilobate, but the posterior lobe of it is characteristically weakly developed and sometimes completely absent. On the other hand, the anterior lobe is very conspicuous though not as long as the posterior process. This lobe makes an angle of c. 50–70° with the anterior process, is broad, and has a rounded end. The posterior lobe, when developed, is very short and bulbous. Orally the lobes have central rows of low, stubby denticles, usually only in small number.

In specimens, which are well developed, the margins of the posterior processes are flexed upwards forming oral marginal furrows between the margins and the central ridges, and a marked ledge that runs along the margins of the processes. The aboral surface is excavated over the whole area, forming a wide but not very deep basal cavity, which however is rather narrow at the anterior processes. In most specimens from Tvären this cavity is more or less filled with a basal filling.

REMARKS.—This subspecies seems in most essentials to agree fairly well with the description of *Amorphognathus ordovicica*, given by Branson & Mehl, but is distinguished by, *inter alia*, the very short posterior lobe of the posterior lateral process. It is also similar to *Am. complicata* Rhodes but distinguished by the usually bilobate posterior lateral process, the anterior lobe of which, furthermore, is shorter than the posterior process, making a sharper angle with the anterior process than in *Am. complicata.*

MATERIAL.—20 specimens and a great number of fragments that probably belong here.

OCCURRENCE.—Common in boulders of crystalline Ludibundus limestone from the Tvären area (however as a rule fragmentary).

Amorphognathus ordovicica Branson & Mehl spp. ***simplicior*** n.ssp. var.?

Pl. 4, figs. 1, 3, 4.

Among the material brought to ssp. *simplicior* there are two specimens that in some characters depart from typical specimens of this subspecies. The differences are: (*a*) that all processes diverge in the same horizontal plane; (*b*) that the posterior lobe of the posterior lateral process is well developed; and (*c*) that the main denticle row is not straight but bent, the anterior and posterior processes thus forming an angle of 130–140° with each other. In fact, this form is very similar to the holotype of *Am. ordovicica* but seems to have a somewhat broader posterior process. Yet, the fact that only two good specimens have been found apart from some transitions to typical ssp. *simplicior*, leads me to the conclusion that quite probably this type is only an extreme form of ssp. *simplicior*. However, the form is so remarkable and so characteristic that distinguishing it as a variety would be legitimate. Because of the scarce material, I prefer to bring it tentatively under the above systematic designation.

MATERIAL.—Two specimens.

OCCURRENCE.—The specimens were found in boulder nr. 10, consisting of crystalline Ludibundus limestone from the Tvären area.

Amorphognathus tvaerensis n.sp.

Pl. 4, figs. 7–10.

DERIVATION OF NAME.—After the bay of Tvären.

HOLOTYPE.—LO 4853 T, pl. 4, figs. 7, 8.

DIAGNOSIS.—An *Amorphognathus* with a slender, blade-like, pointed anterior process, from which a rather weak anterior lateral process diverges, and a broad, platform-like posterior process with two lateral processes, viz. one bilobate, located nearest to the anterior lateral process but on the opposite side, and one unilobate more posterior to them and on the same side as the anterior lateral process. All lateral processes shorter than the posterior process. Central unit arched in lateral view. Main denticle row making a sinuous curve.

DESCRIPTION.—The complex unit consists of five processes, viz. one anterior and one posterior, which form the central unit with the main denticle row, and three lateral ones, two bilobate and one unilobate. One bilobate process branches from the anterior process, and the other, here called "1st posterior lateral process", from the anterior part of the posterior process. The unilobate lateral process, here referred to as "2nd posterior lateral process", originates from about the middle of the posterior process.

The anterior process is as a rule somewhat shorter than the posterior process, slender, is strongly compressed laterally and pointed distally, and has as a whole a blade-like appearance. In oral view it is straight or slightly curved to one side, whereas in lateral view it is straight or directed a little downwards distally. The lateral faces of the anterior process are smooth except for a conspicuous ledge that runs near the aboral margin. Orally the process has a ridge, bearing the denticles. The latter, generally 5–20, are erect, stout, 1–1.5 times as high as wide, confluent at their bases but with free, not very pointed apices. They are somewhat compressed laterally, which makes their lateral faces moderately convex and the anterior and posterior edges sharp. From the distal end, where the denticles are very small, their sizes increase rapidily posteriorly, becoming constant in the posterior part of the anterior process, where there is a tendency towards development of one or a few particularly big denticles; however, the difference in size between these denticles and those more anteriorly in the process is not great enough to justify the designation "top denticle" or "cusp" for the largest of them.

The anterior lateral process originates from a point just below these large denticles. Usually it is broken off but in complete specimens it is bilobate; generally the anterior lobe is somewhat longer than the posterior one, but both are shorter than the anterior process. Orally they bear a central row of low, fused denticles.

The posterior process is flat, broad and has a rounded distal end which often is directed distinctly downwards; in lateral view the process is thus curved downwards in comparison with a horizontal plane through the aboral margin of the anterior process. In oral view the process is curved somewhat to one side, the main denticle row following a sinuous course. The denticles of the posterior process are low, fused, often indistinctly and irregularly developed, as a rule free apically but seldom with sharply pointed ends. Uusually there is only a small number, but sometimes up to 15 denticles may be distinguished in this part of the main denticle row.

From the anterior part of the posterior process diverges the 1st posterior lateral process that is bilobate, with lobes that in general appearance are similar to the

posterior process. The anterior is somewhat longer than the posterior of the lobes but distinctly shorter than the posterior process. The angle between the anterior lobe and the anterior process amounts to c. 40–50°, and that between the two lobes to a little less than 90°. The denticles rows of the lobes include a low number of fused and often confluent denticles.

Posterior to this process, and on the other side of the central axis, the 2nd posterior lateral process originates from the posterior process, making an angle with the process of c. 70–80°, and directed posteriorly. This process may apparently have a varying length, obviously depending on different stages of development of the conodont. In most specimens it is, however, markedly shorter than the posterior process. Orally it may be undenticulated, but generally some low, fused denticles are developed; yet, they seem seldom to reach the main denticle row, but form an isolated row of denticles. The posterior processes of all specimens have more or less raised margins which form conspicuous ledges round the processes. Immediately in front of the 2nd posterior lateral process there is regularly a slight curvature outwards of the aboral margin, which might be interpreted as a rudimentary development of a new process; however, in none of the specimens found does this development seem to have passed the initial stage.

The basal cavity that extends over the whole aboral area is very wide but rather shallow in the posterior processes, and comparatively narrow at the anterior processes. In most specimens from Tvären, it is more or less filled with a basal filling.

REMARKS.—This species is clearly distinguished from all previously described species of *Amorphognathus* by the existence and position of the 2nd posterior lateral process. However, it is obviously related to forms like *Am. ordovicica* and *Am. inaequalis* Rhodes, and may be derived from those and similar species by development of a 2nd posterior lateral process.

MATERIAL.—More than 70 as a rule more or less fragmentary specimens.

OCCURRENCE.—Rather common in boulders of crystalline Ludibundus limestone from the Tvären area.

Dichognathus Branson & Mehl, 1933

TYPE SPECIES.—*Dichognathus prima* Branson & Mehl, 1933.

REMARKS.—This genus stands near *Prioniodus* but is distinguished by, *inter alia*, the undenticulated anterior process, which as a rule is only weakly developed (cf. Rhodes & Müller 1956, pp. 697–698).

Dichognathus typica Branson & Mehl, 1933

Pl. 5, fig. 6.

1933. *Dichognathus typica* Branson & Mehl, p. 113, pl. 9, figs. 27–29.

1935*a*. *Dichognathus typicus* Branson & Mehl–Stauffer, p. 141, pl. 11, figs. ?2–3, 5, ?8, ?10.

?1935*b*. *Dichognathus typicus* Branson & Mehl–Stauffer, p. 604, pl. 71, fig. 23.

cf. 1943. *Dichognathus typica* Branson & Mehl–Branson & Mehl, p. 387, pl. 64, fig. 9.

1944. *Dichognathus typica* Branson & Mehl–Branson, pp. 89–90, pl. 13, figs. ?39, 43, 44, ?45.

1952. *Dichognathus typica* Branson & Mehl–Fay, p. 86.

cf. 1957. *Dichognathus typica* Branson & Mehl–Glenister, p. 735, pl. 88, figs. 4, 6.

1959. *Dichognathus typica* Branson & Mehl–Ethington, p. 274, pl. 40, fig. 17.

1959. *Dichognathus typica* Branson & Mehl–Sweet, Turco, Warner, & Wilkie, p. 1048, pl. 132, fig. 6.

DESCRIPTION.—The posterior process is slightly curved in lateral view and has smooth lateral faces. Orally it carries a series of denticles of slightly varying but as a whole fairly constant size; the denticles are basally confluent but otherwise free, apically pointed, and conspicuously compressed laterally with sharp anterior and posterior edges and faintly convex lateral faces. The lateral process is directed anteriorly and downwards and makes in oral view an angle of c. 160° with the posterior process. It is distinctly shorter than the posterior process, straight with smooth lateral faces, except for a low ridge on the outer side along and somewhat below the bases of the denticles. The denticles differ from those of the posterior process by being somewhat longer and more discrete. The denticles of the lateral process are strongly compressed laterally and rather thin. The anterior process is short, strongly flexed laterally, and has a sharp oral margin that is undenticulated. It continues upwards as a conspicuous costa along the anterior side of the cusp. The cusp is suberect, rather slender, laterally compressed with a fine longitudinal striation on the lateral faces. On the aboral side of the processes there is a well developed basal cavity that is deepest below the cusp. Its greatest width is at about the middle of the posterior process, where the inner basal margin curves inwards.

REMARKS.—Specimens of this type are extremely rare in the samples. Because of their fragile nature, all specimens found are more or less fragmentary, probably because of the extraction process. In all essentials they seem however to agree with the original description. With the exception of the undenticulated anterior process they are very similar to forms of *Prioniodus variabilis* n.sp. that sometimes has but weak denticulation along the anterior process.

According to Ethington (1959, p. 274) this genus has not before been reported from Europe. However, it must be pointed out that Rhodes (1953, p. 317) referred a single specimen from the Llandeilo limestone to *Dichognathus* cf. *D. typica;* because this specimen has all processes denticulated, it might be better to bring it to *Prioniodus.* Probably it is conspecific with forms included in *P. variabilis* n.sp. in this paper. Further, Sannemann (1955*b*, p. 25) reported two species of *Dichognathus,* viz. *D.* cf. *extensa* Branson & Mehl, and *D.* cf. *typica* from Arenigian-Llandeilian strata in Germany. However, as Sannemann remarked, the two specimens found are very badly preserved, and their relation to *Dichognathus* must be regarded as uncertain.

MATERIAL.—Four specimens.

OCCURRENCE.—Very rare in the boulders nr. 6 and 10 of Ludibundus limestone from the Tvären area.

Distacodus Hinde, 1879

TYPE SPECIES.—*Machairodus incurvus* Pander, 1856.

REMARKS.—Pander's original generic name was preoccupied and Hinde (1879) introduced the new name *Distacodus* for the genus. Lindström (1955*a*, p. 554) has pointed out that to *Distacodus* should be referred only those simple conodonts having a lateral costa on each side, which does not run near the posterior edge.

Distacodus? falcatus Stauffer, 1935

Pl. 1, fig. 15. Textfig. 3 C.

1935*a*. *Distacodus falcatus* Stauffer, pp. 142, 159, pl. 12, fig. 16.

1935*b*. *Distacodus falcatus* Stauffer–Stauffer, p. 605, pl. 74, fig. 30.

1941. *Distacodus falcatus* Stauffer–Stauffer & Thiel, pp. 238, 241, 245.

cf. 1959. *Distacodus falcatus* Stauffer–Ethington, p. 275, pl. 39, fig. 9.

