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REMARKS ON THE EVOLUTION OF ORDOVICIAN CONODONTS

Contents

Abstract	395
Introduction	395
Principles of taxonomy of conodonts	396
The course of the phylogeny	398
Organization of the "apparatus" of branching conodonts	413
Affinities of Conodontophorida	416
The outline of evolution of Conodontophorida	417
Regularities in evolution of conodonts	420
Diagnoses of new taxa	421
List of synonyms	425
References	447
Frequency of conodonts in samples	454

Abstract. — The phylogeny of Ordovician Conodontophorida from the Baltic region is reconstructed and homologization of elements of the natural assemblages is presented. A reconstruction of the apparatus of Spathognathodontidae indicates that it was a bilateral medial organ composed of 14 conodonts with denticles turned inwards. Attempts are made to homologize the tissue of conodonts Panderodontidae with enamel of dermal denticles of lower Vertebrata and the basal filling tissue with dentine.

A common phenomenon in conodont evolution is the occurrence of morphological gradient within the apparatus. The evolutionary changes are introduced polarly, and successively spread from the most rapidly evolving element on the adjoining ones. Fifty six species and subspecies of Ordovician conodonts are illustrated and their synonymes given. Two new suborders, three genera, seven species and three temporal subspecies are proposed.

INTRODUCTION

Conodonts are fairly common, easy to free from the rock, and may be studied in fairly large populations which makes them especially suitable for analysis of evolutionary trends. The most interesting results may be obtained when whole conodont assemblages belonging to single animals are analysed. The basis for reconstruction of such apparatuses, mainly by

using statistical techniques, was given by Bergström & Sweet (1966), Lindström (1964, 1971) and Bergström (1971). In this paper the reconstructions of conodont apparatuses are tested using phylogenetic constructions. It is assumed that every element of the apparatus reconstructed should be present at all the evolutionary stages, being subjected to gradual morphological changes. Evolutionary series of elements of the apparatus may be discontinuous only in one direction concordant with time axis, i.e. sudden reduction of an element is possible but not its sudden appearance or, even more, disappearance and repeated appearance in the same morphological form. This excludes a possibility of the occurrence of stages devoid of elements present in ancestral and descendant apparatuses in evolutionary series. This phylogenetic test is a basic (besides statistic analysis) tool in studies on the polymorphism of relics of fossil organisms.

The present study covers conodonts derived from erratics of the Baltic origin occurring in northern Poland. The chronological sequence is based on Mójcza limestone sequence (about 8 m in thickness; uppermost Arenigian — Upper Caradocian; Dzik, in prepar.) and samples from Sukhrumägi sections (Estonia; Viira, 1974). As far as possible the published data concerning earlier (Lindström, 1971; McTavish, 1973) and later (Bergström, 1971) phylogeny were supplemented with the newly gathered data.

SEM micrographs were taken in the Laboratory of Electron Microscopy of the Nencki Institute of Experimental Biology, Warsaw.

The conodont material analysed is housed in the Paleozoological Institute of the Polish Academy of Sciences (abbreviated as ZPAL). The symbols used in description of the samples are:

- E — erratic boulder dissolved by the author,
- O — erratic boulder dissolved by Prof. Roman Kozłowski,
- S — Sukhrumägi section (Estonia)
- M — Mójcza limestone from the Holy Cross Mts (Poland).

Acknowledgements

Warm thanks are due to Prof. Adam Urbanek and Dr. Jerzy Trammer for critical comments and fruitful stimulating discussions, and to Dr. Hubert Szaniawski for his help in gathering literature. Professor Roman Kozłowski kindly supplied his samples extracted from erratic boulders, and Ryszard Wrona, M. Sc., from the Ordovician of Estonia.

PRINCIPLES OF TAXONOMY OF CONODONTS

The species of Conodontophorida is understood by Lindström (1971) and other authors as a section of evolutionary line (temporal species), i.e. in entirely different way than in biology. Delineation of limits of temporal

species is highly subjective. Nevertheless, it is accepted here taking care that the section of evolutionary changes comprised by such "species" at least roughly corresponds to morphological differences between contemporaneous species of the same genus. The term "subspecies", which has nothing in common with biological subspecies (geographic race), is used for more discrete time taxonomic units as it was done by Mashkova (1971) and others. In the neontology the genus is used for grouping contemporaneous, usually numerous species, whereas as used by Lindström (1971) and others it is monospecific almost always in every time section. The latter is also the case of taxa of higher rank in conodont taxonomy. Such approach has resulted in excessive splitting of the systematics. If the paleontological taxa have to correspond to neontological ones and, at the same time, to be monophyletic, then they should comprise markedly more taxa of the lower rank than the latter. The former should comprise all the species living in a given period of time (as it is done in the zoological systematics for the case of the Recent organisms), those which lived in the past as well as those which will originate later; in other words, from the appearance till extinction of higher rank taxon. Morphological variability of paleontological taxon may be compared with that of the neontological only in possibly the shortest section of the history of the former.

In this study the systematics of Conodontophorida is based on the structure of apparatuses and it is different of that of Lindström (1971). Orientation of conodonts on illustrations is accepted after Lindström (1971) and Bergström (1971).

At the present state of knowledge of conodont "apparatuses" it is possible to make an attempt to homologize their component elements and to unify the nomenclature. "Apparatuses" may be divided into three groups of homology here recognized as three monophyletic suborders. Within these suborders comprising forms with similar structure of "apparatuses" it is possible to carry out full homologization of elements.

Group. I. Suborder Westergaardodinina Lindström, 1970 emend.

"Apparatuses" of conodonts of the type family are still not reconstructed. Possibly they comprised both symmetric and asymmetric element similarly as Chirognathidae (Webers, 1966). Assignment of primitive family Panderodontidae to any group is arbitrary.

Group II. Suborder Prioniodontina nov.

"Apparatuses" comprise:

1. asymmetric elements with lateral rib or branch — Prioniodiform — in some groups differentiated into three types:
 - (a) with branches set at obtuse angle — amorphognathiform,
 - (b) with branches set at acute angle — ambalodiform,
 - (c) flattened — keislognathiform;
2. asymmetric elements without lateral ribs — cordylodiform;
3. asymmetric elements with four ribs or branches — tetraprioniodiform;

4. symmetric elements — trichonodelliform (= roundyiform; suberectiform);
5. asymmetric elements with incision below main cusp — oistodiform (= falodiform/holodontiform):

The most primitive conodonts of that group have elements of two types only: symmetric (trichonodelliform) and asymmetric ("drepanodiform").

Group III. Suborder Ozarkodinina nov.

"Apparatuses" comprise:

1. asymmetric elements with branches set at obtuse angle, ozarkodiniform, differentiated in some groups into:
 - (a) platform elements — polygnathiform,
 - (b) flat elements — ozarkodiniform s.s. (sometimes modified into platform ones);
2. asymmetric elements with two branches laterally bent, hindeodelliform, differentiated into:
 - (a) short-branched twisted elements — plectospathodiform, (= zygognathiform),
 - (b) long-branched elements — hindeodelliform s.s. (= ligonodiniform, cordylodiform);
3. symmetric elements — trichonodelliform (= diplododelliform, enantiognathiform);
4. asymmetric elements with one branch reduced in size — neoprioniodiform — probably homologous with asymmetric elements with incision beneath main cusp — oistodiform.

THE COURSE OF THE PHYLOGENY

1. Simple conodonts with a marked contribution of organic matter (Westergaardodinidae Müller, 1959) — text-fig. 1. Typical Cambrian Westergaardodinidae are only occasionally found in Ordovician deposits (Hamar, 1966; Druce & Jones, 1971). These Ordovician forms are closely related to evolutionary advanced Late Cambrian *Westergaardodina bicuspidata* as they do not display rudiments of medial denticle present in *W. bicuspidata* from lower horizons of the Upper Cambrian. The presence of the denticle indicates that *W. bicuspidata* evolved from the forms of the *W. tricuspadata* type. Basal cavity of these two forms is rudimentary, extended along conodont arms. Middle Cambrian *W. muelleri*, characterized by deep basal cavity, represents a transitional link between the genera *Westergaardodina* and *Furnishina*. *Westergaardodina* presumably originated through flattening and bending of lateral margins of conodonts of the *Furnishina* type. According to Druce and Jones (1971) Ordovician Chirognathidae originated from tridentate primitive *Westergaardodina* through increase in number of denticles. According to Sweet & Schönlaub (1975) Chirognathidae are

connected with *Oulodus* (Prioniodinidae). Chirognathidae and possibly affined Coleodontidae are fairly abundant in the Caradocian of North America and Siberia. There are known some forms close to Chirognathidae, characterized by solid, massive basal filling of a specific shape (Cullison, 1938; Mosher & Bodenstein, 1969; Moskalenko, 1972).

The morphology of typical Westergaardodina indicates that they armed medial fissure in animal body.

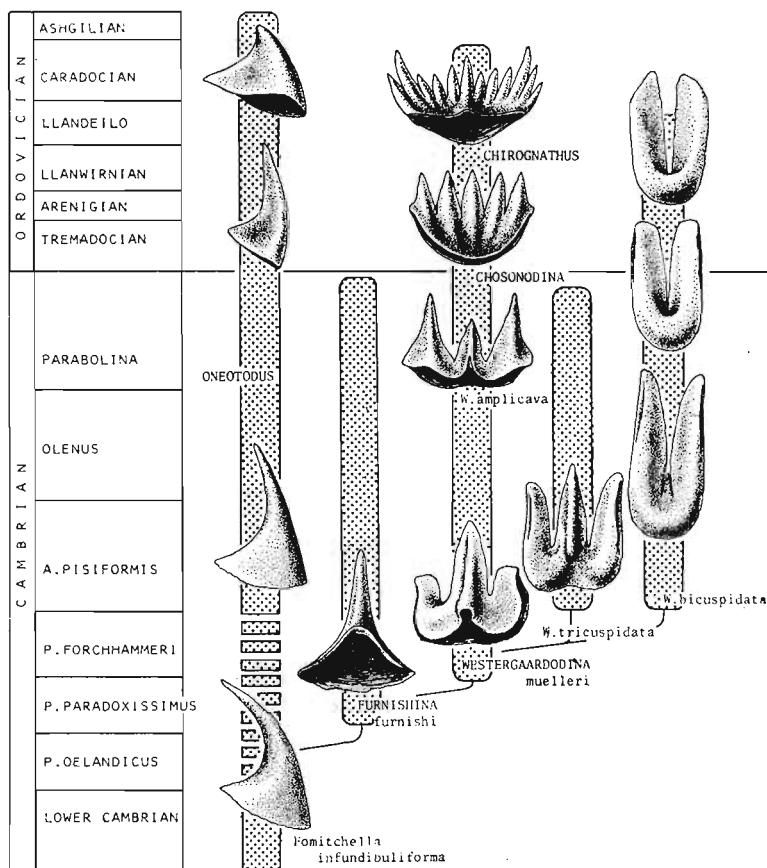


Fig. 1. Phylogenetic relationships between Cambrian and Ordovician conodonts (partly after Druce & Jones, 1971). The data concerning stratigraphic ranges after Müller (1971). In the *Furnishina*-*Westergaardodina*-*Chirognathus* evolutionary line only symmetric elements are illustrated. According to Sweet & Schönlaub (1975) *Chirognathus* is connected with *Oulodus* (Prioniodinidae).

2. Simple conodonts forming assemblage without oistodiform element (Panderodontidae Lindström, 1970) — text-fig. 2. The genus *Semiacontiodus* Miller, 1969, ranging from the Lower Tremadocian (Miller, 1969; Druce & Jones, 1971) up to Upper Caradocian (Bergström & Sweet, 1966), is presumably the ancestral form of Panderodontidae. *Semiacontiodus* comprises

both symmetric elements with three rounded ridges (text-fig. 13 *l, m, p, u*) and asymmetric elements with oblique lateral ridge (text-fig. 13 *g-k, q, t*). It evolved directly from Late Cambrian *Oneotodus* (Druce & Jones, 1971). Morphological simplicity and the lack of oistodiform element in *Semiacontiodus* appear to be original features. A very high variability in samples of conodonts *Semiacontiodus* (text-fig. 13) indicates a remarkable number of conodonts belonging to assemblage of a single animal.

Early Ordovician genus *Scolopodus*, characterized by asymmetric hyaline conodonts only, presumably evolved from primitive *Semiacontiodus* via forms described as *Scolopodus quadriplicatus* and *S. gracilis* by Druce & Jones (1971).

A stratigraphically important genus *Protopanderodus* evolved from *Semiacontiodus* through the development of sharp ridges and compressed denticles and modification of all the elements into asymmetric. "*Scolopodus*" *asymmetricus* Druce & Jones is the transitional form here. All the elements of *Protopanderodus* are asymmetric and characterized by a high inter-population and growth variability (text-fig. 16). No elements with auxiliary lateral furrow were found in *P. rectus* assemblages of the Early Arenigian age (Van Wamel, 1974). Such elements are known from the Upper Arenigian (text-fig. 19*b*). *Protopanderodus* did not undergo any distinct evolutionary changes during the Llanvirnian. Symmetric elements with two lateral furrows first appeared in the apparatuses of the Llandeillian age (Hamar, 1964; *P. varicostatus* Sweet & Bergström, text-fig. 2) and they gradually forced out elements with single furrow. This resulted in repeated development of symmetric elements. Elongation of base of all the elements of the apparatus took place in upper horizons of the Caradocian and in Ashgilian (text-fig. 2, 16 *h, k*). Some independent lines of *Protopanderodus* retain primitive morphology of conodonts during Caradocian, Ashgilian and Llandoveryan (*Decoriconus* Cooper, 1975).

The genus *Drepanodus*, another possible derivative of primitive *Semiacontiodus*, comprises two principal forms of conodonts displaying a very high variability of the continuous nature (text-fig. 17). Van Wamel (1974) differentiated 4 forms of conodonts of *D. arcuatus* assemblage. Middle Ordovician *Drepanodus* differ from the Early Ordovician ones in being more massive and in ribbed denticles (text-figs 2, 17).

The genus *Scalpellodus* gen.n. comprises asymmetric conodonts with flattened and sharpened posterior edge (text-fig. 14*a-e*). The onset of denticulation in *S. cavus* (Webers) is sometimes marked in the form of slightly visible bands of "white matter". Several forms such as *Semiacontiodus carinatus* sp.n. and *Scalpellodus* (?*Cornuodus*) *laevis* sp.n. represent morphological links between the genera *Semiacontiodus* and *Scalpellodus*. *Scalpellodus latus* evolved presumably from the most primitive *Semiacontiodus* via *Scalpellodus* (?*Cornuodus*) *longibasis* or directly from *Oneotodus*.

The genus *Panderodus* is characterized by lateral fissure reaching base of the conodont (text-fig. 15). However, this feature is lacking in some forms of conodonts in assemblage (text-fig. 15g, m). It may be considered as homologous with lateral incision of the base, observable in some elements of *Drepanodus* (text-fig. 17d) and *Scolopodus*. *Panderodus gracilis*, common in the Upper Ordovician and Silurian, displays a marked, rather gradual evolution connected with increase in relative compression of some elements and elongation of others (text-figs 2, 15a, b, e, f).

First *Walliserodus*, *W. costatus* sp.n. from the Lower Llanvirnian, originated from *Scalpellodus* (?*Cornuodus*) *longibasis* through thickening of fine longitudinal ribbing. Further evolution of the former was connected with increase in height of ribs at the expense of their number. Assemblages of conodonts belonging to a single species comprise highly diverse types

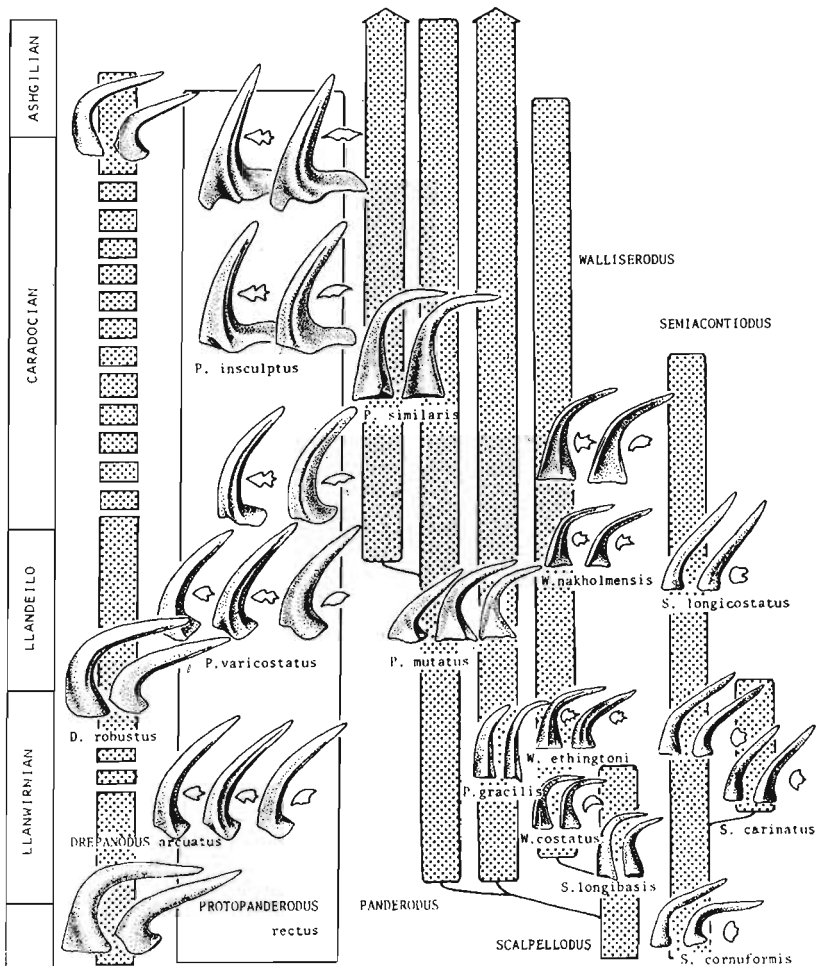


Fig. 2. Evolutionary changes in some Panderodontidae between the Arenigian and Ashgillian. Only main types of elements are illustrated.

of elements; those characterized by the maximum number of ridges are the most important for taxonomy.

Typical *Belodina* occurs in subordinate amounts in the Ashgillian of the Baltic region (Bergström & Sweet, 1966). The presence of lateral fissure (text-fig. 14g) indicates close affinity with *Panderodus*. Denticulation repeatedly occurred in forms close to *Panderodus* (e.g. in evolutionary line of the genus *Belodella*; see text-fig. 14f). The similarity of some elements of *Belodina* to oistodiform elements of Distacodontidae is superficial and convergential.

The affinities of *Strachanognathus parvus* Rhodes (text-fig. 14i-k) and *Histiodela serrata* Harris (text-fig. 12d) are not clear.

A high variability and marked continuity of morphological transitions within natural assemblage suggest that the conodonts of the family Panderodontidae did not form apparatuses with small number of elements but they rather represented dermal denticles covering the surface of animal body.

3. Simple flattened conodonts with oistodiform elements in the assemblage (Distacodontidae Bassler, 1925) — text-fig. 3. Form-species *Proconodontus carinatus* and *Oistodus cambricus* may belong to *Drepanoistodus*. They appeared in Notch Peak Limestone (Utah) earlier than Tremadocian *Cordylodus* (Miller, 1969). *Drepanoistodus* apparatus contains a few types of asymmetric simple elements which may be homologized with elements of branched conodonts, as well as symmetric and oistodiform elements (text-fig. 19). The most primitive species of this genus, *D. inaequalis* (Pander), has oistodiform element resembling simple asymmetric elements (Van Wamel, 1974). Full morphological transitions between some elements of the apparatus of *D. suberectus* are known which would suggest that also at least some conodonts of Distacodontidae were dermal denticles covering animal body. The differences between the two types of oistodiform elements increased during the Arenigian and Early Llanvirnian. I have not found any asymmetric elements with sharp lateral ridge in assemblages of *Drepanoistodus* from the strata younger than the Arenigian. However, a very similar element was illustrated from Llandeillian (Pratt Ferry Formation) by Sweet & Bergström (1962). At the present stage of knowledge of conodonts of the genus *Drepanoistodus* I do not see any possibility of clear differentiation of species *D. forceps*, *D. basiovalis* and *D. suberectus*, contrary to the point of view of Lindström (1971).

Genus *Paroistodus* (text-fig. 3, 18g, h) originated as an off-shoot *Drepanoistodus* in the earliest Arenigian as a small evolutionary line characterized by partial inversion of conodont basal cavity. *Paroistodus* had "apparatus" consisting of two types of asymmetric elements only and it became extinct before the end of Arenigian.

The genus *Paltodus* (allocated in *Drepanoistodus* by Van Wamel, 1974) is characterized by asymmetric elements with sharp lateral ridges and differing from *Drepanoistodus* in less differentiated apparatus. *Paltodus inconstans* (Lindström) presumably evolved from *D. inaequalis*, retaining primitive morphology of oistodiform element and having also a symmetric element in the apparatus (Van Wamel, 1974). Llanvirnian "apparatuses" assigned here to that genus contain asymmetric elements only (text-fig. 18e-f). Morphology of these elements was retained at least till the Llandeilian (Sweet & Bergström, 1962: *Oistodus* ? n.sp.). The evolution of oistodiform element was connected with elongation of denticle and decrease in

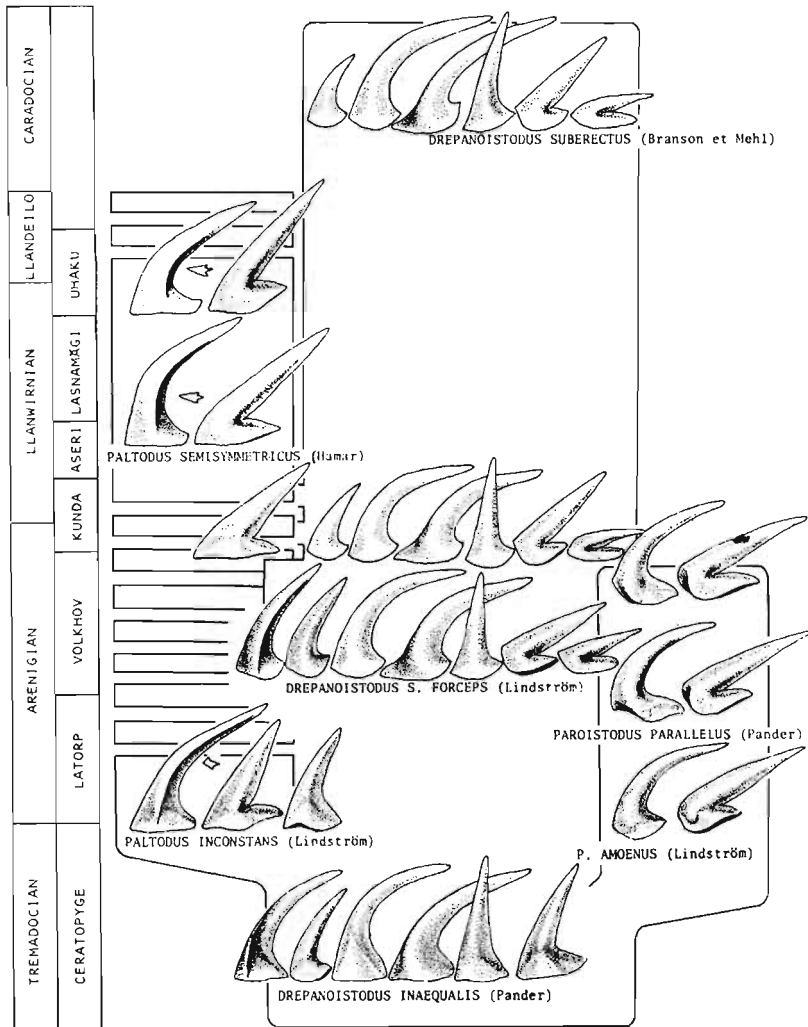


Fig. 3. Phylogeny of Distacodontidae and homologization of main types of elements. Structure of apparatuses of *D. inaequalis* and *P. amoenus* after Van Wamel (1974) and that of *D. suberectus* after Bergström & Sweet (1966). Reconstruction of composition of the "apparatus" of *P. semisymmetricus* based on scarce data.

angle between the denticle and the base (text-fig. 3). "Drepanodiform" element retains lateral ridges shifted backward whereas its base increases in length and the angle of curvature of denticle decreases. The material is too scarce for any reliable reconstruction of the apparatus.

