Geologica et Palaeontologica	SB 1	S. 29 - 42	4 Abb.	Marburg, 15. 4. 1972

Multielement Taxonomy and Ordovician Conodonts

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With 4 Figures

Abstract: Studies of the last five years, building on sound work published between 1930 and 1966, have resulted in development of a multielement taxonomy that now embraces many of the simple cones and most of the ramiform and platform-type elements known from Ordovician rocks in the North Atlantic and North American Midcontinent Provinces. The history of taxonomy for Ordovician conodonts is reviewed; the current status of multielement taxonomy is summarized; and the evolutionary development of stocks with nonfibrous ramiform-element apparatuses is discussed, with a view toward establishment of the framework for a realistic suprageneric classification of these forms. Although much work remains to be done, it is now clear that all major lineages of conodonts were established in or before Middle Ordovician times. Origins of these stocks, however, remain obscure in nearly every instance and constitute not only one of the major unsolved problems in conodont taxonomy but also serve as the principal impediment to suprageneric classification. It is suggested that a thorough evaluation of late Lower and early Middle Ordovician conodont faunas, with special attention to simple-cone genera, be made before suprageneric classification is allowed to crystallize.

Introduction

Conodonts are still a zoologic enigma, but active research in the last five years has yielded a vast amount of information that has in many ways revolutionized ideas about their taxonomy, evolution, and stratigraphic distribution. This rapid progress is strikingly illustrated by the many new results reached in recent studies of Ordovician conodonts. Among others, these results include establishment of a fundamentally new taxonomy based on the concept of multielement species. We recently contrasted this taxonomic approach with form taxonomy (SWEET & BERGSTRÖM 1970) and noted that because it treats conodonts as organisms rather than only as stratigraphic tools, it provides new means of clarifying previously unknown or misinterpreted relationships within conodont stocks and permits establishment of a taxonomy that is both simpler and more soundly based zoologically than the one previously in use.

Developments in the taxonomy of Ordovician conodonts have been very rapid in the last few years and this symposium provides a timely opportunity to review its current status, particularly with respect to major elements of faunas from North America and northwest Europe. Unfortunately, information available to us about Ordovician conodonts in other areas is still too fragmentary for taxonomic analysis at the multielement level. Also, space limits make it impossible for us to deal with more than a few important examples. Others have been treated elsewhere (BERGSTRÖM & SWEET 1966; WEBERS 1966; SCHOPF 1966) and an additional few must be deferred for later discussion pending study of more material. We hope that our comments about the genera assembled in the appendix to this report will also be useful as a supplementary summary of the current status of Ordovician conodont taxonomy.

Historical Review

At the outset we should emphasize that recent developments in the taxonomy of Ordovician conodonts represent merely the latest phase in studies that began more than a century ago. Without the base provided by earlier work, taxonomic ideas of the present could not have been achieved so readily and recognition of now-evident patterns would have been much delayed. Thus a brief review of the progress of Ordovician conodont taxonomy is a good introduction to a summary of its current status, which forms the bulk of our report.

Studies of Ordovician conodonts began, of course, with PANDER's remarkable monograph of 1856, in which the central taxonomic problem was clearly recognized. That is, as we pointed out recently (SWEET & BERGSTRÖM 1970), PANDER considered both form and what is now termed multielement taxonomy. He chose the former – not, apparently because it was the sounder biologically, but because it was the more practical means of describing the disjunct remains of a new group of unknown affinities. The choice was a wise one, we believe, for imposition of a multielement philosophy so early on a group so rich in form diversity would surely have inhibited others in assembly of the distributional and associational data from which multielement taxonomy now emerges so easily.

Although a few important reports appeared between 1856 and 1953, studies of European Ordovician conodonts were few in this long period. Six form-species were described from the American Ordovician by HINDE in 1879 and others were noted peripherally between 1879 and 1930. However, little work that bears significantly on the taxonomy of these forms was accomplished until the 1930's when C. R. STAUFFER (of the University of Minnesota) and the Missouri University group headed by E. B. BRANSON and M. G. MEHL began their important investigations. Between 1930 and 1955, information accumulated more or less regularly about the geographic and stratigraphic distribution of conodonts in the American Ordovician. We do not list all these reports individually, but we note that the taxonomy employed in them was Panderian and it was well suited to thorough description of the wide variety of forms encountered in small collections derived largely from easily disaggregated terrigenous rocks. Although such an approach came later to be regarded as "nuts and bolts" taxonomy by its detractors, we are convinced that any attempt to employ the more sophisticated views of multielement systematics in this epoch of primary data accumulation would not only have rendered the data useless but would have needlessly prolonged normal evolution of the multielement system we now advocate. The principal failing of the form-taxonomy approach was that, despite evidence from natural assemblages described as early as 1934, its users came to regard form-taxa as real biologic entities.

Acetic and monochloracetic acids came to be generally used for extraction of conodonts from calcareous rocks in the early 1950's and we regard this technical advance as a significant milestone in the more widespread use of conodonts stratigraphically and indirectly in the progress of conodont taxonomy. In the study of Ordovician conodonts, this technical improvement had more than ordinary impact. That is, on both the European and North American platforms, Ordovician rocks are developed largely in conodont-rich carbonate (or at least calcareous) facies, and the freedom to sample all parts of these sections systematically conferred by acid-reduction techniques resulted rather promptly in assembly of the large, sequential collections required by both detailed biostratigraphy and multielement taxonomy. At first, of course, and naturally, the larger collections assembled from both European and American carbonate rocks were described in existing Panderian terms. Indeed, it is now amusing to note that between 1955 and about 1964, success in using conodonts stratigraphically stimulated application of a form-taxonomy even more rigorous than before in descriptions of Ordovician faunas.

An early defection from form-taxonomy, as applied to Ordovician conodonts, was made by Sweet & Bergström in 1962, when their studies of a large collection from the Pratt Ferry Formation of Alabama convinced them that a group of simple cones representing an obvious symmetry-transition series was more logically regarded as the remains of a single species, *Scolopodus varicostatus,* than as the record of three species of as many form-genera. Lindström (1964) employed the same approach on a large scale. He illustrated the pervasive occurrence of form-transition series in Ordovician and younger conodont faunas, called attention quite forcefully to existence of similar patterns in successive faunas, and speculated on a general model for conodont apparatuses. This was an important nudge in the direction of a multielement taxonomy for Ordovician conodonts.

General use of multielement taxonomy in description and evaluation of Ordovician conodont faunas was delayed, however, until 1966, when it was used independently by Webers in his important study of Middle and Upper Ordovician forms from Minnesota, by Bergström & Sweet in their report on faunas from the Lexington Limestone of the Cincinnati Region, and, to a limited extent by Schopf in his study of conodonts from the Trenton Group of New York and southern Ontario. We emphasize that all these studies were based on large collections, systematically tabulated, and strong dependance on descriptions of form-taxa by previous authors is evident in discrimination of elements of the several apparatuses recognized. Thus these reports appeared more as logical culminations of 25 years of study of Midcontinent Ordovician conodonts than as radical and adventuresome departures from Panderian orthodoxy.

Since 1966, multielement taxonomy has guided many studies of American and European Ordovician conodonts, and the results we summarize in later parts of this report (and its appendix) have mostly been achieved in the last five years. In this period Serpagli (1967) recognized that the skeletal apparatuses of several species from the Upper Ordovician of the Carnic Alps included form-transition series, and Kohut (1969) applied quantitative grouping techniques to collections of Middle and Upper Ordovician conodonts from the Cincinnati Region. Kohut's work also demonstrated conclusively that nearly all the multielement associations described empirically as species by Bergström & Sweet (1966) survive rigorous statistical analysis. Additionally, Bergström (1968) worked out the skeletal architecture of *Prioniodus* and Sweet & Bergström (1970) showed that the prioniodont plan is fundamental as a model for the skeletal apparatus of other Ordovician genera. Our task in the remainder of this report is thus to elucidate the major results of taxonomic work in the last five years, particularly as it involves Ordovician faunas with which we have worked directly.