REMARKS.—The specimens referred to this species agree fairly well with the figure and the somewhat spartan description given by Stauffer (1935*a*). My specimens, however, agree even more closely with the specimen from the Decorah shale, which is also figured by Stauffer (1935*b*). Yet, the specimens seem to have a slightly longer cusp, which, however, may possibly depend on the fact that the cusp is fragmentary in Stauffer's specimens. The lateral costae appear to be more accentuated in the Tvären specimens, but in this respect there seems to be a rather wide variation from specimen to specimen. One might wonder if this species, at least the type that is most common in the Tvären material, really belongs to *Distacodus*. In fact, the lateral costae run in part near the posterior edge, particularly at the upper part of the cusp, and according to Lindström (see 1955 *a*) this characterizes the genus *Acontiodus*. However, as in *Distacodus expansus* (Graves & Ellison), where the costae sometimes are located very near the posterior edge (cf. Lindström 1955*a*, pl. 3, fig. 14), these costae do not reach the posterior margin. In the American holotype, which is figured by Stauffer, the costae seem even to be located somewhat more anteriorly as in typical species of *Distacodus*. In some specimens from Tvären there is a shallow furrow in the oral margin, particularly in its upper part at the point of maximum curvature of the cusp. The margins of this furrow are often developed as low carinae. Specimens with these characters could perhaps better be referred to *Scolopodus*. However, I think there are not sufficient reasons at present to definitely separate this species from *Distacodus* on the material that has hitherto been found and described, and in this paper it is questionably referred to the latter genus.

MATERIAL.—Seven specimens.

OCCURRENCE.—Rare in boulders of Ludibundus limestone from the Tvären area.

Drepanodus Pander, 1856

TYPE SPECIES.—*Drepanodus arcuatus* Pander, 1856.

REMARKS.—Depending on broad and somewhat vague original definitions, the systematic characters distinguishing the genera *Drepanodus* and *Oistodus* remained long unclear, and this led to a certain looseness in the nomenclature as regards these genera. However, Lindström (1955*a*) has proposed redefinitions for both *Drepanodus* and *Oistodus*, formulating that of the former genus thus: "I have regarded all symmetrical and subsymmetrical species with smooth lateral faces, sharp anterior and posterior edges, and the posterior edge of the cusp meeting the oral margin in a curve as belonging to *Drepanodus*" (Lindström op. cit., p. 558).

This redefinition and that of *Oistodus* give clear separating characters for the two genera, and it would be valuable for conodont systematics if they could be generally adopted.

Drepanodus homocurvatus Lindström, 1955

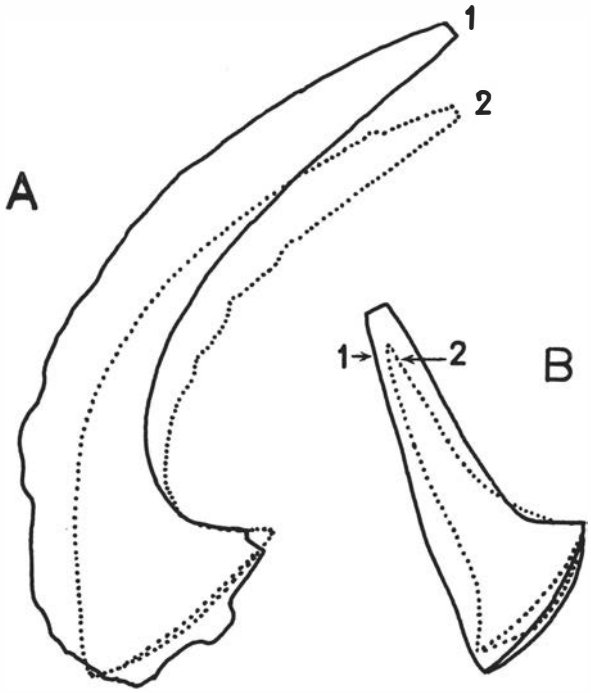
Pl. 2, figs, 13, 14; pl. 5, fig. 19. Textfig. 3 E, 4 A.

1933. *Oistodus curvatus* Branson & Mehl, p. 110, pl. 9, figs. 4, 10, 12.

1935*a*. *Oistodus curvatus* Branson & Mehl–Stauffer, p. 146, pl. 12, figs. 20, 23, ?24, 27, ?29, 30, ?36.

1935*b*. *Oistodus curvatus* Branson & Mehl–Stauffer, p. 609, pl. 74, figs. 5, ?10, ?12, 17, 20–23, 25, 26, 27–29, ?31, 33–37, ?38, ?39, 40, 47, 48, ?49.

1941. *Oistodus curvatus* Branson & Mehl–Graves & Ellison, pl. 3, figs. 17, 24.



Text-fig. 4. Comparison between general outlines of Middle Ordovician and closely related Lower Ordovician conodonts. A, *Drepanodus homocurvatus* Lindström: (1) specimen LO 4036 t from Tväreп; (2) specimen LO 3577 t from the Lower Ordovician. B, *Drepanodus suberectus* (Branson & Mehl): (1) specimen LO 4059 t from Tväreп; (2) specimen LO 3575 t from the Lower Ordovician. Approx. × 55, × 100, × 60, and × 80, respectively.

1953. *Oistodus curvatus* Branson & Mehl–Rhodes, p. 295, pl. 21, figs. 82, 83, 89, 90, 157, ?158, 159, 160, ?161.

aff. 1955*a*. *Drepanodus homocurvatus* Lindström, p. 563, pl. 2, figs. 23, 24, 39.

1957. *Drepanodus homocurvatus* Lindström–Glenister, p. 725, pl. 86, fig. 13, pl. 87, figs. 5, 6, 8.

1959. *Drepanodus homocurvatus* Lindström–Ethington, p. 276, pl. 39, fig. 16.

1959. *Drepanodus homocurvatus* Lindström–Sweet, Turco, Warner, & Wilkie, p. 1049, pl. 130, fig. 7.

For further synonyms see Fay (1952, p. 134).

REMARKS.—This species is not very common in the material here treated, but several specimens are found. They agree well with the description of *Oistodus curvatus*, given by Branson & Mehl (1933) and fairly well with the description of *Drepanodus homocurvatus* Lindström, 1955. In all events, no remarkable difference could be found. Yet, after a direct comparison with Lindström's original specimens, it was possible to recognize some minor differences between Lindström's specimens from the Lower Ordovician and those from the Middle Ordovician of Tväreп. The former specimens have a somewhat smaller width of the lower part of the cusp, a little more rounded lateral faces, and a straighter basal margin in lateral view. These differences may seem trifling, but they appear rather significant for the whole material. It can thus not

be excluded that they could have stratigraphical significance. If this should be the case, it is evident that *Oistodus curvatus* Branson & Mehl, described from the Plattin (Middle Ordovician) of Missouri, is not quite identical with "*Drepanodus homocurvatus*" from the Lower Ordovician of Sweden. However, further research, incl. direct comparisons between the original specimens, is necessary, before anything more definite can be said on this question.

A remarkable fact is that in the Tvären material the species occurs in two forms considerably different in size. One form (cf. pl. 2, fig. 14) is in every detail nearly twice as large as the other (cf. pl. 2, fig. 13), but otherwise both are identical, except in colour: the large form is light brown, the small ivory-coloured. Although no single intermediary between these forms is found, I do not think that mere differences in size justify the erection of a variety. In all probability size differences do not represent a solid foundation for spitting up a conodont species.

MATERIAL.—41 specimens.

OCCURRENCE.—Not very common in boulders of Ludibundus limestone from the Tvären areas.

Drepanodus suberectus (Branson & Mehl, 1933)

Pl. 5, fig. 7. Textfig, 3 K, 4 B.

1933. *Oistodus suberectus* Branson & Mehl, pl. 111, pl. 9, fig. 7.
1951. *Oistodus suberectus* Branson & Mehl–Branson, Mehl, & Branson, p. 8, pl. 2, figs. 1–4.
aff. 1955*a*. *Drepanodus suberectus* (Branson & Mehl)–Lindström, p. 568, pl. 2, figs. 21, 22.
1957. *Oistodus*? *suberectus* Branson & Mehl–Glenister, p. 726, pl. 86, figs. 12, ?14.
1959. *Drepanodus suberectus* (Branson & Mehl)–Stone & Furnish, p. 222, pl. 31, fig. 7.
1959. *Drepanodus suberectus* (Branson & Mehl)–Ethington, p. 276, pl. 39, fig. 17.
1959. *Drepanodus suberectus* (Branson & Mehl)–Sweet, Turco, Warner, & Wilkie, p. 1049, pl. 130, fig. 4.

For further synonyms see Fay (1952, p. 136).

REMARKS.—The Tvären specimens agree closely with Branson & Mehl's original description. As a rule the base is subelliptical in aboral view, with pointed anterior and posterior ends. The cusp is slightly proclined, almost straight or a little curved at the base, and laterally compressed. Along its anterior and posterior edges wide keels are developed that give the lateral faces of the cusp the appearance of broad carinae. The basal cavity is very shallow with its apex directed forwards.

The few specimens found are very uniform in general appearance and do not show any variation similar to that figured by Glenister (1957).

A comparison with Lindström's original specimens from the Lower Ordovician of Sweden shows certain characteristic differences. Thus the cusp of those specimens is more slender, having a smaller width, more rounded lateral faces, and narrower anterior and posterior keels than that of the Tvären specimens. The discussion under *Drepanodus homocurvatus* regarding eventual differences of stratigraphic value between Swedish specimens from Lower Ordovician and the American originals from Middle Ordovician is thus applicable even in the case of this species.

MATERIAL.—Five specimens.

OCCURRENCE.—Very rare in boulders of Ludibundus limestone from the Tvären area.

Falodus Lindström, 1955

TYPE SPECIES.—*Falodus prodentatus* (Graves & Ellison, 1941).

Falodus n.sp.

Pl. 5, figs. 4, 5. Textfig. 3 A.

DESCRIPTION.—The base is rather long, and in lateral view roughly triangle-shaped. The basal margin is somewhat curved with a distinct undulation upwards at a point about one-third of the distance from the antero-basal angle to the oral-basal angle. Anteriorly the base is thin and strongly compressed laterally; posteriorly it is somewhat widened. While the inner face of the base is flat, the outer face is slightly convex, depending on a flaring out of the wall of the basal cavity. This cavity, being triangular in lateral view, is very narrow and has its greatest width posteriorly. The antero-basal and oral-basal angles are c. 70°, and 45°, respectively. Along the rather thin anterior edge a small number of very weak denticles are developed with fused, blunt apices. The oral edge is almost straight, forming a keel which makes an angle of c. 45° with the posterior edge of the cusp. The cusp is reclined, and in the available specimen broken off, but is probably at least as long as the oral edge. In cross section it is rather thin, and with sharp anterior and posterior edges. On each of its lateral faces a very conspicuous carina runs a short distance above the base; however, it soon becomes indistinct higher on the cusp.

REMARKS.—Hitherto only three species have been referred to this genus, viz., except the genotype mentioned above, *Falodus extensus* (Graves & Ellison), and *Falodus* n.sp. (cf. Lindström 1957). The latter species is rather similar to the Tvären species, but they are not identical. A comparison with Lindström's original specimens shows that my species is distinguished, *inter alia*, by its higher base, very prominent lateral carinae, and the course of its basal margin. Thus, I think there is no doubt that the Tvären specimen really belongs to a new species, but because the available material, as mentioned, only includes one specimen, which also seems to be rather fragile, I yet hesitate to erect a new species.

MATERIAL.—One specimen.

OCCURRENCE.—Only found in boulder No. 3 of Ludibundus limestone from the Tvären area.

Ligonodina Ulrich & Bassler, 1926

TYPE SPECIES.—*Ligonodina pectinata* Ulrich & Bassler, 1926.

ULRICH & BASSLER'S GENERIC DEFINITION (Ulrich & Bassler 1926, p. 12).—"General form of tooth as in *Prioniodus* but distinguished by the development of a series of sucker-like impressions on one side of the downward extension of the main cusp."

REMARKS.—As has been pointed out by Rhodes (1953, p. 305) the "sucker-like impressions" are scars of broken denticles.

The genus *Eoligcnodina* Branson, Mehl. & Branson, 1951 was erected to include forms with a well developed basal cavity, but in other respects obviously similar to *Ligonodina*. Rhodes (1953) regarded this character as insufficient to distinguish a new genus. Ethington (1959) noticed that Ordovician species of *Ligonodina*-type,

in addition to a deep basal cavity, have crowded or fused denticles on the posterior process, and he regarded these characters as sufficient to motivate retention of the genus *Eoligonodina*.