4. Simple conodonts yielding elements with high lateral ribs and oistodi-form elements in the assemblage (Oistodontidae Lipdström, 1970) — text-fig. 4. Conodonts belonging to this family have apparatus identical in com-

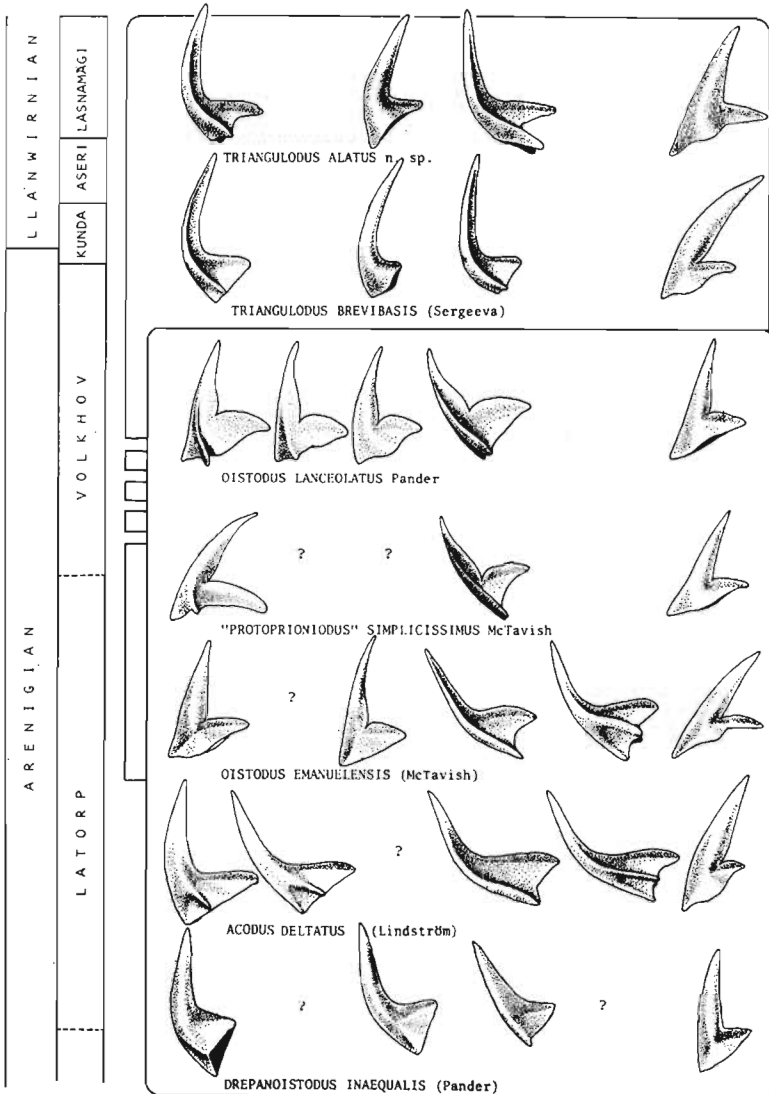


Fig. 4. Phylogeny of Oistodontidae (partly after McTavish, 1973). From the left to the right: prioniodiform, keislagnathiform, cordylodiform, trichonodelliform, tetraprioniodiform and oistodiiform elements.

position as that of primitive Prioniodontidae (see McTavish, 1973). According to Lindström (1971) and McTavish (1973) there are differences in the microstructure as *Oistodus* and *Scandodus* are hyaline. However, the degree of development of "white matter" was shown to be highly variable even at the population (sample) level (see also Barnes, Sass & Monroe, 1973) in several conodonts therefore it cannot be regarded as of any greater importance for the taxonomy.

Oistodus lanceolatus Pander (text-fig. 23a-b) is identical (text-fig. 4) as *Protoprioniodus simplicissimus* McTavish (? = *Oelandodus elongatus* (Lindström) Van Wamel, 1974) in structural pattern and almost identical in the morphology. *Protoprioniodus* and *Oistodus* do not seem to be homeomorphs because of stratigraphic proximity, but rather closely related. The evolution from *Scandodus tetrahedron* (Lindström) to *Protoprioniodus simplicissimus* McTavish was discussed by McTavish (1973) (see text-fig. 4) It was connected with development of *Oistodus*-type incision on all the elements.

Triangulodus brevibasis (Sergeeva) closely resembles *Acodus deltatus* Lindström in composition of the apparatus and morphology of conodonts (text-figs 4, 22a-e). The former most probably evolved from the later via *Triangulodus subtilis* Van Wamel. In the Llanvirnian there appears *Triangulodus alatus* sp.n. with strongly widened basal ridges (text-fig. 22f-k, pl. 1), which presumably originated from *S. brevibasis*. However, its direct connections with the most primitive branched conodonts are not excluded. *Distomodus ? tamarae* Lindström, Rachebeauf & Henry, 1974, is presumably another representative of *Triangulodus*.

5. Branched conodonts comprising a few types of asymmetric elements with three branches in the assemblage (Prioniodontidas Bassler, 1925 — text-figs. 5, 6, 7. *Prioniodus navis* Lindström (text-fig. 24) appears so similar to *P. elegans* Pander (see Bergström, 1971) in structural pattern and morphology that a close affinity between them seems to be beyond any doubt. *Prioniodus elegans* differs from *P. navis* in lower differentiation of three-branched asymmetric elements (text-fig. 5). *Prioniodus navis*, as interpreted by Van Wamel (1974), presumably comprises some transitional species.

There is no unequivocal evidence for the sequence in which conodonts occur in *Prioniodus* apparatus. They form a distinct morphological series from three-branched elements with branches set at obtuse angle and with widened base (amorphognathiform), through three-branched element with steeply inclined branches (prioniodiform = ambalodiform) or tree-branched flattened element to two-branched element (gothodiform = ligonodiform). The "apparatus" also comprises four-branched asymmetric (tetraprioniodiform), three-branched symmetric (roundiform = trichonodel

liform) and asymmetric oistodiform (= falodiform) elements. Keislognathi- form and ligonodiniform elements became completely similar in the Late Llanvirnian (text-fig. 27). Transformation of amorphognathiform and am- balodiform elements in massive platform element proceeded asynchronously: in this case the similarity of elements did not increase but decreased.

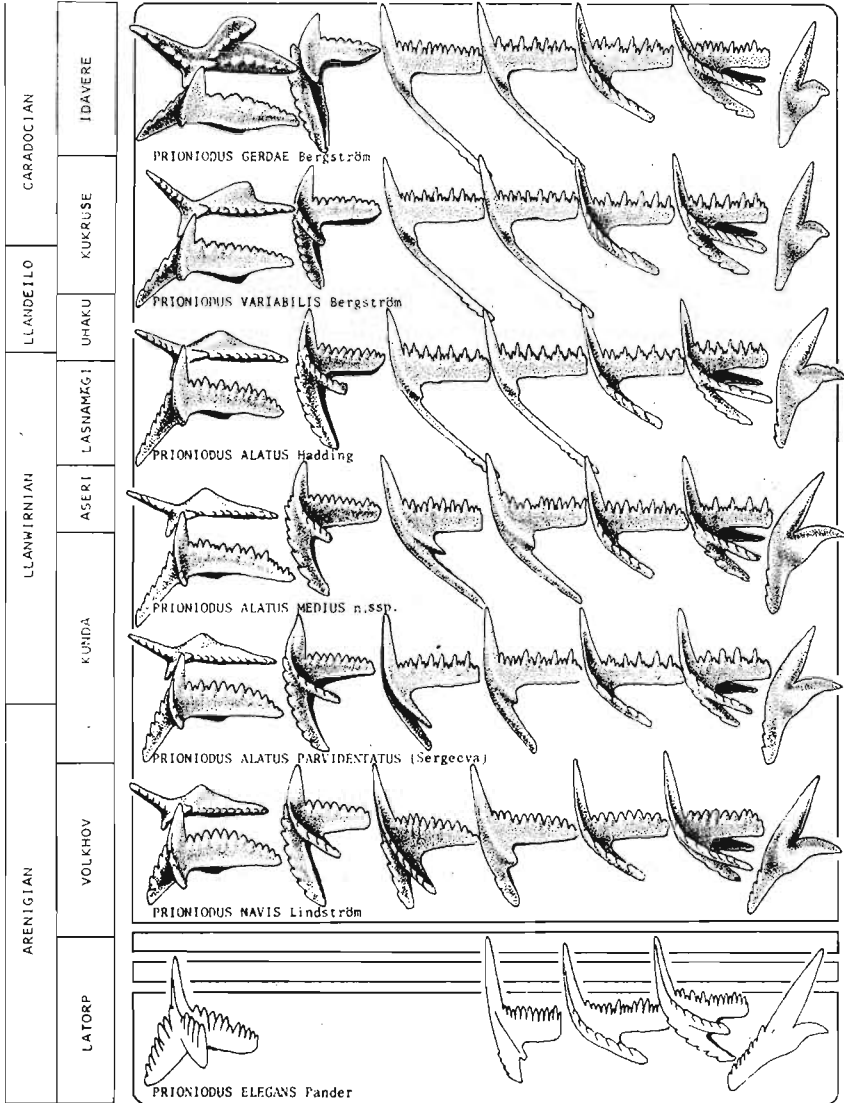


Fig. 5. Post-Middle Arenigian phylogeny of the genus *Prioniodus*. The structure of *P. elegans* apparatus after Bergström (1971). From the left to the right: elements of the amorphognathiform, ambalodiform, keislognathiform, cordylodiform, trichonodel- liform, tetraprioniodiform and oistodiform types. The evolutionary changes effect length of lateral branch of keislognathiform element and size of lateral swelling of base of amorphognathiform element.

Evolution in direction of development of platform elements took place not before the end of reduction of third branch of the keislognathiform element (text-fig. 5). This was accompanied by an increase in differences between shape and size of platform (amorphognathiform and ambalodiform and branched elements (text-fig. 29). The number of forms of elements, which is difficult to establish because of the intra-population variability, is presumably under-estimated in the schemes presented here.

Llanvirnian *Spinodus spinatus* (Hadding) is close to the most primitive Prioniodontidae. Despite of the above mentioned differences in microstructure this species may be related to hyaline *Multioistodus* as the structural patterns of the apparatuses are identical (see Lindström, 1964).

The apparatus of *Amorphognathus* is fully homological with that of *Prioniodus*. *Prioniodus navis*, the range of which overlaps with the range of the oldest species of the former, *A. variabilis*, is characterized by elements most similar to those of the former in morphology (text-fig. 6). The differences concern additional branch developed on amorphognathiform element of *A. variabilis*. The evolution from one species to another presumably proceeded in the same way as in the case of the development of platform element in *Prioniodus gerdæ*, i.e. through onset of denticulation on widened basal shelf of amorphognathiform element. The genus *Amorphognathus* lived only in earlier part of the Kunda stage in the Baltic region as only *Eoplacognathus* elements are found in upper part of the Kunda stage. In the Upper Llanvirnian there are, however, found single elements of the genus *Amorphognathus* which presumably immigrated from the south-west (this genus occurs throughout Llanvirnian stage in Mójcza limestone) (text-fig. 31d, g, h, and k). These elements retained primitive four-branched amorphognathiform element despite of often swollen upper margin of upper branch. The species *A. inaequalis* known from the Llandeilo Limestone (England) and Mójcza Limestone (Poland) displays onset of denticulation on that swollen margin (text-figs 6, 31 I-c). This resulted in origin of the fifth branch which became progressively more elongated during the Caradocian and Ashgillian (text-fig. 6). The intra-population variability precludes differentiation of closely related species on the basis of single amorphognathiform elements. The amorphognathiform elements of evolutionary advanced species of *Amorphognathus* differ within a pair (Bergström, 1971). According to Viira (1974) ambalodiform elements did not form symmetric pair.

The oistodiform (holodontiform) element is the most sensitive index of evolutionary advancement of *Amorphognathus*. The evolution of that element proceeded mainly through increase in number and size of denticles as well as modification of lateral swelling of the base into denticulated branch.

The genus *Eoplacognathus* presumably evolved from *Amorphognathus variabilis* Sergeeva. The transition from the former to the latter was probably related to reduction of branching elements of the apparatus so only platform remained. The morphology of platform elements is initially almost the same in *E. zgierzensis* sp.n. and *A. variabilis* Sergeeva (text-fig. 31). The differences in morphology, steadily increasing along with evolution, involve a marked elongation of lower branch of amorphognathiform

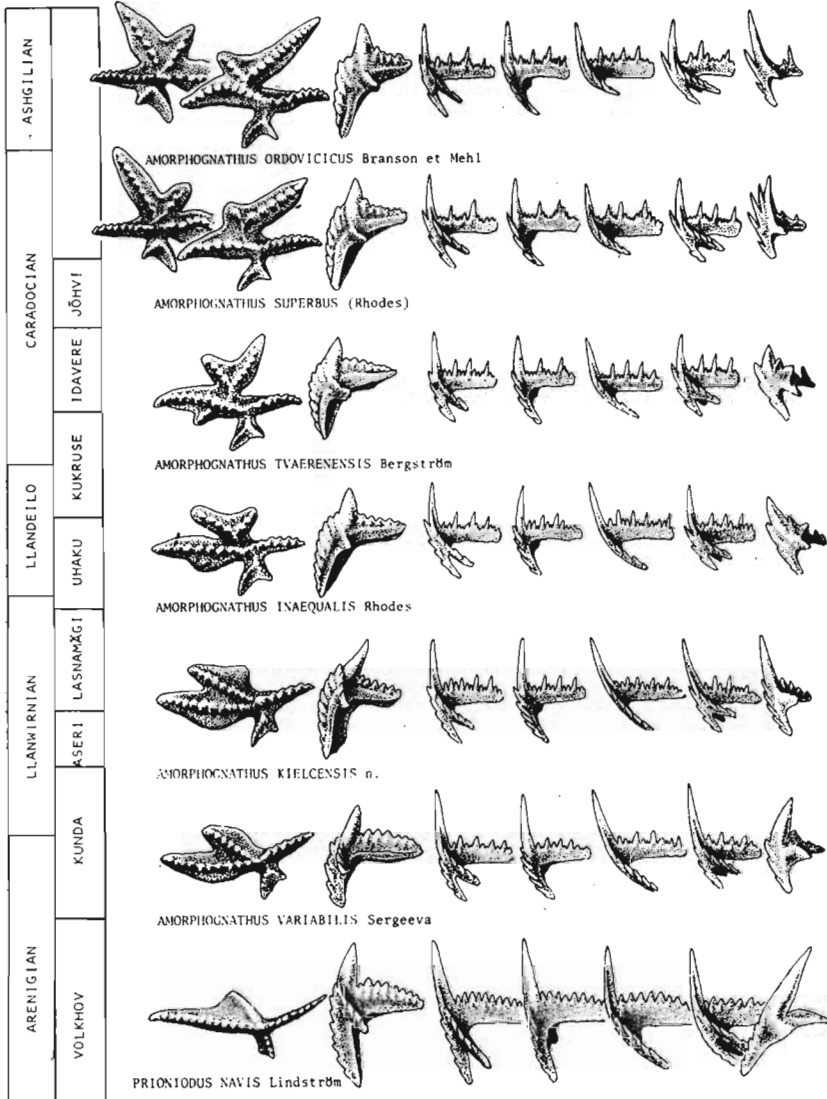


Fig. 6. Phylogeny of the genus *Amorphognathus*. Structure of apparatuses of *A. superbus* and *A. ordovicicus* after Bergström (1971). The sequence of elements as in text-fig. 5; different orientation of cordylodiform element. The variability of amorphognathiform element as a rule exceeds differences between related species.

element and lateral-posterior branch of ambalodiform element of *Eoplacognathus* (text-fig. 7).

Amorphognathiform elements are highly variable in morphology thus it is very difficult to state whether they were originally symmetric or asymmetric. The only fairly stable and distinct trend in their evolution is that involving shifting of upper branch from upper-posterior position in *E. pseudoplanus* and *E. suecicus* through almost vertical in *E. foliaceus* to

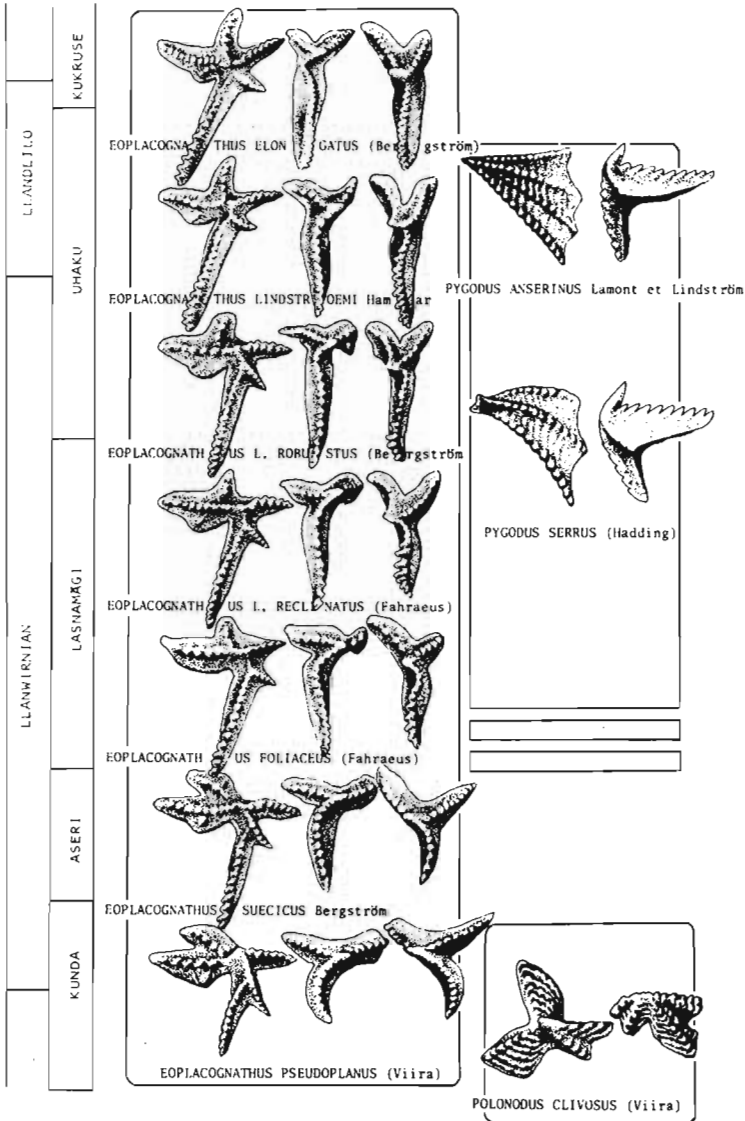


Fig. 7. Phylogeny of the genera *Eoplacognathus* and *Pygodus* (partly after Bergström, 1971). Comparison with the genus *Polonodus*. Amorphognathiform and ambalodiform elements (left and right in the case of *Eoplacognathus*).

upper-anterior in *E. reclinatus*, which was followed by elongation of that branch (text-fig. 7). The occurrence of a small, lower-posterior projection on upper branch is highly variable. In the course of the evolution of ambalodiform elements of *E. pseudoplanus*, almost symmetric elements (text-fig. 35) became progressively more asymmetric. The left element retained its T-shape whereas the right achieved Y-shaped pattern of branches. *Eoplacognathus lindstroemi* displays partial revival of symmetry as both ambalodiform elements become Y-shaped. Some samples, as e.g. E-085 yield fully symmetric ambalodiform elements (text-fig. 33e-g).

The evolutionary position of the species *Polonodus clivosus* (Viira), occasionally found in the Middle Kunda stage (similar form is known from Table Head Formation of Newfoundland — Fahraeus, 1970), is not clear (text-fig. 29c, d; pl. 43, fig. 1a-b). The ornamentation comprising radial and concentric rows of tubercles brings it close to Early Cambrian *Tommotia* (probably acrotretid brachiopod). However, similar ornamentation is typical of early ontogenic stages of *Eoplacognathus*. Despite the lack of knowledge of composition of the natural assemblage I assume that this form evolved from the most primitive *Eoplacognathus* similar to those described as "*Eoplacognathus suecicus*" by Barnes & Poplawski (1973).

Similar problems are connected with interpretation of the evolutionary position of the genus *Pygodus* (text-fig. 7, 29a, b, e, f). The occurrence of the two elements, one of which is almost identical as primitive ambalodiform element and another morphologically close to amorphognathiform element, may indicate connections between the genus *Pygodus* and the genera *Amorphognathus*, *Eoplacognathus* and *Polonodus*. According to Bergström (1971) the apparatus of *Pygodus* may also comprise elements of the tetraprioniodiform and trichonodelliform (*Roundya*) type. In the course of evolution the number of rows of tubercles increased in amorphognathiform element and angle of opening of arms increased in ambalodiform element (Bergström, 1971). These evolutionary trends may indicate increasing separateness from original morphology of elements of apparatus of affined *Prioniodus*.

Rhodesgnathus elegans polonicus n. ssp., occurring in *Prioniodus gerdae* zone of Mójca Limestone, has apparatus consisting of only two types of platform elements. The elements morphologically closer to *P. gerdae* achieved denticulation on lateral swellings on the basis of both elements. It is highly probable that *R. elegans* evolved from *P. gerdae*.

Complexodus pugionifer (Drygant, 1974) from the Llandeillian may be related to primitive Icriodontidae. Its apparatus comprises amorphognathiform elements only. The origin of that species is not clear. The species is morphologically similar to primitive species of the genus *Amorphognathus*, differing in not thickened margins of basal cavity (typical of platform Prioniodontidae elements); and the elements became more massive through widening and doubling of denticles as in *Icriodella*.

6. Conodonts having amorphognathiform elements with multiple rows of denticles on anterior (?) branch in the apparatus (Icriodontidae Müller & Müller, 1957). The oldest representative of that family, *Icriodella superba* Rhodes, has apparatus consisting of massive amorphognathiform (icriodontiform) element with double row of tubercles on anterior (?) branch (text-fig. 25k) of simplified ambalodontiform (sagittodontiform) and two types of branching elements (symmetric and asymmetric, rhynchognathiform). The direct ancestor of *I. superba* — *I. praecox* Lindström, Racheboeuf & Henry, 1974 (the lowermost Llandeillian as it would follow from its cooccurrence with *A. kielcensis*) — did not achieve doubled rows of denticles whereas all the remaining elements are similar to that of *I. superba*. Therefore it seems to be better accommodated in the genus *Prioniodus*.

The trend to decrease in number of elements is typical of the evolution of Icriodontidae. It was as a rule accompanied by simplification of all the remaining types of elements except for the amorphognathiform type.

7. Conodonts having two-branched ozarkodiniform and oistodontiform elements in the assemblage (Periodontidae Lindström, 1970) — text-fig. 8-9. Periodontidae presumably evolved from *Drepanoistodus* of the *D. inaequalis* group. Van Wamel (1974) found transitional undenticulated elements in the oldest populations of *Periodon flabellum*. Denticulation of the margin developed in *Periodon* earlier and independently from that of Prionodontidae (McTavish, 1973). *Periodon adentatus* (McTavish) is presumably the oldest representative of Periodontidae, appearing somewhat earlier than „*Acodus*” *deltatus* in Emanuel Formation (Australia; McTavish, 1973). The denticulation on lateral branches of trichonodelliform and plectospathodontiform (cladognathiform) elements and anterior margin of ozarkodiniform element must have appeared before origin of chronologically later species of Periodontidae — *Periodon flabellum*. The evolutionary line of the genus *Periodon* displays reduction of lateral branches of both symmetric and asymmetric plectospathodontiform three branched elements and development of denticulation on anterior margins of ozarkodiniform and oistodontiform elements (text-figs 8, 39). This trend was slowly realized till the end of Caradocian.

In the evolutionary line of the genus *Microzarkodina* the reduction affected medial branch of symmetric and plectospathodontiform elements, and the latter became more asymmetric. The development of denticulation of anterior margin of ozarkodiniform element is also marked here (text-figs 9, 40).

Forms intermediate between *Microzarkodina* and *Phragmodes* are found in Upper Llanvirnian and Llandeillian of Mójca limestone (text-fig. 9, 35m-o). They differ from *Microzarkodina ozarkodella* in additional lateral branch on ozarkodiniform element.