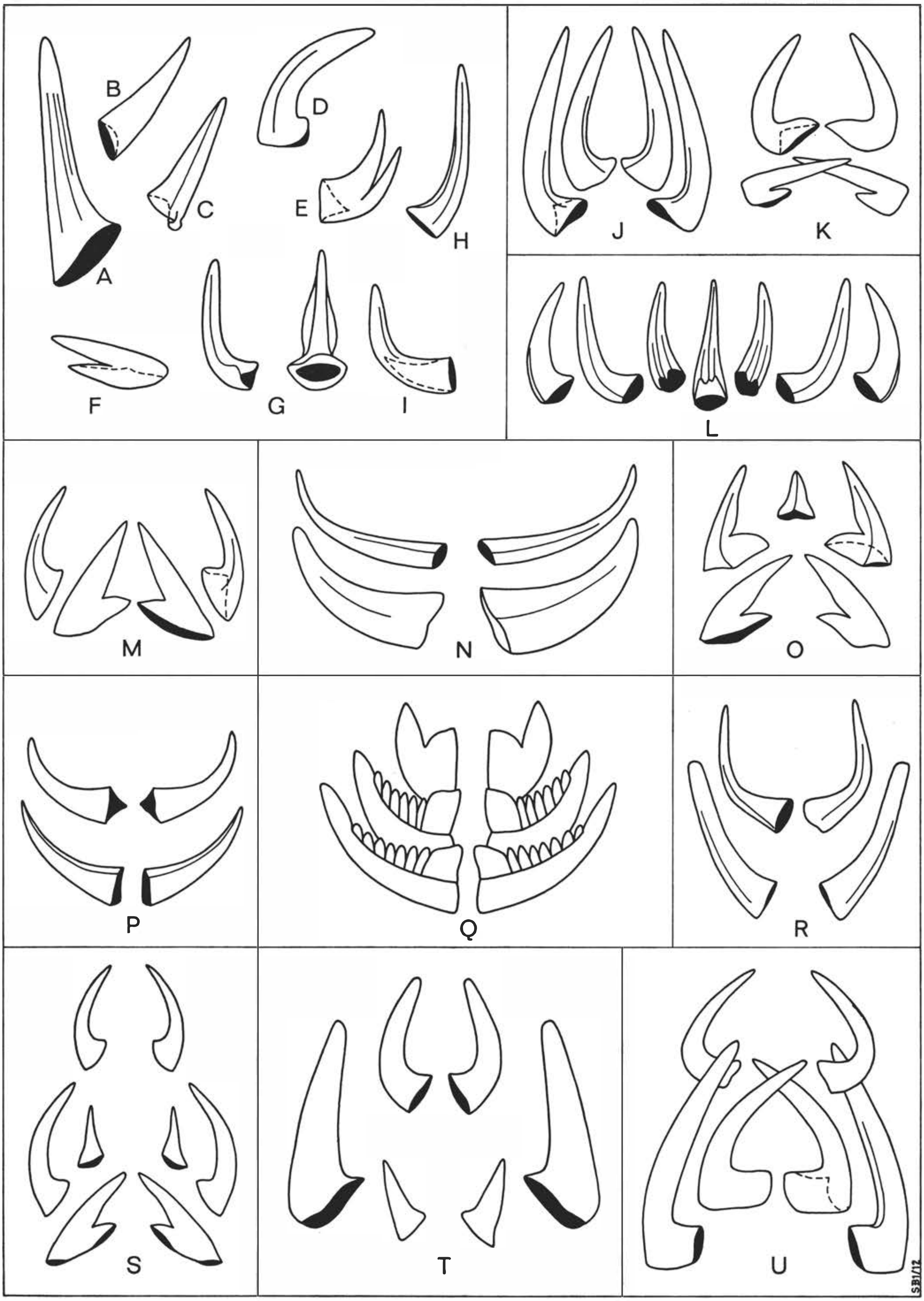
The Multielement Approach

In 1966, we described an empirical approach to the recognition of multielement Ordovician taxa (Bergström & Sweet 1966), and in 1968 Kohut provided a much more elegant and probably sounder means to the same end. Basically, both approaches aim at discriminating groups of regularly associated disjunct elements that may be regarded as components of the skeletal apparatuses of conodont species.

Application of both empirical and quantitative grouping techniques to large collections of disjunct elements from Ordovician rocks of the North American Midcontinent and North Atlantic Provinces has resulted in recognition of numerous groups of essentially constant associates. Individual components of these groups, previously described as form-species, are related to others in size, mode of denticulation, shape and conformation of basal cavity, distribution of white matter, and surface micromorphology. We regard each group as the representative of a fossil species, the acceptable specific name for which is that of its first-named skeletal component. Successions of groups related in major skeletal organization, but differing in minor features, are regarded as genera, but these are much less objective taxa than those on the specific level and we can offer no very useful list of criteria by which genera can be distinguished from species. Somewhat lamely, we suggest that relationship, expressed as similarities in major features in skeletal organization, is the only useful character in recognizing genera.

A major result of multielement analysis of disjunct Ordovician conodont-elements has been the discovery that virtually all groups we regard as species follow one of three major skeletal plans. In one, all skeletal components are simple cones; in another, skeletal elements are basically all ramiform elements (that is, bars and blades), although one or more of the components may secondarily be reduced to a simple cone; and in a third, a ramiform assembly is basic, but a few elements develop into platforms or develop platform-like processes and others may be reduced to simple cones. For convenience, these basic plans may be termed

Fig. 1: Simple-cone apparatuses. A. *Mixoconus;* B. "*Oneotodus*" *ovatus*; C. *Ulrichodina*; D. *Stereoconus*; E. *Strachanognathus*; F. "*Oistodus*" *venustus*; G. "*Acontiodus*" *alveolaris*; H. "*Scolopodus*" *quadraplicatus*; I. *Cornuodus*; J. *Protopanderodus*; K. *Paroistodus*; L. *Acodus oneotensis*, *Paltodus bassleri*, and *Oistodus*? *triangularis*; M. *Paltodus*; N. *Panderodus*; O. *Oistodus*; P. *Coelocerodontus*; Q. *Belodina*; R. "*Distacodus*" *falcatus*; S. *Drepanoistodus*; T. *Scandodus;* U. *Drepanodus.* Figures generalized from either type species or from another species that is better known. ▶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simple-cone, *ramiform-element*, and *ramiform-platform* skeletal apparatuses. There are many variations on these three themes in Ordovician faunas, but we discuss only a few before considering their suprageneric classification.

Simple-Cone Apparatuses

In this group we distinguish two categories. *Monoelemental apparatuses* are characterized not by just one, but by a single type, of conodont-element. These may be paired, but they exhibit no obvious symmetry transitions even though they may vary in minor morphologic details. *Multielemental apparatuses*, which might be described as bi-, tri-, tetra-, or pentaelemental depending on the number of morphologically distinct components, have two to several different elements that commonly (but not invariably) exhibit form transition but would probably be referred to different genera by form-taxonomists.

So far as we know, monoelemental apparatuses were developed by relatively few Ordovician conodonts in either the Midcontinent or North Atlantic Provinces. Indeed, we currently recognize only two genera of this type in North Atlantic Ordovician faunas and just seven in those of the North American Midcontinent. The limited variation among elements of the type species of *Strachanognathus* RHODES, 1955 (Fig. 1, E) was described by BERGSTRÖM (1962), and generalized elements of the type species of *Cornuodus* FÅHRAEUS, 1966 (Fig. 1, I) exhibit few obvious differences from specimen to specimen in North Atlantic Province collections available to us. Monoelemental simple-cone taxa of the Midcontinent Ordovician include "*Scolopodus*" *quadraplicatus* BRANSON & MEHL, 1933 (Fig. 1, H), the several species of *Ulrichodina* FURNISH, 1938 (Fig. 1, C), *Mixoconus* SWEET, 1955 (Fig. 1, A), "*Oistodus*" *venustus* STAUFFER, 1935 (Fig. 1, F), "*Oneotodus*" *ovatus* (STAUFFER 1935) (Fig. 1, B), "*Acontiodus*" *alveolaris* STAUFFER, 1935 (Fig. 1, G), and the species of *Stereoconus* BRANSON & MEHL, 1933 (Fig. 1, D). Of these, only "*Scolopodus*" *quadraplicatus* and "*Oneotodus*" *ovatus* are particularly common or well known, and it is possible that the monoelemental condition of at least some of the others results from inadequate knowledge of their associations. For example, "*Acontiodus*" *alveolaris* is very commonly associated with elements of "*Distacodus*" *falcatus* STAUFFER, 1935 (Fig. 1, R) and might be the trichonodelliform element of that apparatus. However, both are rare and we need to know more than we do about co-occurrence before reaching any conclusion on relationship.

Multielemental simple-cone apparatuses characterize the type species of *Drepanodus* PANDER, 1856 (Fig. 1, U); *Drepanoistodus* LINDSTRÖM, 1971 (Fig. 1, S); *Oistodus* PANDER, 1856 (Fig. 1, O); *Paltodus* PANDER, 1856 (Fig. 1, M); *Paroistodus* LINDSTRÖM, 1971 (Fig. 1, K); *Protopanderodus* LINDSTRÖM, 1971 (Fig. 1, J); *Scandodus* LINDSTRÖM, 1955 (Fig. 1, T); *Scolopodus* PANDER, 1856; and *Walliserodus* SERPAGLI, 1967, all of which are characteristic of Ordovician faunas in the North Atlantic Province. In Midcontinent Ordovician faunas, species of *Acanthodus* FURNISH, 1938, formed skeletal apparatuses that included not only the distinctly serrate drepanodiform elements originally referred to the form-genus, but probably also an array of scandodiform, acodiform, and possibly oistodiform elements, as well. Another genus, which needs a name (Fig. 1, L), includes a succession of similar species in the North American Lower Ordovician, one of which had a skeletal apparatus composed of the elements FURNISH (1938) assigned to the form-species *Acodus oneotensis*, *Oistodus? triangularis*, and *Paltodus bassleri*. *Proconodontus* MILLER, 1969, shows obvious form variation, but we do not understand its apparatus because MILLER (1969) gives no information on sample-by-sample distributions. *Coelocerodontus* ETHINGTON, 1959 (Fig. 1, P) and *Oneotodus* LINDSTRÖM, 1955, show obvious symmetry transitions, as does the suite of variable Middle and Upper Ordovician forms most commonly included in "*Distacodus*" *falcatus* STAUFFER, 1935 (Fig. 1, R). An association of drepanodiform and oistodiform elements distinguishes several common species of *Drepanoistodus* LINDSTRÖM, 1971 (Fig. 1, S) that may be the only ones common to both North Atlantic and North American Midcontinent faunas. Finally, we include as multielemental simple-cones not only *Belodella* ETHINGTON, 1959, but also *Panderodus* ETHINGTON, 1959 (Fig. 1, N), *Plegagnathus* ETHINGTON & FURNISH, 1959, and *Belodina* ETHINGTON, 1959 (Fig. 1, Q). The latter two genera formed elements that are "compound" in traditional terminology, but these elements were obviously built in quite a different way than the ramiform and platform-type elements to which we restrict the term "compound".