Ligonodina elongata Rhodes, 1953

Pl. 5, figs. 14, 15, 17, 18.

1953. *Ligonodina elongata* Rhodes, pp. 305–306, pl. 21, figs. 130, 131.
?1955. *Ligonodina* cf. *L. elongata* Rhodes–Rhodes, p. 134, pl. 8, figs. 7, 8.
1959. *Eoligonodina elongata* (Rhodes)–Ethington, p. 277, pl. 40, fig. 5.
1959. *Ligonodina elongata* Rhodes–Lindström, p. 440, pl. 3, figs. 26, 27.
1959. *Eoligonodina elongata* (Rhodes)–Sweet, Turco, Warner, & Wilkie, p. 1051, pl. 132, fig. 4.

REMARKS.—A number of specimens in the Tvären material are referred to this species. In most respects they agree closely with the excellent description, given by Rhodes, but because my specimens seem to be in better condition than those from Great Britain, some small additions can be made to the description. Thus, the cusp of complete specimens is pointed, generally suberect, and of about the same length as the anterior process. The denticulation of the posterior process is also well preserved in the Tvären specimens. Posterior to the cusp there are 4–8 rather small but pointed, basally fused, denticles; in some cases there is in this series one discrete denticle about twice as big as the others. Behind these follows one very large denticle, as a rule being of the same size as the cusp, erect, pointed, compressed laterally and with sharp anterior and posterior edges. This denticle is followed by a series of small, erect, basally confluent denticles, similar to those in the first series of the posterior process.

In some specimens a well developed basal funnel is preserved situated between the anterior and posterior processes. As usual this funnel is very fragile and often it is more or less destroyed. In some specimens both the basal funnel and the funnel filling are lost, and the only structural features that indicate their previous existence are the longitudinal excavations on the aboral sides of the processes. These excavations which constitute a part of the basal cavity are described from several genera, e.g. *Trichonodella* Branson & Mehl, *Roundya* Hass, and *Keislognathus* Rhodes. It seems probable that also specimens of these genera have been provided with a basal funnel, which, however, is less frequently preserved. As mentioned above, I regard it as depending on secondary causes whether there is or is not a basal funnel in specimens that in all other details agree. The funnel is thus a feature, the presence or absence of which is without systematic value. According to this, I have not distinguished any such forms in this material, and all specimens are referred to *Ligoncdina elongata*.

In a recent paper, Lindström (1959) discussed the generic characters of *Pericdon* Hadding, 1913. According to the generic definition given by Lindström (1955*b*, p. 110), *Periodon* is characterized by an anterior and a posterior process, both denticulated, and a lateral, undenticulated, costa or process. In specimens of the genotype, *Periodon aculeatus*, the anterior process is feebly developed, and the lateral costa may sometimes be completely missing. Another characteristic feature in the type species of *Periodon* is the very large denticle on the posterior process behind the cusp. Now, *Ligonodina elongata* has in fact a similar large denticle on the posterior process and denticulated anterior and pcsterior processes. However, the denticles on the long

anterior process are discrete, rather long, and placed laterally on the process, and the species must thus be regarded as a typical *Ligonodina*.

MATERIAL.—11 specimens.

OCCURRENCE.—Sparse in boulders of Ludibundus limestone from the Tvären area.

Oistodus Pander, 1856

TYPE SPECIES.—*Oistodus lanceolatus* Pander, 1856.

REMARKS.—The following redefinition of the genus was given by Lindström (1955*a*, p. 573): "To *Oistodus* belong simple conodonts with a more or less wide basal cavity. The posterior edge makes a sharp angle with the oral edge. As a rule, either or both of the lateral faces are carinate."

Among the characters, mentioned in this redefinition, the sharp angle between the oral and posterior edges seems to me to be the most significant for the genus.

Oistodus excelsus Stauffer, 1935

Pl. 2, figs. 18, 19.

1935*b*. *Oistodus excelsus* Stauffer, p. 610, pl. 74, fig. 43.

?1957. *Oistodus excelsus* Stauffer–Glenister, p. 725, pl. 86, figs. 4, 7.

?1959. *Oistodus excelsus* Stauffer–Stone & Furnish, p. 224, pl. 31, fig. 5.

1959. *Oistodus excelsus* Stauffer–Ethington, p. 282, pl. 39, fig. 20.

cf. 1959. *Oistodus excelsus* Stauffer–Sweet, Turco, Warner, & Wilkie, p. 1053, pl. 130, fig. 5.

REMARKS.—The few specimens referred to this rather typical species agree well with Stauffer's description and figure. Possibly the cusp is more markedly straight in the Tvären specimens than in the holotype. Yet, this may depend on the fact that the cusp is broken in the holotype and that the reconstruction made is perhaps not quite adequate.

MATERIAL.—Three (four?) specimens.

OCCURRENCE.—Very rare in boulders of crystalline Ludibundus limestone from the Tvären area.

Oistodus sp. aff. *O. inclinatus* Branson & Mehl, 1933

Pl. 1, fig. 16. Text-fig. 3 J.

DESCRIPTION.—The basal cavity is rather shallow, open anteriorly and posteriorly and has a not very distinct apex. The semicircular basal margin makes an angle of c. 80° with the anterior edge and c. 50° with the oral edge. In aboral view the base is slightly asymmetrical in one specimen but in others it is symmetrical. The cusp is about twice as long as the base, strongly reclined, elongated, and it has an almost straight posterior edge in lateral view. Its anterior edge is slightly but continually curved from the antero-basal angle to the apex. In cross section the cusp is rather thin with keeled anterior and posterior edges. On each of the lateral faces of the cusp there is developed a broad carina. It is more accentuated on the inner side. The posterior edge makes an angle of c. 60° with the short, almost straight oral edge which also is provided with a keel. As a rule, the cusp seems to be flexed somewhat inwards, and often a growth axis may be visible.

REMARKS.—The specimens from Tvären differ from typical *O. inclinatus* in having a somewhat longer base which is not always distinctly asymmetrical, and in that the oral edge makes a sharper angle with the posterior edge. From *O. abundans* Branson & Mehl they are distinguished by their anterior margin and the semicircular basal margin. Possibly this is a new species, but because the available material only includes five specimens, I do not think it advisable as yet to erect a new species, particularly because this is a rather critical series of species, which in limited material may be hard to separate from each other.

MATERIAL.—Five specimens.

OCCURRENCE.—Very rare in boulders of Ludibundus limestone from the Tvären area.

Oistodus robustus n.sp.

Pl. 3, figs. 7–10. Textfig. 3F.

DERIVATION OF NAME.—The base of the species is very robust.

HOLOTYPE.—LO 4043 T, pl. 3, figs. 7–9.

DIAGNOSIS.—A simple conodont with an anteriorly-posteriorly extended base and rather short, suberect or slightly reclined cusp. The angle between the posterior edge and the oral edge is sharp. Cusp lacking carinae and costae. Base triangular in cross section with a flat or concave inner side and an angular outer side.

DESCRIPTION.—The base is very long, the length of the basal margin being 3 times the height of the base. In lateral view the base is triangular in general appearance, with a slightly curved oral margin. The inner basal margin is arched, the outer is divided into two parts, one anteriorly and one posteriorly to a very distinct flexing out of the basal sheath; this flare is located at a point about one-third of the distance from the oral-basal angle to the antero-basal angle. In cross section the flare makes the base triangular. The inner side of the base is flat or sometimes concave. The basal cavity is narrow, shallow but long. In the Tvären specimens it is regularly filled with a basal filling.

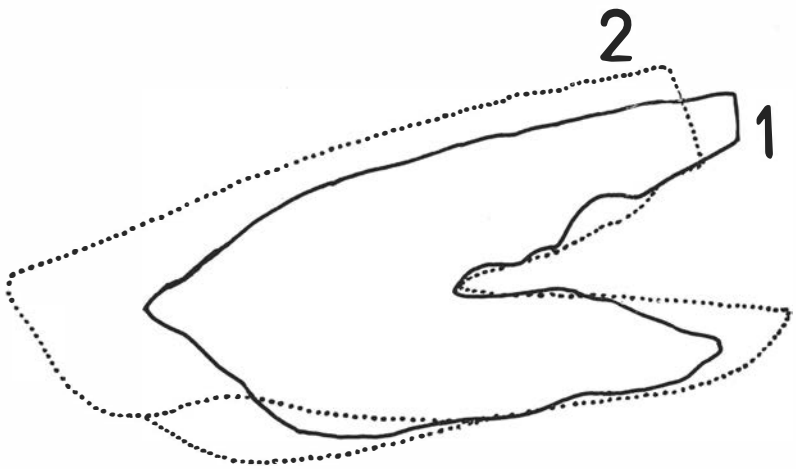
The cusp is short, stout, suberect or reclined and compressed laterally. Generally it is flexed somewhat outwards. The posterior margin is straight, sharp and makes an angle of c. 70–80° with the keeled oral margin. The antero-basal angle is c. 30°. From this angle the anterior margin runs straight at first at the base, but then curves posteriorly at the base of the cusp, after which it again becomes straight and remains until it reaches the pointed end of the cusp. The lateral faces of the cusp are flattened or moderately convex, and lack costae and carinae but have a very fine, longitudinal striation. In some specimens, structures somewhat resembling basal canalules (cf. Lindström 1955*a*) are visible at the lower part of the anterior margin.

REMARKS.—In one specimen a weak denticle is developed at the posterior part of the oral margin. If the oral margin were regularly denticulated, this species should be referred to *Cordylodus*, but because the denticulation in this case seems to be accidental and missing in the majority of the specimens, I think the species must be regarded as a good *Oistodus*.

From *Oistodus breviconus* Branson & Mehl, 1933 the new species is distinguished, *inter alia*, in having a longer anterior part of the base and a longer cusp.

MATERIAL.—36 specimens.

OCCURRENCE.—Not rare in boulders of crystalline Ludibundus limestone from the Tvären area.



Text-fig. 5. Comparison between general outlines of *Oistodus* cf. *venustus* Stauffer, specimen LO 4061 t (1), and *Oistodus forceps* Lindström, specimen LO 3647 t (2). Approx. × 130 and × 150, respectively.

Oistodus cf. *venustus* Stauffer, 1935

Pl. 5, figs. 8, 9. Text-figs. 3B, 5.

cf. 1935*a*. *Oistodus venustus* Stauffer, p. 147, pl. 12, fig. 12.
1953. *Oistodus venustus* Stauffer–Rhodes, p. 295, pl. 22, figs. 168–170.
1957. *Oistodus* sp.–Lindström, p. 174, pl. 1, fig. 8, text-fig. 2.
1959. *Oistodus venustus* Stauffer–Ethington, p. 282, pl. 39, fig. 22.
not 1957. *Oistodus venustus* Stauffer–Glenister, p. 727, pl. 86, fig. 6.

DESCRIPTION.—The base is very long, but low, with a shallow basal cavity which is rather wide at its anterior and posterior ends. Posteriorly the cavity is rather narrow but anteriorly it becomes deeper and wider. From the oral-basal angle, which is very sharp, the basal margin runs rather straight in an anterior direction, but a short distance before the antero-basal angle it makes a curve upwards and meets the anterior edge at an angle of c. 70–90°. At the inner basal margin there is a little undulation at a point below the junction of the posterior and oral edges. The oral edge is sharply keeled and, particularly posteriorly, curved. The faces of the base are moderately convex.

The cusp is as a whole slender, about 1.5 times as long as the base, strongy reclined, and flexed somewhat inwards. Its anterior and posterior edges are sharply keeled and thin. Above the antero-basal angle the anterior edge is slightly curved posteriorly, but becomes nearly straight upwards, and is then subparallel to the posterior part of the basal margin. The angle between the oral and the posterior edges is sharp. The posterior edge is fairly straight basally, but higher on the cusp it makes a curve, and approaches the anterior edge, after which it runs subparallel to that edge to the pointed distal end of the cusp. Laterally the cusp has conspicuous carinae, one on each face.