8. Conodonts having only two-branched and oistodiform elements in the apparatus (Cyrtoniodontidae Hass, 1959). The uppermost part of Mójcza Limestone (from the *P. gerdae* zone upwards) yields occasional elements of apparatus resembling *Phragmodus* (text-fig. 4). The most characteristic of these is *Hamarodus europaeus* (Serpagli) (text-fig. 36a, e). The material is

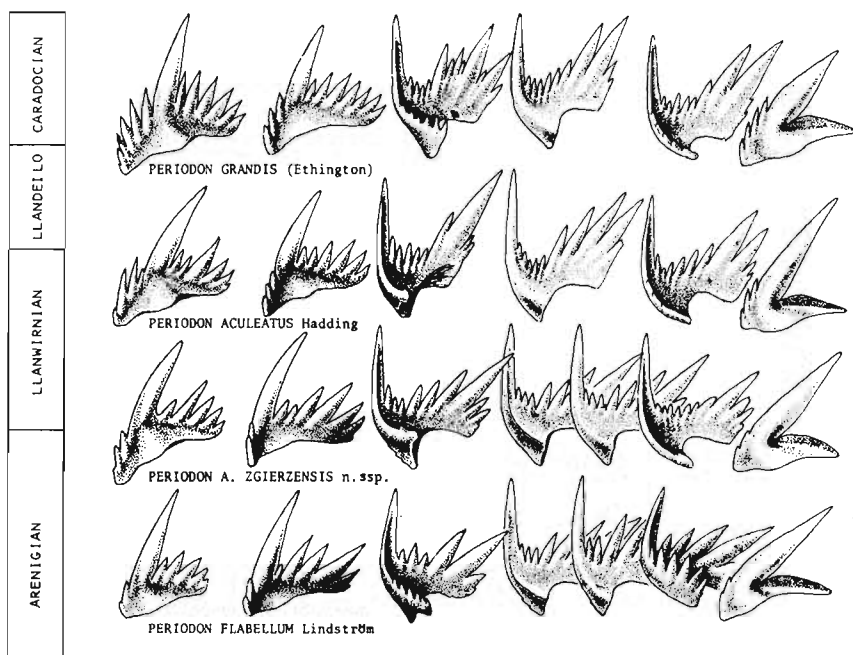


Fig. 8. Stratigraphic sequence of species of the genus *Periodon*. From the left to the right: ozarkodiniform, (two types), plectospathodiform, cordylodiform (two types), trichonodelliform and oistodiform elements.

too innumerable for reconstruction of the whole apparatus. However, these elements occur together also in other regions (Rhodes, 1955; Walliser, 1964; Serpagli, 1967; Viira, 1974), therefore it is highly probable that they belonged to a single apparatus. Particular elements may be easily homologized with those of *Phragmodus* sp. Moskalenko (1972) from the Volginsky subhorizon of Siberia (an equivalent of the Llandeillian). *Hamarodus europaeus* presumably evolved from *Phragmodus* sp. Moskalenko and "*Scandodus*" *manifestus* Moskalenko from the Mangazeisky horizon of Siberia may represent a transitional stage.

The genus *Oulodus* (Prioniodinidae Bassler, 1925) evolved from Periodontidae (from forms close to *Periodon flabellum*). It differs from *Microzarkodina* in transformation of oistodiform into neoprioniodiform element only. Sweet & Schönlaub (1975) postulated derivation of *Oulodus* from Chirognathidae. However, composition of chirognathid natural assemblage (Webrs, 1966) is strongly different from that of *Oulodus*. *Oulo-*

us (?) flexus is probably the most primitive and oldest species in this genus. Single elements of its apparatus were described by Rhodes (1953) from the Llandeilo Limestone. Periodontidae are connected with all post-Ordovician branching conodonts via that genus. I suppose that *Ligonodina* (Prioniodinidae) evolved directly from *Oulodus* through transformation of cordylodiform element into hindeodelliform (ligonodiniform) element and differentiation of ozarkodiniform elements. *Ozarkodina* (Spathognathodontidae) differs from Prioniodinidae in having different shape of ozarkodiniform and hindeodelliform elements.

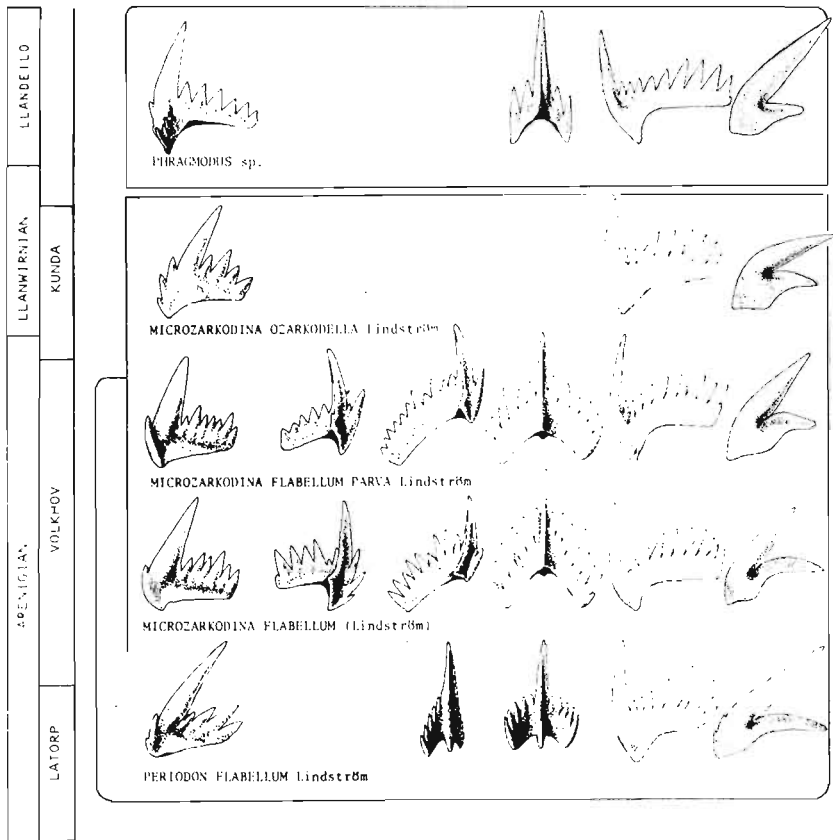


Fig. 9. Stratigraphic sequence of species of the genus *Microzarkodina* and comparison with the species *Periodon flabellum* and *Phragmodus* sp. From the left to the right: ozarkodiniform, plectospathoditiform (two types), trichonodelliform, cordylodiform and oistodiform elements. Orientation of neoprioniodiform and trichonodelliform elements different of that from text-fig. 8.

ORGANIZATION OF THE "APPARATUS" OF BRANCHING CONODONTS

There are no finds which could enable reconstruction of arrangement of Ordovician conodonts in the "apparatus". However, the arrangement may be reconstructed on the basis of indirect evidence, i.e. homologization

of the elements of Ordovician assemblages with those of geologically younger assemblages with the known structural pattern.

Several conodont "apparatuses" were found in the Silurian, Devonian, Carboniferous and Permian strata (Rhodes, 1952; Lange, 1968; Pollock, 1969, Behnken, 1975). The majority of them are of coprolite origin and the original arrangement of conodonts is obliterated. Some of them are, however, slightly deformed and they may serve as a basis for reconstructing original arrangement of conodonts in the apparatus. This is especially the case of *Ozarkodina steinhornensis* illustrated by Mashkova (1972) and "*Scotella typica*" illustrated by Rhodes (1952) (text-fig. 10b, c). The mutual arrangement of the conodonts in the apparatus may be interpreted only in one way (see text-fig. 10a). The conodonts were set in pairs with their denticles turned inwards. The sequence of the elements was as follows: platform (polygnathiform) pair, ozarkodiniform pair, plectospathodiform pair, three hindeodelliform pairs and neoprioniodiform pair. The sequence of occurrence of the plectospathodiform and hindeodelliform elements which are very similar to each other in highly advanced species and usually broken, is not clear. The apparatus of Mashkova (1972) is oblique-laterally deformed (text-fig. 10c) and that of Rhodes (1952 — oblique-medially deformed (text-fig. 10b). This reconstruction of the apparatus of Conodontophorida is different of those hitherto presented (see Lindström, 1974). Trichonodelliform elements, although common in coprolites, were not found in any of the complete apparatuses hitherto recorded. These elements presumably occupied an isolated position in the animal body, acting, e.g., as an armament of medial fold of fin. There were at least two trichonodelliform elements in the apparatus as they became differentiated into two types of elements in Late Paleozoic and Triassic conodontophorids. It issues also from statistical data.

The data concerning undisturbed fragments of apparatuses occurring in the form of "clusters" (Pollock, 1969) suggest that the above discussed model is matched by the apparatuses of both *Ozarkodina* and *Ligonodina* types. Therefore it may be expected that the apparatus of Periodontidae, i.e. the ancestors of *Ozarkodina* and *Ligonodina*, had similar structural pattern. Elements homologous to *Ozarkodina* elements were also set parallel to one another in a definite succession. The data on quantitative relations of the types of elements of *Microzarkodina* apparatus (Marsal & Lindström, 1972) indicate that its structure was identical as that of *Ozarkodina* apparatus, providing that homologization of elements accepted here is correct.

A similar gradient from platform to this branching conodonts is found in the apparatuses of Prioniodontidae (text-figs 5-6). The arrangement of elements could have been here the same as in *Ozarkodina*. I could not carry out a reliable homologization of apparatuses of Prioniodontidae with those of Periodontidae. Prioniodiform (amorphognathiform + ambalodi-

form) elements are probably homologous with ozarkodiniform (polygnathiform + ozarkodiniform) elements of *Ozarkodina* whilst tetraprioniodiform element — with plectospathodiform, keislognathiform, and cordylodiform — with hindeodelliform ones, and oistodiform — with neoprioniodiform ones. The data available show that trichonodelliform elements occurred in subordinate amounts in Prioniodontina “apparatuses” which is in contradiction with the data presented by Marsal & Lindström (1972).

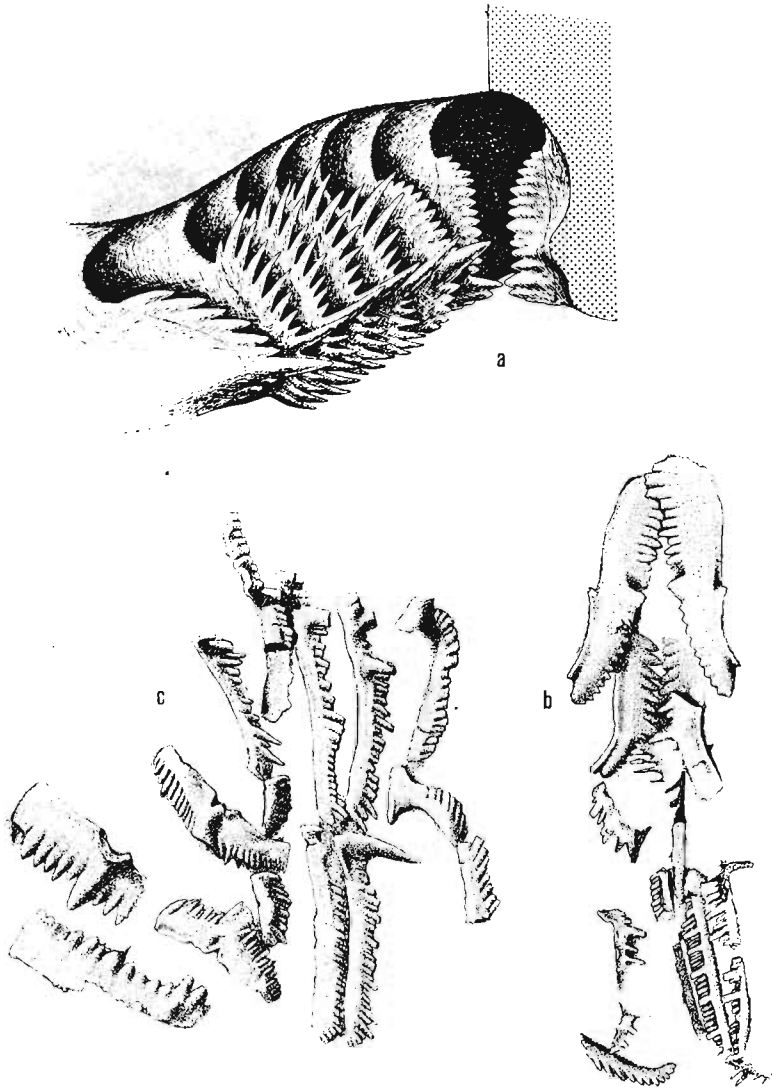


Fig. 10. Pattern of apparatus of *Ozarkodinina* n. subordo, a reconstruction of apparatus of *Ozarkodina confluens* (Branson & Mehl); succession of elements: neoprioniodiform, three hindeodelliform, plectospathodiform, ozarkodiniform and polygnathiform elements; right part omitted; b apparatus of *Idiognathodus* (?) sp. after Rhodes (1952, pl. 126, fig. 11); c apparatus of *Ozarkodina steinhornensis* (Ziegler) after Mashkova (1972, pl. 1).

A high differentiation in hydrodynamic properties of apparatus elements results in deformation of numerical ratios in the majority of samples. This results in limited reliability of the reconstructions made using statistical techniques.

The pairs of conodonts set together commonly found with interfingering blades as well as the above reconstruction seem to indicate biting function of the conodont apparatus. On the other hand numerous examples of regeneration of broken denticles indicate that the conodonts were covered with epithelium throughout the development which is also supported by the results of studies on their microstructure. Despite all the objections against the biting or chewing function of conodonts of the suborder Ozarkodinina it is worth to note that the degree of abrasion of denticles depends on several factors such as: (1) hardness of food, (2) hardness of the tooth, (3) time of functioning and (4) the mode of functioning (biting, chewing, crushing). The conodonts are equally resistant to abrasion as tooth of vertebrate (similar mineral composition). The Conodontophorida presumably lived on fine planktonic organisms; therefore, providing that the conodonts were used for a relatively short time their filtering-holding-and-chewing (linear differentiation of the conodonts within the apparatus) function is not excluded. This function would explain a heavy selective pressure and differentiation of evolutionary trends of particular elements of the apparatus.

Irrespective of the function of Ozarkodinina it is almost certain that they were arming fissure-like medial (!) structure in animal body. Strictly bilateral symmetry of that fissure (not invalidated by asymmetry of some elements of the apparatus) precludes its interpretation as lateral branchial fissures which, as a rule, are asymmetric. Therefore, most probably the conodonts were arming mouth opening. Some of the oldest Chordate (*Anaspida* and some *Ostracodermi*) presumably had fissure-like mouth.

AFFINITIES OF CONODONTOPHORIDA

The only group of conodonts, which may be supposed to be directly affined with *Agnatha* or *Pisces* are *Panderodontidae*. Continuous morphological transitions between forms of elements of natural assemblages of these conodonts suggest that they did not belong to highly specialized apparatuses consisting of innumerable elements. Their function was presumably analogous if not homologous with that of dermal denticles of *Thelodonti* and fishes. The tissue of the conodont cusp, growing from the outside and with compact microstructure, may be homologous with enamel of vertebrate teeth (see Barnes, Sass & Poplawski, 1973; Lindström & Ziegler, 1971). The mode of growth of the conodonts indicates their ectodermal origin. It is not surprising, therefore, that their tissue differs from that of

dentine of Heterostraci (Gross, 1954) which is of mesodermal origin. Only the "basal filling" tissue, growing to the inside and thus probably of mesodermal origin, may be homologized with the dentine. This tissue resembles dentine also in spherulitic microstructure (see Lindström & Ziegler, 1971, pl. 7, fig. 6; Halstead, 1974, fig. 11.4) and in its canals (Barnes, Sass & Poplawski, 1973, fig. 5e). It follows that the structural patterns of Panderoodontidae conodonts and dermal denticles of Agnatha are markedly similar. The differences are related to markedly higher contribution of mesodermal dentine in tooth of Agnatha as typical conodonts are almost exclusively of ectodermal origin. The lack of any sharp boundary between enamel and dentine probably results from delay in calcification in the course of histogenesis (see Kerr, 1955) and penetration of the enamel by Tomes processes of the odontoblasts (see Schmidt & Keil, 1971, fig. 287).

I do not agree with Bengtson's (1976) suggestion on homology between tissue of Cambrian *Furnishina* cusp and basal filling tissue of geologically younger conodonts. Basal filling tissue has been originating at the later stage of organogeny and seems to be also phylogenetically younger than the tissue of conodont cusp. The mode of origin of *Furnishina* cusp is much more similar to that of other conodonts than to that of basal filling tissue. If denticles of *Hertzina* were actually growing by basal internal accretion then their affinity to conodonts is doubtful.

The conodont-bearing animal, *Odontogriphus omalus*, described from the Middle Cambrian of Burgess Shale by Morris (1976), probably belongs to Agnatha. Segmented medial part of the body and darkcoloured lateral ends of the segments strongly resemble branchial sacs of early Heterostraci (*Turinia*, *Lanarkia*, *Logania* etc). Tail, narrow as far as visible, and remains of lateral sensory organs marked on the head support this supposition. The analogy between oral apparatus of that organism and the lophophore is superficial. All the representatives of Lophophorata are sedentary forms and the development of lophophore evidences adaptation to sedentary mode of life. Internal skeleton in the lophophore tentacles would be functionless.

THE OUTLINE OF EVOLUTION OF CONODONTOPHORIDA

The mode of origin of new branches in Prioniodontidae conodonts (text-fig. 5) indicates that mineral parts of conodonts were closely related to the pattern of skin folds on animal body. The modifications of these folds were preceding modifications of conodonts. Thus it may be concluded that Early Cambrian conodonts originated as an armament of already existing dermal projections. The mode of growth of primitive Cambrian conodonts (Müller & Nogami, 1972) seems to indicate that the primitive

conodonts were not completely covered with epithelium throughout the growth.

The typical Cambrian Westergaardodinidae persisted till the end of Llanvirnian without any greater changes (text-fig. 1).

The conodonts with long massive denticle and shallow basal cavity, typical of the Ordovician, appeared at the turn of the Cambrian and Ordovician. Conodonts of that group (Panderodontidae) often yield both symmetric and asymmetric elements in the assemblage. In several evolutionary lines the symmetric element disappeared and denticulation developed. Only genera *Panderodus* (= *Dapsilodus* Cooper, 1976), *Protopanderodus* (= *Decoriconus* Cooper, 1975) and *Walliserodus* (asymmetric elements only), have passed the Ordovician-Silurian boundary. The descendants of first lived till the Middle Devonian. Elements of assemblages of that group form series with continuous transitions, similar to that of dermal denticles of sharks (see Reif, 1974). Conodonts of these assemblages were presumably covering the whole body of animal. Forms closely resembling thelodonts in shape are very common here (Moskalenko, 1972). The microstructure is somewhat similar to that of Heterostraci (Barnes, Sass & Monroe, 1973). Therefore the eventual connections between conodonts and Agnatha should be looked for here.

The primary conical conodonts yielding symmetric elements in the apparatuses gave rise to later branched conodonts. The development of asymmetric, blade-like oistodiform element with incision below the main denticle was an important event in the history of that group. The evolutionary branch of forms characterized by the assemblage comprising both oistodiform element and simple, sharp-ridged (Distacodontidae) elements continued till the end of the Caradocian (text-fig. 3). Some forms (*Paltodus*, *Paroistodus*) secondarily have lost their symmetric elements. These conodonts were presumably numerous, covering the surface of animal body. In one group the ridges were modified into fine, high crests (Oistodontidae). Such forms lived till the end of Llanvirnian (text-fig. 4). Prioniodontidae originated through the development of denticulation on such crests (McTavish, 1973). Numerous elements in their assemblages were also covering the surface of animal body; however, they display distinct functional differentiation indicating that at least a part of them were arranged in the apparatus. Two types of massive three-branched elements (amorphognathiform and ambalodiform) displayed a trend differentiation from that of the remaining ones, connected with increase in size and complexity (text-fig. 5). This trend was realized independently at least four times in the evolutionary lines of *Prioniodus* (text-fig. 5), *Amorphognathus* (text-fig. 6), *Complexodus* (text-fig. 25i) and *Icriodella* (text-fig. 25k) a special attention should be paid to the evolution of *Icriodella*. The genus (Llandeillian-Caradocian), which presumably evolved from *Prioniodus*, has an apparatus consisting of a few types of branching elements and single platform (amorphognathi-

form) element with doubled row of tubercles (Bergström & Sweet, 1966; Lindström, Racheboeuf & Henry, 1974). In the Early Silurian a part of forms displayed a trend to increase lateral arms of platform element, accompanied by simplification of the remaining branching elements resulting in external similarity to primitive Early Ordovician *Scolopodus* (*Pelekysgnathus*, see Klapper & Philip, 1972). In other groups only one arm of plat-

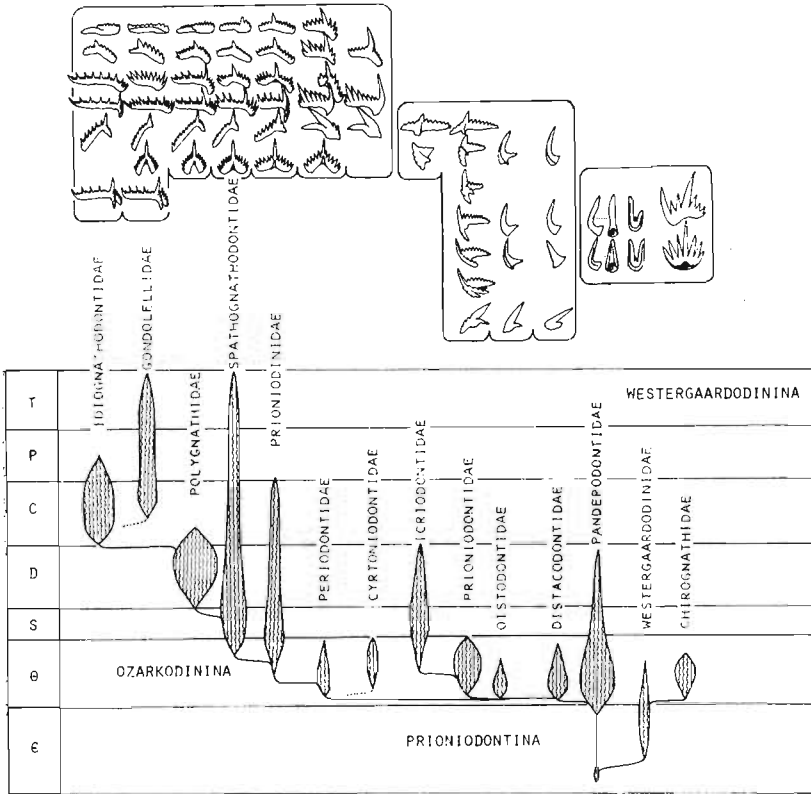


Fig. 11. Phylogenetic relationships between the families of Conodontophorida. Homologization of apparatuses within Ozarkodinina subordo n. and Prioniodontina subordo n. The family Panderodontidae may be allocated in the suborder Westergaardodinina despite of differences in microstructure. Family Cyrtionodontidae *sensu* Sweet & Bergström 1972 is polyphyletic and can be divided into Periodontidae (*Phragmodus*) and Prioniodinidae (*Oulodus*).

form element enlarges whereas the other undergo complete reduction (*Icriodus*).

Denticulation of conodont arms developed independently in Prioniodontidae and Periodontidae. All the remaining conodonts (Ozarkodinina subordo n. evolved from the latter. In the evolution of Ozarkodinina there are marked trends to differentiation of two-branched element, modification of

three- into two-branched elements (trichonodelliform) and to transformation of the remaining ones (first oistodiform and later cordylodiform elements). The resulting apparatus, in which the modifications were almost exclusively limited to the platform element, persisted to the Late Triassic times. Somewhat more conservative apparatus of Ligonodina (Prioniodinidae) persisted till the end of the Carboniferous (Baeseman, 1973) (text-fig. 11).

REGULARITIES IN EVOLUTION OF CONODONTS

The occurrence of morphological gradient in serially arranged conodonts is the common phenomenon in evolution of that group. The most intensive evolutionary changes are polarly introduced and successively spread from the most rapidly evolving element on the adjoining ones (text-fig. 5—6). Besides the above examples of the evolution of that type in Prioniodontidae there are several examples from the post-Ordovician history of platform apparatuses. The trend to increase in robustness, best displayed by the first (polygnathiform) element of the apparatus, is subsequently displayed by the successive ozarkodiniform element which becomes platform in some evolutionary lines (e.g. "*Notognathella*" — *Mesotaxis* ozarkodiniform element — see Klapper & Philip, 1971). Similarly, the trend to extension of arms of hindeodelliform element gradually affects plectospathodiform element (Mashkova, 1972). This phenomenon is interpreted here as the result of differences in distance of conodonts belonging to the apparatus from the centers of embryonal induction (organizers). Evolution in action of an organizer is marked with the intensity directly proportional to spatial or physiological distance of an element of apparatus and it radiates on the adjoining elements. This mechanism originated because of polar differentiation of functions within the apparatus. Independent evolution of element assemblages within the apparatus indicates complexity of its organogenesis and genetic control of numerous gene assemblages. A marked and selectively controlled asymmetry of elements of *Eoplacognathus* apparatuses may be related to the effect of spatial arrangement (in occlusion position) of dermal folds on which conodont originates on the organogenesis or asymmetric spatial arrangement of structures inducing organogenesis of these conodonts. In evolutionary lines characterized by increase of complexity of conodont structure the juvenile stages of the ontogeny recapitulate features of the ancestral forms. This is well-displayed by the organogenesis of *Amorphognathus*. I have found the same phenomena in the organogenesis of platform element of Silurian species *Ozarkodina confluens*. The recognition of such regularity may be highly useful for further studies on the phylogeny.