Ramiform-Element Apparatuses

North Atlantic and American Midcontinent Ordovician faunas included a large number of species whose skeletal apparatuses were composed of elements with one to several processes. We have noted previously (BERGSTRÖM & SWEET, 1970; SWEET & BERGSTRÖM, 1970) that most of these skeletal apparatuses can be derived readily from that of *Prioniodus elegans* (Fig. 2, G; 4, A), type species of *Prioniodus* PANDER, 1856, which includes prioniodiform, belodiform, falodiform, tetraprioniodiform, and hibbardelliform elements (BERGSTRÖM 1968, 1971; SWEET & BERGSTRÖM 1970). Parenthetically, we should point out that our opinion about the skeletal architecture of *Prioniodus elegans* differs somewhat from that of LINDSTRÖM (1971), but this is probably because our collections include several thousand representatives of *P. elegans*, whereas his included fewer than 200 specimens distributed among many samples.

North Atlantic Ordovician ramiform-element genera whose skeletal organization had a more or less modified prioniodont plan include *Prioniodus* (in which we also place *Baltoniodus* LINDSTRÖM 1971) (Fig. 2, A; 2, G; 4, A); *Microzarkodina* LINDSTRÖM, 1971 (Fig. 2, K); *Paracordylodus* LINDSTRÖM, 1955 (Fig. 2, D); and *Periodon* HADDING, 1913 (Fig. 2, J). The genera *Disparodus* KNÜPFER, 1967, *Dichodella* SERPAGLI, 1967, and *Istorinus* KNÜPFER, 1967, may also belong in this category but are not well enough known to permit conclusions about their skeletal apparatuses.

Prioniodus (s. l.) is varied and abundantly represented in Balto-Scandic Ordovician faunas and five species have also been recognized in the Appalachian Ordovician of eastern North America. Some important species, many of major stratigraphic utility, are described by BERGSTRÖM (1971).

The type species of *Microzarkodina* (Fig. 2, K) has a skeletal apparatus of cordylodiform, trichonodelliform, ozarkodiniform, and oistodiform elements (LINDSTRÖM 1971), which is similar in some ways to that of *Plectodina* STAUFFER, 1935 (BERGSTRÖM & SWEET, 1966; SWEET & BERGSTRÖM 1970; Fig. 4, F–G).

The skeletal apparatus of *Periodon aculeatus* HADDING (Fig. 2, J) has cordylodiform, ligonodiniform, cladognathodiform, hibbardelliform, prioniodiniform, and falodiform components (BERGSTRÖM & SWEET 1966). Homology between elements of this apparatus and those of the *Prioniodus*

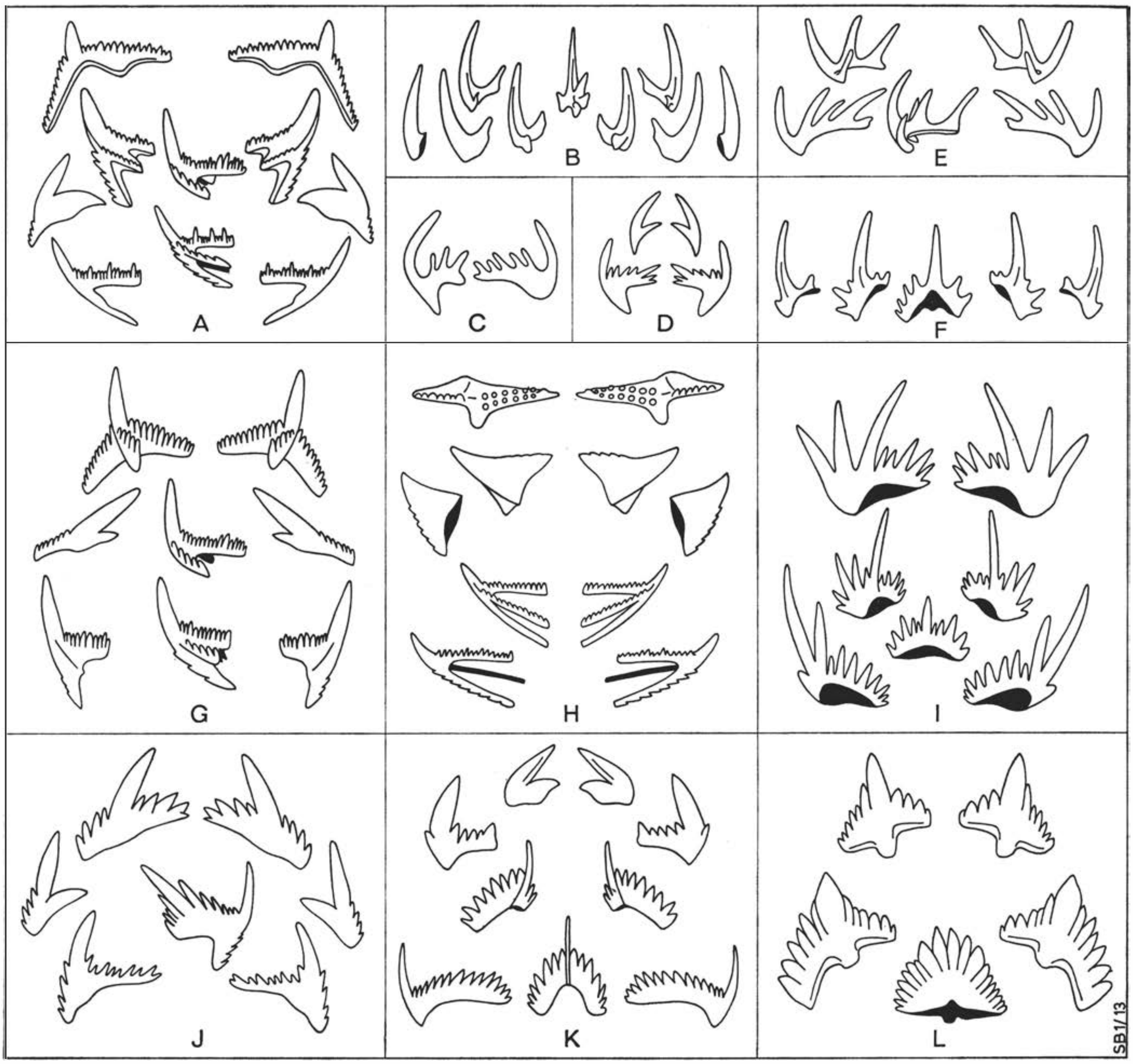


Fig. 2: Ramiform-element apparatuses. A. *Prioniodus variabilis*; B. *Multioistodus compressus*; C. *Cordylodus angulatus* and *C. ramosus*; D. *Paracordylodus*; E. Middle Ordovician "*Cordylodus*"; F. *Microcoelodus* (or *Erismodus*); G. *Prioniodus elegans*; H. *Icriodella superba*; I. *Chirognathus monodactylus*; J. *Periodon aculeatus*; K. *Microzarkodina*; L. *Rhipidognathus*. Magnifications vary; figures generalized from either type species or best-known species.

elegans apparatus has been discussed by Sweet & Bergström (1970). However, the oldest species of *Periodon*, *P. flabellum* (Lindström), may lack falodiform elements (Lindström 1971).

Structure of the skeletal apparatus of *Paracordylodus* Lindström, 1955, is not definitely known, but representatives of the form-species *P. gracilis* Lindström, type of the genus, appear to be consistently associated with those of the somewhat similar form-species, *Oistodus gracilis* Lindström (not Branson & Mehl), and the two may be parts of the same apparatus (Fig. 2, D).

Cordylodus Pander, 1856, with a skeleton that does not follow the prioniodont plan, may be the most primitive genus with a ramiform-element apparatus. Specimens of *C. angulatus* Pander, type of the genus, occur constantly in the lowermost Ordovician of the Baltic Region with closely similar elements described as *C. rotundatus*, and Bergström & Sweet (1966) suggested that these two types of elements represent the same skeletal apparatus (Fig. 2, C). We do not know if there were other types of elements in that apparatus. We should note, however, that elements closely similar to those of *C. angulatus* are known from the Middle Ordovician at widely scattered localities (Bergström 1971; Hadding 1913; Kay 1962; Lindström 1964; Sweet & Bergström 1962), but the skeleton of the species they represent (Fig. 2, E) seems to have been more complex than that of *C. angulatus* in that it also included elements of a transition series (Lindström 1964). Relations between Lower and Middle Ordovician species of *Cordylodus* are made even more obscure by the fact that typical representatives of the genus have not as yet been found in the interval between lowermost Lower and Middle Ordovician.