REMARKS.—This species seems very similar to *Oistodus venustus* Stauffer, which, however, has no lateral carinae, at least to judge from the description and figures given by Stauffer. Rhodes (1953) referred some specimens from the Llandeilo limestone

to Stauffer's species, without any description or remarks about their appearance. Yet, from what may be seen in his figures, at least two of the figured specimens probably are carinate (cf. Rhodes, op. cit., pl. 22, figs. 168, 170). Carinate forms of a similar appearance but with cusp twice as long as base were brought by Lindström (1955*a*) to a new species, *O. forceps*. Glenister (1957) also referred carinate specimens to *O. venustus*.

The Tvären specimens agree closely with Rhodes' figures but are not similar to the specimens figured by Glenister. On comparison with the original of Lindström's form *Oistodus* sp., it is clear that this form is very closely related to, or identical with, the Tvären form; unfortunately, the specimen figured by Lindström (1957, pl. 1, fig. 8) is preserved largely as a mould, which makes a closer examination of it impossible. The type specimens of *Oistodus forceps* Lindström are similar to the Tvären species, but they seem to be distinguished by a straight anterior edge, longer cusp, straighter oral edge, and by the upward curve of the basal margin being located somewhat more anteriorly (cf. text-fig. 5). It must however be emphasized that these differences are small, and that all of them are not distinct in every specimen.

MATERIAL.—Six specimens.

OCCURRENCE.—Rare in boulders of Ludibundus limestone from the Tvären area.

Paltodus Pander, 1856

TYPE SPECIES.—*Paltodus subaequalis* Pander, 1856.

Paltodus n.sp.

Pl. 1, figs. 6–9. Text-fig. 3 D.

DESCRIPTION.—The conodont is rather long and slender with a proclined or suberect cusp. The base is rather wide at the opening of the basal cavity, almost circular in cross section with well rounded anterior and posterior margins; this gives the base as a whole a conical appearance. The basal margin, which is straight or nearly so in lateral view, borders a conical basal cavity which extends rather deeply into the cusp, in the few available specimens to a point about a third of the distance to the apex of the cusp. As a rule the cavity is filled with a basal filling. Above the basal margin there runs in some specimens a shallow groove round the base. The oral edge is rounded and makes an angle of c. 80° with the basal margin; it is almost straight or slightly curved. The cusp forms an angle of a little more than 100° with the base and is about twice as long as this. It has rounded anterior and posterior edges and moderately convex lateral faces. Posteriorly at one side, and more anteriorly at the other, there is a high, very conspicuous costa that runs from the base to the sharply pointed apex of the cusp. This placing of the costae thus makes the cross section of the cusp asymmetrical. On one specimen one of the lateral costae is distinctly weaker and lower than the other, and on a third specimen both costae are comparatively weakly developed; this character seems thus to vary to some degree. At the anterior margin of the lower part of the cusp two rather short, very shallow grooves run upwards in one specimen; however, after a short distance they become indistinctly developed, and higher up the anterior margin of the cusp is smooth. At high magnification a very fine longitudinal striation may be visible on the lateral faces of the cusp.

REMARKS.—In all probability this is a new species, and it was placed in *Paltodus* only after some hesitation. In general appearance it is similar to an *Acontiodus* but its marked lack of symmetry justifies its placing in *Paltodus*. To my knowledge no

Paltodus with a cross section similar to that of this species has previously been described.

Acontiodus n.sp. 3, described by Lindström (1957) from the zone of *Climacograptus wilsoni* of Morroch Bay, Scotland, is superficially similar to the Tvären species but appears, according to Lindström's figures, to be distinguished by a more extended base. A direct comparison between the originals from Morroch Bay and my specimens showed, however, that it cannot be excluded that these specimens are identical. Because of the bad state of preservation of Lindström's specimens it is impossible to make any more detailed comparisons. At all events they seem to be closely related.

MATERIAL.—Four specimens.

OCCURRENCE.—Very rare in boulders of crystalline Ludibundus limestone from the Tvären area.

Panderodus Ethington, 1959

TYPE SPECIES.—*Paltodus unicostatus* Branson & Mehl, 1933.

REMARKS.—Ethington (1959) referred to this genus forms, earlier brought to *Paltodus*, but characterized by a deep basal cavity, which extends into half the height of the cusp or higher. He proposed that only species with a shallow basal cavity like those figured by Pander (1856) should be placed in *Paltodus*.

Panderodus acostatus (Branson & Branson, 1947)

Pl. 1, figs. 13, 14.

1947. *Paltodus acostatus* Branson & Branson, p. 554, pl. 82, figs. 1–5, 23, 24.

1953. *Paltodus acostatus* Branson & Branson–Rhodes, p. 296, pl. 21, figs. 111, 112, pl. 22, figs. 163, 164, pl. 23, figs. 212, 213.

1957. *Paltodus? acostatus* Branson & Branson–Glenister, p. 727, pl. 85, fig. 7.

REMARKS.—In the available material from Tvären only two specimens were referred to this species. One of them was complete and, in my opinion, undoubtedly belongs to this species; the other is fragmentary at the base and has a more atypical appearance. Unfortunately the typical specimen was lost after illustrating, and the remaining specimen may only questionably be referred to this species. This specimen is noteworthy, however, in that the tip of the cusp is stunted and does not have the dimensions that could be expected from the curvature of the anterior and posterior edges below. This structure might indeed be interpreted as an example of regeneration of broken parts of conodonts. In the Tvären material also at least one specimen of *Strachanognathus parva* has been found showing a distinct regeneration of the anterior denticle. Regeneration of broken parts of conodonts in a similar manner are reported by, *inter alia*, Furnish (1938, p. 324, pl. 41, fig. 31), Hass (1941, p. 77), and Müller (1956*a*, p. 12). This phenomenon strongly supports the hypothesis that the conodonts originally had an internal location in tissues of the conodont-bearing animal.

MATERIAL.—One (two) specimen.

OCCURRENCE.—Only found in boulder nr. 3 of Ludibundus limestone from the Tvären area.

Panderodus sp. aff. *P. unicostatus* (Branson & Mehl, 1933)

Pl. 1, figs. 10–12. Text-fig. 3G.

DESCRIPTION.—The base is rather long, often fairly expanded, with greater height than width. In cross section it is roughly triangular with a broadly rounded anterior

margin, and a posterior margin somewhat compressed laterally. The oral-basal angle is c. 70–90°, and the antero-basal angle less than 90°. The basal cavity is very long, pyramidal, and narrow, and extends through one-half to two-thirds of the length of the cusp. Very often fragments of a basal funnel are preserved in the opening of the basal cavity; yet, the funnel filling is as a rule missing. The base continues into the cusp without any sharp limit. The oral margin carries at its lower part a very low costa, but is rounded upwards. The anterior margin of the cusp is very broad and almost flat in the lower part, but becomes rounded upwards. Somewhat laterally there runs along it a costa which is often very conspicuous and which continues to the apex of the cusp. The cusp is as a whole rather slender, suberect to proclined, and not very pointed. Its lateral faces are moderately convex. Distally, near the apex, the cusp is laterally compressed and the margins are sharp. On both faces of the cusp a rather deep, longitudinal groove runs upwards from a notch in the basal margin. These grooves are nearer to the posterior than to the anterior margin; on the cusp they become gradually more shallow and indistinctly developed. At one side the groove is often somewhat deeper than at the other but, except for the laterally flexed anterior costa, the cross section of the cusp is otherwise nearly symmetrical. The specimens show some variations in the length and curvature of the cusp, the height of the base, and the depth of the lateral grooves, but as a whole they represent a rather uniform type.

REMARKS.—Rather many species of *Panderodus* have been described, and some of these seem to stand so near each other that an exact determination without original specimens for comparison may be hard to make. This depends largely on a relatively wide variation within several species and not infrequently on spartan original descriptions. Before a critical revision of this genus is made, I think the use of an "open nomenclature" in doubtful cases is preferable, instead of erecting new species, which might further complicate the systematics. The present species is very closely related to *Panderodus unicostatus* according to the scope Rhodes (1953) gave the species. However, I am not sure that the Tvären specimens are quite identical with the original form from the Silurian that was described by Branson & Mehl (1933); between their figured cotype (pl. 3, fig. 3) and the specimens from Tvären there are some differences, *inter alia*, in the length and curvature of the cusp and the shape of the lateral faces. In the material from Tvären some specimens have a certain resemblance to *Panderodus recurvatus* (Rhodes) (cf. pl. 1, fig. 12). These specimens have a shorter oral margin, more strongly recurved cusp, higher base, and a very weak anterior costa. However, as a whole they differ but slightly from the other specimens, and it seems hardly justified to separate these specimens into a special species.

MATERIAL.—28 specimens.

OCCURRENCE.—Not common in boulders of Ludibundus limestone from the Tvären area.

Paracordylodus Lindström, 1955

TYPE SPECIES.—*Paracordylodus gracilis* Lindström, 1955*a*.

LINDSTRÖM'S GENERIC DEFINITION (Lindström 1955*a*, p. 584).—"Compound conodonts with a cusp, a posterior denticulate edge or process, no lateral processes, and an anterior undenticulated process that is distinctly set-off."

REMARKS.—This genus is closely related to *Cordylodus*, the only difference being the appearance of the anterior process, which is longer in *Paracordylodus* than in

Cordylodus. However, this is a relative character, and from a systematic point of view I think it would be desirable to give a more precise wording of the definition of *Paracordylodus* as regards this character. I therefore propose that only species in which the anterior undenticulated process is about as long as, or longer than the cusp, should be referred to *Paracordylodus*.

Belodus Pander, 1856, stands near *Paracordylodus* but is distinguished by having no anterior and posterior processes; the unit consists of a continually curved cusp that is orally denticulated. Recently, Ethington (1959) split the genus *Belodus* and brought most of the species earlier referred to *Belodus* to two new genera, *Belodina* and *Belodella*. *Belodina* was proposed to include forms characterized in particular by crowded denticles and a rather deep basal cavity, which as a rule is bifid posteriorly, whereas *Belodus* was restricted to include only forms with widely spaced denticles under the assumption that the type species of the latter genus, *B. gracilis* Pander, has the denticles placed in that way. However, according to one, and in all probability the most accurate, of Pander's two figures of the type species of *Belodus*, this species probably has also crowded denticles (cf. Pander 1856, pl. 3, fig. 8). This character is thus of little use in distinguishing the two genera.

As regards the proposed genus *Belodella*, its generic characters are not treated in detail by Ethington (op. cit.). However, the type species, *B. devonicus* Stauffer, 1940, seems to represent a type rather different from typical species of *Belodus* (cf. Stauffer 1940, pl. 59, figs. 47, 48), wherefore the erection of a new genera for these supposed Devonian forms may be regarded as well justified.

Paracordylodus lindstroemi n.sp.

Pl. 2, figs. 8–12. Text-fig. 2 C.

DERIVATION OF NAME.—In honour of Dr. Maurits Lindström, who erected the genus.

HOLOTYPE.—LO 4033 T, pl. 2, figs. 8–10.

DIAGNOSIS.—A *Paracordylodus* with a rather slender, proclined, inwards flexed cusp, a straight, multidenticulated posterior process, and a subequally long, undenticulated anterior process which makes an angle of c. 40° with the posterior process. On the outer face of the anterior process is developed a more or less distinct lateral carina.

DESCRIPTION.—The posterior process is straight or somewhat curved anteriorly, 3.5 times or more as long as high, and with smooth, convex lateral faces. Often a not very marked ledge runs near the aboral margin. Orally the process carries a series of denticles of varying sizes; as a rule groups of 2–3 small denticles alternate with single denticles about 3 times as big. All denticles are pointed, laterally compressed with convex lateral faces and sharp anterior and posterior edges, and are fused basally.

The undenticulated anterior process makes a continuous curve with the cusp, and is of about the same length as the posterior process, but somewhat more slender. The angle between these processes amounts to c. 40°. Along the rather sharp anterior margin of the anterior process there runs a low and often indistinct costa which continues up on the cusp. On the outer side of the anterior process, generally on its upper part, a broad carina is developed. Sometimes this carina is very conspicuous, but often it is more or less indistinct.

The cusp is proclined, of the same length as the processes or somewhat shorter, rather slender, and pointed apically. At its anterior and posterior margins there

are costae which come from the processes. The lateral faces of the cusp are moderately convex and finely striated longitudinally. The cusp is as a rule conspicuously flexed inwards, giving the conodont a convex outer side.