DIAGNOSES OF NEW TAXA

Genus *Semiacontiodus* Miller, 1969

Type species: Acontiodus (Semiacontiodus) nogamii Miller, 1969.

Semiacontiodus carinatus sp.n.

(text-fig. 13m-o; pl. XLI, fig. 5, 6)

Holotype: ZPAL C.VI/1-069, text-fig. 13k.

Type locality: Erratic boulder E-143, Międzyzdroje, NW Poland.

Type horizon: Upper Llanvirnian, *Eopl. reclinatus* Zone.

Derivation of the name: carinatus (Lat.) — keeled.

Diagnosis. — *Semiacontiodus* with sharpened posterior margins of symmetric and asymmetric conodonts.

Material. — Thirty specimens.

Occurrence. — Upper Llanvirnian, erratic boulders from Poland.

Genus *Scalpellodus* nov.

Type species: Protopanderodus latus Van Wamel, 1974.

Derivation of the name: scalpellum (Lat.) — penknife.

Diagnosis. — Only asymmetric conodonts with flattened and posteriorly sharpened denticle. A trend to development of denticulation.

Species assigned: *S. (?) laevis* sp.n., *Drepanodus longibasis* Lindström, 1955, *Protopanderodus latus* Van Wamel, 1974, *Drepanodus cavus* Webers, 1966.

Occurrence. — Upper Llanvirnian to Caradocian of the Baltic region (Sweden, Estonia, Poland) and N. America.

Remarks. — Differs from closely related genus *Panderodus* in the lack of lateral fissure.

Scalpellodus (? *Cornuodus*) *laevis* sp.n.

(text-fig. 13a-c; pl. XLI, fig. 1)

Holotype: ZPAL C.VI/1-008, text-fig. 13a.

Type locality: Erratic boulder E-081, Mochty, Central Poland.

Type horizon: Middle Llanvirnian, *Eopl. foliaceus* Zone.

Derivation of the name: laevis (lat.) — smooth.

Diagnosis. — Funnel-shaped, with oval base, and denticle strongly bent and laterally flattened in medial and apical parts.

Material. — Over 30 specimens.

Occurrence. — Middle Arenigian (Volkhov) to Uppermost Llanvirnian. Baltic region.

Remarks. — Very primitive form of uncertain generic status. From *Cornuodus erectus* Fahraeus differs in lack of lateral — posterior ridges.

Genus *Walliserodus* Serpagli, 1967

Type species: Paltodus debolti Rexroad, 1967.

Walliserodus costatus sp.n.

(text-fig. 14m, n; pl. XLI, fig. 2)

Holotype: ZPAL C. VI/1-307; text-fig. 14 m.

Type locality: Mójcza near Kielce, Central Poland.

Type horizon: Lower Llanvirnian.

Derivation of the name: *costatus* — ribbed.

Diagnosis. — Conodonts morphologically close to *Panderodus gracilis*, differing in numerous sharp ridges on lateral surfaces.

Material. — Six specimens.

Occurrence. — Lower Llanvirnian of Poland.

Genus *Belodella* Ethington, 1959

Type species: *Belodus devonicus* Stauffer, 1940.

Belodella serrata sp.n.

(text-fig. 14f, pl. XLI, fig. 3)

Holotype: ZPAL C.VI/1-021, text-fig. 14f.

Type locality: Erratic boulder E-141, Międzyzdroje, NW Poland.

Type horizon: Upper Llanvirnian, *E. reclinatus* Zone.

Derivation of the name: *serrata* (Lat.) — serrate.

Diagnosis. — Conodonts with serrate posterior margin and with thin, apical part of denticle bent in the middle.

Material. — Five specimens.

Occurrence. — Upper Llanvirnian, erratic boulders from Poland.

Remarks. — Conodonts almost identical in morphology as *S. longibasis* from which they evolved. They seem not related to Silurian *Panderodus* also characterized by serrate margin.

Suborder **Prioniodontina** nov.

Diagnosis. — Asymmetric three-branched (tricarinate) elements predominating functionally in the apparatus. Secondary simplification common.

Range: see text-fig. 11.

Genus *Triangulodus* Van Wamel, 1974

Type species: *Paltodus volchovensis* Sergeeva, 1963.

Triangulodus (?) *alatus* sp.n.

(text-fig. 20f-k; pl. XLI, fig. 2—5)

Holotype: ZPAL C.VI/1-105, text-fig. 20k.

Type locality: Erratic boulder E-149, Międzyzdroje, NW Poland.

Type horizon: Upper Llanvirnian, *E. reclinatus* Zone.

Derivation of the name: *alatus* (Lat.) — winged.

Diagnosis. — Ridges strongly developed and elongated in basal part of the conodonts. Cusps short.

Material. — Over 35 specimens.

Occurrence. — Upper Llanvirnian, Estonia, erratic boulders from Poland.

Genus *Prioniodus* Pander, 1856

Type species: *Prioniodus elegans* Pander, 1856

Prioniodus alatus Hadding, 1913*Prioniodus alatus medius* ssp.n.

(text-fig. 23a-l; pl. XLII, fig. 1)

Holotype: ZPAL C.VI/1-139, text-fig. 23f.*Type locality*: Erratic boulder E-079, Mochty, Central Poland.*Type horizon*: Lower Llanvirnian, upper part of the *E. pseudoplanus* Zone.*Derivation of the name*: *medius* (Lat.) — medium.*Diagnosis*. — Lateral branch of keislognathiform element short, sharpened.*Material*. — Over 340 specimens.*Occurrence*. — Lower Llanvirnian (upper part of the Kunda stage and Aseri stage), Estonia, erratic boulders from Poland.Genus *Amorphognathus* Branson & Mehl, 1933*Type species*: *A. ordovicicus* Branson & Mehl, 1933.*Amorphognathus kielcensis* sp.n.

(text-fig. 26h-l; pl. XLIV, fig. 1)

Holotype: ZPAL C.VI/1-176, text-fig. 26h.*Type locality*: Mójcza near Kielce, Central Poland.*Type horizon*: Lower Llandeillian, *P. anserinus* Zone.*Derivation of the name*: from Kielce — town in the Holy Cross Mts, Poland.*Diagnosis*. — Oistodiform element with small, reduced posterior branch and long main denticle.*Material* — Seventy five specimens.*Occurrence*. — Middle Llanvirnian to Lower Llandeillian, Baltic region (Estonia and erratic boulders from Poland) and Mójcza limestone (Holy Cross Mts, Poland).Genus *Polonodus* nov.*Type species*: *Ambalodus clivosus* Viira, 1974.*Derivation of the name*: from *Polonia* (Lat.) — Poland.*Diagnosis*. — Conical conodonts with 4 lobes covered with concentric and radial rows of tubercles. Very large basal cavity.*Species assigned*: Only type-species.*Occurrence*. — Lower Llanvirnian (Upper Kunda stage). Baltic region (Estonia and erratic boulders from Poland), Mójcza limestone (Poland).Genus *Complexodus* nov.*Type species*: *Balognathus pugionifer* Drygant, 1974.*Derivation of the name*: from *complexio* (Lat.) — junction.*Diagnosis*. — Amorphognathiform element with additional upper branches and transversally widened (or doubled) denticles. Presumably only one type of elements.*Species assigned*: only type species.*Occurrence*. — Upper Llandeillian to Lower Caradocian, Central Poland and Volhynia.Genus *Eoplacognathus* Hamar, 1966*Type species*: *Ambalodus lindstroemi* Hamar, 1964.

Eoplacognathus zgierzensis sp.n.

(text-fig. 30a-f; pl. XLIII, fig. 2)

Holotype: ZPAL C.VI/1-223, text-fig. 30d.*Type locality*: Erratic boulder E-096, Zgierz, Central Poland.*Type horizon*: Lower Llanvirnian, Kunda stage BIII α or β .*Derivation of the name*: from Zgierz — town in Central Poland.*Diagnosis*. — Amorphognathiform element with lower-anterior branch only somewhat shorter than lower branch.*Material*. — Twenty specimens.*Occurrence*. — Lower part of the Kunda stage, Baltic region (erratic boulders).Genus *Rhodesgnathus* Bergström & Sweet, 1966*Type species*: *Ambalodus elegans* Rhodes, 1952.*Rhodesgnathus elegans polonicus* ssp.n.

(text-fig. 25g, h, pl. XLIV, fig. 3, 4)

Holotype: ZPAL C.VI/1-136, text-fig. 25g.*Type locality*: Mójcza near Kielce, Central Poland.*Type horizon*: Lower Caradocian, *P. gerdae* Zone.*Derivation of the name*: from *Polonia* (Lat.) — Poland.*Diagnosis*. — Lateral basal shelf of amorphognathiform element transformed into real, denticulated branch. Basal shelf of ambalodiform element wide with prominent marginal ridge.*Material*. — One hundred sixty specimens.*Occurrence*. — Lower Caradocian, Poland.Genus *Spinodus* nov.*Type species*: *Cordylodus spinatus* Hadding, 1913.*Derivation of the name*: from *spina* (Lat.) — spine.*Diagnosis*. — All the elements of the apparatus (with the composition such as in primitive Prioniodontidae) with strongly elongated branches and long denticles circular in cross-section.*Species assigned*: — Only type species.*Occurrence*. — Upper Llanvirnian of the Baltic region and Central Poland.*Remarks*. — The relation to the genus *Subprioniodus* Smith, 1907 (type species *S. paucidentatus* from the Lower Ordovician of Scotland) is not clear.

Suborder Ozarkodinina nov.

Diagnosis. — Asymmetric two-branched (ozarkodiniform and hindeodelliform) elements predominant functionally in the apparatus.*Range*. — See text-fig. 10.Genus *Periodon* Hadding, 1913*Type species*: *P. aculeatus* Hadding, 1913.*Periodon aculeatus zgierzensis* ssp.n.

(text-fig. 34e-k, pl. XLIV, fig. 5—6)

Holotype: ZPAL C.VI/1-265, text-fig. 34g.*Type locality*: Erratic boulder, Zgierz, Central Poland.

Type horizon: Lower Llanvirnian, lower part of the *Pseudoplanus* Zone.
Derivation of the name: from Zgierz — town in Central Poland.

Diagnosis. — Trichonodelliform element with reduced denticulation on lateral branches (as in *P. aculeatus aculeatus*), oistodiform element without or with 2 denticles at anterior margin at the most (as in *P. flabellum*).

Material. — Over 50 specimens.

Occurrence. — Lower Llanvirnian, Baltic region (erratic boulders).

LIST OF SYNONYMS
(not including the full synonymy)

Amorphognathus kielcensis sp.n.

Amorphognathus sp. A, Viira, 1967, text-fig. 3, no 22a, b.

Amorphognathus sp. n. 4 Viira, 1974, pl. 7, fig. 7-9.

Amorphognathus sp. n. 5, Viira, 1974, pl. 7, fig. 11, 14.

Amorphognathus aff. *variabilis* Sergeeva,

Viira, 1974, pl. 7, fig. 12, 13.

Amorphognathus inaequalis Rhodes, Lindstrom, Racheboeuf & Henry, 1974, p. 16, pl. 1, fig. 8-11, pl. 2, fig. 1, 2, 7.

„*Prionotodus*” (*Rhodesgnathus*?) n.sp. aff. *prionotodus variabilis* Bergström and *P. gerdæ* Bergström, Lindstrom, Racheboeuf & Henry, 1974, p. 19, pl. 1, fig. 17, 18.

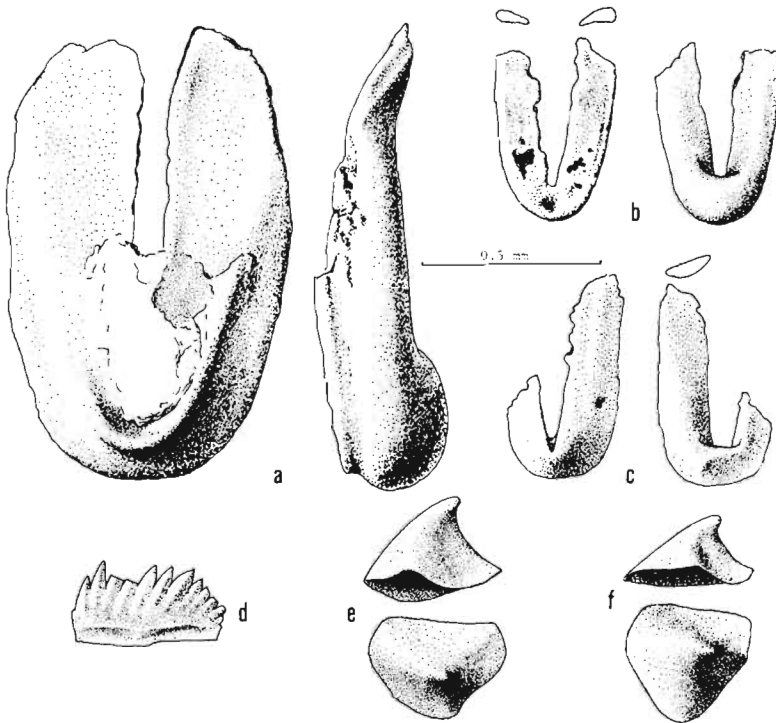


Fig. 12. a—c *Westergaardodina* ex. gr. *bicuspidata* Müller: a, b Sukhrumägi B II β, Estonia, ZPAL C. VI/1-001, 002; c Sukhrumägi B III, Estonia, 1-003. d *Histiodelia serrata* Harris: Mójca limestone, sample A. 14, ZPAL C. VI/1-348, Lower Llanvirnian. e, f *Oneotodus mitratus* Moskalenko: e erratic boulder E-113, 1-004, Upper Llanvirnian, E. *robustus* Zone; f Mójca limestone, sample A-18, 1-300, Llandeillian.

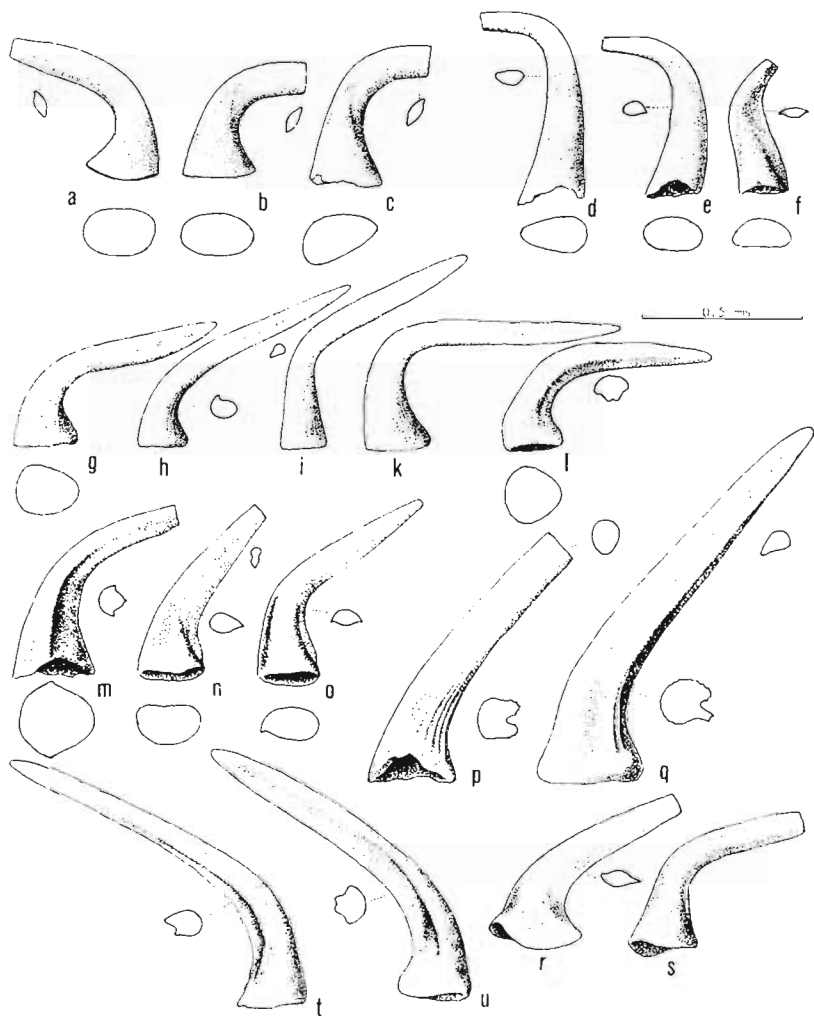


Fig. 13. a—c *Scalpellodus* (? *Cornuodus*) *laevis* sp.n.: a erratic boulder E-081, 1-008, holotype, Middle Llanvirnian, *E. foliaceus* Zone; b—c erratic boulder E-116, 1-010, 011, Upper Arenigian, *P. originalis* Zone. d—f *Scalpellodus longibasis* (Lindström): d—e erratic boulder E-135, 1-012, 013, Lower Llanvirnian, *E. suecicus* Zone; f erratic boulder E-080, 1-015, lowermost Llanvirnian. g—l, t, u *Semiacontiodus cornuiformis* (Sergeeva): g—l erratic boulder E-113, 1-060—064, Upper Llanvirnian, *E. robustus* Zone; t, u erratic boulder E-085, 1-71, 72, uppermost Llanvirnian, *E. lindstroemi* Zone. m—o *Semiacontiodus carinatus* sp.n.: boulder E-113, 1-302—304, Upper Llanvirnian, *E. robustus* Zone. p, q *Semiacontiodus longicostatus* (Drygant): Mójcza limestone, sample A-19, 1-305, 306, Llandeillian.



Fig. 14. *a-e Scalpellodus cavus* van Wamel: *a-c* erratic boulder E-194, 1-016—018, Middle Llanvirnian, *E. reclinatus* Zone; *d* erratic boulder E-130, Middle Llanvirnian, *E. reclinatus* Zone; *e* erratic boulder E-113, 1-019, Upper Llanvirnian, *E. robustus* Zone. *f Belodella serrata* sp.n.: erratic boulder E-141, 1-021, holotype, Middle Llanvirnian, *E. reclinatus* Zone. *g, h Belodina compressa* (Branson & Mehl): *g* erratic boulder E-082, 1-022; *h* erratic boulder E-207, 1-307, Upper Caradocian or Ashgillian. *i Scalpellodus* sp.: erratic boulder E-079, 1-023, Lower Llanvirnian, *E. pseudoplanus* Zone. *j, k Strachanognathus parvus* Rhodes: erratic boulder E-143, 1-024, 25, Middle Llanvirnian, *E. reclinatus* Zone. *l Scolopodus peselephantis* Lindström: erratic boulder E-117, 1-026, uppermost Arenigian, *A. variabilis* Zone. *m, n Walliserodus costatus* sp.n.: Mójcza limestone sample A-14, 1-307—308, Lower Llanvirnian, *E. pseudoplanus* Zone. *o, p Walliserodus ethingtoni* (Fahraeus): erratic boulder E-143, 1-046, 047, *E. reclinatus* Zone. *q, t Walliserodus nakholmensis* (Hamar): Mójcza limestone, sample A-22, 1-309—312, *P. gerdae* Zone.

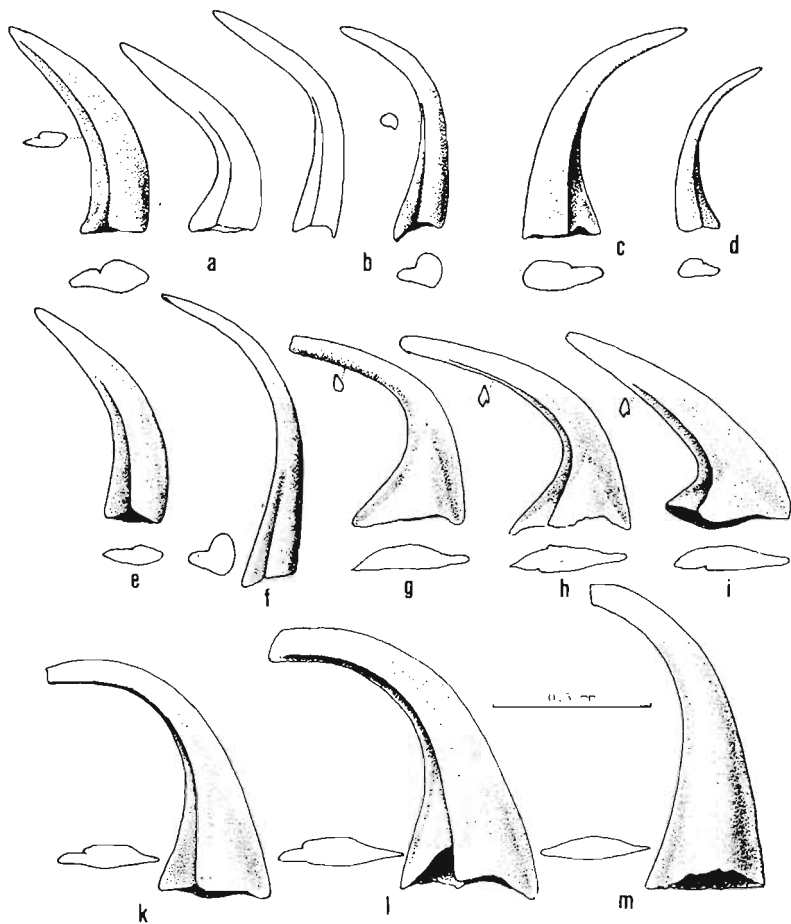


Fig. 15. a, b, e, f *Panderodus gracilis* (Branson & Mehl): a, b, erratic boulder E-143, 1-026—029, *E. reclinatus* Zone; e, f erratic boulder E-090, 1-030—031, Ashgillian or Silurian, c, d, k-m *Panderodus (Dapsilodus) similaris* (Rhodes): c, d erratic boulder E-197, 1-032, 033, Llandeillian; k—m Mójcza limestone sample A-2, 1-034, 36, *A. superbus* Zone. g—i *Panderodus (Dapsilodus) mutatus* (Branson & Mehl): Mójcza limestone, sample A-10, *E. robustus* Zone.

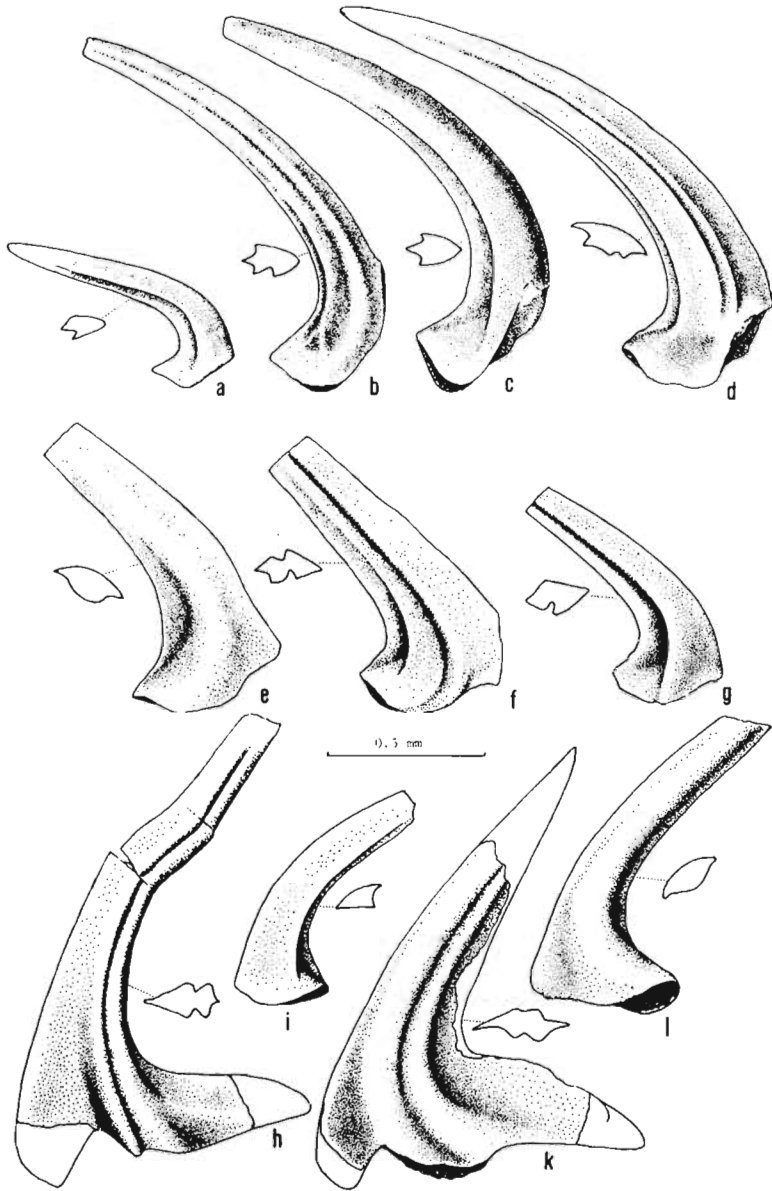


Fig. 16. *a-d, i, l* *Protopanderodus rectus* (Lindström): *a* erratic boulder E-116, 1-055, *P. originalis* Zone; *b-d* erratic boulder E-130, 1-071—073, *E. reclinatus* Zone; *i* erratic boulder E-135, 1-074, *E. suecicus* Zone; *l* erratic boulder E-116, 1-075, *P. originalis* Zone. *e-g* *Protopanderodus varicostatus* (Bergström): Mójcza limestone, sample A-17, 1-313—315, Llandeillian. *h, k* *Protopanderodus insculptus* (Branson & Mehl): Mójcza limestone; *h* sample A-2d, 1-076; *k* sample A-2, 1-077, *A. superbus* Zone.