Species with ramiform-element apparatuses built on the prioniodont plan dominate Middle and Upper Ordovician faunas in the American Midcontinent. In "fibrous" genera such as *Multioistodus* CULLISON, 1938 (Fig. 2, B), *Erismodus* BRANSON & MEHL, 1933 (Fig. 2, F), *Curtognathus* BRANSON & MEHL, 1933, *Chirognathus* BRANSON & MEHL, 1933 (Fig. 2, I), and *Leptochirognathus* BRANSON & MEHL, 1943; in the non-fibrous, but closely related *Rhipidognathus* BRANSON, MEHL & BRANSON, 1951 (Fig. 2, L); and in *Histiodella* HARRIS, 1962, the prioniodont apparatus is simplified, although some (but not all) species had prioniodiform elements or their functional equivalents. In *Plectodina* STAUFFER, 1935 (Fig. 4, F–G), *Phragmodus* BRANSON & MEHL, 1933 (Fig. 4, B–E), and *Oulodus* BRANSON & MEHL, 1933 (Fig. 4, J–K), however, most or all of the prioniodont components are recognizable, although they may be much modified in the youngest species of all these genera.

Ramiform-Platform Apparatuses

Species with skeletons characterized by a combination of ramiform and platform-like elements were not common components of Ordovician faunas in either the North American Midcontinent or North Atlantic Provinces. In both, however, they are represented in some abundance at certain levels in the Middle Ordovician and in the North Atlantic Province they are rather varied and of considerable stratigraphic significance at those levels.

Middle and Upper Ordovician ramiform-platform genera of the North Atlantic Province are discussed in detail in another paper by one of us (BERGSTRÖM, in preparation), hence it is sufficient here to note that the more important ones are *Amorphognathus* BRANSON & MEHL, 1933, *Eoplacognathus* HAMAR, 1966, *Icriodella* RHODES, 1953, and *Pygodus* LAMONT & LINDSTRÖM, 1957. We know too little as yet about *Nericodus* LINDSTRÖM, 1955, *Priomorphognathus* KNÜPFER, 1967, *Sagittodontina* KNÜPFER, or *Serratognathus* LEE, 1970, to include them in this discussion.

The apparatus of *Amorphognathus ordovicicus* BRANSON & MEHL, 1933, can readily be homologized with that of *Prioniodus elegans* (SWEET & BERGSTRÖM 1970; BERGSTRÖM 1971) and there is little doubt that the genus was derived from prioniodont ancestors in the Early Ordovician (BERGSTRÖM & SWEET, 1970). Lower Ordovician species are still almost unknown, but in Middle and Upper Ordovician rocks a succession of distinct species is distinguished primarily by differences in the amorphognathiform and holodontiform elements (BERGSTRÖM 1971; SWEET & BERGSTRÖM 1971).

Eoplacognathus lindstroemi (HAMAR 1964) has a skeletal apparatus that apparently included only asymmetrical polyplacognathiform and ambalodiform elements (BERGSTRÖM 1971). The apparatus may thus be regarded as a reduced prioniodont one and is similar to that of *Polyplacognathus* STAUFFER, 1935.

The skeletal apparatus of *Icriodella superba* RHODES, 1953 (Fig. 2, H) is also of slightly modified prioniodont type and consists of a transition series (formerly included in the form-genera *Roundya* and *Rhynchognathodus*) and prioniodiform elements (assigned previously to form-genera *Icriodella* and *Sagittodontus*). A much more modified, or reduced, apparatus characterizes *Rhodesognathus* BERGSTRÖM & SWEET, 1966, whose skeleton was composed solely of prioniodiform elements with ledge-like lateral extensions on some of their processes.

Pygodus LAMONT & LINDSTRÖM, 1957, is quite useful stratigraphically and apparently also had a modified prioniodont apparatus. Middle Ordovician species of *Pygodus* developed an apparatus consisting of pygodiform and haddingodiform (or ambalodiform) elements and possibly hibbardelliform and tetraprioniodiform elements of a form-transition series (BERGSTRÖM 1971). There is evidence that indicates that at least the pygodiform elements of primitive *Pygodus* species developed by gradual reduction from a complexly branched platform-type element in the late Lower and early Middle Ordovician.

Ramiform-platform apparatuses were developed in Midcontinent Ordovician faunas only by *Polyplacognathus* STAUFFER, 1935, and *Scyphiodus* STAUFFER, 1935. Only one long-ranging species of the former, *P. ramosus*, is known from interior parts of the Midcontinent Province, but several others developed in adjacent areas dominated by species of the North Atlantic Province (BERGSTRÖM 1971). In *Polyplacognathus*, the skeletal apparatus was reduced to platform-like ambalodiform and amorphognathiform elements (WEBERS 1966; BERGSTRÖM & SWEET 1966) in a fashion comparable to that exhibited by *Eoplacognathus* in North Atlantic Province faunas. Typical elements of *Scyphiodus*, on the other hand, are like those of the form-genus *Icriodella*, of the North Atlantic Province (WEBERS 1966), but in samples containing representatives of *Scyphiodus* we have been unable to identify homologues of the non-platform sagittodontiform and rhynchognathodiform components of multielement *Icriodella*. Thus the skeletal apparatus of *Scyphiodus*, like that of *Polyplacognathus* and *Rhodesognathus*, may be a fundamentally prioniodont assembly reduced to one of its prioniodiform components.

Evolution and Suprageneric Classification

In the heyday of form-taxonomy, most students of conodonts wisely avoided speculation about suprageneric categories, for, although several schemes involving such categories were proposed (BASSLER 1925; BRANSON & MEHL 1944; HASS 1962), it seems to have been tacitly understood that, if genera were admittedly artificial, suprageneric groupings would be even more so. However, as SWEET & BERGSTRÖM (1970) and LINDSTRÖM (1970) have noted, development of multielement taxonomy, which seems to be more natural, opens the door to consideration of the broader relationships that can be expressed on the suprageneric level. Indeed, LINDSTRÖM (1970) has already provided a useful preliminary survey of conodonts at the suprageneric level, and that survey is the point of departure for the following remarks about Ordovician forms and their derivatives.

Before considering suprageneric classification of Ordovician conodonts, we attempted to delineate and understand the range of variation of morphologically intergradational sequences of multielement species. Gradually, these have been grouped into genera and related to other elements of the provincial faunas they represent. We have also paid considerable attention to stratigraphic range, although many critical intervals are as yet unsampled or have produced collections too small to aid our analysis. Although we have studied most forms known to us from Ordovician faunas, we confess a limited knowledge of the simple-cone genera and of those with skeletal elements of the type termed "fibrous", or "hyaline". Simple-cones are undoubtedly of basic importance, but many European and nearly all North

American species are as yet too poorly known to be considered productively on the suprageneric level. As for the "fibrous" genera, we note only that a majority of them developed ramiform-element skeletal apparatuses and are probably related closely to contemporaneous non-fibrous forms. We suspect that "fibrous" structure, which is not confined to Ordovician conodonts, and the apparently reduced apparatuses of "fibrous" species are expressions in many cases of adaption to shallow-water, possibly even hypersaline, environments. Thus "fibrous" species may well be classified eventually with the non-fibrous forms to which many appear most closely related. However, we have no definite information on these matters and prefer not to speculate further about them. In short, we confine our remarks here to a consideration of the development of Ordovician and related non-fibrous genera with ramiform-element and ramiform-platform apparatuses. These remarks, we believe, will be sufficient to indicate that all major stocks of conodonts have their roots in Ordovician faunas.

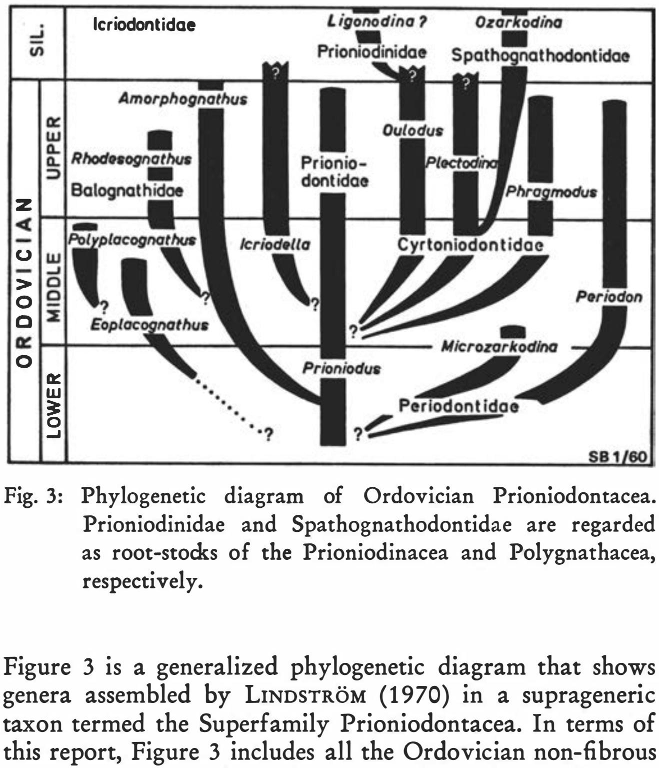


Fig. 3: Phylogenetic diagram of Ordovician Prioniodontacea. Prioniodinidae and Spathognathodontidae are regarded as root-stocks of the Prioniodinacea and Polygnathacea, respectively.