The basal cavity has its apex below the base of the cusp and extends in the form of furrows along the processes. In the Tvären specimens it is often filled by a well developed basal funnel of somewhat varying colour: sometimes black-brown, but often of the same colour as the rest of the conodont. Its cavity, the funnel cavity, sometimes contains remains of the funnel filling.

REMARKS.—Hitherto *Paracordylodus* has been a monotypic genus. From the genotype, *P. gracilis* Lindström, the present species is very well distinguished by, *inter alia*, being much more robust with suberect denticles on the posterior process.

As far as I know, no conodont of a type closely similar to this has previously been described. Perhaps it may be remarked that Pander (1856, pl. 3, fig. 9) figured a specimen, determined by him as *Prioniodus elegans* which actually has a certain superficial resemblance to *Paracordylodus lindstroemi*.

MATERIAL.—31 specimens.

OCCURRENCE.—Not rare in boulders of crystalline Ludibundus limestone from the Tvären area.

Prioniodus Pander, 1856

TYPE SPECIES.—*Prioniodus elegans* Pander, 1856.

REMARKS.—Öpik (1936) and Lindström (1955*a*) have shown that Pander's original definition of the genus (Pander 1856, p. 29) was based on fragmentary specimens. On the basis of more complete material from the Upper Planilimbata limestone of Sweden, Lindström (1955*a*, p. 589) has proposed a redefinition of *Prioniodus* in the following words: "To the genus *Prioniodus* belong compound conodonts with a suberect cusp, from the base of which diverge three denticulate edges or processes, one posteriorly, one anteriorly, and one laterally."

Rhynchognathodus Ethington, 1959 appears, according to the original description (cf. Ethington 1959, p. 286), to stand very near to *Prioniodus*. In fact, the genotype of the former genus, *Rh. typica* Ethington, seems to have the appearance of a *Prioniodus* with a preserved basal funnel (cf. Ethington op. cit., pl. 41, fig. 4).

Prioniodus variabilis n.sp.

Pl. 2, figs. 1–7.

1959. *Prioniodus variabilis* Bergström–Lindström, p. 444, pl. 3, figs. 17–19 (*nomen nudum*).

DERIVATION OF NAME.—The species is rather variable.

HOLOTYPE.—LO 4032 T, pl. 2, figs. 6, 7,

DIAGNOSIS.—A *Prioniodus* with a stout, suberect cusp and subequally long, orally multidenticulated posterior and lateral processes, and a generally shorter anterior process. The lateral process is directed anteriorly, the anterior process deflexed and recurved. The angle between the anterior and the posterior processes amounts to c. 60–80°, and the one between the anterior and lateral processes to c. 50°. The denticles are of subequal size, basally confluent, but apically free. On the faces of the processes there is, as a rule, a more or less conspicuous ledge running near the aboral margin.

DESCRIPTION.—The basal cavity is rather deep with its apex situated below the base of the cusp. The cavity continues as narrow furrows along the aboral sides of the processes; sometimes, particularly in the anterior process, it may be seen only as a shallow groove, extending along the process. Often there are remains of a basal funnel in the basal cavity and occasionally parts of the funnel filling have been preserved.

The anterior process varies greatly, but seems as a rule to be shorter than the posterior and lateral processes. Being strongly deflexed and recurved this process has the appearance of a lateral one; that this process must be regarded as the anterior is evident, when one follows its upwards continuation which runs as a distinct costa along the anterior edge of the cusp to its apex. The denticles of the anterior process are small, erect, blunt and basally confluent; in some specimens the denticulation is very weak in this process.

The lateral process is often directed anteriorly, and in such specimens it greatly resembles an anterior process. It is straight, at least twice as long as high, distally often somewhat pointed, and orally bearing a series of denticles which are bigger than those of the anterior process, more discrete, somewhat proclined and laterally compressed, with sharp anterior and posterior edges.

The posterior process is of about the same length as, or longer than the lateral process, straight or a little curved, and has orally well developed denticles. The denticles are proclined, c. 1.5 times as high as wide, not very pointed, and basally fused; they are somewhat compressed from the sides.

Along one or both faces of the processes a more or less distinct ledge may be developed along and near the aboral margin. Sometimes this ledge is only weak and occasionally almost completely absent, particularly along the posterior process and on the posterior face of the anterior process, but as a rule it is very prominent. The faces of the ledge are smooth except the oral (upper) one which sometimes is provided with irregularly placed pits, only visible at a high magnification. In the available material there are transitions between types, some almost lacking a ledge and others which in this respect are very well developed; thus, as far as I can see, the development of the ledge has limited diagnostic value in the specimens in the Tvären material, at least on the species level.

The cusp is stout, more than 3 times as high as wide, apically pointed, and suberect or slightly proclined. Its anterior margin runs in a regular curve over into the oral margin of the anterior process. From the denticulated margins of the other processes, conspicuous but rather low costae rise to the apex of the cusp. The moderately convex lateral faces of the cusp between these costae are very finely striated longitudinally.

REMARKS.—To this species a series of closely related forms is referred, the most striking morphological characteristics of which is the variable development of the anterior process and the ledges. In specimens where the anterior process is comparatively robust, this process and the lateral one are often arranged almost symmetrically to the cusp. Other forms (cf. pl. 2, figs. 1–3, 4) have only a weak anterior process, the postero-lateral face of which lacking or having only an undistinctly developed ledge; such types have often a certain resemblance to *P. navis* Lindström. Thus it is possible to distinguish several forms in the Tvären material belonging to *Prioniodus*, but hitherto it has not, on the basis of this limited material, been possible to find distinct and constant characters separating the types that would justify separating the material into more than one species. Yet I am conscious of the fact that when more material becomes available it will perhaps be possible to split this species.

MATERIAL.—More than 62 specimens.

OCCURRENCE.—Rather common in boulders of crystalline Ludibundus limestone from the Tvären area. Crûg limestone, Great Britain (Lindström 1959).

Roundya Hass, 1953

TYPE SPECIES.—*Roundya barnettana* Hass, 1953.

REMARKS.—Hass (1953, p. 88) founded the genus on forms, formerly referred to *Trichonodella* but with also the posterior process denticulated. At about the same time Lindström (1955*a*), not yet aware of the existence of Hass' paper, remarked that species with the posterior process denticulated perhaps should not be referred to *Trichonodella*, but he did not erect a new genus. Most subsequent authors have accepted Hass' genus (cf., *inter alia*, Rhodes 1955; Sannemann 1955*b*; Bischoff & Ziegler 1957; Flügel & Ziegler 1957; Glenister 1957), but Sweet (1955) and Rexroad (1957) still brought species with denticulated posterior process to *Trichonodella*. Ethington (1959) remarked that the posterior process in the Ordovician forms of this genus is compressed laterally with more or less crowded denticles whereas post-Ordovician species, also including the type species of *Roundya*, are characterized by a wide posterior process with widely spaced denticles. He therefore suggested that only the latter forms should be referred to *Roundya*.

The specimens of "*Trichonodella*-type" from Tvären are characterized by a very long, laterally compressed posterior process which orally carries a great number of denticles of varying sizes. This development of the posterior process should, in my opinion, preclude reference of these forms to *Trichonodella*, species of the latter genus being characterized by a very short, undenticulated or only weakly denticulated posterior process. On the other hand, the Tvären specimens also differ in several respects from most species referred to *Roundya*, the genotype *R. barnettana* Hass inclusive, as to the appearance of the posterior process. However, until additional material of this type has been described I do not think it justified to erect a new genus for these forms, and in this report they are referred to *Roundya*.

Roundya inclinata (Rhodes, 1953)

Pl. 5, figs. 10–13.

1953. *Trichonodella inclinata* Rhodes, p. 315, pl. 22, figs. 176, 177, 186.
1955. *Roundya inclinata* (Rhodes)–Rhodes, p. 137.
1957. *Roundya inclinata* (Rhodes)–Glenister, p. 733, pl. 88, fig. 19.
1959. *Trichonodella inclinata* Rhodes–Ethington, p. 290, pl. 41, fig. 6.

REMARKS.—The specimens from Tvären agree fairly well with the description and figures given by Rhodes (1953). The posterior process in complete specimens is very long, but as a rule distally broken off; a number of long fragments of processes that in all probability belong to this species have been found in the samples. The oral denticulation of the posterior process rather varies but in most specimens it is composed of short series of comparatively small, thin, sharply pointed denticles which alternate with single, discrete, larger denticles which sometimes are of the same size as the cusp. According to Rhodes (op. cit.) there are generally only two small denticles between the larger ones in the Welsh specimens. In the Tvären specimens the number of denticles varies considerably, and as a whole the denticulation of the posterior

process in the Tväre n specimens is fairly irregular. Sometimes the processes are connected with a basal funnel, but often this funnel is absent.

In some specimens one of the lateral processes is somewhat less curved than the other. This character often seems to be combined with a weaker denticulation on the former process; thus the specimens concerned are somewhat asymmetrical. In fact, some of these specimens could be brought to *Keislognathus* Rhodes, 1955. A study of the few specimens of this type met with in the Tväre n material however suggests that probably these forms only represent an extreme variation type, which by transitions pass over into typical *R. inclinata*.

MATERIAL.—38 specimens.

OCCURRENCE.—Not very common in boulders of Ludibundus limestone from the Tväre n area.

Roundya sp.

Pl. 5, fig. 16.

DESCRIPTION.—The unit consists of a proclined cusp from the base of which one posterior and two lateral denticulated processes diverge. The posterior process is straight or slightly arched, rather slender, has convex lateral faces, and carries orally a series of denticles. The denticles are fused basally, not sharply pointed, and are of varying size; 1–3 small denticles alternate with ones about twice as big. The lateral processes make an angle of c. 30° at their bases but become posteriorly almost parallel. Orally they carry a series of anteriorly and upwards directed, pointed, partly discrete denticles. At the bases of the denticles there is along the processes a more or less distinct ridge. The cusp is rather long, stout, and proclined. From the processes one posterior and two lateral costae rise to the apex of the cusp. The faces of the cusp are rounded between these costae, and finely striated longitudinally. The basal cavity is not very deep and extends as furrows along the processes. Often a basal funnel is developed.

REMARKS.—The specimens brought to the present species are very similar to those specimens in the Tväre n material, which in this study are referred to *R. inclinata*, but they are distinguished, *inter alia*, by a bigger cusp; less varying sizes of the denticles of the posterior process, where the biggest, discrete denticles are distinctly shorter than the cusp; and on the whole a more robust appearance. The available specimens are few and partly fragmentary and do not allow a complete description.

MATERIAL.—Four specimens.

OCCURRENCE.—Very rare in boulders of Ludibundus limestone from the Tväre n area.

Strachanognathus Rhodes, 1955

TYPE SPECIES.—*Strachanognathus parva* Rhodes, 1955.

Strachanognathus parva Rhodes, 1955

Pl. 3, figs. 1–6. Text-figs. 2 B, 3 H, I.

1955. *Strachanognathus parvus* Rhodes, p. 132, pl. 7, fig. 16; pl. 8, figs. 1–4.

REMARKS.—This species is abundant in the limestones from Tväre n, particularly the dense ones, and several hundreds of specimens have been found in the samples.

The Tvären specimens agree perfectly with the excellent description given by Rhodes but show in certain details a considerable variation, though most types seem to fall within the normal variation scope of the species as defined by Rhodes' figures. Because my material appears to be better preserved than the original specimens from the Keisley limestone, some remarks about the variation can be made.

The angle between the anterior and the posterior denticle in anterior view diverges from 5° to 35° (cf. pl. 3, figs. 2, 5). As a rule the posterior denticle does not make an angle with a median line through the base, but sometimes there is a lateral flexing of 5–10°. The length of the basal margin, the height of the base, and the length of the oral margin also vary considerably (cf. pl. 2, figs. 1, 3, 6). Occasionally both the anterior and the posterior denticles have low but distinct carinae on the lateral faces, but as a rule these faces are only moderately convex. The basal cavity may be very deep, but often it is rather shallow. Its apex, which Rhodes described as situated "... vertically above its basal midpoint and immediately below the junction of the two denticles", very often protrudes into the lowest part of the anterior denticle of the Tvären specimens; curiously enough, not a single specimen has been found, where this apex is directed into the bigger posterior denticle.