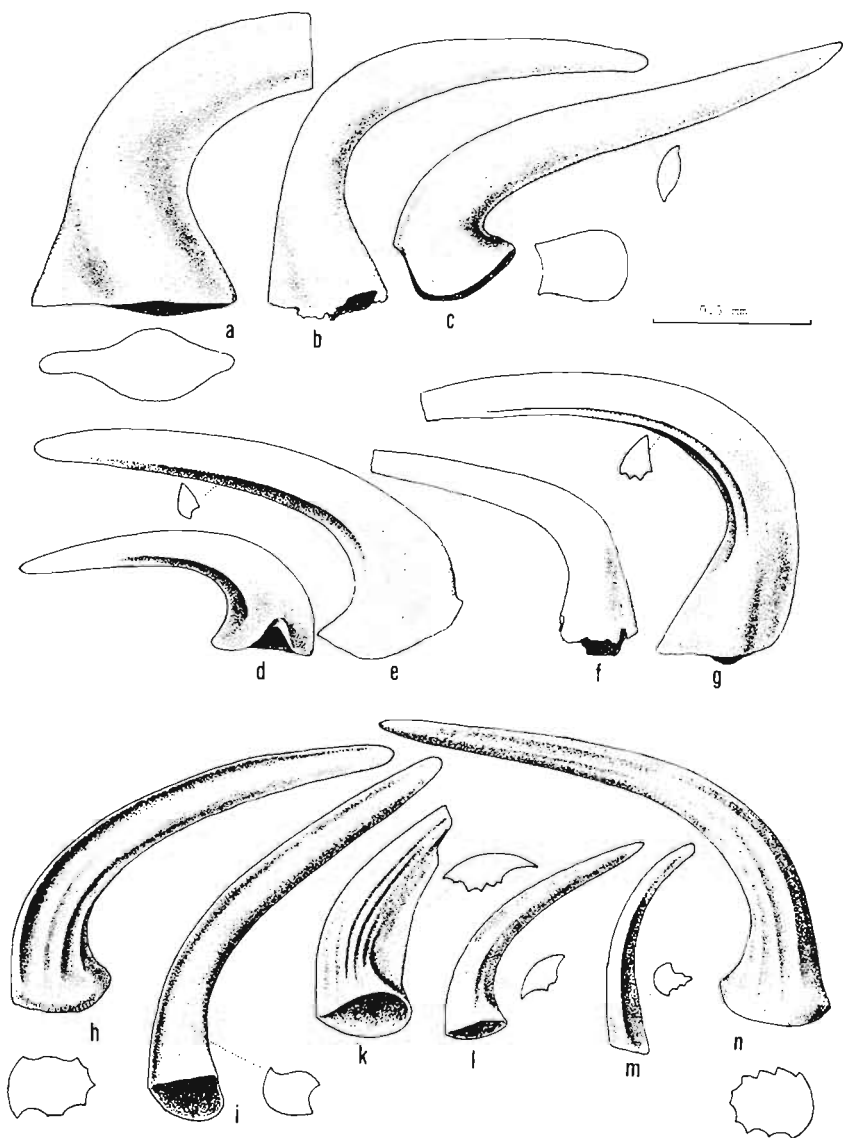


Fig. 17. a—c *Drepanodus arcuatus* Pander: erratic boulder E-116, 1-052—054, *P. originalis* Zone. d—g *Drepanodus robustus* (Hadding): Mójcza limestone, sample A-8, 1-056—059, *E. lindstroemi* Zone. h—n *Scolopodus rex* Lindström h—k erratic boulder E-116, 1-040—042, *P. originalis* Zone; l—n erratic boulder E-119, 1-043—045, *P. originalis* Zone.

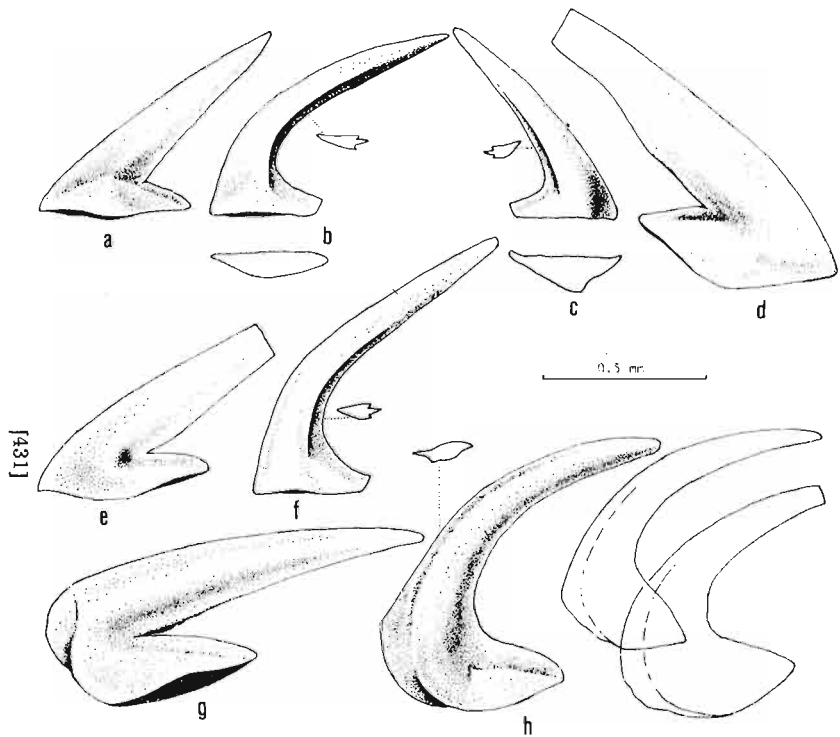


Fig. 18. *a* *Paltodus* (?) sp.: erratic boulder E-089, 1-078, Lower Llanvirnian, *E. pseudoplanus* Zone, oistodiform element. *b-f* *Paltodus* (?) *semisymmetricus* (Hamar): *b-d* erratic boulder E-113, 1-079-081, Upper Llanvirnian, *E. robustus* Zone; *e, f* erratic boulder E-130, 1-082-083, Middle Llanvirnian, *E. reclimatus* Zone. *g, h* *Paroistodus parallelus originalis* (Sergeeva): erratic boulder E-116, 1-084-087, Upper Arenigian, *P. originalis* Zone.

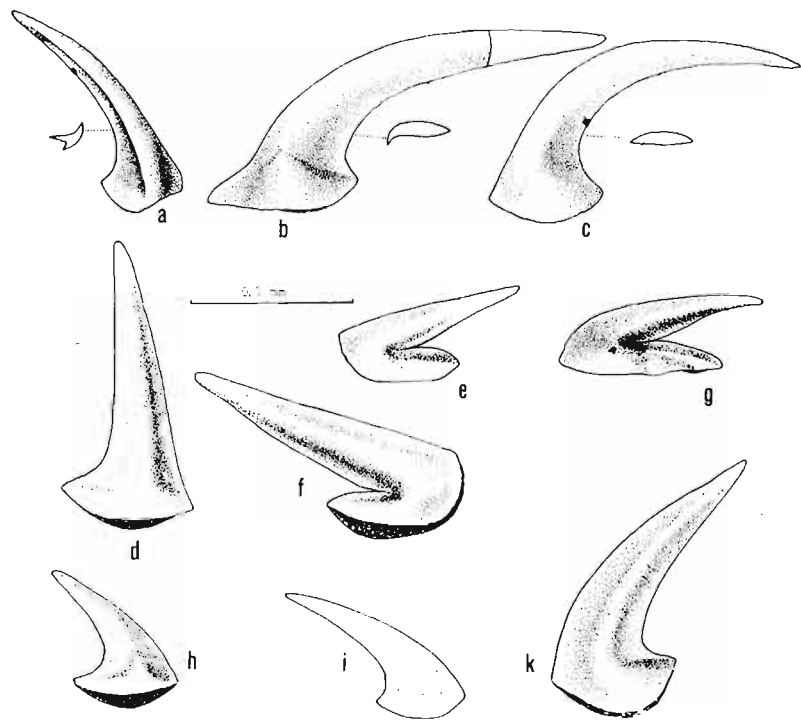


Fig. 19. *Drepanoistodus suberectus forceps* (Lindström): *a-g, k* erratic boulder E-116, 1-088-094, 096, Upper Arenigian, *P. originalis* Zone; *h* erratic boulder E-080, 1-095, Lowermost Llanvirnian, *E. pseudoplanus* Zone. *i* erratic boulder E-137, 1-097, Middle Llanvirnian, *E. reclimatus* Zone; *a* prioniodiform (?) el., *b* another type of prioniodiform (?) el., *c* cordylodiform (?) el., *d* trichonodelliform el., *e, g* oistodiform elements, *h, k* "scandodiform" el.

Amorphognathus tvaerenensis Bergström, 1962
Amorphognathus ordovicica (Branson & Mehl), Bednarczyk, 1971a, pl. 4, fig. 8a-c.
Amorphognathus variabilis Sergeeva, 1963
Amorphognathus n.sp. 1, Lindström, 1960, Lindström, 1964, text-fig. 33B.
Ambalodus planus Sergeeva, Viira, 1974, p. 53, pl. 6; fig. 22-24, 27, 30, text-fig. 40-42.
Lenodus falodiformis Sergeeva, Viira, 1974, p. 93, pl. 6, fig. 6.
Lenodus clarus Sergeeva, Viira, 1974, p. 93, pl. 6, fig. 7.
Drepanodus arcuatus Pander, 1856
Scandodus pipa Lindström, Bednarczyk, 1969, pl. 1, fig. 1.
Drepanodus robustus (Hadding, 1913)

Acontiodus robustus (Hadding), Lindström, 1955b, p. 108, pl. 22, fig. 1, 2, 6, non 4.
 ?*Acontiodus falcatus* (Hadding), Lindström, 1955b, p. 106, pl. 22, fig. 8, 9.
Acontiodus reclinatus Lindström, Spassov & Teller, 1963, p. 77, pl. 1, fig. 1.
Cornuodus bergstroemi n.sp., Serpagli 1967, p. 57, pl. 12, fig. 1a-2c.
Cornuodus montanaroe n.sp. Serpagli 1967, p. 58, pl. 12, fig. 3-46.
Acontiodus arcuatus Lindström, Viira, 1974, p. 47, pl. 11, fig. 1, 2, text-fig. 27b-v.
Drepanoistodus suberectus forceps (Lindström, 1955)
Oistodus forceps Lindström, Wolska, 1961,

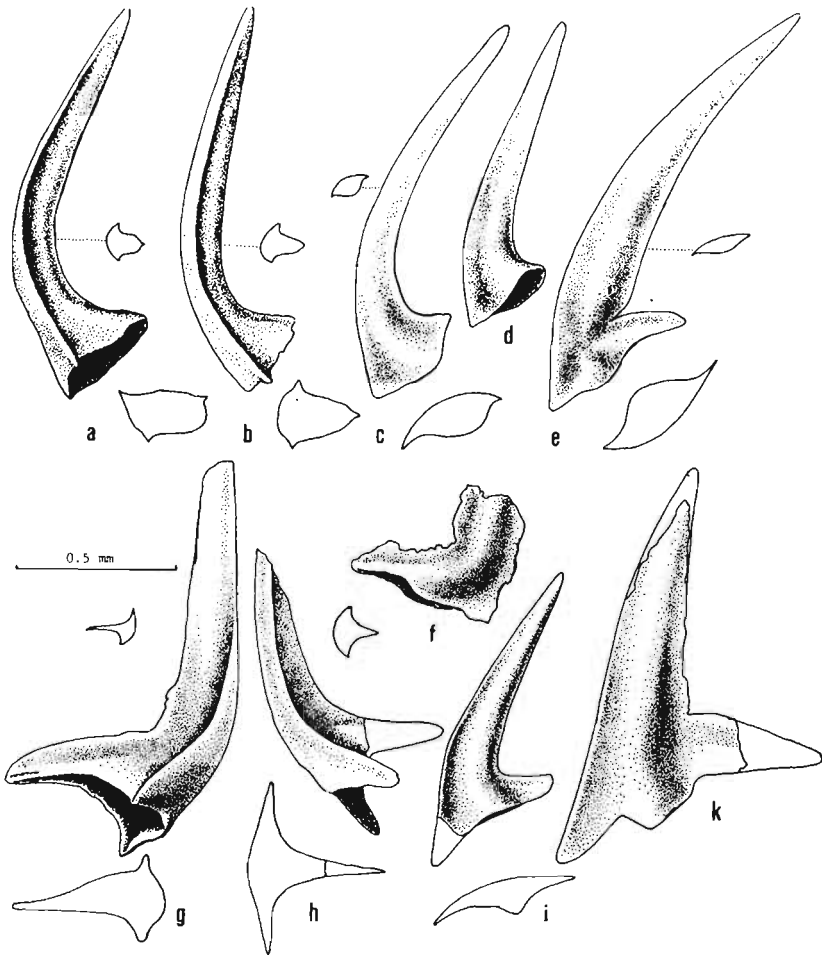


Fig. 20. a—e *Triangulodus brevibasis* (Sergeeva): erratic boulder E-116, 1-098—102, Upper Arenigian, *P. originalis* Zone. f—k *Triangulodus* (?) *alatus* sp.n.: f, g, k erratic boulder E-149, 1-103—105, holotype—1-105; h, i erratic boulder E-145, 1-106—107, Middle Llanvirnian, *E. reclinatus* Zone. a, g prioniodiform element, b, h trichonodelliform el., c, d, f, i cordylodiform el., e, k (?) oistodiform el.

p. 351, pl. 3, fig. 6, Bednarczyk, 1971a, pl. 1, fig. 1.
Drepanodus homocurvatus Lindström, Wolska, 1961, p. 348, pl. 2, fig. 7a, b, Bednarczyk, 1971b, pl. 6, fig. 5, Baranowski & Urbanek, 1972, pl. 2, fig. 10.
Oistodus excelsus Stauffer, Bednarczyk, 1971b, pl. 4, fig. 3.
Oistodus venustus Stauffer, Spasov & Teller, 1963, p. 79, pl. 1, fig. 10.
Drepanodus suberectus (Branson & Mehl), Bednarczyk, 1971b, pl. 5, fig. 6, Baranowski & Urbanek, 1972, pl. 2, fig. 8.
Drepanodus planus Lindström, Bednarczyk, 1971b, pl. 4, fig. 3.
Oistodus parallelus Pander, Bednarczyk, 1971b, pl. 4, fig. 10.
Oistodus basiovalis Sergeeva, Bednarczyk, 1971a, pl. 1, fig. 2, Bednarczyk, 1969, pl. 1, fig. 2.
Oistodus inclinatus Branson & Mehl, Baranowski & Urbanek, 1972, pl. 2, fig. 8.
Drepanoistodus forceps (Lindström), Serpagli, 1974, p. 30, pl. 10, fig. 8a-12c, pl. 21, fig. 9-14, Van Wamel, 1974, p. 64, pl. 2, fig. 14-22.
Eoplacognathus pseudoplanus (Viira, 1974)
Ambalodus pseudoplanus n.sp., Viira, 1974, p. 54, pl. 6, fig. 25, 29, 31, text-fig. 43-46.
Amorphognathus sp.n. 1, Viira, 1974, pl. 7, fig. 1-4.
 ?*Amorphognathus variabilis* Sergeeva, Viira, 1974, pl. 7, fig. 3, 4.
Amorphognathus sp.n. 2, Viira, 1974, pl. 7, fig. 5, 6.

Eoplacognathus foliaceus (Fahraeus, 1966)
Polyplacognathus humilis sp.n., Viira, 1974, p. 106, pl. 9, fig. 1, 2, text-fig. 135.
Polyplacognathus ramosus sp.n., Viira, 1974, p. 110, text-fig. 140.
Eoplacognathus foliaceus (Fahraeus), Viira, 1974, p. 77, pl. 8, fig. 10, 11, text-fig. 85-86.
Eoplacognathus lindstroemi lindstroemi Hammar, 1964
Polyplacognathus mirus sp.n., Viira, 1974, p. 107, pl. 10, fig. 10-12, text-fig. 136.
Polyplacognathus gallus sp.n., Viira, 1974, p. 106, pl. 9, fig. 19, 20, 27, 28, 31, 32, text-fig. 134.
Polyplacognathus stella Viira, Viira, 1974, text-fig. 10 no 1, 1a, b, 2a, b.
Eoplacognathus lindstroemi Hammar, Viira, 1974, p. 74, pl. 8, fig. 14, 15, 19-22, text-fig. 81.
Eoplacognathus lindstroemi reclinator (Fahraeus, 1966)
 non *Ambalodus reclinator* Fahraeus, Bednarczyk, 1971a, pl. 3, fig. 4a, b.
 ?*Eoplacognathus ambaloides* Viira, Viira, 1972, fig. 6, no. 1, 2.
 ?*Eoplacognathus acros* Viira, Viira, 1972, fig. 9, no. 1a, b, 2a, b.
 ?*Eoplacognathus tridens* Viira, Viira, 1972, fig. 6, no. 3, 4.
Eoplacognathus reclinator (Fahraeus), Viira, 1974, pl. 8, fig. 12, 13, text-fig. 93, 94.
Eoplacognathus lindstroemi robustus Bergström, 1971
Ambalodus reclinator Fahraeus, Bednarczyk, 1971a, pl. 3, fig. 4a, b.
Eoplacognathus lobulus Viira, Viira, 1972, fig. 8.

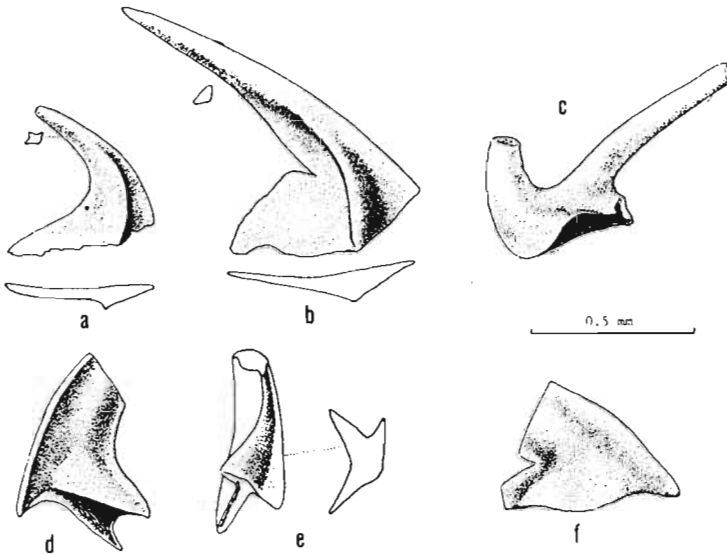


Fig. 21, a, b *Oistodus lanceolatus* Pander: erratic boulder E-148, 1-108, 109, Middle Arenigian, prioniodiform el. d, f *Triangulodus* sp.: erratic boulder E-148, 1-110-111, prioniodiform and oistodiform el. c *Spinodus spinatus* (Hadding): Mójca limestone, sample A-10, 1-112, Upper Llanvirnian, E. robustus Zone.

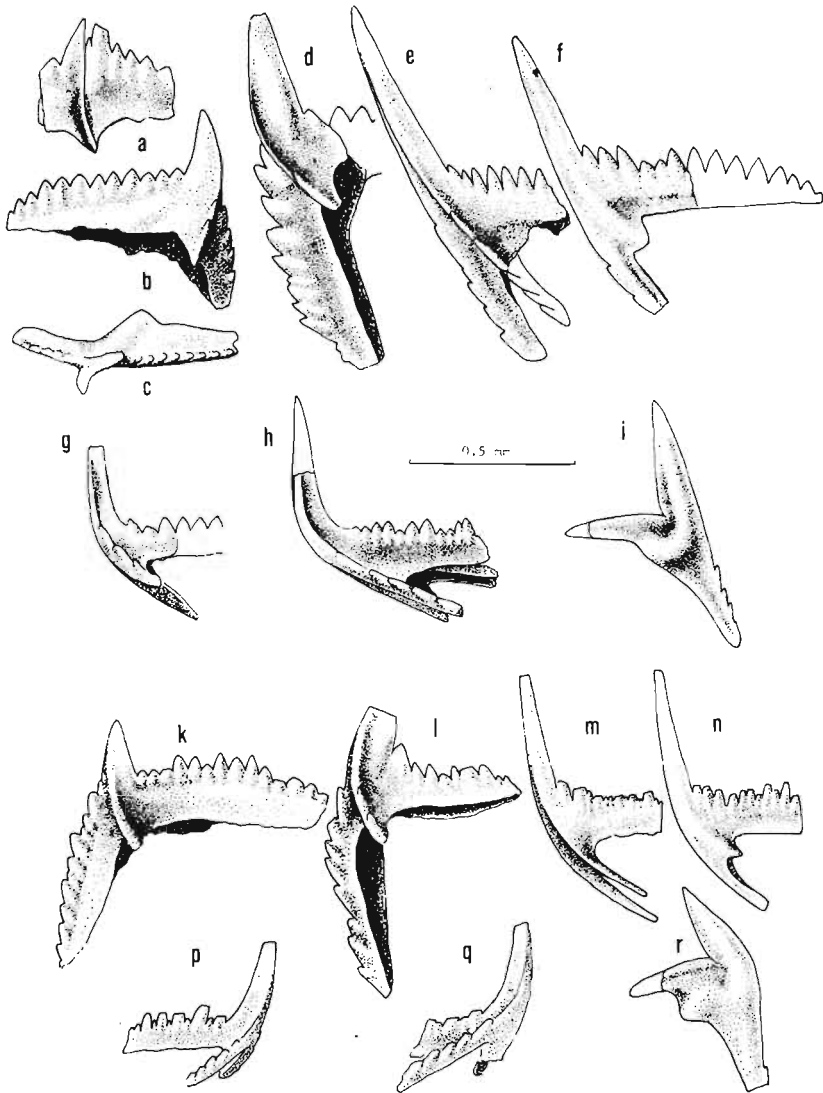


Fig. 22. a—i *Prioniodus navis* Lindström: erratic boulder E-116, 1-113—121, *P. originalis* Zone. k—e *Prioniodus alatus parvidentatus* (Segeeva): Mójcza limestone, sample A-14, 1-333-339, *E. pseudoplanus* ? Zone, a—c, k amorphognathiform elem., d, l ambalodiform el., e, m keislognathiform el., f, n cordylodiform el., g, p trichonodelliform el., h, q tetraprioniodiform el., i, r oistodiform el.