Figure 3 is a generalized phylogenetic diagram that shows genera assembled by Lindström (1970) in a suprageneric taxon termed the Superfamily Prioniodontacea. In terms of this report, Figure 3 includes all the Ordovician non-fibrous genera with ramiform-element and ramiform-platform skeletal apparatuses except *Cordylodus* Pander, and *Paracordylodus* Lindström. Development and taxonomy of the ramiform-platform complex, which includes *Amorphognathus, Eoplacognathus, Rhodesognathus,* and *Polyplacognathus* (the Balognathidae of Figure 3), will be discussed by Bergström (in preparation). Consequently, we limit ourselves here to discussion of the relationships and possible derivatives of the ramiform-element genera assembled on the right side of Figure 3.

The oldest assembly of elements exhibiting the skeletal plan of the Prioniodontacea includes *Acodus deltatus* Lindström, 1955, and probably some other forms, all of which are simple cones in traditional parlance. These elements are probably the skeletal components of an unnamed genus, but this needs further study and taxonomy is somewhat confused. That is, Lindström (1970, 1971) includes *Acodus deltatus* as part of the apparatus of *Gothodus costulatus*. However, the type of the latter, which is also type of *Gothodus*, comes from beds with *Prioniodus elegans*, is indistinguishable from the belodiform element of *P. elegans*, and is not found with *Acodus deltatus* through the entire range of the latter. Indeed, *A. deltatus* appears without *G. costulatus* in beds that are older than ones that yield either the first *P. elegans* or the type of *G. costulatus*. Thus we regard *G. costulatus* as a junior synonym of the form-species *Belodus gracilis* Pander, and *Gothodus* as a junior synonym of multielement *Prioniodus* Pander.

Prioniodus elegans (Fig. 2, G; 4, A) appears first in beds just above the ones with the oldest *Acodus deltatus* and the latter may well be ancestral to the former. It is presently difficult to assess Lindström's (1970) assertion that two lineages – *Prioniodus* and *Baltoniodus* – were involved in this initial prioniodont radiation, for we do not agree that *Gothodus*, which Lindström regards as ancestral to *Baltoniodus*, is distinct from *Prioniodus elegans*. For the time being, then, we include both in the same genus, *Prioniodus* (which forms the central trunk of Figure 3), although it is useful to segregate species of this complex with two types of prioniodiform elements as a subgenus, *Baltoniodus*.

Prioniodus elegans has a short range in the lower Arenig, but is followed in younger North Atlantic faunas by a long succession of rapidly evolving species, all with two types of prioniodiform elements (Fig. 2, A) and referable, therefore, to the subgenus *Baltoniodus*. Lower and Middle Ordovician species of *Prioniodus* are especially well known (Bergström 1971), but younger forms exist and apparently survived until at least the end of the Ordovician.

Periodon and *Microzarkodina* (Figs. 2, J; 2, K), whose skeletal apparatuses are also built on prioniodont lines, appear in Balto-Scandic Ordovician faunas at about the same time (Lindström 1971) and only a little later than the first *Prioniodus*. Skeletal apparatuses of these two genera differ most prominently from that of *Prioniodus elegans* in lacking quadraxial prioniodiform elements – they have ozarkodiniform or prioniodiniform elements in this position, instead. The earliest *Periodon* lacks falodiform elements. However, once these are added, the genus maintains its distinctness, with little more than minor modifications in individual elements, into the Upper Ordovician. *Microzarkodina* is not known above the Llanvirn (Lindström 1971), but the skeleton of its youngest species does not differ appreciably from that of its oldest. In other words, skeletal patterns, set very early in the stocks represented by *Periodon* and *Microzarkodina*, were retained with only minor variation to extinction of these stocks. Although *Periodon* and *Microzarkodina* seem closely related structurally, the differences that separate them from one another or from contemporary species of *Prioniodus*, their presumed ancestor, are not predicted in *Prioniodus elegans*. Thus we cannot point with assurance to an origin for these two genera in *Prioniodus*, although it seems logical on structural grounds. To our knowledge, neither *Microzarkodina* nor *Periodon* exhibits trends that lead logically to species of other prioniodont genera with ramiform-element apparatuses. Most, if not all, of those genera appear to have developed in faunas of North American Midcontinent type, not in North Atlantic faunas. Thus we assign *Microzarkodina* and *Periodon* to a family of their own, the Periodontidae of Lindström (1970).

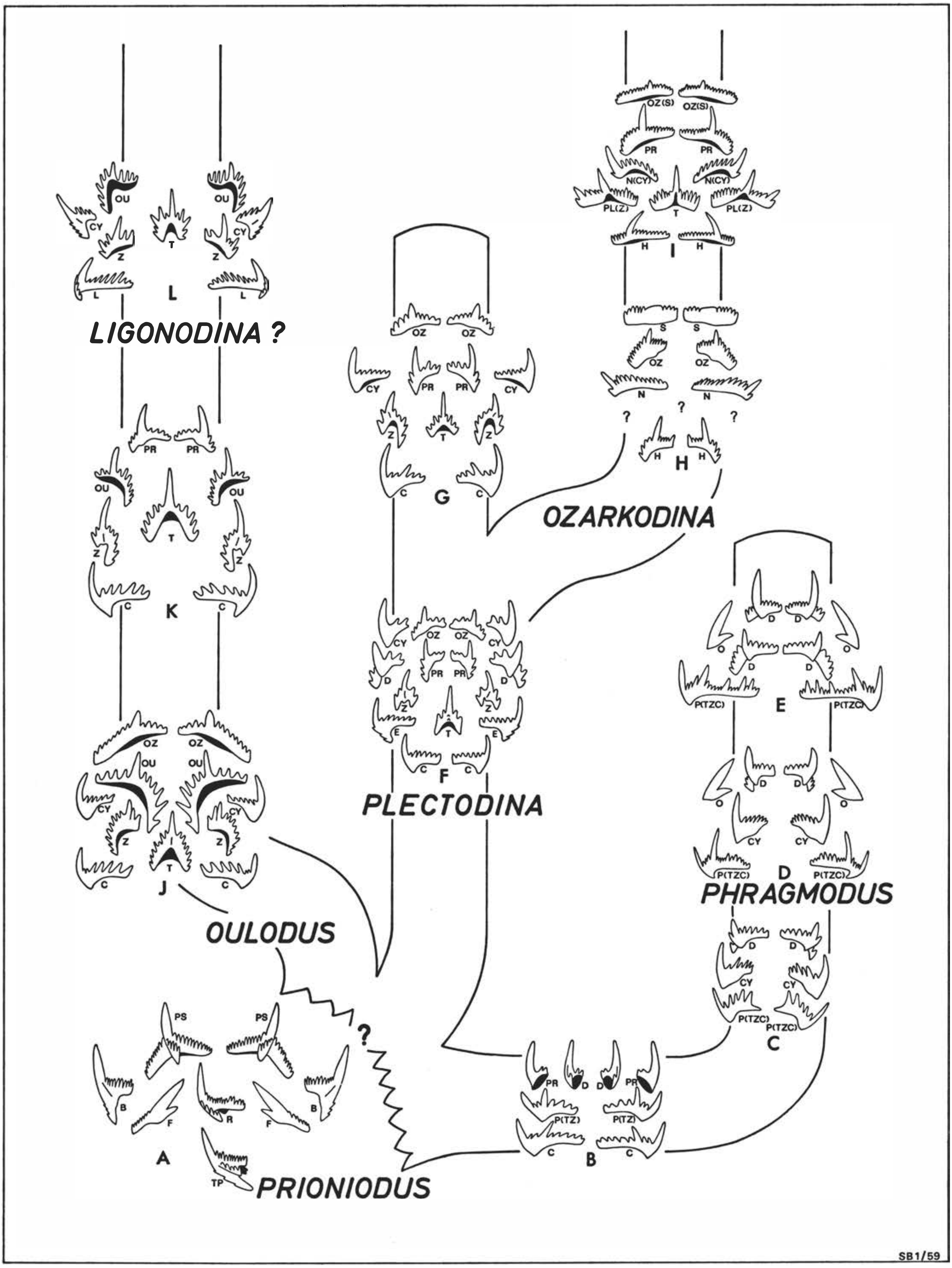
Phragmodus, characteristic of the North American Midcontinent, mimics *Periodon* in some features and is represented by a succession of four distinct species in Middle and Upper Ordovician rocks. The oldest species (Fig. 4, B), which is named and described by Sweet in a report now in preparation, is distinguished by prominently sinuous phragmodiform elements, a skeletal apparatus that included cyrtoniodiform elements, and a central form-transition series divided between phragmodiform and cordylodiform elements. In somewhat younger *P. inflexus* (Stauffer) (Fig. 4, C), which may be a junior synonym of *P. primus* (Branson & Mehl), the form-transition series is composed entirely of slightly sinuous phragmodiform elements; prioniodiform (or dichognathiform) elements bear a single denticle on the anterior process; and the falodiform position in the otherwise prioniodont apparatus is occupied by a distinctive cyrtoniodiform structure. *P. cognitus* Stauffer (Fig. 4, D), which succeeds *P. inflexus* stratigraphically, is morphologically intermediate between *P. inflexus* and *P. undatus*. That is, elements of *P. cognitus* differ in only minor ways from those of older and younger species; however, its dichognathiform element is distinctly unlike that of *P. inflexus*, and a cyrtoniodiform structure occupies the position of the oistodiform element of *P. undatus*. In younger parts of its range, *P. cognitus* grades into *P. undatus*. That is, a few of its cyrtoniodiform elements lose posterior denticles and are thus oistodiform in plan. Some of these oistodiform elements were referred by Webers (1966) to the form-species *Oistodus pseudoabundans* Schopf. *Phragmodus undatus* Branson & Mehl (Fig. 4, E) is the youngest *Phragmodus* and the best-known multielement conodont species. Its skeletal apparatus included a central form-transition series of phragmodiform form-variants; a variable assembly of prioniodiform (or dichognathiform) elements; and an oistodiform element that can now be shown to be a reduced cyrtoniodiform structure occupying the falodiform position of a typical prioniodont apparatus.