During examination of the specimens the interesting question arose whether the above variation in a certain character was connected with a similar variation in another character or the variations were independent of each other. If the former alternative proved to be correct, it would be possible to distinguish a series of closely related forms with constant characters, and soon, it became evident that this was the case in the Tvären material. Thus a short oral margin, the denticles continuously curved and making a very small angle with one another, and a rounded basal margin characterize a common type (cf. pl. 3, figs. 1, 2). Another type has a broad base, straight basal margin, almost straight posterior denticle, and the anterior denticle strongly flexed laterally (cf. pl. 3, figs. 3–5). A third type has a long oral margin, denticles somewhat proclined and comparatively short, and the anterior denticle not much shorter than the posterior (cf. pl. 3, fig. 6). In their typical forms these types are indeed rather characteristic, but a statistical examination of certain characters showed that they only represented stages in a long, continuous series of variations, so that it seemed impossible to draw sharp limits between different types. Under such circumstances a systematic splitting of the material seems meaningless to me, because the characters for every type would be vague, and transitional forms abundant.

MATERIAL.—More than 550 specimens.

OCCURRENCE.—Characteristic for the *Strachanognathus*-fauna of Tvären (see above) but also occurring in boulders of crystalline Ludibundus limestone from Tvären.

Tetraprioniodus Lindström, 1955

TYPE SPECIES.—*Tetraprioniodus robustus* Lindström, 1955*a*.

Tetraprioniodus asymmetricus n.sp.

Pl. 2, figs. 15, 16, 17.

DERIVATION OF NAME.—The cross-section of the base is asymmetrical.

HOLOTYPE.—LO 4038 T, pl. 2, figs. 16, 17.

DIAGNOSIS.—A *Tetraprioniodus* with a suberect, rather stout cusp, and all or at

least three of the processes denticulated. All processes are as long as the cusp or longer. The lateral processes form different angles with the posterior process, the cross-section of the base thus being asymmetrical. Denticles in all processes of varying sizes.

DESCRIPTION.—The basal cavity has its apex below the base of the cusp, is rather deep and extends along all the processes. In the Tvären specimens a very well developed basal funnel as a rule fills the cavity, the walls of this funnel connecting the processes with rather thin laminae; thus, the processes seem not to be free in most specimens. The funnel cavity is very deep, at the opening rather wide, and in cross-section somewhat rhomboidal; as a whole the funnel cavity is pyramidal though not symmetrical.

The four processes are of about the same length and all directed posteriorly. The posterior one is straight, not very high, and with convex lateral faces. Orally it carries a series of apically free but basally confluent denticles, which are pointed, a little compressed laterally, with sharp anterior and posterior edges and convex lateral faces. These denticles vary considerably in size; a few small ones alternate regularly with others more discrete, and about twice as big. Most denticles of the posterior process are erect, but the ones near the cusp often have a tendency to be somewhat proclined.

The lateral processes are of a similar appearance but make different angles with the posterior process, viz. c. 30° and 40°, resp. As a rule these processes carry denticles, but sometimes one process is undenticulated. The denticles are rather widely spaced on the oral side of the lateral processes, and they are pointed and directed anteriorly and upwards.

The anterior process is of the same type as the lateral ones, in a curve bent posteriorly, and making an angle of 40–50° with the posterior process. Sometimes it is flexed slightly laterally. At the anterior edge of it there is always a series of sharply pointed denticles which, however, are only free apically. The cusp is suberect and of about the same size as the posterior process, or shorter. It is rather stout, and apically pointed. From the denticle rows of the processes, low but conspicuous costae rise to the apex of the cusp, making its cross-section trapezoidal. The lateral faces between the costae are finely striated longitudinally.

REMARKS.—From the rather closely related *Tetraprioniodus superbus* (Rhodes) and *T. parvus* Ethington this species is distinguished by, *inter alia*, the multidenticulated anterior process. *T. denticulatus* Lindström and *T. robustus* Lindström do not have a "hindeodellid" denticulation as in the case of the Tvären species.

MATERIAL.—43 specimens.

OCCURRENCE.—Only found in boulders of crystalline Ludibundus limestone from the Tvären area.

Tvaerenognathus n.gen.

DERIVATION OF NAME.—After the bay of Tvären, the type locality.

TYPE SPECIES.—*Tvaerenognathus ordovicica* n.sp.

GENERIC DEFINITION.—Lamellar compound conodonts, consisting of a denticulated central unit, here called "the oral margin", from which three processes diverge, viz. one anterior directed downwards (aborally), and two lateral processes, placed posteriorly, one on each side of the oral margin. All processes orally denticulated and aborally excavated, the excavations forming a distinct basal cavity. The denticles of the oral margin are of a subequal size, no one being developed like a typical cusp.

REMARKS.—The most important characteristics of this genus include the single anterior process and the two posteriorly placed lateral processes. Also the absence of a distinct cusp must be regarded as a significant character for the genus. No similar type of conodonts has previously been described, and the generic affinities of the genus are problematic. In its general organization plan *Tvaerenognathus* is somewhat related to *Tripodellus*, described from the Upper Devonian of Germany by Sannemann (1955*a*). However, *Tvaerenognathus* is clearly distinguished from *Tripodellus*, *inter alia*, in lacking a distinct cusp. Further, although Sannemann (op. cit., p. 155) did not mention anything about it in his generic description, the hitherto described species of *Tripodellus* (*T. flexuosus* Sannemann, 1955, *T. robustus* Bischoff, 1957, and *T. tenuis* Helms, 1959) seem to lack a basal cavity of the the type occurring in *Tvaerenognathus*. In a certain orientation, viz. when one of the lateral processes is oriented horizontally, specimens of the genotype of *Tvaerenognathus* have a superficial resemblance to a *Roundya*, yet being asymmetrical and lacking cusp. From *Oulodus* Branson & Mehl, and *Pristognathus* Stone & Furnish, *Tvaerenognathus* differs, *inter alia*, in having three processes.

ORIENTATION.—The specimens are orientated with the denticulated oral margin horizontally. A review of the general organization of the genotype with some morphological terms is given in text-fig. 2F.

Tvaerenognathus ordovicica n.sp.

Pl. 1, figs. 1–5. Text-fig. 2F.

DERIVATION OF NAME.—The species was found in Ordovician strata.

HOLOTYPE.—LO 4020 T, pl. 1, figs. 3–5.

DIAGNOSIS.—A *Tvaerenognathus* with an almost straight, slender, downwards directed anterior process and the posteriorly placed lateral processes making an angle of c. 50° with each other. All processes denticulated, the anterior one however sometimes only weakly. Denticles of the laterally compressed oral margin rather strong, of subequal size, and flexed in somewhat varied directions but as a whole posterolaterally. One of the lateral processes weaker than the other. Because the denticles of the oral margin are flexed to this side, the species is highly asymmetrical with a convex (here designated "outer") side and a concave (inner) side. Basal cavity extending as aboral furrows along the processes.

DESCRIPTION.—The central part of this conodont is the oral margin, from the anterior end of which the anterior process originates, and at the posterior end of which the two lateral processes branch out. All processes are directed more or less downwards. The oral margin is short, laterally compressed and carries a small number (often about five) of denticles which are placed in a row. The denticles are as a rule of about the same size, no one being very large and making a distinct cusp; occasionally however one or two of the central denticles in the row are somewhat bigger than the others. Apically the denticles are sharply pointed, and basally confluent but otherwise they are free along most of their lengths. Being somewhat compressed laterally the denticles have sharp anterior and posterior margins and moderately rounded lateral faces. The denticles are somewhat irregularly flexed posterolaterally.

The anterior process is almost straight in lateral view, but is flexed somewhat inwards in oral view. In some specimens, where it is well preserved, it is rather long, slender, and bears a series of small, fused, upwards directed denticles on the anterior

margin. Sometimes this denticulation may be only weakly developed, and more or less undistinct, but as a rule, at least one denticle is distinguishable.

The two lateral processes make an angle of c. 40° with the anterior process and c. 50° with each other. The inner of the lateral processes is more slender, and often somewhat longer, than the outer. As a rule the denticulation of these processes is different also: the inner lateral process carries small, often irregularly developed denticles, while those of the outer lateral process are stronger, apically pointed, and partly discrete; sometimes some of these denticles are as big as those of the oral margin. The number of denticles of each of the lateral processes seems to vary greatly but as a rule totals more than five.

The aboral side of the unit is excavated, and this basal cavity extends also out on the processes. Sometimes the processes are more or less completely connected with thin laminae which form a structure, resembling a basal funnel.

The outer side of the unit is convex, the inner concave; thus, this conodont is conspicuously asymmetrical.

REMARKS.—No entirely complete specimen of this species has hitherto been met with in the Tväre material, but by study of a number of comparatively well preserved specimens, it has been possible to give the above description. The specimens found agree closely with each other but some variations, especially in denticulation, have been noted. Although representing a type earlier undescribed, this species, as mentioned above, has in a certain orientation some resemblance to *Roundya*-like forms, from which it might be derivable by, *inter alia*, a reduction of the cusp.

MATERIAL.—10 specimens.

OCCURRENCE.—Rare in boulders of Ludibundus limestone from the Tväre area.

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Abbreviations:

BGU Bulletin of the geological institutions of the University of Uppsala.
GFF Geologiska Föreningens Förhandlingar. Stockholm.
JP Journal of Paleontology.
LUÅ Lunds Universitets Årsskrift.
SGU Sveriges geologiska undersökning. Stockholm.

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PLATES

The catalogue numbers refer to the collections of the Institute of Paleontology of the Lund University, where the specimens are deposited.

Plate 1.

Figs. 1–5. *Tvaerenognathus ordovicica* n.gen. et sp., p. 57. *Fig. 1:* LO 4019 t, sample 3, lateral view. *Fig. 2:* same, anterior view. *Fig. 3:* LO 4020 T, *holotype*, sample 12, postero-innerlateral view. *Fig. 4:* same, postero-outerlateral view. *Fig. 5:* same, posterior view. All figures × 75.

Figs. 6–9. *Paltodus* n.sp., p. 47. *Fig. 6:* LO 4021 t, sample 11, anterior view. *Fig. 7:* LO 4022 t, sample 11, outer lateral view. *Fig. 8:* same, inner lateral view. *Fig. 9:* same as fig. 6, outer lateral view. All figures × 65.

Figs. 10–12. *Panderodus* sp. aff. *P. unicostatus* (Branson & Mehl, 1933), p. 48. *Fig. 10:* LO 4023 t, sample 12, lateral view. *Fig. 11:* same, other side. *Fig. 12:* LO 4024 t, sample 12, lateral view. All figures × 60.

Figs. 13, 14. *Panderodus acostatus* (Branson & Branson, 1947), p. 48. *Fig. 13:* lost specimen, sample 3, lateral view. *Fig. 14:* LO 4025 t, sample 3, lateral view. Both figures × 60.

Fig. 15. *Distacodus*? *falcatus* Stauffer, 1935, p. 38. LO 4026 t, sample 7, lateral view. × 65.

Fig. 16. *Oistodus* sp. aff. *O. inclinatus* Branson & Mehl, 1933, p. 44. LO 4027 t, sample 6, lateral view. × 60.