- Polyplocognathus robustus* (Bergström), Viira, 1974, p. 108, pl. 9, fig. 3-9, 13-18, text-fig. 137-139.
- Eoplacognathus robustus* Bergström, Viira, 1974, p. 79, pl. 8, fig. 16-18, text-fig. 88-92.
- Hamarodus europaeus* (Serpagli, 1967)
- Distomodus europaeus* n.sp., Serpagli, 1967, p. 64, pl. 14, fig. 1-6c, Bergström, 1971, text-fig. 4-5, no. 15.
- Cordylodus elongatus* Rhodes, Rhodes, 1955, p. 135, pl. 7, fig. 5, 6.
- Microcoleodus* ? sp., Rhodes, 1955, p. 133, pl. 10, fig. 19, 22.
- Oistodus* sp., Rhodes, 1955, p. 126, pl. 10, fig. 9.
- ?*Neoprioniodus breviremeus* n.sp., Walliser, 1964, p. 47, pl. 4, fig. 5, pl. 29, fig. 5-10, aff. gen. indet., n.sp. c, Walliser, 1964, p. 91, pl. 4, fig. 4, 11, pl. 10, fig. 28-30, pl. 11, fig. 1-3.
- N. genus*, n.sp., Hamar, 1966, p. 77, pl. 3, fig. 8-10, text-fig. 5, no. 5a-b.
- Plectodina breviremea* (Walliser), Serpagli, 1967, p. 89, pl. 18, fig. 5-9c.
- Oistodus niger* n.sp., Serpagli, 1967, p. 79, pl. 20, fig. 1-7d.
- Hamarodus europeus* (Serpagli), Viira, 1974, p. 81, pl. 13, fig. 22-25, text-fig. 106.
- Hamarodus estonicus* gen. et sp.n., Viira, 1974, p. 88, pl. 13, fig. 26-27, text-fig. 107.
- Hamarodus norvegicus* gen. et sp.n., Viira, 1974, pl. 13, fig. 22-25.
- Periodon undosus* n.sp., Viira, 1974, p. 103, pl. 13, fig. 4-7, text-fig. 130.
- Histiodela serrata* Harris, 1962
- Spathognathus* n.sp. Lindström, 1960, Fahrreus, 1970, fig. 31.
- Spathognathus* sp., Viira, 1974, p. 125, pl. 5, fig. 39, 40, text-fig. 163.
- Microzarkodina flabellum parva* Lindström, 1971
- Prioniodina* cf. *flabellum* Lindström, Wolska, 1961, p. 354, pl. 4, fig. 4a, b.
- Cordylodus delicatus* Branson & Mehl, Baranowski & Urbanek, 1972, pl. 2, fig. 3.
- Trichonodella recurva* (Branson & Mehl), Baranowski & Urbanek, 1972, pl. 1, fig. 5.
- ?*Zygognathus deformis* (Stauffer), Baranowski & Urbanek, 1972, pl. 1, fig. 1.
- Ozarkodina flabellum* (Lindström), Baranowski & Urbanek, 1972, pl. 1, fig. 4.
- Oistodus lanceolatus* Pander, Baranowski & Urbanek, 1972, pl. 2, fig. 4.
- Oneotodus mitratus* (Moskalenko, 1973)
- Ambalodus mitratus* Moskalenko, Moskalenko, 1973, pl. 21, fig. 23.
- Ambalodus mitratus nostras* Moskalenko, Moskalenko, 1973, pl. 21, fig. 24-25.
- Gen. et sp. indet. A, Serpagli, 1967, p. 107, pl. 29, fig. 2a-c.
- Gen. et sp. indet. B, Serpagli, 1967, p. 107, pl. 29, fig. 1a, b.
- Paltodus semisymmetricus* (Hamar, 1966)
- Distacodus variabilis* n.sp., Webers 1966, p. 28, pl. 12, fig. 15, 16, 17.
- Anontiodus* n.sp. 2, Lindström, 1960, fig. 6, no. 11, 10.
- ?*Oistodus pseudoabundans* Schopf, Webers 1966, p. 34, pl. 2, fig. 20, 21.
- Acontiodus semisymmetricus* n.sp., Hamar, 1966, p. 51, pl. 7, fig. 5, 6, text-fig. 3, no. 6.
- Acodus viruensis* n.sp., Fahrreus, 1966, p. 12, pl. 2, fig. 2a, b, text-fig. 2a.
- Acontiodus nevadensis* n.sp., Ethington & Schumacher, 1969, p. 450, pl. 67, fig. 21-22.
- Oistodus* sp.n.B, Viira, 1974, p. 97, pl. 11, fig. 13, 14, text-fig. 117.
- Panderodus gracilis* (Branson & Mehl, 1933)
- Panderodus cornutus* (Stauffer), Wolska, 1961, p. 353, pl. 4, fig. 1a, b.
- Panderodus gracilis* (Branson & Mehl), Wolska 1961, p. 353, pl. 4, fig. 2a, b, Bednarczyk, 1971b, pl. 5, fig. 2, Viira, 1974, pl. 12, fig. 1, 10-12, pl. 13, fig. 1, 3, text-fig. 126, 128.
- Panderodus unicosatus* (Branson & Mehl), Wolska, 1961, p. 353, pl. 4, fig. 3a, b.
- Panderodus compressus* (Branson & Mehl), Bednarczyk, 1971b, pl. 5, fig. 4, Viira, 1974, p. 101, pl. 12, fig. 2, pl. 13, fig. 2, text-fig. 126-128.
- Panderodus (Decoriconus) similaris* (Rhodes, 1953)
- Scandodus inflexus* Hamar, Bednarczyk, 1971a, pl. 4, fig. 5.
- Acodus similaris* Rhodes, Viira, 1974, p. 43, pl. 9, fig. 23, 24, pl. 12, fig. 14, 15, text-fig. 19, 20.
- Paroistodus parallelus originalis* (Sergeeva, 1963)
- Oistodus parallelus* Pander, Wolska, 1961, p. 351, pl. 3, fig. 4.
- Distacodus expansus* (Graves & Ellison), Wolska, 1961, p. 347, fig. 4.
- Distacodus* sp., Wolska, 1961, p. 348, pl. 2, fig. 6.
- Oistodus forceps* Lindström, Bednarczyk, 1971a, pl. 1, fig. 5, Bednarczyk, 1971b, pl. 4, fig. 9.
- Drepanodus originalis* (Sergeeva), Viira, 1974, p. 69, pl. 5, fig. 11-18, text-fig. 72.
- Panderodus (Dapsilodus) mutatus* (Branson & Mehl, 1933)
- Acodus mutatus* (Branson & Mehl), Webers 1966, p. 21, pl. 3, fig. 5, 6.
- Acontiodus procerus* (Ethington), Serpagli 1967, p. 46, pl. 9, fig. 6-11c.
- Periodon flabellum* (Lindström, 1955)
- Trichonodella flabellum* Lindström, Viira, 1974, pl. 4, fig. 8, 9.
- Prioniodina ? deflexa* Lindström, Viira, 1974, pl. 4, fig. 10, 15, 16.
- Prioniodina inflata* Lindström, Viira, 1974, pl. 4, fig. 18-20.
- Periodon flabellum* (Lindström); Serpagli, 1974, p. 63, pl. 14, fig. 1-17b, pl. 25, fig. 1-6, Van Wamel, 1974, p. 80, pl. 4, fig. 14-20.
- Periodon aculeatus aculeatus* Hadding, 1913
- Oulodus* cf. *tortilis* (Sweet & Bergström), Viira, 1974, p. 98, text-fig. 121.
- Periodon aculeatus* Hadding, Viira, 1974, p. 102, text-fig. 129.
- Periodon* sp.n., Viira, 1974, p. 104, text-fig. 131.

- Periodon*? sp., Viira, 1974, p. 105, text-fig. 132.
- Polonodus clavosus* (Viira, 1974)
- Amorphognathus* n.sp., Lindström, 1964, p. 92, fig. 33C.
- Ambalodus clavosus* n.sp., Viira, 1974, p. 51, pl. 8, fig. 1, text-fig. 37, 38.
- Amorphognathus*? n.sp., Viira, 1974, p. 62, text-fig. 58.
- Ambalodus*? n.sp., Viira, 1974, p. 52, pl. 8, fig. 2, 3, text-fig. 39.
- ?*Amorphognathus variabilis* Sergeeva, Fahraeus 1970, fig. 3E.
- Prioniodus gerdae* Bergström, 1971
- Amorphognathus gerdae* (Bergström), Viira, 1974, p. 60, pl. 11, fig. 38, text-fig. 56, 57.
- Prioniodus* aff. *variabilis* Bergström, Viira, 1974, pl. 9, fig. 24, 25.
- Prioniodus alatus alatus* Hadding, 1913
- non *Prioniodus*? *alatus* Hinde, Hinde, 1879, p. 362, pl. 16, fig. 5 (neoprioniodiform element of the Polygnathidae).
- Prioniodus alatus* Hadding, Wolska, 1961, p. 355, pl. 4, fig. 5a, b, Spassov & Teller, 1963, p. 80, pl. 1, fig. 3a, b, Bednarczyk, 1971b, pl. 5, pl. 5, fig. 2, Viira, 1974, pl. 10, fig. 12.
- Prioniodus* sp. 1 Lindström, Wolska, 1961, pl. 2, fig. 10, Spassov & Teller, 1963, p. 81, pl. 1, fig. 11a, b.
- Prioniodus* cf. *variabilis* Bergström, Wolska, 1961, p. 356, pl. 5, fig. 2a, b.
- Paracordylodus* sp. 2 Lindström, Wolska, 1961, p. 354, pl. 2, fig. 9, pl. 3, fig. 3a, b.
- Keislognathus gracilis* Rhodes, Wolska, 1961, p. 350, pl. 2, fig. 2, 3, 5.
- Tetraprioniodus* cf. *robustus* Lindström, Wolska, 1961, p. 358, pl. 5, fig. 3a, b.
- ? *Distacodus stola* Lindström, Wolska, 1961, p. 348, pl. 2, fig. 4.
- Tetraprioniodus superbus* (Rhodes). Wolska, 1961, p. 358, pl. 6, fig. 1-3, Spassov & Teller, 1963, p. 82, pl. 1, fig. 18.
- Falodus* sp., Wolska, 1961, p. 350, pl. 2, fig. 1a, b, Spassov & Teller, 1963, p. 78, pl. 1, fig. 8, 9.
- Oepikodus smithensis* Lindström, Spassov & Teller, 1963, p. 48, pl. 1, fig. 15.

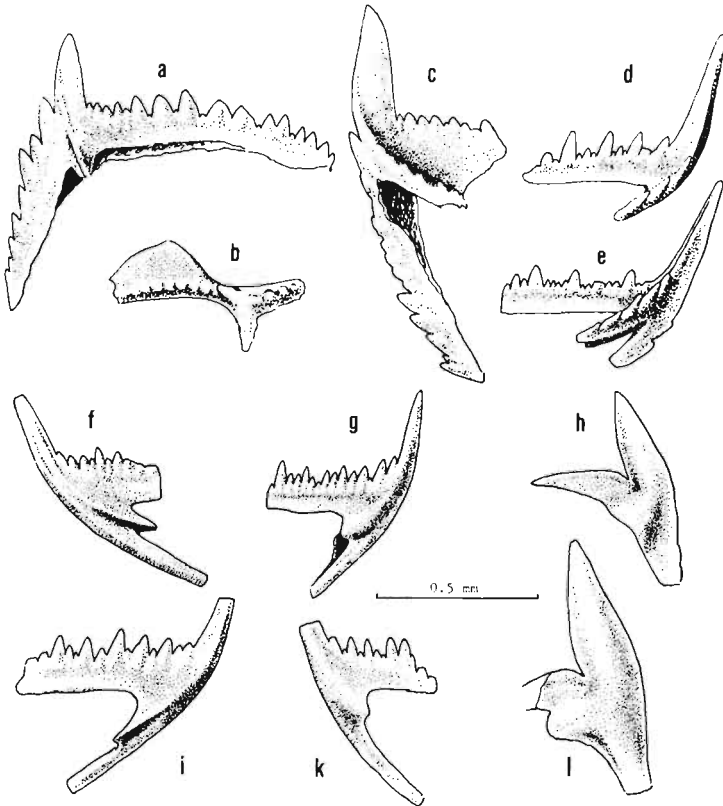


Fig. 23. *Prioniodus alatus medius* ssp.n.: a—h erratic boulder E-079, 1-134—141, holotype—1-138, *E. pseudoplanus* Zone; i—l erratic boulder E-138, 1-142—144; *E. suecicus* Zone a, b amorphognathiform el., c ambalodiform el., d trichonodelliform el., e tetraprioniodiform el., f, i keislognathiform el., g, k cordylodiform el., h, l oistodiform.

Prioniodus navus Lindström, Spassov & Teller, 1963, p. 80, pl. 1, fig. 16, 17.

Prioniodus praevariabilis Fahraeus, Bednarczyk, 1971b, pl. 5, fig. 2. Bergström, 1971, p. 146, pl. 2, fig. 1.

Baltoniodus praevariabilis (Fahraeus), Lindström, 1971, p. 56.

Tetraprioniodus asymmetricus Bergström, Bednarczyk, 1971b, pl. 5, fig. 5a, b.

Prioniodus variabilis Bergström, Viira, 1974, pl. 10, fig. 13, 14, 16, 17.

Baltoniodus n.sp., Lindström, Racheboeuf & Henry 1974, p. 17, pl. 1, fig. 12.

Remarks.—*Prioniodus* ? *alatus* Hinde, 1879 cannot be assigned, as a Devonian form, to this genus. It was also assigned to the genus *Prioniodus* only tentatively by its author. Thus, it is not necessary in my opinion to treat it as an older homonym. The Hadding's name is widely used in the proper meaning.

Prioniodus alatus parvidentatus (Sergeeva, 1963)

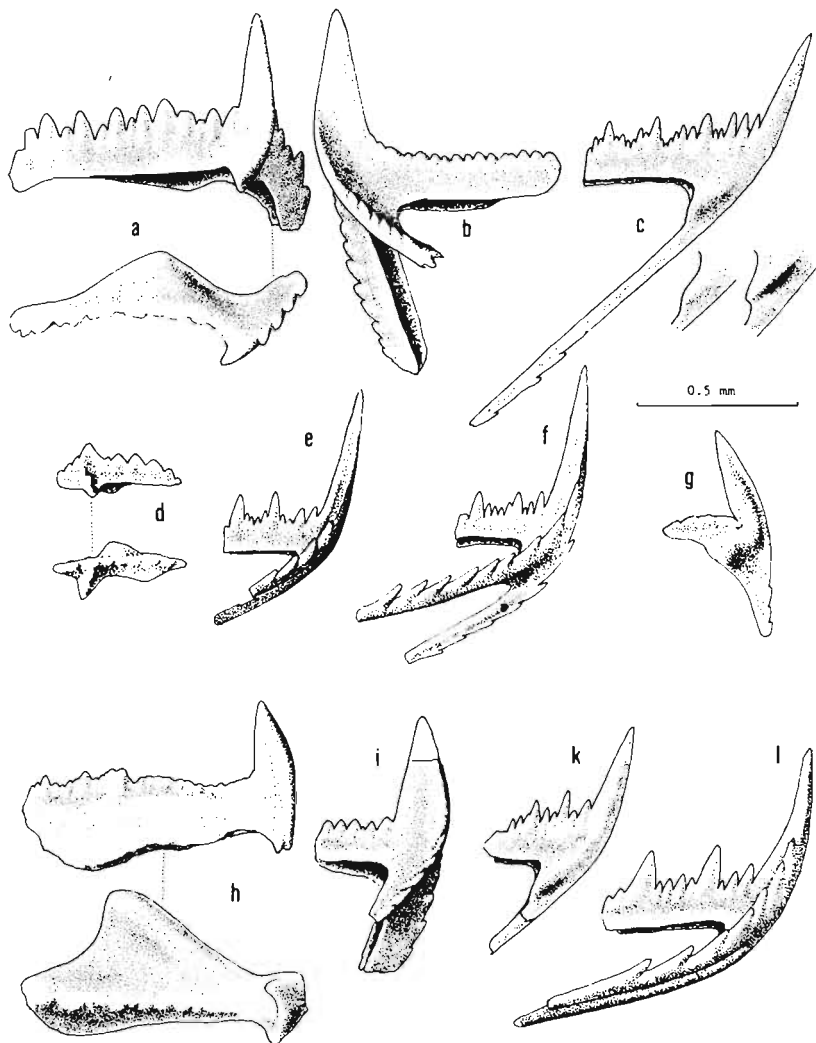


Fig. 24. a—g *Prioniodus alatus alatus* Hadding: erratic boulder E-113, 1-145—153, E. robustus Zone. h—l *Prioniodus variabilis* Bergström: erratic boulder E-112, 1-154—159, P. variabilis Zone. a, d, h amorphognathiform el., b, i amabalodiform el., c, k keislognathiform and ligonodiniform el., e, l trichonodelliform el., f tetraprioniodiform el., g oistodiform el.

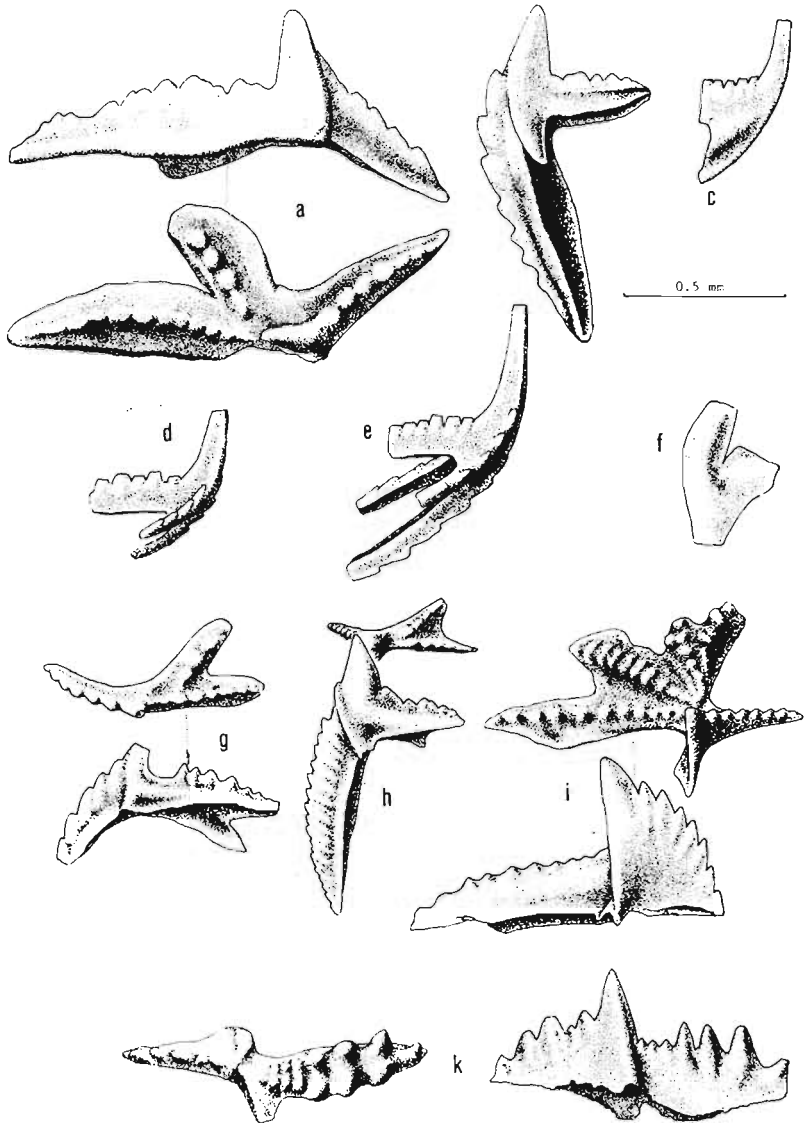


Fig. 25. a—f *Prioniodus gerdae* Bergström: erratic boulder E-154, 1-163—168, *P. gerdae* Zone. g—h *Rhodesgnathus elegans polonicus* ssp.n: Mójcza limestone, sample A-21, 1-316, 317, *P. gerdae* Zone. i *Complexodus pugionifer* (Drygant): Mójcza limestone, sample A-19, 1-318, Llandeilian. k *Icriodella superba* (Rhodes): erratic boulder E-212, 1-344, Upper Caradocian.

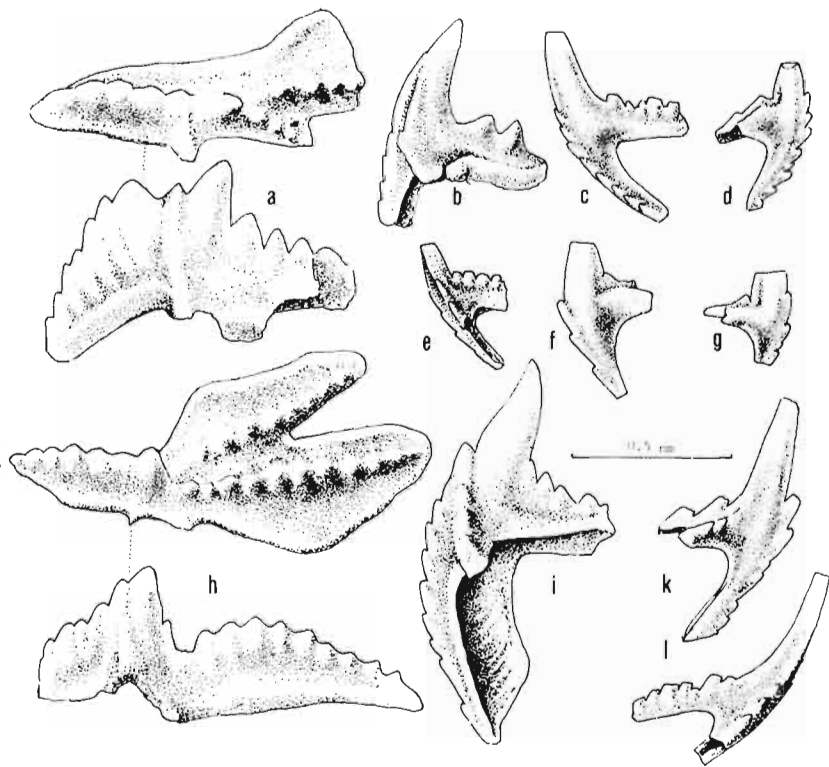


Fig. 26. a—g *Amorphognathus variabilis* Sergeeva: a, d Mójcza limestone, sample A-14, 1-319-320, *E. pseudoplanus* Zone; e, g Mójcza limestone, sample A-12, 1-171-173, 176, 177, *E. pseudoplanus* Zone; f Mójcza limestone, sample A-10, 1-174, *E. robustus* Zone; h—l *Amorphognathus kielcensis* sp.n.: h—i Mójcza limestone, sample A-18, 1-178, 179, holotype—1-178, Llandeillian a, h amorphognathiform el., b, i ambalodiform el., c cordylodiform el., e keislognathiform el., d, f, g, k oistodiform el.

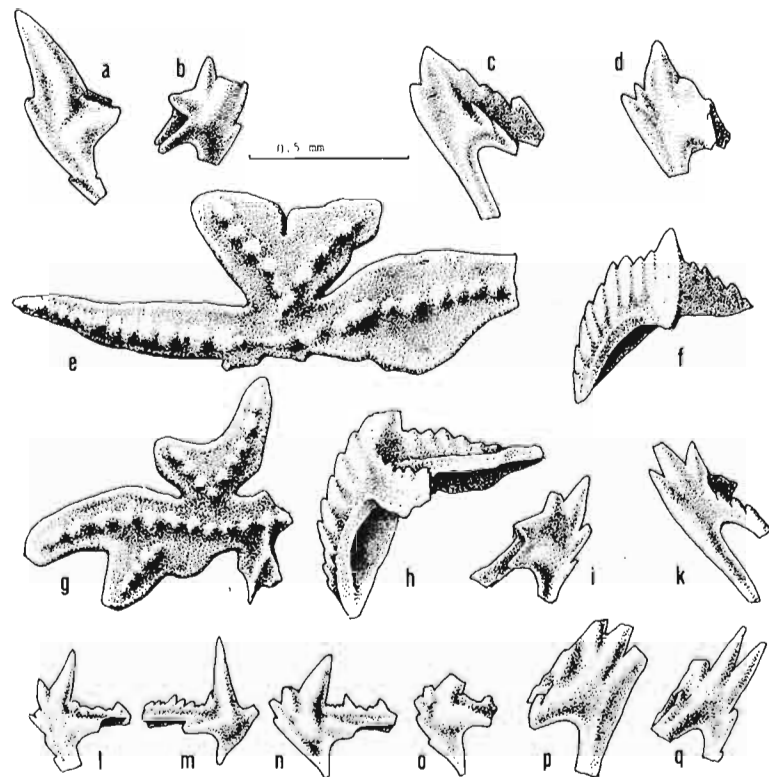


Fig. 27. a—f *Amorphognathus inaequalis* Rhodes: a, b Mójcza limestone, sample A-7, 1-185, 186; c—f sample A-6, 1-189-192, Llandeillian. g—q *Amorphognathus tvaerenensis* Bergström: g—k Mójcza limestone, sample A-5, 1-340-343, *P. variabilis* Zone; l—o Mójcza limestone, sample A-21, 1-323-326, p, q sample A-22, *P. gerdae* Zone. e, g amorphognathiform el., f, h ambalodiform el., a—d, i—q oistodiform el.