Plectodina is in many ways closely related to *Phragmodus*. However, the central form-transition series of its skeletal apparatus is more elaborately differentiated and includes elements previously assigned to the form-genera *Trichonodella, Zygognathus, Eoligonodina, Cordylodus, Subcordylodus,* and *Plectodina*. In *P. aculeata* (Stauffer) (Fig. 4, F), the type and oldest known species, a dichognathiform element with short processes, a similar prioniodiniform element, and a sinuous ozarkodiniform element occupy prioniodiform position in the apparatus, and a cyrtoniodiform element is in the falodiform position. Study of sequential collections indicates that in apparatuses of younger species, such as the well-known *P. furcata* (Hinde) (Fig. 4, G), the dichognathiform element is transformed gradually into a second prioniodiniform structure, but other elements remain little changed in major features.

Representatives of *Phragmodus* and *Plectodina* commonly occur together in Middle and Upper Ordovician rocks of the North American Midcontinent. *Phragmodus* appeared somewhat before *Plectodina*, but, despite study of hundreds of large collections and obvious similarities in the skeletal architecture and geographic distribution of these two genera, we have been unable to trace either into the other, nor have we identified a directly ancestral group for either genus. Lindström (1970), emphasizing obvious similarities, referred both *Phragmodus* and *Plectodina* to the Periodontidae, in which he also included *Periodon* and *Microzarkodina*. Thus he apparently viewed these genera as a single interrelated stock, with common ancestry in *Prioniodus*. This may have been the case. However, we note that *Microzarkodina* and *Periodon*, and *Phragmodus* and *Plectodina*, developed at different times in faunas of different provinces. Furthermore, only slightly modified prioniodiform elements are present in the apparatuses of the oldest species of *Phragmodus* and *Plectodina*, and this suggests to us that both are closer in this respect to *Prioniodus* than they are to *Microzarkodina* or *Periodon*, the oldest species of which have ozarkodiniform or prioniodiniform elements in the prioniodiform position. Thus we suggest that both the obvious relationship between *Phragmodus* and *Plectodina* and the obvious differences between these genera and *Periodon-Microzarkodina* would be best expressed by referring the former to a separate family, the oldest name for which, unfortunately, is Cyrtoniodontidae Hass, 1962 (ex Cyrtoniodontinae Hass, 1962).

Published information about the skeletal architecture of *Oulodus* Branson & Mehl is incomplete. Study of new collections and reassessment of old ones, however, indicates that the apparatus of *Oulodus oregonia* (Branson, Mehl & Branson) includes the array of elements illustrated in Figure 4, K, and the apparatus of older species was apparently similar (Fig. 4, J). Insofar as the central form-transition series is concerned, the skeletal apparatus of *Oulodus* is closely similar except in mode of denticulation to that of *Plectodina*, which appears somewhat earlier than *Oulodus* and is a likely ancestor. None of the *Oulodus* apparatuses known to us, however, contains dichognathiform elements, and, at least in younger species, like *O. oregonia*, cyrtoniodiform elements have not been positively identified. More important, probably, is the fact that the *Oulodus* apparatus apparently included only one type of ozarkodiniform or prioniodiniform element, rather than the two types characteristic of the *Plectodina* apparatus. We interpret the distinctive oulodiform and prioniodiniform (or ozarkodiniform) elements of multielement *Oulodus* as modified prioniodiform structures, and we suspect (but do not know) that *Oulodus* developed from *Plectodina* through reduction in complexity of the more elaborate *Plectodina* apparatus. In any event, differentiation of *Oulodus* and *Plectodina* in the early Middle Ordovician of the American Midcontinent was an event of major significance, for we believe these genera originated the two important groups that Lindström (1970) identifies as the superfamilies Polygnathacea and Prioniodinacea. If so, *Oulodus* and *Plectodina* initiated the stocks from which virtually all major conodont lineages diverged in Ordovician and later times.

Fig. 4: Phylogenetic diagram of Cyrtoniodontidae. A. *Prioniodus elegans* Pander (not included in Cyrtoniodontidae; apparatus shown only for comparison); B. *Phragmodus* n. sp. Sweet; C. *Phragmodus inflexus* (Stauffer); D. *Phragmodus cognitus* Stauffer; E. *Phragmodus undatus* Branson & Mehl; F. *Plectodina aculeata* (Stauffer); G. *Plectodina furcata* (Hinde); H. *Ozarkodina* n. sp. Bergström (apparatus includes plectospathodiform and trichonodelliform elements, but none available is complete enough for illustration); I. *Ozarkodina excavata* (Branson & Mehl); J. *Oulodus serratus* (Stauffer); K. *Oulodus oregonia oregonia* (Branson, Mehl & Branson); L. *Ligonodina? elegans* Walliser. Comparable elements shown in same positions in apparatus arrays and identified by small letters, the meaning of which is as follows: B = belodiform; C = cordylodiform; CY = cyrtoniodiform; D = dichognathiform; E = eoligonodiniform; F = falodiform; H = hindeodelliform; L = ligonodiniform; N = neoprioniodiform; O = oistodiform; OU = oulodiform; OZ = ozarkodiniform; P = phragmodiform; PL = plectospathodiform; PR = prioniodiniform; PS = prionioidiform; R = roundyiform; S = spathognathodiform; T = trichonodelliform; TP = tetraprioniodiform; Z = zygognathiform. Apparatus H lacks element designations and the plectospathodiform and trichonodelliform components because it is known from limited, undescribed material not yet thoroughly studied. ▶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To substantiate our claims to heritage for *Oulodus* and *Plectodina*, we call attention to Figures 4, K–L and 4, G–I. In Figures 4, K and 4, L, we compare elements of the skeletal apparatuses of *Oulodus oregonia* with those of the Silurian species Jeppsson (1969) identifies as *Ligonodina elegans* Walliser, 1964. Neither we nor Jeppsson know, of course, if the apparatus of the latter is indeed that of *Ligonodina* (which has much younger types), but the two element assemblies illustrated in Figures 4, K and 4, L are clearly of the sort Lindström (1970) regards as characteristic of the Prioniodinacea and they are so similar to one another that we question separation on the generic level. However such problems may ultimately be solved, we assert that the similarities illustrated in Figures 4, K and 4, L are compelling evidence for origin of the Prioniodinacea in *Oulodus*, which probably evolved in the Middle Ordovician from *Plectodina*, but could have had an independent origin in some as yet unknown species of *Prioniodus*.

In Figures 4, G–4, I, we call attention to close similarity between the skeletal apparatus of *Plectodina furcata* (Hinde) and that of Ordovician and Silurian species of the sort assigned to *Hindeodella* by Jeppsson (1969) or *Ozarkodina* by Lindström (1970). Especially significant in the apparatus of both genera is the occurrence of two types of blades, derived by way of early *Plectodina* species from prioniodiform elements of the basic prioniodont apparatus. In *Plectodina* these are ozarkodiniform and prioniodiniform elements, whereas in *Ozarkodina* they are ozarkodiniform and spathognathodiform elements. We attach little significance to this largely semantic difference or to the fact that a rather distinctive "hindeodelloid" denticulation comes to distinguish at least some of the elements in many (but not all) of the derivatives of *Plectodina*. What seems most important at this stage is not just the identification of a likely ancestral stock *(Plectodina)* for the Polygnathacea in Middle Ordovician Prioniodontacea, but recognition of the fact that *Ozarkodina* itself was also present (and represented by several species) well before the end of the Ordovician.

Our survey of Ordovician prioniodont genera would be incomplete without mention of multielement *Icriodella* Rhodes (Fig. 2, H), which has a complete prioniodont skeletal apparatus (Bergström & Sweet 1966; Webers 1966; Sweet & Bergström 1970), but no known ancestors in *Prioniodus* or other genera of the Prioniodontacea. Although commonly regarded as a member of the North Atlantic Ordovician fauna, the oldest representative of the genus we have seen is a specimen from the the early Middle Ordovician Fort Peña Formation of Texas sent to us for study by Dr. Lael Bradshaw. Connections between Ordovician *Icriodella*, Silurian *Icriodina*, and Devonian *Icriodus* and *Pelekysgnathus* postulated by Lindström (1970) seem assured on structural grounds, but stratigraphic gaps punctuate the lineage. We agree, however, that all these genera are logically united in a single family (Icriodontidae Müller & Müller, 1957) and the best place for it seems to be in the Prioniodontacea, where Lindström (1970) put it.

On an earlier page of this report, we listed reasons for a tentative conclusion that *Scyphiodus* Stauffer, 1935, might have had a reduced skeletal apparatus composed only of icriodelliform elements, but the relationship between *Icriodella* and *Scyphiodus* implied by such comparative statements cannot be substantiated at this time. In addition, there are minor but significant differences between typical *Scyphiodus* elements and the icriodelliform components of *Icriodella* and the two genera were apparently members of different provincial faunas. In brief, we have no evidence that *Scyphiodus* and *Icriodella* are very closely related – it is just as likely, or perhaps more likely, that *Scyphiodus* developed from *Plectodina* rather than from *Icriodella*, and represents perhaps the first of several times that platform development in the Polygnathacea was accompanied by reduction in the ramiform apparatus.