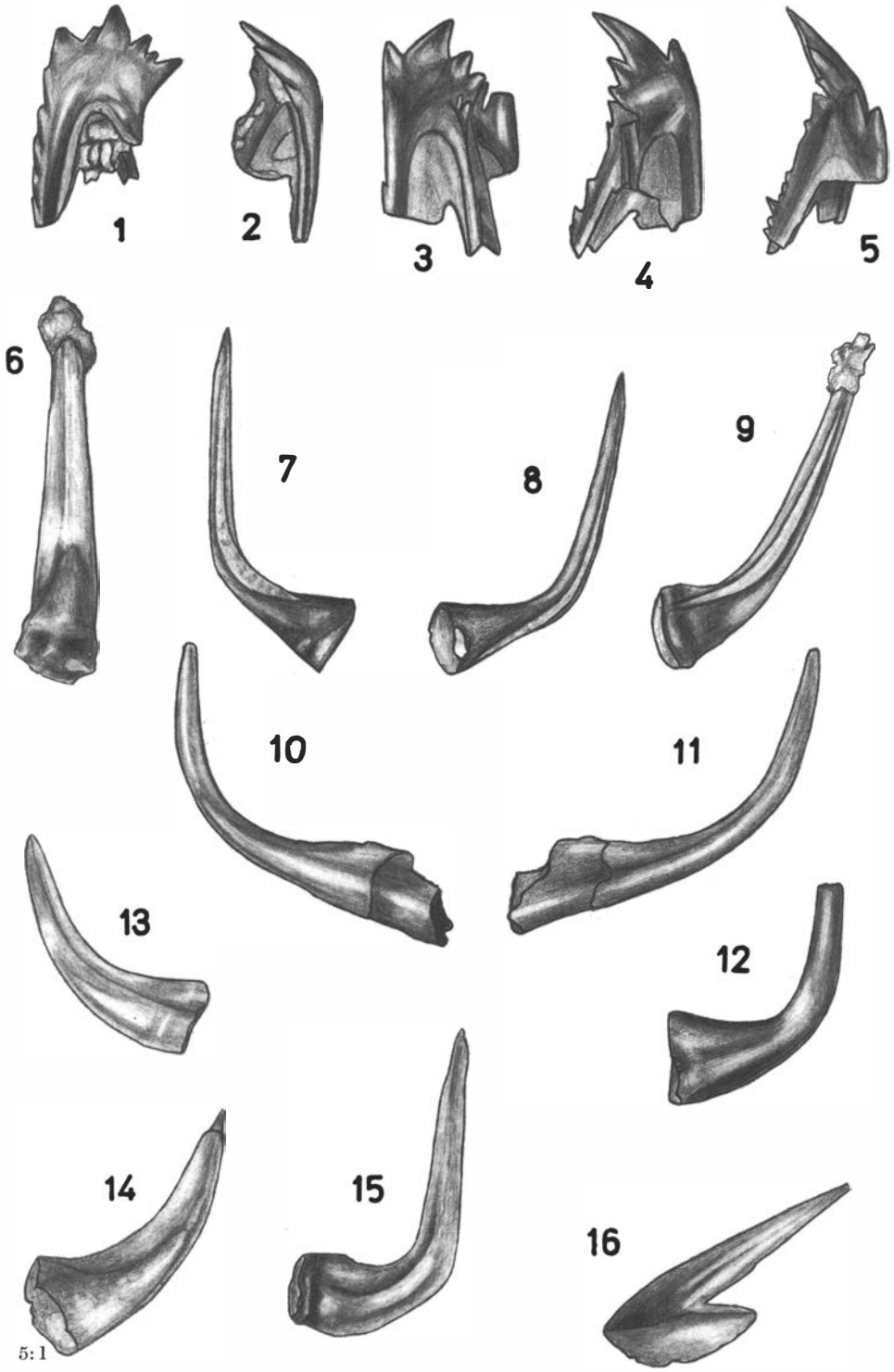
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Plate 2.

Figs. 1–7. *Prioniodus variabilis* n.sp., p. 51. *Fig. 1:* LO 4028 t, sample 11, lateral view. *Fig. 2:* same, posterior and slightly lateral view. *Fig. 3:* LO 4029 t, sample 8, lateral view. *Fig. 4:* LO 4030 t, sample 11, lateral view. *Fig. 5:* LO 4031 t, sample 8, lateral view. *Fig. 6:* LO 4032 T, *holotype*, sample 11, lateral view. *Fig. 7:* same, posterior view. All figures × 50.

Figs. 8–12. *Paracordylodus lindstroemi* n.sp., p.50 . *Fig. 8:* LO 4033 T, *holotype*, sample 9, inner lateral view. *Fig. 9:* same, oral view. *Fig. 10:* same, outer lateral view. *Fig. 11:* LO 4034 t, sample 8, inner lateral view. *Fig. 12:* same, outer lateral view. All figures × 50.

Figs. 13, 14. *Drepanodus homocurvatus* Lindström, 1955, p. 39. *Fig. 13:* LO 4035 t, sample 7, lateral view. *Fig. 14:* LO 4036 t, sample 7, lateral view. Both figures × 42.5.

Figs. 15–17. *Tetraprioniodus asymmetricus* n.sp., p. 55. *Fig. 15:* LO 4037 t, sample 11, lateral view. *Fig. 16:* LO 4038 T, *holotype*, sample 11, posterior view. *Fig. 17:* same, lateral view. All figures × 50.

Figs. 18, 19. *Oistodus excelsus* Stauffer, 1935, p. 44. *Fig. 18:* LO 4039 t, sample 11, inner lateral view. *Fig. 19:* same, outer lateral view. Both figures × 40.

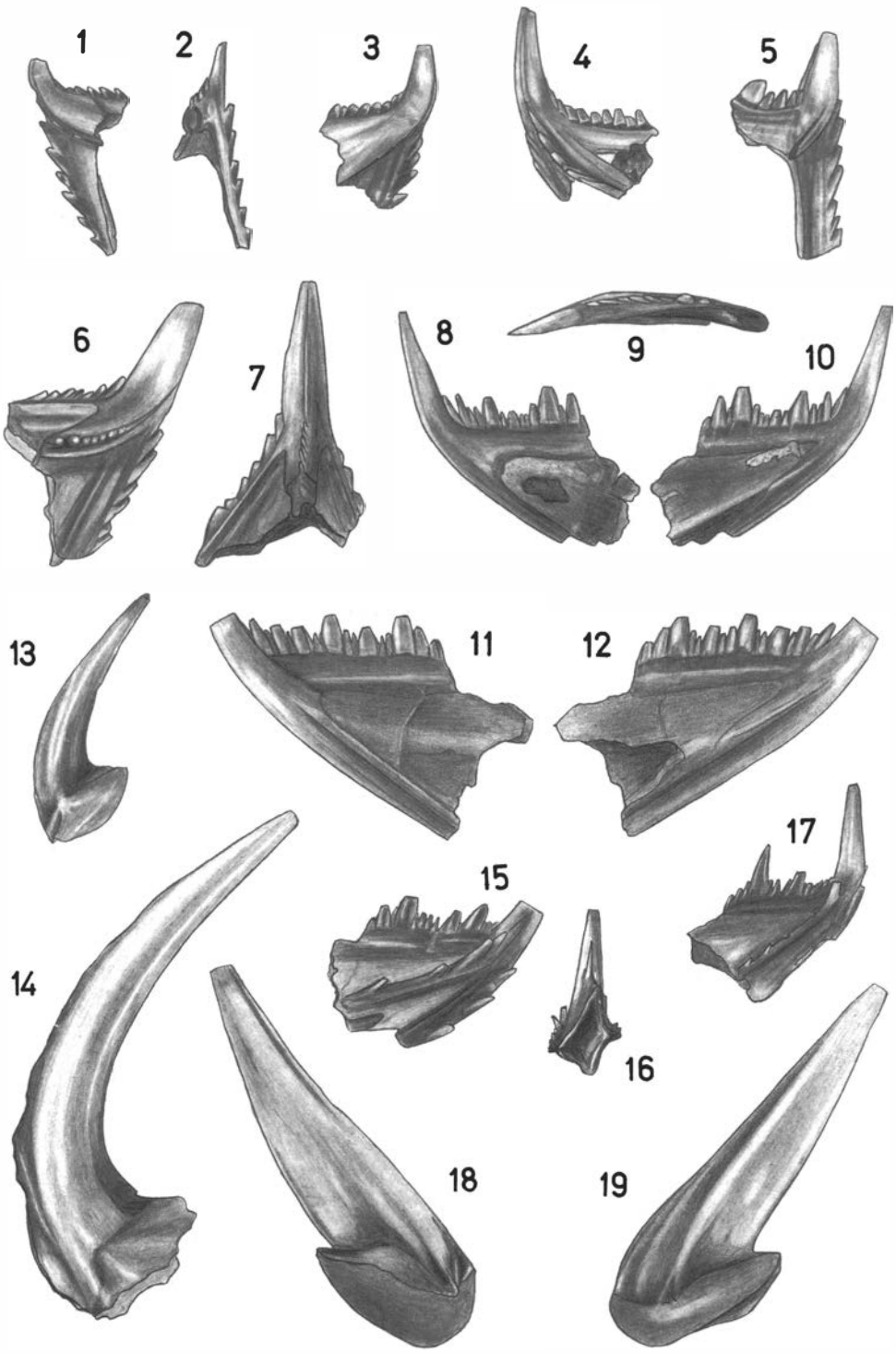
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Plate 3.

(All figures × 60.)

Figs. 1–6. *Strachanognathus parva* Rhodes, 1955, p. 54. *Fig. 1:* LO 4040 t, sample 12, outer lateral view. *Fig. 2:* same, anterior view. *Fig. 3:* LO 4041 t, sample 5, inner lateral view. *Fig 4:* same, outer lateral view. *Fig. 5:* same, anterior view. *Fig. 6:* LO 4042 t, sample 12, lateral view.

Figs. 7–10: *Oistodus robustus* n.sp., p. 45. *Fig. 7:* LO 4043 T, *holotype*, sample 11, oral view. *Fig. 8:* same, outer lateral view. *Fig. 9:* same, inner lateral view. *Fig. 10:* LO 4044 t, sample 8, outer lateral view.

Figs. 11–14. *Ambalodus triangularis* Branson & Mehl, 1933 ssp. *suecicus* n.ssp., p. 28. *Fig. 11:* LO 4045 t, sample 7, lateral view. *Fig. 12:* LO 4046 T, *holotype*, sample 7, lateral view. *Fig. 13:* LO 4047 t, sample 7, lateral view. *Fig. 14:* same, oral view.

Figs. 15–17. *Ambalodus triangularis* Branson & Mehl, 1933 ssp. *erraticus* n.ssp., p. 26. *Fig. 15:* LO 4048 t, sample 11, lateral view. *Fig. 16:* LO 4049 T, *holotype*, sample 11, oral view. *Fig. 17:* same, lateral view.

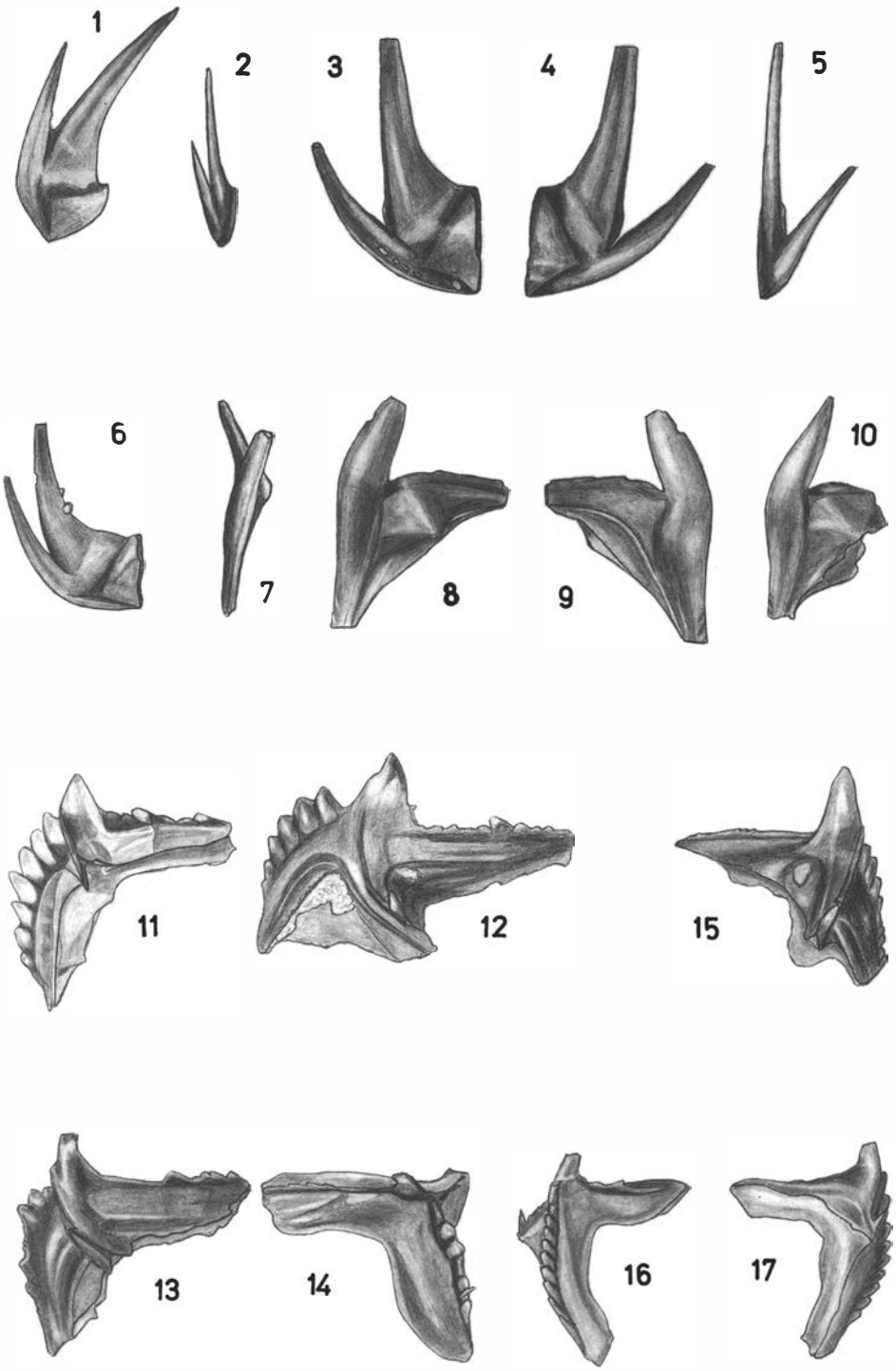
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Plate 4.