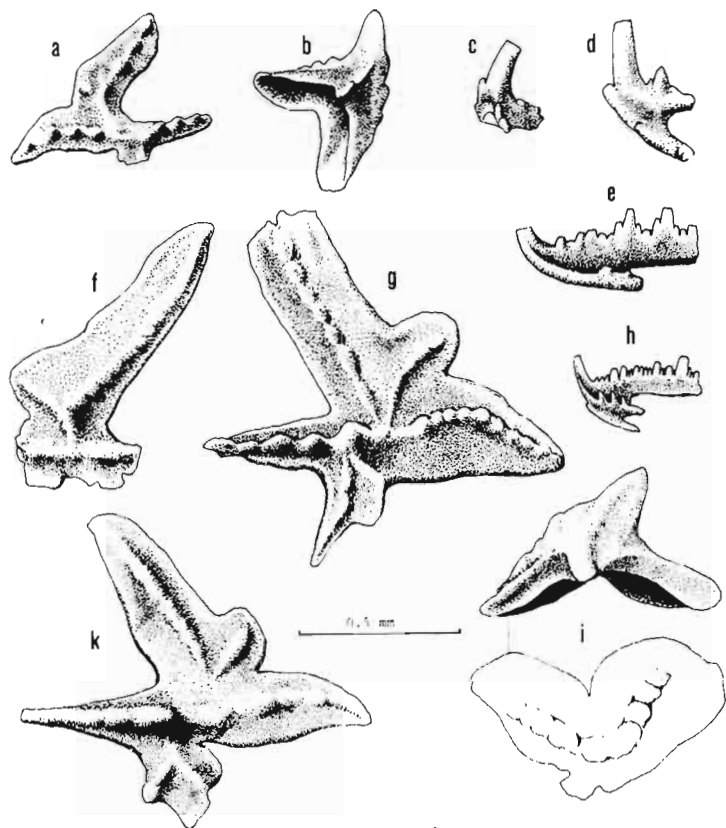


Fig. 28. *a-i* *Amorphognathus superbis* (Rhodes): *a-e* Mójcza limestone, sample A-2, 1-204—208, *A. superbis* Zone; *f-i*, erratic boulder 0-390, 1-209—212, *A. superbis* (?) Zone. *k* *Amorphognathus ordovicicus* (Branson & Mehl)?: erratic boulder E-082, 1-213, Ashgillian (?). *a, f, g, k* amorphognathiform el., *b, i* ambalodiform el., *c* keislognathiform el., *d* cordylodiform el., *e* trichonodelliform el. *h* tetraprioniodiform el.

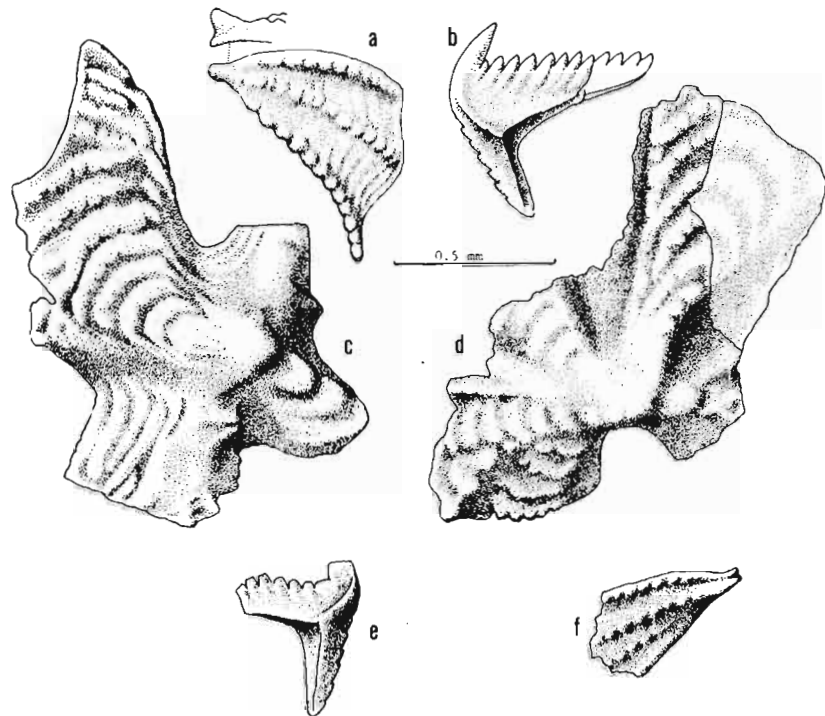


Fig. 29. *a, b, e* *Pygodus serrus* (Hadding): *a, b* erratic boulder E-113, 1-214, 215, Upper Llanvirnian, *E. robustus* Zone; *e* Mójcza limestone, sample A-17, 1-329, *c, d* *Polonodus clivosus* (Viira): erratic boulder E-080, 1-216, lowermost Llanvirnian, *E. pseudoplanus* Zone; *d* Mójcza limestone, sample A-11, 1-218, uppermost Arenigian or lowermost Llanvirnian. *f* *Pygodus anserinus* Lamont & Lindström, Mójcza limestone, sample A-18, 1-330, Llandeilian *a, c, d, t* amorphognathiform (?) el., *b* ambalodiform el.

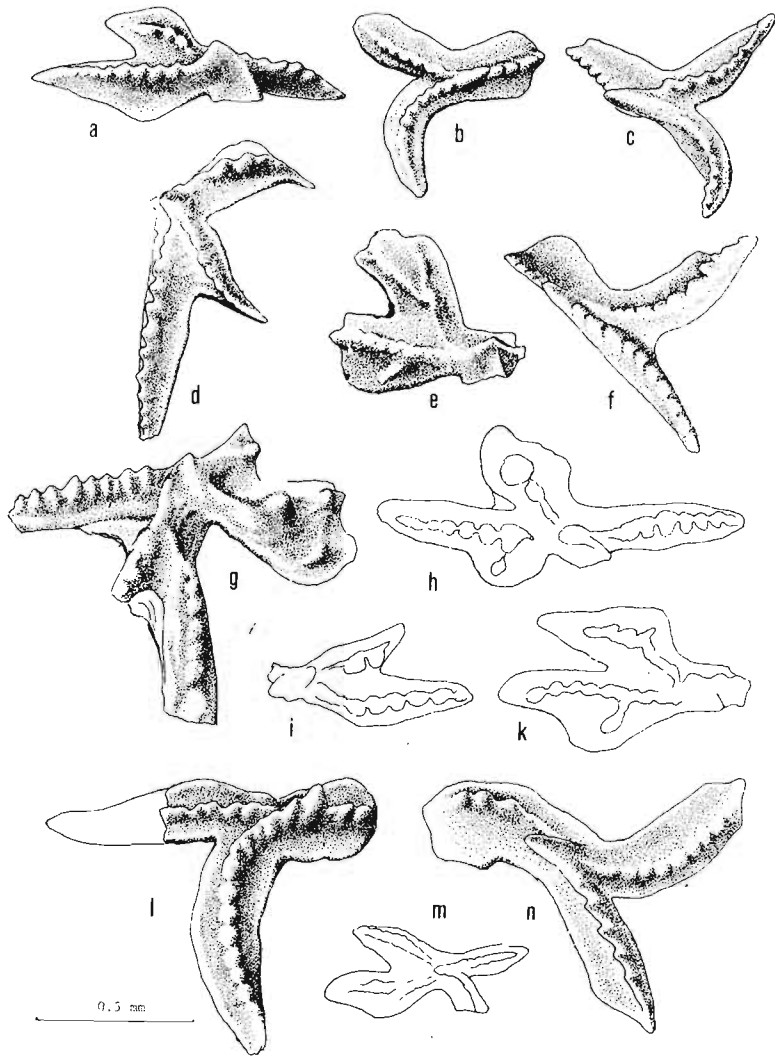


Fig. 30. *a-f Eoplacognathus zgierzensis* sp.n.: *a-c, e* erratic boulder E-089, 1-219-222, lowermost Llanvirnian (BIII α or BIII β); *d, f* erratic boulder E-096 1-223, 224 (BIII α or BIII β). *g-n Eoplacognathus pseudoplanus* (Viira): erratic boulder V-079, 1-225-231, upper part of the *E. pseudoplanus* Zone (BIII γ), late form. *a, d, e, g-k, m* amorphognathiform el., *b, c, f, l, n* ambalodiform el.

?*Tetraprioniodus minax* n.sp., Sergeeva, 1963, p. 102-103, pl. 8, fig. 1-6 (can be assigned to *Amorphognathus variabilis*).

Falodus parvidentatus n.sp., Sergeeva, 1963, p. 103-104, pl. 8, fig. 4-7.

?*Baltoniodus navis* (Lindström) late form, Lindström, 1971, pl. 1, fig. 18-23.

Prioniodus navis Lindström, 1955

Prioniodina densa Lindström, Bednarczyk, 1971b, pl. 4, fig. 7, Viira, 1974, pl. 6, fig. 1, 2.

Prioniodus alatus Hadding, Baranowski & Urbanek, 1972, pl. 1, fig. 6.

Prioniodus elegans Pander, Baranowski & Urbanek, 1972, pl. 1, fig. 7.

Falodus prodentatus (Graves & Ellison), Baranowski & Urbanek, 1972, pl. 1, fig. 8.

Prioniodus navis Lindström, Viira, 1974, pl. 6, fig. 8, 9, Van Wamel, 1974, p. 89, pl. 8, fig. 10-19 (partim).

Volchodina densa (Lindström), Sergeeva, 1974, p. 83, pl. 1-4, fig. 4-5.

Protopanderodus rectus (Lindström, 1955)

Acontiodus cf. *rectus* var. *sulcatus* Lindström, Wolska, 1961, p. 345, pl. 1 fig. 2.

Acontiodus sp., Wolska, 1961, p. 346, pl. 1, fig. 3.

Acontiodus rectus Lindström, Spassov & Teller, 1963, p. 78, pl. 1, fig. 4, Bednarczyk, 1969, pl. 1, fig. 7, Baranowski & Urbanek, 1972, pl. 2, fig. 2, Viira, 1974, p. 48, pl. 4, fig. 21-23, text-fig. 29.

Acontiodus rectus sulcatus Lindström, Bednarczyk, 1969, pl. 1, fig. 10.

Acontiodus robustus Hadding, Bednarczyk, 1971a, pl. 3, fig. 3

Acontiodus cf. *kullerudensis* Hamar, Baranowski & Urbanek, 1972, pl. 1, fig. 3.

Scandodus rectus Lindström, Baranowski & Urbanek, 1972, pl. 2, fig. 2.

Acodus triangulatus Fahraeus, Viira, 1974, p. 46, pl. 5, fig. 25-26, text-fig. 25-26.

?*Scandodus* cf. *unistriatus* Sweet & Bergström, Viira, 1974, p. 119, pl. 5, fig. 30, text-fig. 151.

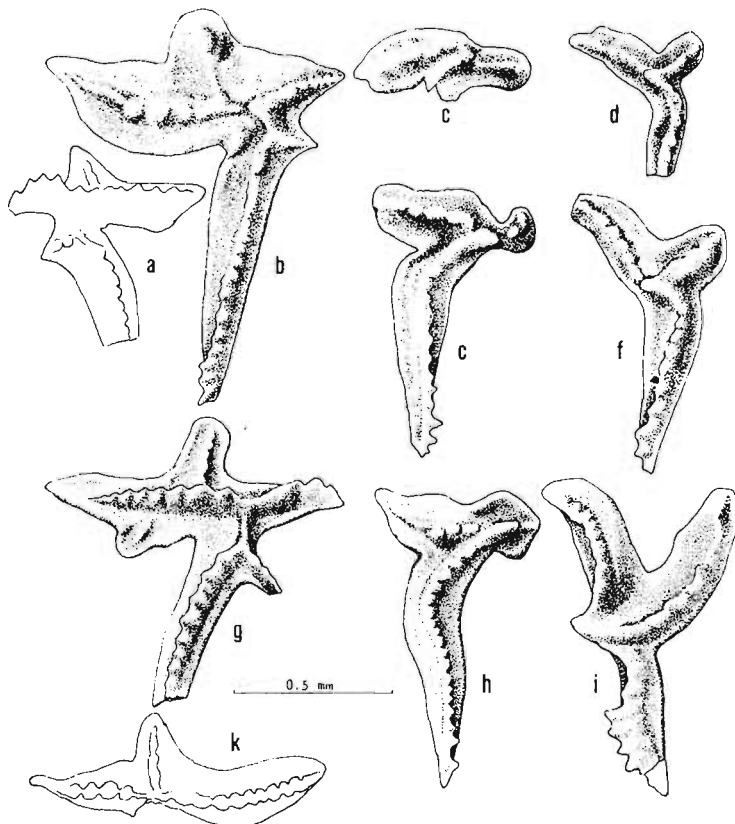


Fig. 31. a-f *Eoplacognathus foliaceus* (Fahraeus): a-d erratic boulder E-081, 1-232-236, Middle Llanvirnian, *E. foliaceus* Zone; e, f erratic boulder E-138, 1-237, 238, *E. foliaceus* Zone. g-k *Eoplacognathus lindstroemi reclinatus* (Fahraeus): erratic boulder E-149, 1-239-242, Middle Llanvirnian, *E. reclinatus* Zone. a, b, g, k amorphognathiform el., c, d, e, f, h, i ambalodiform el.

Scolopodus varicosatus Sweet & Bergström, Viira, 1974, p. 123, pl. 5, fig. 23-24, text-fig. 160.

Protopanderodus insculptus (Branson & Mehl, 1933)

Scandodus dissimilaris (Branson & Mehl), Serpagli, 1967, p. 94, pl. 24, fig. 5-6c.

Scolopodus? *insculptus* (Branson & Mehl), Serpagli, 1967, p. 97, pl. 28, fig. 1-6b.

"*Scolopodus*" n.sp. cf. "*S.*" *insculptus* (Branson & Mehl), Bergström, 1971, fig. 5, no. 13.

Pygodus serrus (Hadding, 1913)

Pygodus anserinus Lamont & Lindström, Wolska, 1961, p. 357, pl. 14, fig. 4, 5.

Haddingodus serra (Hadding), Viira, 1974, p. 86, pl. 11, fig. 28, text-fig. 105.

Semtacontiodus cornuiformis (Sergeeva, 1963)

Drepanodus cf. *subarcuatus* Furnish, Wolska, 1961, p. 349, pl. 1, fig. 5-7.

Drepanodus simplex Branson & Mehl, Wolska, 1961, p. 349, pl. 2, fig. 8.

Scandodus polonicus n.sp., Spassov & Teller, 1963, p. 81, pl. 1, fig. 5.

Semtacontiodus longicostatus (Drygant, 1974)

Scandodus longicostatus sp.n., Drygant, 1974, p. 57, fig. 9-13.

? *Scolopodus cordis* n.sp., Hamar, 1966, p. 74, pl. 3, fig. 4-6, text-fig. 2, no. 5.

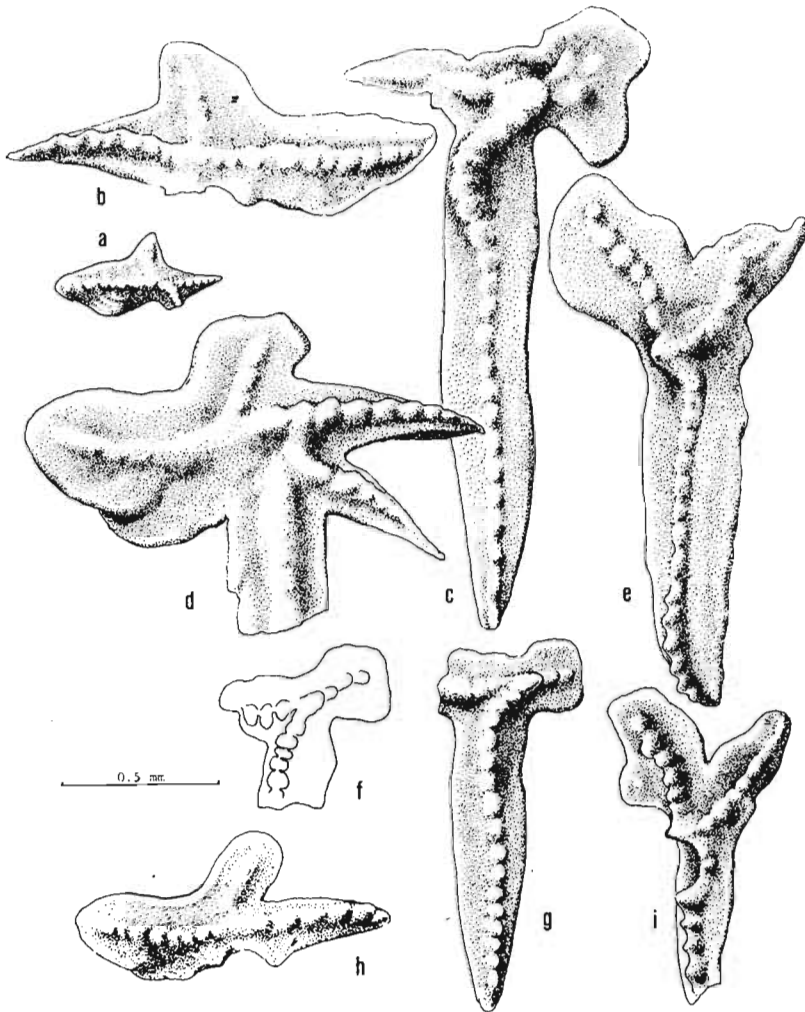


Fig. 32. *Eoplacognathus lindstroemi robustus* Bergström: a—e erratic boulder E-113, 1-243—247, Upper Llanvirnian, *E. robustus* Zone: f—i Mójcza limestone, sample A-10, 1-248—251, *E. robustus* Zone, a, b, d, h amorphognathiform el., c, e, f, g, i ambalodi-form el.

non *Distacodus falcatus* Stauffer, Bergström & Sweet, 1966, p. 329, pl. 35, fig. 10-13.
Cornuodus erectus Fahraeus, Bednarczyk, 1971a, pl. 3, fig. 5.
Scandodus sp. 1 Lindström, 1960, Viira, 1974, p. 121, text-fig. 156, 157.
 ? *Scandodus tortus* sp.n., Viira, 1974, p. 118, pl. 5, fig. 32-33, text-fig. 149, 150.
Scolopodus cornuformis Sergeeva, Viira, 1974, p. 123, pl. 5, fig. 27, 29, pl. 11, fig. 18, text-fig. 161.
Scalpellodus cavus (Webers, 1966)
Drepanodus cavus n.sp., Webers, 1966, p. 28, pl. 12, fig. 4, 5.
Protopanderodus latus n.sp., Van Wamel, 1974, p. 91, pl. 4, fig. 1-3.
Drepanodus amplissimus n.sp., Serpagli, 1967, p. 66, pl. 15, fig. 1a-5b.
Scalpellodus longibasis (Lindström, 1955)

Scolopodus peselephantis Lindström, Bednarczyk, 1971b, pl. 4, fig. 6, Viira, 1974, p. 124, text-fig. 162, Van Wamel, 1974, p. 94, pl. 5, fig. 16, 17.
Strachanognathus parvus Rhodes, 1955
Strachanognathus parvus Rhodes, Wolska, 1961, p. 358, pl. 5, fig. 6a, b, Bednarczyk, 1971a, pl. 3, fig. 6.
Triangulodus brevitasis (Sergeeva, 1963)
Triangulodus brevitasis (Sergeeva), Van Wamel, 1974, p. 96, pl. 5, fig. 1-7.
Triangulodus alatus n.sp.
Oistodus sp.n.A, Viira, 1974, p. 96, pl. 11, fig. 4, 5, text-fig. 116.
Walliserodus ethingtoni (Fahraeus, 1966)
Panderodus ethingtoni n.sp., Fahraeus, 1966, p. 26, pl. 3, fig. 5, ab.
Paltodus sp., Viira, 1967, fig. 4, no. 15.
Walliserodus nakholmensis (Hamar 1966)

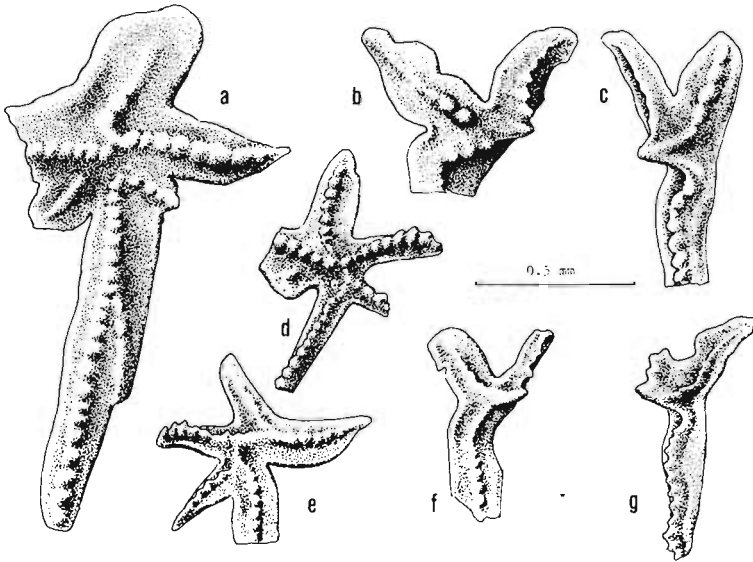


Fig. 33. *Eoplacognathus lindstroemi* Hamar: a-c Mójcza limestone, sample A-8, 1-252-255, Upper Llanvirnian, *E. lindstroemi* Zone. e-g erratic boulder E-085, 1-256-258, *E. lindstroemi* Zone. d *Eoplacognathus elongatus* (Bergström): Mójcza limestone, sample A-5, 1-331; a, d, e amorphognathiform el., b, c, f, g ambalodiform el.

Drepanodus aff. *longibasis* Lindström, Viira, 1974, p. 68, text-fig. 69.
Protopanderodus longibasis (Lindström, Van Wamel, 1974, p. 92, pl. 4, fig. 4-6.
Scandodus gracilis n.sp., Sergeeva, 1974, p. 80, fig. 6-9.
Scolopodus rex Lindström, 1955
Scolopodus rex Lindström, Bednarczyk, 1969, pl. 1, fig. 11, Baranowski & Urbanek, 1972, pl. 2, fig. 10, Viira, 1974, pl. 3, fig. 22, 23.
Paltodus scolopodiformis n.sp. Sergeeva, 1974, p. 79, fig. 10-11.
Scolopodus peselephantis Lindström, 1955

Panderodus nakholmensis n.sp., Hamar, 1966, p. 66, pl. 7, fig. 22-24, text-fig. 3, no. 3.
 ? *Acodus trigonius* (Schopf), Serpagli, 1967, p. 43, pl. 8, fig. 1-10c.
Walliserodus debolti (Rexroad), Serpagli, 1967, p. 104, pl. 31, fig. 5-13c.
Paltodus iniquus sp.n., Viira, 1974, p. 99, pl. 11, fig. 16-17, text-fig. 124, 125.
Westergaardodina ex gr. *bicuspidata* Müller, 1959
Westergaardodina bicuspida Müller, Hamar, 1966, p. 80, pl. 16, fig. 1, text-fig. 2, no. 3, Druce & Jones, 1971, p. 100, pl. 7, fig. 1-4d, text-fig. 32.