Our remarks about relationships among prioniodont genera and families have been based on the assumption that comparative anatomy of multielement skeletal apparatuses is the best means of establishing relationships between ramiform-element apparatuses of prioniodont type. While we believe this approach has been successful in tracing evolutionary development within genera, it has not helped very much to establish connections between genera or between the several suprageneric groups of the Prioniodontacea just discussed. That is, although it has been definitely established that the skeletal plan of *Prioniodus* is recognizable with only a little imagination in all the genera assembled in the Prioniodontacea, we are as yet unable to document objectively the origin of a single prioniodont genus with a ramiform-element apparatus in *Prioniodus*. To be sure, differences that separate the various prioniodont genera may have arisen rapidly through allopatric speciation in geographically limited areas marginal to the realms of various species of *Prioniodus* or other prioniodont genera. On the other hand, the current lack of established connections between prioniodont genera may suggest that, despite strong skeletal similarities, the Prioniodontacea is an unnatural group within which direct genetic connections never existed. That is, we cannot at present rule out the possibility that, as was probably the case with *Prioniodus*, each of the ramiform-element genera now assembled in the Prioniodontacea had an independent origin in genera or species with simple-cone apparatuses, a number of which exhibit the same array of forms that characterize ramiform-element prioniodont apparatuses. In short, the prioniodont plan may turn out to be merely a map of the way in which all but a few conodont skeletons were organized and we may be deceiving ourselves at this point by conferring genetic respectability on a group of diverse origins just because their skeletal apparatuses achieved the same (or a similar) stage of development in the Ordovician. Although we suspect that the Prioniodontacea, as we have discussed it, will turn out to be a viable natural taxon, we suggest that judgment on this matter be reserved until we know much more than we now do about the youngest Lower and the oldest Middle Ordovician conodonts, especially about those species that formed simple-cone apparatuses.

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Appendix
Status of Ordovician Conodont Genera

(In the following notes, T = type and TS = "type species"; unless otherwise noted, TS was established at same time and by same author as genus).

Acanthodus Furnish, 1938 *(A. uncinatus).* TS apparatus unknown; included only simple cones.

Acodus Pander, 1856 *(A. erectus).* TS identified but not redescribed from Estonian collections (Viira 1966, 1970). One range chart (Viira 1966) indicates the only other form-species with same range and not known to be part of another apparatus is *Acontiodus latus* Pander, TS of *Acontiodus*; apparatus of neither species known.

Acontiodus Pander, 1856 *(A. latus).* TS recently identified by Viira (1966, 1970) in lowermost Ordovician of Estonia; affinities unclear (see *Acodus*).

Ambalodus Branson & Mehl, 1933 *(A. triangularis).* TS is ambalodiform element of *A. ordovicicus*, TS of *Amorphognathus* (Bergström & Sweet 1966); synonym of that genus.

Amorphognathus Branson & Mehl, 1933 *(A. ordovicius).* TS is amorphognathiform element of *A. ordovicicus* (see *Ambalodus).*

Aphelognathus Branson, Mehl & Branson, 1951 *(A. grandis).* TS type is a blade like those of *Oulodus* or *Plectodina* apparatuses: other elements of apparatus unknown; may be like those of multielement *Oulodus.*

Archaeognathus Cullison, 1938 (*A. primus*). Affinities obscure; probably not conodont; similar specimen with prominent basal structure described by Mosher & Bodenstein (1969).

Balognathus Rhodes, 1953 *(B. expansus).* TS type a fragmentary amorphognathiform element of *Amorphognathus superbus* (Rhodes); synonym of *Amorphognathus.*

Baltoniodus Lindström, 1971 (*Prioniodus navis* Lindström, 1955). TS type a prioniodiform element of *Prioniodus*-type apparatus; regarded here as subgenus of *Prioniodus;* synonym of *Prioniodus* in Bergström (1971).

Barbarodina Stauffer, 1935 *(B. typicala).* T of TS a cordylodiform element; part of multielement *Oulodus* apparatus; jr. synonym of *Oulodus.*

Belodella Ethington, 1959 (*Belodus devonicus* Stauffer, 1940). Ordovician species combine belodelliform elements with a form-transition series (Serpagli 1967); relation to Silurian and Devonian species unclear.

Belodus Pander, 1856 *(B. gracilis).* Ts of TS belodiform elements of multielement *P. elegans* Pander, TS of *Prioniodus* (Bergström 1968); synonym of *Prioniodus.*

Bryantodina Stauffer, 1935 *(B. typicalis).* Ts of TS part of apparatus with hibbardelliform, phragmodiform and prioniodiniform elements (Webers 1966); this has not been confirmed.

Cardiodella Branson & Mehl, 1955 (*Cardiodus tumidus* Branson & Mehl, 1933). Probably part of apparatus with *Curtognathus* and *Trucherognathus,* but not confirmed; if so, jr. synonym of one of those genera.

Cardiodus Branson & Mehl, 1933 (see *Cardiodella*).

Chirognathus Branson & Mehl, 1933 *(C. duodactyla).* TS has multielement ramiformelement apparatus including several *Chirognathus* species of Branson & Mehl (1933); synonymies not worked out.

Chosonodina Müller, 1965 *(C. herfurthi).* TS apparatus unknown.

Clavohamulus Furnish, 1938 *(C. densus).* TS apparatus unknown.

Coelocerodontus Ethington, 1959 *(C. trigonius).* T of TS a trigonid element; accompanying tetragonid probably part of same apparatus (Webers 1966).

Coleodus Branson & Mehl, 1933 *(C. simplex).* TS cotypes incomplete; apparatus unknown.

Cordylodus Pander, 1856 *(C. angulatus).* TS apparatus included two cordylodiform elements, *C. angulatus* and *C. rotundatus* of Pander (1856).

Cornuodus Fåhraeus, 1966 *(C. erectus).* T of TS a simple, generalized, distinctive element; may be only type present in apparatus.

Cornuramia Smith, 1907 *(C. monodonta).* Unrecognizable; name should be used only for type material.

Curtognathus Branson & Mehl, 1933 *(C. typus).* Ts of TS may be part of apparatus with cardiodelliform and trucherognathiform elements; apparatus not known.

Cyrtoniodus Stauffer, 1935 *(C. complicatus).* Ts of TS posteriorly denticulate oistodiform elements, probably of *Phragmodus* but possibly of *Plectodina.*

Dichognathus Branson & Mehl, 1933 *(D. typicus).* Ts of TS prioniodiform elements of *Phragmodus undatus* Branson & Mehl; genus a synonym of *Phragmodus.*

Dirhadicodus Harris, 1964 (*Multioistodus lateralis* Cullison, 1938). Jr. synonym of *Multioistodus* Cullison, 1938; TS is element of *M. subdentatus* Cullison.

Disparodus Knüpfer, 1967 *(D. simplex).* T of TS fragmentary; affinity uncertain.

Distacodus Hinde, 1879 *(Machairodus incurvus* Pander, 1856). Illustrated T of TS suggests drepanodiform element of bielemental apparatus like *Drepanoistodus;* TS not identified in Baltic area since 1856; affinities uncertain.

Drepanodus Pander, 1856 *(D. arcuatus).* TS apparatus of drepanodiform and oistodiform elements (Lindström 1971).

Drepanoistodus Lindström, 1971 (*Oistodus forceps* Lindström, 1955). TS apparatus of drepanodiform and oistodiform elements (Lindström 1971).

Eobelodina Sweet and others, 1959 (*Oistodus fornicalus* Stauffer, 1935). Ts of TS part of apparatus of *Belodina compressa* (Branson & Mehl); jr. synonym of *Belodina.*

Eofalodus Harris, 1962 *(E. brevis).* TS apparently denticulate oistodiform (or falodiform) element of otherwise unknown (?bielemental) apparatus; genus probably distinct, especially after Lindström's (1971) revision of *Oistodus.*

Eoligonodina Branson, Mehl & Branson, 1951 *(E. robusta).* TS laterally denticulate cordylodiform element of *Plectodina* apparatus (Kohut & Sweet 1968); genus jr. synonym of *Plectodina.*

Eoneoprioniodus Mound, 1965 *(E. cryptodens).* TS affinities unknown.

Eoplacognathus Hamar, 1966 (*Ambalodus lindstroemi* Hamar, 1964). Ts of TS ambalodiform elements of *E. lindstroemi* (Hamar 1964) (Bergström 1971).

Erismodus Branson & Mehl, 1933 *(E. typus).* TS part of form-transition series of compound fibrous elements (Andrews 1967); described apparatus may not be complete.

Evencodus Moskalenko, 1970 *(E. sibiricus).* Fibrous simple cones; apparatus unknown; TS resembles simple form-species of *Erismodus*; other species may be fish tubercles.

Falodus Lindström, 1955 (*Oistodus prodentatus* Graves & Ellison, 1941). T of TS is falodiform element of multielement *Periodon aculeatus*, TS of *Peridon*; jr. synonym of *Periodon* (Bergström & Sweet 1966).

Fryxellodontus Miller, 1969 *(F. inornatus).* TS apparatus a transition series with 4 types of simple elements, one denticulated (Miller 1969).