(All figures × 60.)

Figs. 1, 3, 4. *Amorphognathus ordovicica* Branson & Mehl, 1933 ssp. *simplicior* n.ssp. var.?, p. 35. *Fig. 1:* LO 4050 t, sample 10, lateral view. *Fig. 3:* same, aboral view. *Fig. 4:* same, oral view.

Figs. 2, 5, 6. *Amorphognathus ordovicica* Branson & Mehl, 1933 ssp. *simplicior* n.ssp., p. 34. *Fig. 2:* LO 4051 T, *holotype*, sample 8, lateral view. *Fig. 5:* same, oral view. *Fig. 6:* LO 4052 t, sample 10, oral view.

Figs. 7–10. *Amorphognathus tvaerensis* n.sp., p. 36. *Fig. 7:* LO 4053 T, *holotype*, sample 12, oral view. *Fig. 8:* same, lateral view. *Fig. 9:* LO 4054 t, sample 7, oral view. *Fig. 10:* LO 4055 t, sample 7, oral view.

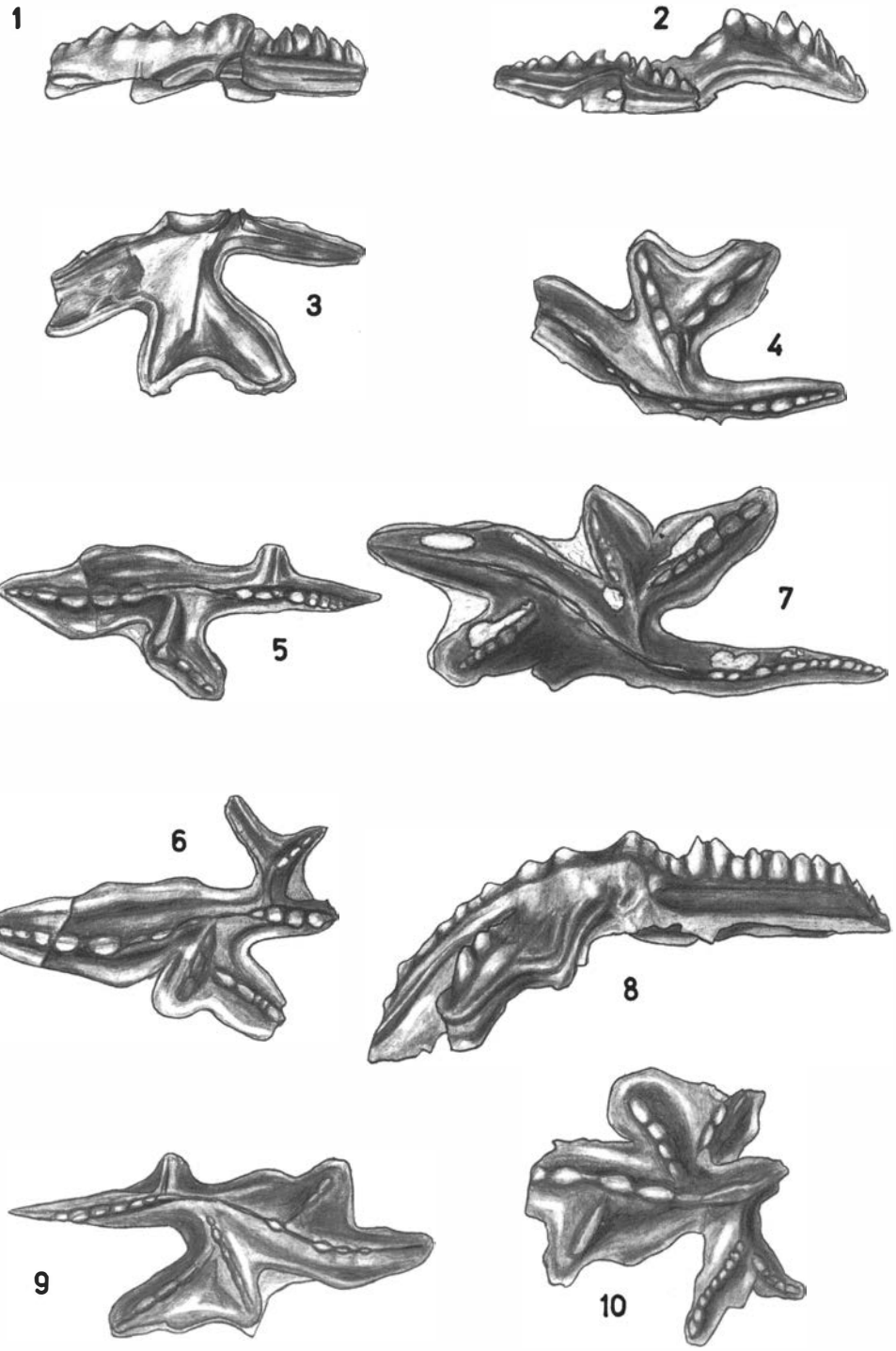
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Plate 5.

Figs. 1–3. *Amorphognathus elongata* n.sp., p. 31. *Fig. 1:* LO 4056 T, *holotype*, sample 6, oral view. *Fig. 2:* same, lateral view. *Fig. 3:* same, aboral view. All figures × 60.

Figs. 4, 5. *Falodus* n.sp., p. 42. *Fig. 4:* LO 4057 t, sample 3, lateral view. *Fig. 5:* same, other side. Both figures × 60.

Fig. 6. *Dichognathus typica* Branson & Mehl, 1933, p. 38. LO 4058 t, sample 10, lateral view. × 60.

Fig. 7, *Drepanodus suberectus* (Branson & Mehl, 1933), p. 41. LO 4059 t, sample 7, lateral view. × 47.

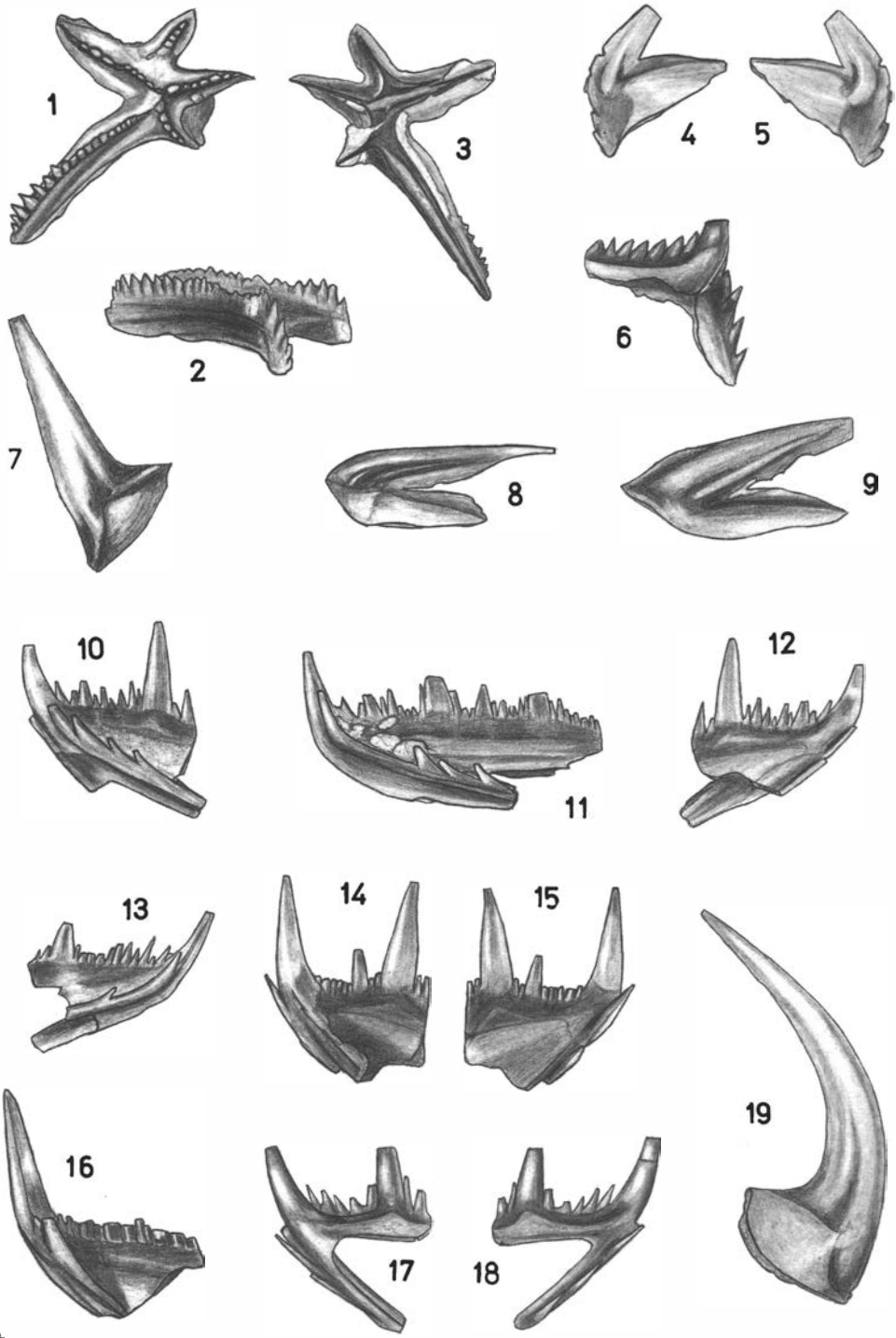
Figs. 8, 9. *Oistodus* cf. *venustus* Stauffer, 1935, p. 46. *Fig. 8:* LO 4060 t, sample 3, lateral view. *Fig. 9:* LO 4061 t, sample 8, lateral view. Both figures × 60.

Figs. 10–13. *Roundya inclinata* (Rhodes, 1953), p. 53. *Fig. 10:* LO 4062 t, sample 12, lateral view. *Fig. 11:* LO 4063 t, sample 12, lateral view. *Fig. 12:* same as fig. 10 but other side. *Fig. 13:* LO 4064 t, sample 12, lateral view. All figures × 60.

Fig. 16. *Roundya* sp., p. 54. LO 4065 t, sample 8, lateral view. × 60.

Figs. 14, 15, 17, 18. *Ligonodina elongata* Rhodes, 1953, p. 43. *Fig. 14:* LO 4066 t, sample 10, lateral view. *Fig. 15:* same, other side. *Fig. 17:* LO 4067 t, sample 3, lateral view. *Fig. 18:* same, other side. All figures × 55.

Fig. 19. *Drepanodus homocurvatus* Lindström, 1955, p. 39. LO 4068 t, sample 7, lateral view. × 50.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