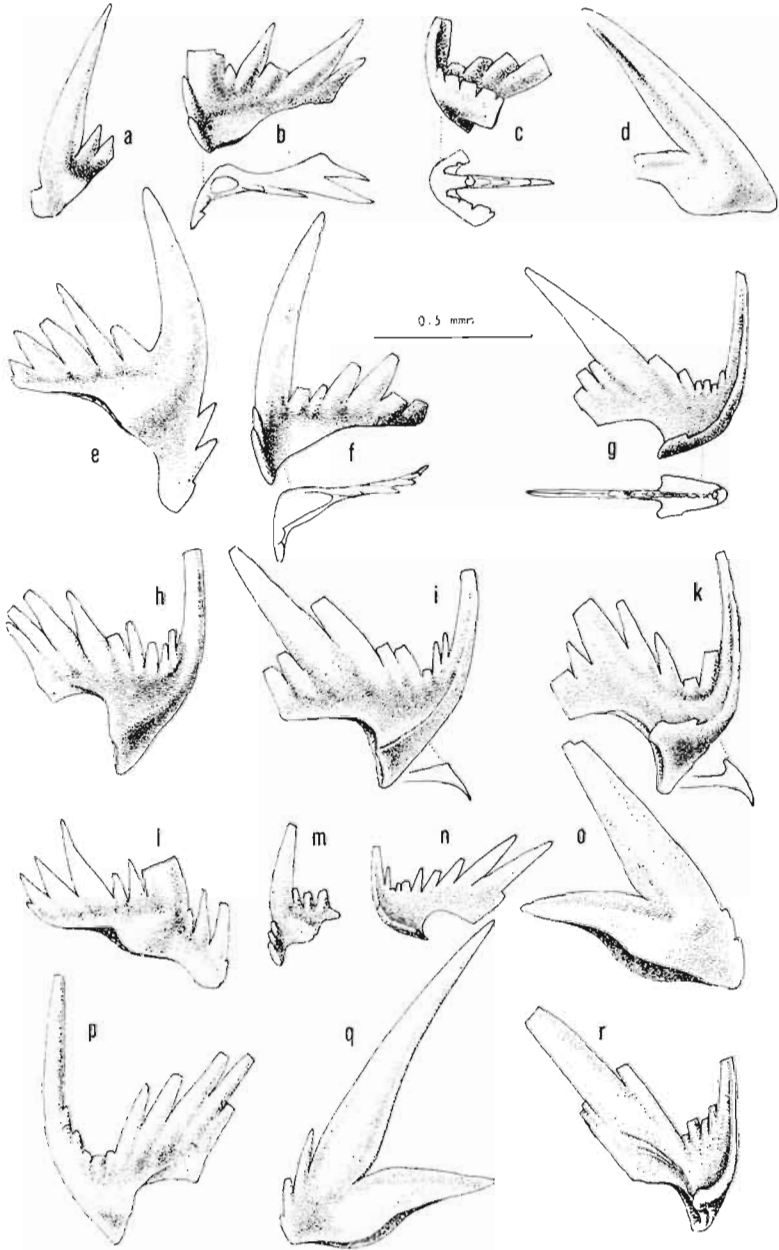


Fig. 34. *a—d* *Periodon flabellum* (Lindström): erratic boulder E-116, 1-259—262, Upper Arenigian, *P. originalis* Zone. *e—k* *Periodon aculeatus zgierzensis* ssp.n.: erratic boulder E-089, 1-263—268, holotype—1-265, lowermost Llanvirnian, *E. pseudoplanus* Zone. *l—r* *Periodon aculeatus aculeatus* Hadding: erratic boulder E-113, 1-269—275, Upper Llanvirnian, *E. robustus* Zone. *a, e, l* ozarkodiniform el., *b, f, m* ozarkodiniform (?) el., *c, g, n* trichonodelliform el., *h, p* cordylodiform el., *i* II cordylodiform el., *k, r* plectospathodiform el., *d, o, q* oistodiform el.

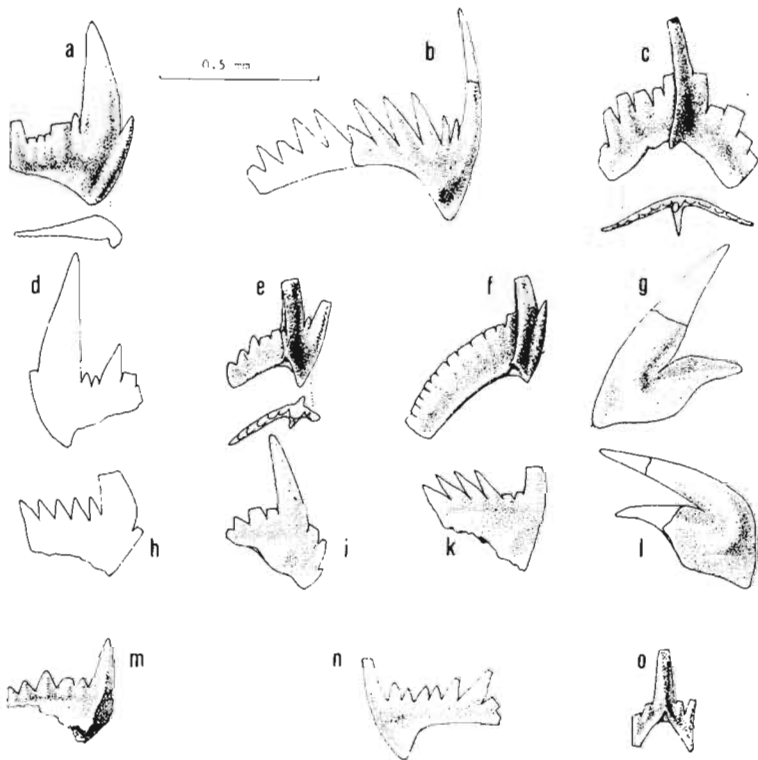


Fig. 35. a—h *Microzarkodina flabellum parva* Lindström: erratic boulder E-116, 1-276—283, Upper Arenigian, *P. originalis* Zone. i—l *Microzarkodina ozarkodella* Lindström; erratic boulder E-117, 1-284—286, uppermost Arenigian, *A. variabilis* Zone. m—o *Phragmodus* sp.: Mójcza limestone, sample A-19, 1-332, a, d, h, i ozrakodini-form el., c trichonodelliform el., e, f plectospathodiform el., b, k cordylodiform el., g, l oistodiform el.

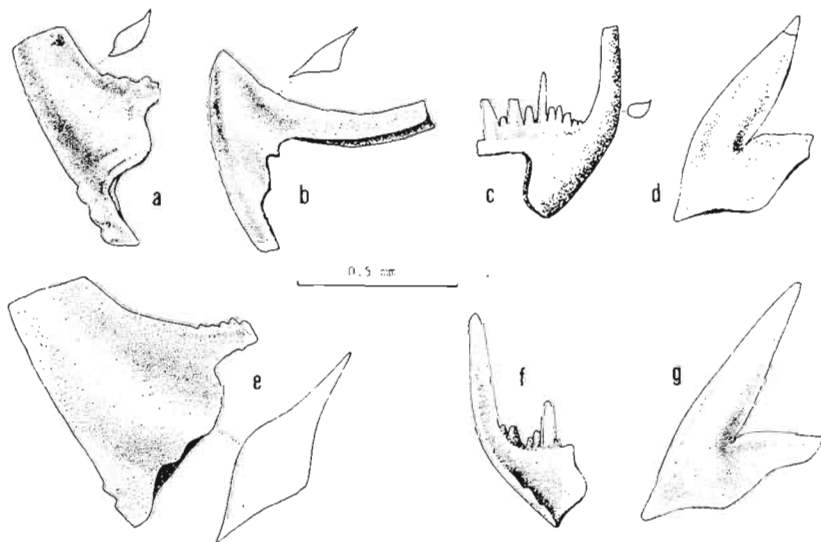


Fig. 36. *Hamarodus europaeus* (Serpagli): Mójcza limestone, a—d sample A-4, 1-287—290, Upper Caradocian, *A. superbus* Zone; e—g sample A-2, 1-291—293, Upper Caradocian. a, b, e ozarkodini-form el., c, f cordylodiform el., d, g oistodiform el.

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UWAGI O EWOLUCJI KONODONTÓW ORDOWICKICH

Streszczenie

Cały zespół konodontów, zazwyczaj zróżnicowanych morfologicznie, należał do jednego zwierzęcia konodontowego. Rekonstrukcje składu takich zespołów oparte są na badaniach statystycznych: zakłada się, że konodony należące do jednego zwierzę-

cia powinny występować w statystycznie istotnych próbach zawsze razem a nigdy oddzielnie. W poniższym opracowaniu przedstawiono wyniki badań ewolucji zespołów, pozwalające na sprawdzenie prawidłowości rekonstrukcji statystycznych, przy założeniu, że linie ewolucyjne poszczególnych elementów winny być równoległe do siebie (co nie oznacza równoczesności wydarzeń ewolucyjnych) i ciągłe (zespoły nie zawierające elementów występujących w zespołach wyjściowych i potomnych nie mogą być częścią ciągu ewolucyjnego).

Sądząc z charakteru przejść morfologicznych w obrębie zespołu najprymitywniejszych konodontów ordowickich (Panderodontidae), konodonty te pierwotnie pokrywały znaczną część powierzchni ciała zwierzęcia i były analogami a zapewne i homologami ząbków skórnych najpierwotniejszych strunowców.

Z kambru do ordowiku przeszły tylko dwie linie ewolucyjne konodontów. Jedną z nich stanowi rodzaj *Westergaardodina*, który wg. Druce & Jones (1971) dał początek ordowickiej rodzinie Chirognathidae. Wszystkie pozostałe konodonty wywodzą się od kambryjskiego rodzaju *Oneotodus*. Prymitywne proste konodonty pierwotnie lub wtórnie nie zawierające elementów symetrycznych w zespole dotrwały do dewonu. Zapewne w końcu dolnego ordowiku konodonty te dały początek bezszczętkowcom Heterostraci — wskazuje na to ich morfologia i mikrostruktura. Ważnymi wydarzeniami w ewolucji konodontów było powstanie konodontów zawierających w zespole trójżebrowe elementy symetryczne, a później wykształcenie elementu oistodiform — płaskiego z wcięciem krawędzi pod głównym zębem. Proste konodonty zawierające ten element w zespole powstały w termadoku i dotrwały do końca karadoku (Distacodontidae). Największy rozwój osiągnęły linie ewolucyjne konodontów u których na krawędziach rozwinęło się ząbkowanie. Jedną z nich, cechującą się przewagą w zespole elementów trójgałzkowych (Prioniodontidae) powstała z Distacodontidae w dolnym arenigu (McTavish, 1973). Część elementów zespołów konodontów z tej rodziny wykazuje tendencję do wytworzenia platformy przez wykształcenie dodatkowych, ząbkowanych gałęzi na rozszerzeniach bazy. Prioniodontidae wymarły w końcu karadoku, natomiast pochodząca od nich gałąź ewolucyjna form, które wykształciły platformę przez zwielokrotnienie szeregów ząbków (Icriodontidae) dotrwała do górnego dewonu, podlegając uproszczeniu morfologii gałzkowych elementów zespołu.

Niezależnie od Prioniodontidae rozwinęło się ząbkowanie ramion Periodontidae dając początek liniom ewolucyjnym konodontów tworzących zespoły z przewagą elementów dwugałzkowych. Od Periodontidae za pośrednictwem Prioniodontidae wywodzą się wszystkie pozostałe konodonty poordowickie. Aparat sylurskich i późniejszych konodontów z tej grupy składa się z 14 konodontów zróżnicowanych morfologicznie i zapewne funkcjonalnie, ustawionych kolejno za sobą i ząbkami skierowanych do siebie. Niezależnie w wielu liniach rozwija się platforma u pierwszego elementu (polygnathiform) — zazwyczaj przez zwielokrotnienie rzędów zębów. Poza aparatem pozostawały elementy symetryczne.

ЕЖИ ДЗИК

ЗАМЕЧАНИЯ О ЭВОЛЮЦИИ ОРДОВИКСКИХ КОНОДОНТОВ

Резюме

Весь комплекс конодонтов, как правило морфологически дифференцированный, относится к одному конодонтному животному. Реконструкции состава таких комплексов основываются на статистических анализах. Принимается, что конодонты, принадлежащие одному животному, должны встречаться в статистически важных пробах всегда совместно и никогда отдельно. В работе изложены результаты изучения эволюции комплексов, позволяющие поверить достоверность статистических реконструкций, принимая, что эволюционные линии отдельных элементов, должны быть параллельны (что не обозначает одновременности эволюционных событий) и непрерывны (комплексы, не содержащие элементов, представленных в исходных комплексах и в производных комплексах, не являются частью эволюционного ряда).

Характер морфологических рядов в комплексе самых примитивных ордовикских конодонтов (*Panderodontidae*) показывает, что эти конодонты покрывали первично значительную часть поверхности тела животного и представляли аналоги и, повидимому, гомологи кожных зубчиков простейших хордовых.

Из кембрия в ордовик перешли лишь два эволюционных ряда конодонтов. К одному из них относится род *Westergaardodina*, который, по мнению Друсса и Джонса (1971), дал начало ордовикскому семейству *Chirognathidae*. Все остальные конодонты происходят от кембрийского рода *Oneotodus*. Примитивные простые конодонты, лишённые элементов симметрии, сохранились до среднего девона. Вероятно в конце раннего ордовика от этих конодонтов произошли бесчелюстные *Heterostraci*, что показывает их морфология и микроструктура. Важными событиями в эволюции конодонтов было появление трехреберных симметрических элементов, а позже появление элемента *oistodiform* — плоского, с углублением края под главным зубом. Простые конодонты с этим элементом появились в тремадоке и существовали до конца карадока (*Distacodontidae*). Самое большое развитие получили эволюционные ряды конодонтов с зазубренными краями. Один из них, характеризующийся преобладанием в сообществе трехветвистых элементов (*Prioniodontidae*) произошёл от *Distacodontidae* в раннем арениге (Мак-Тевис, 1973). Некоторые элементы комплекса конодонтов этого семейства проявляют признаки образования платформы путем образования дополнительных, зубчатых ветвей на расширениях базиса. *Prioniodontidae* исчезли в конце карадока, а происходящая от них эволюционная ветвь, формы которой имели платформу, образовавшуюся за счет увеличения количества рядов зубчиков (*Ucriodontidae*) сохранилась до позднего девона, подвергаясь упрощению морфологии ветвистых элементов сообщества.

Независимо от Prioniodontidae развилась зазубренность лучей Periodontidae, что было началом эволюционных рядов конодонтов, образующих комплексы с преобладанием двухветвистых элементов. От Periodontidae посредством Prioniodontidae выводятся все остальные послеордовикские конодонты. Аппарат силурийских и последующих конодонтов этой группы состоит из 14 разных по морфологии и функциям конодонтов, расположенных последовательно друг за другом, с зубчиками обращенными к себе взаимно. Во многих рядах развивается платформа у первого элемента (polygnathiform), как правило путем умножения рядов зубчиков. Вне аппарата находились симметрические элементы.

EXPLANATION OF PLATES

Plate XLI

- Fig. 1. *Scalopellodus laevis* sp.n. Upper Arenigian, erratic boulder E-116, *P. originalis* Zone, ZPAL C. VI/1-341, $\times 150$.
- Fig. 2. *Walliserodus costatus* sp.n. Lower Llanvirnian, Mójcza limestone, sample A-14, *E. pseudoplanus* Zone, ZPAL C. VI/1-342, $\times 140$.
- Fig. 3. *Belodella serrata* sp.n. Upper Llanvirnian, erratic boulder E-141, *E. reclinatus* Zone, ZPAL C. VI/1-343, $\times 200$.
- Fig. 4,7. *Semiacontiodus cornuformis* (Sergeeva). Lower Llanvirnian, erratic boulder E-079, *E. pseudoplanus* Zone. 4 Asymmetric element with well developed basal filling. ZPAL C. VI/1-344. $\times 120$; 7 Symmetric element ZPAL C. VI/1-345, $\times 150$.
- Fig. 5. *Semiacontiodus carinatus* sp.n. Upper Llanvirnian, erratic boulder E-113, *E. robustus* Zone. Symmetric element, ZPAL C. VI/1-346. $\times 150$.
- Fig. 6. The same species and boulder. Asymmetric element, ZPAL C. VI/1-347, $\times 150$.

Plate XLII

- Fig. 1. *Prioniodus alatus medius* ssp.n. Lower Llanvirnian. Erratic boulder E-079, upper part of the *E. pseudoplanus* Zone. Keislognathiform element, ZPAL C. VI/1-340, $\times 140$.
- Fig. 2. *Triangulodus* (?) *alatus* sp.n. Middle Llanvirnian. Oistodiform (?) element, erratic boulder E-081, *E. foliaceus* Zone, ZPAL C. VI/1-295, $\times 120$.
- Fig. 3. The same species. Middle Llanvirnian. Cordylodiform element, erratic boulder E-149, *E. reclinatus* Zone, ZPAL C. VI/1-294, $\times 72$.
- Fig. 4. The same species. Middle Llanvirnian. Trichonodelliform element, erratic boulder E-149, ZPAL C. VI/1-296, $\times 90$.
- Fig. 5. The same species. Middle Llanvirnian. Cordylodiform element, erratic boulder E-149, ZPAL C. VI/1-297, $\times 120$.

Plate XLIII

- Fig. 1. *Polonodus clivosus* (Viira). Lowermost Llanvirnian, erratic boulder E-080, lower part of the *E. pseudoplanus* Zone. Amorphognathiform (?) element, ZPAL C. VI/1-217: a apical view, $\times 120$, b lateral view, $\times 130$.
- Fig. 2. *Eoplacognathus zgierzensis* sp.n. Lowermost Llanvirnian, erratic boulder E-080. Amorphognathiform element, apical view, ZPAL C. VI/1-298, $\times 72$.
- Fig. 3. *Pygodus serrus* (Hadding). Upper Llanvirnian, erratic boulder E-113, *E. robustus* Zone. Amorphognathiform (?) element, basal view, ZPAL C. VI/1-299, $\times 130$.

Plate XLIV

- Fig. 1. *Amorphognathus kielcensis* sp.n. Lower Llandeillian, Mójcza limestone, sample A-18, *P. anserinus* Zone. Oistodiform element, ZPAL C. VI/1-334, $\times 140$.
- Fig. 2. *Complexodus pugionifer* (Drygant). Upper Llandeillian, Mójcza limestone, sample A-19, *A. inaequalis* Zone. Amorphognathiform element, ZPAL C. VI/1-335, $\times 90$.
- Fig. 3. *Rhodesgnathus elegans polonicus* ssp.n. Lower Caradocian, Mójcza limestone, sample A-21, *P. gerdæ* Zone. Amorphognathiform element, ZPAL C. VI/1-336, $\times 100$.
- Fig. 4. The same species and sample. Ambalodiform element, ZPAL C. VI/1-337, $\times 100$.
- Fig. 5. *Periodon aculeatus zgierzensis* ssp.n. Lower Llanvirnian, erratic boulder E-089, lower part of the *E. pseudoplanus* Zone. Trichonodelliform element, ZPAL C. VI/1-338, $\times 140$.
- Fig. 6. The same species and boulder. Oistodiform element, ZPAL C. VI/1-339, $\times 140$.
- Fig. 7. *Prioniodus alatus medius* ssp.n. Lower Llanvirnian, erratic boulder E-079, upper part of the *E. pseudoplanus* Zone. Keislognathiform element, ZPAL C. VI/1-340, $\times 140$.
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Table 1
 THE FREQUENCY OF
 Sequence of samples from erratic

Species	Sample	ABERRANT										SERRATED									
		<i>P. originalis</i>	<i>P. variabilis</i>	<i>P. gerdæ</i>	<i>A. variabilis</i>	<i>E. pseudocylindricus</i>	<i>E. caecus</i>	<i>E. rostratus</i>	<i>E. acutus</i>	<i>E. foliaceus</i>	<i>E. rostratus</i>	<i>E. serratus</i>	<i>E. serratus</i>	<i>E. serratus</i>	<i>E. serratus</i>	<i>E. serratus</i>	<i>E. serratus</i>	<i>E. serratus</i>			
1. <i>Asterocerosidina</i> <i>exur. bispinulata</i>	7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
2. <i>Histiodelia</i> <i>atlantica</i>	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
3. <i>Phragmodus</i> <i>microtus</i>	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
4. <i>Polipodus</i> <i>rex</i>	18	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
5. <i>Polipodus</i> <i>pseudophantia</i>	53	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
6. <i>Phragmodus</i> <i>sp. sp.</i>	50	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
7. <i>Asterocerosidina</i> <i>gerdae</i>	97	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
8. <i>Polipodus</i> <i>longispinus</i>	42	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
9. <i>Polipodus</i> <i>laevis</i>	20	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
10. <i>Polipodus</i> <i>ovatus</i>	120	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
11. <i>Phragmodus</i> <i>caecus</i>	60	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
12. <i>Phragmodus</i> <i>caecus</i>	246	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
13. <i>Phragmodus</i> <i>caecus</i>	595	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
14. <i>Histiodelia</i> <i>serrata</i>	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
15. <i>Phragmodus</i> <i>compressus</i>	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
16. <i>Polipodus</i> <i>sp. sp.</i>	82	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
17. <i>Asterocerosidina</i> <i>cornuformis</i>	145A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
18. <i>Asterocerosidina</i> <i>longicostatus</i>	26A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
19. <i>Asterocerosidina</i> <i>causatus</i>	30	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
20. <i>Phragmoderus</i> <i>sp. sp.</i>	50	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
21. <i>Polipodus</i> <i>77</i> <i>oceanographicus</i>	20	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
22. <i>Asterocerosidina</i> <i>subrotunda</i>	120	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
23. <i>Asterocerosidina</i> <i>originalis</i>	249	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
24. <i>Histiodelia</i> <i>lamellosa</i>	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
25. <i>Polipodus</i> <i>sp. sp.</i>	20	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
26. <i>Polipodus</i> <i>spinatus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
27. <i>Polipodus</i> <i>sp. sp.</i>	1695	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
28. <i>Polipodus</i> <i>sp. sp.</i>	207	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
29. <i>Polipodus</i> <i>sp. sp.</i>	508	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
30. <i>Polipodus</i> <i>sp. sp.</i>	64	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
31. <i>Polipodus</i> <i>sp. sp.</i>	96	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
32. <i>Polipodus</i> <i>sp. sp.</i>	353	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
33. <i>Polipodus</i> <i>sp. sp.</i>	391	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
34. <i>Polipodus</i> <i>sp. sp.</i>	28	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
35. <i>Polipodus</i> <i>sp. sp.</i>	46	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
36. <i>Polipodus</i> <i>sp. sp.</i>	60	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
37. <i>Polipodus</i> <i>sp. sp.</i>	20	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
38. <i>Polipodus</i> <i>sp. sp.</i>	100	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
39. <i>Polipodus</i> <i>sp. sp.</i>	132	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
40. <i>Polipodus</i> <i>sp. sp.</i>	204	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
41. <i>Polipodus</i> <i>sp. sp.</i>	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
42. <i>Polipodus</i> <i>sp. sp.</i>	9	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
43. <i>Polipodus</i> <i>sp. sp.</i>	7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
44. <i>Polipodus</i> <i>sp. sp.</i>	12A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
45. <i>Polipodus</i> <i>sp. sp.</i>	21	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
46. <i>Polipodus</i> <i>sp. sp.</i>	26	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
47. <i>Polipodus</i> <i>sp. sp.</i>	38	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
48. <i>Polipodus</i> <i>sp. sp.</i>	185	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
49. <i>Polipodus</i> <i>sp. sp.</i>	25	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
50. <i>Polipodus</i> <i>sp. sp.</i>	6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
51. <i>Polipodus</i> <i>sp. sp.</i>	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
52. <i>Polipodus</i> <i>sp. sp.</i>	6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
53. <i>Polipodus</i> <i>sp. sp.</i>	22	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
54. <i>Polipodus</i> <i>sp. sp.</i>	44	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
55. <i>Polipodus</i> <i>sp. sp.</i>	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
56. <i>Polipodus</i> <i>sp. sp.</i>	18	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
57. <i>Polipodus</i> <i>sp. sp.</i>	19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
58. <i>Polipodus</i> <i>sp. sp.</i>	11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			

Errata to the Table 1: for M.A-21 *P. variabilis* Zone read M.A-21 *P. gerdae* Zone; for M.A-22 *P. gerdae* Zone read M.A-22 *P. alvatus* Zone; for *Histiodelia atlantica* read *Histiodelia serrata*; for *Microzarkodina* sp., sample E-087 read *Phragmodus* sp., sample M.A-19.

(continued)

CONODONTS IN SAMPLES

boulders of a given horizon is random

	LAWRENINIAN										LARGILLIAN										GRADOCIAN										ARTILL. P. artill.					
	E. reclinator		S. roborator		L. lindstroemi		P. amareus		A. inaequalis		P. variabilis		P. p. p.		A. superbus																					
	La-6	La-7	La-8	La-9	La-10	La-11	La-12	La-13	La-14	La-15	La-16	La-17	La-18	La-19	La-20	La-21	La-22	La-23	La-24	La-25	La-26	La-27	La-28	La-29	La-30	La-31	La-32	La-33	La-34	La-35	La-36	La-37	La-38	La-39	La-40	
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