Goniodontus Ethington, 1959 *(G. superbus).* T of TS a holodontiform element of *A. ordovicicus* Branson & Mehl, TS of *Amorphognathus* (Bergström 1971); synonym of *A.*

Gothodus Lindström, 1955 *(G. costulatus).* Restudy of TS type confirms opinion (Bergström 1968) that TS is conspecific with *Belodus gracilis*, a part of multielement *P. elegans*, TS of *Prioniodus* Pander. *Gothodus* thus jr. synonym of *Prioni-*

odus. Lindström (1971) regards *G. costulatus* as part of apparatus including, among others, "*Acodus*" *deltatus* Lindström, 1955, but type collections and ours from strata coeval with those that produced "*A.*" *deltatus* holotype lack *G. costulatus*.

Gyrognathus Stauffer, 1935 (*G. primus*). Ts of TS oulodiform elements; jr. synonym of *Oulodus* Branson & Mehl, 1933 (Bergström & Sweet 1966).

Haddingodus Sweet & Bergström, 1962 (*Arabellites serra* Hadding, 1913). Part of apparatus of *Pygodus* Lamont & Lindström, 1957; jr. synonym of *Pygodus* (Bergström 1971).

Hindeodella Bassler, 1925 (*H. subtilis* Ulrich & Bassler, 1926). Jeppsson (1969) and Lindström (1970) discuss this genus and its apparatus. Identical forms occur in Ordovician rocks; taken most broadly, *Hindeodella* might be used for them, but *Ozarkodina* ist better.

Hirsutodontus Miller, 1969 (*H. hirsutus*). Apparatus unknown.

Histiodella Harris, 1962 (*H. altifrons*). TS includes blades on which it is based and trichonodelliform elements (*H. triquetra* Mound 1966).

Holodontus Rhodes, 1953 (*H. superbus*). T of TS a holodontiform element of *Amorphognathus superbus* (Rhodes) (Bergström 1971); jr. synonym of *Amorphognathus*.

Icriodella Rhodes, 1953 (*I. superba*). TS a prioniodiform element in apparatus of multielement *I. superba* (Bergström & Sweet 1966; Sweet & Bergström 1970).

Istorinus Knüpfer, 1967 (*I. postdentatus*). Apparatus unknown.

Keislognathus Rhodes, 1955 (*K. gracilis*). TS is asymmetric hibbardelliform element of *Amorphognathus ordovicicus* Branson & Mehl (Bergström 1971); jr. synonym of *Amorphognathus*.

Lenodus Sergeeva, 1963 (*L. clarus*). T of TS probably a holodontiform element (Bergström 1971); other elements of *Amorphognathus* apparatus not known from type strata.

Lepodus Branson & Mehl, 1933 (see *Lepognathodus*).

Lepognathodus Fay, 1959 (*Lepodus minutus* Branson & Mehl, 1933). T a small tooth-like element; may not be a conodont.

Leptochirognathus Branson & Mehl, 1943 (*L. quadratus*). TS a variable ramiform element; may be part of transition series; apparatus not known in detail.

Loxodus Furnish, 1938 (*L. bransoni*). Apparatus unknown; not known to be associated with other compound elements.

Loxognathus Graves & Ellison, 1941 (*L. flabellata*). T of TS part of apparatus of *P. aculeatus*, TS of *Periodon* Hadding (Bergström & Sweet, 1966); synonym of *Periodon*.

Microcoelodus Branson & Mehl, 1933 (*M. typus*). T a zygognathiform element; probably part of form-transition series including elements indistinguishable from *Erismodus*; Andrews (1967) regards *M.* as synonym of *E.*; our studies suggest two genera may be distinct.

Microzarkodina Lindström, 1971 (*Prioniodina flabellum* Lindström, 1955). TS apparatus includes ozarkodiniform, cordylodiform, trichonodelliform and oistodiform elements (Lindström 1971).

Mixoconus Sweet, 1955 (*M. primus*). T of TS a fibrous simple cone; apparatus unknown.

Multicornus Moskalenko, 1970 (*M. anonymus*). TS probably belongs in form-genus *Ptiloconus* Sweet, 1955; thus is part of apparatus of *Erismodus* or *Microcoelodus*, or both.

Multioistodus Cullison, 1938 (*M. subdentatus*). TS part of form-transition series (Lindström 1964) with cordylodiform, cladognathodiform, tetraprioniodiform, and hibbardelliform elements.

Neocoleodus Branson & Mehl, 1933 (*N. spicatus*). Apparatus unknown.

Neomultioistodus Harris, 1965 (*N. compressus*). T apparently a cladognathodiform element of *Multioistodus*.

Nericodus Lindström, 1955 (*N. capillamentum*). Affinities obscure; probably a conodont and possibly related to *Hirsutodontus* Miller, 1969; several more specimens have been collected since 1955.

Nordiodus Serpagli, 1967 (*N. italicus*). T of TS a drepanodiform element apparently associated with *N. proclinatus* Serpagli and *Oistodus rhodesi* Serpagli; apparatus needs further study.

Oepikodus Lindström, 1955 (*O. smithensis*). TS part of apparatus of *Prioniodus evae* Lindström; genus a jr. synonym of *Prioniodus* Pander (Bergström, 1968).

Oistodella Bradshaw, 1969 (*O. pulchra*). Apparatus unknown; ?related to *Belodina*.

Oistodus Pander, 1856 (*O. lanceolatus*). TS part of transition series of hyaline simple cones (Lindström 1964; 1971).

Oneotodus Lindström, 1955 (*Distacodus? simplex* Furnish, 1938). Apparatus unknown.

Oulodus Branson & Mehl, 1933 (*O. mediocris*). TS apparatus includes oulodiform, trichonodelliform, zygognathiform, cordylodiform, and probably prioniodiniform elements.

Ozarkodina Branson & Mehl, 1933 (*O. typica*). TS part of apparatus with spathognathodiform, neoprioniodiform, hindeodelliform, plectospathodiform and trichonodelliform elements; assigned to *Hindeodella* by Jeppsson (1969) but to *Ozarkodina* by Lindström (1970); rare in Ordovician.

Pachysomia Smith, 1907 (*P. wanlockensis*). T a compound element; may be scolecodont; if T is conodont, affinities obscure.

Paltodus Pander, 1856 (*P. subaequalis*). TS may be sr. synonym of *P. inconstans* Lindström 1955, which has apparatus of oistodiform and asymmetric drepanodiform elements (Lindström 1971).

Panderodus Ethington, 1959 (*Paltodus unicostatus* Branson & Mehl, 1933). Silurian TS probably bielemental simple-cone apparatus, as is case with some Ordovician species assigned to this genus (Bergström & Sweet 1966).

Paracordylodus Lindström, 1955 (*P. gracilis*). TS apparatus of paracordylodiform and oistodiform elements (= *O. gracilis* Lindström); may be others.

Paroistodus Lindström, 1971 (*Oistodus parallelus* Pander, 1856). Bielemental simple-cone apparatus with drepanodiform and oistodiform elements.

Periodon Hadding, 1913 (*P. aculeatus*). Multielement; TS apparatus of periodontiform, falodiform and prioniodiniform elements (Bergström & Sweet 1966).

Phragmodus Branson & Mehl, 1933 (*P. primus*). TS apparatus unknown; others of phragmodiform, dichognathiform and oistodiform (or cyrtonidiform) elements (Bergström & Sweet 1966).

Plectodina Stauffer, 1935 (*P. dilata*). TS a cordylodiform element of *P. aculeata* (Stauffer, 1930), which must be regarded as T of multielement genus; apparatus of cordylodiform, trichonodelliform, zygognathiform, dichognathiform, ozarkodiniform, prioniodiniform, cyrtoniodiform elements.

Plegagnathus Ethington & Furnish, 1959 (*P. nelsoni*). Few specimens of TS known; apparatus unknown; related to *Belodina*.

Polycaulodus Branson & Mehl, 1933 (*P. inclinatus*). May be part of apparatus of fibrous forms assigned to *Curtognathus*, *Cardiodella*, and *Trucherognathus*; relationship still not clear.

Polyplacognathus Stauffer, 1935 (*P. ramosus*). TS apparatus with polyplacognathiform and modified ambalodiform elements (Bergström & Sweet 1966).

Pravognathus Stauffer, 1935 (*Heterognathus idoneus* Stauffer, 1935). Little known; apparatus included two types of blades (Webers 1966).

Priomorphognathus Knüpfer, 1967 *(P. alatus)*. T of TS a fragmentary platform like some upper L. Ordovician *Eoplacognathus; P.* may be jr. synonym of *E.*

Prioniodus Pander, 1856 *(P. elegans)*. TS apparatus of prioniodiform, falodiform, belodiform, hibbardelliform, tetraprioniodiform elements (Bergström 1968).

Pristognathus Stone & Furnish, 1959 *(P. bighornensis)*. TS apparatus unknown; T of TS resembles an oulodiform element of distinctive type.

Protopanderodus Lindström, 1971 (*Acontiodus rectus* Lindström, 1955). Multielement; apparatus includes symmetrical and asymmetrical panderodiform elements.

Pteracontiodus Harris & Harris, 1965 *(P. aquilatus)*. T of TS a distinctive compound element; apparatus unknown; possibly part of *Multioistodus* transition series.

Ptiloconus Sweet, 1955 (*Pteroconus gracilis* Branson & Mehl, 1933). TS part of apparatus of *Microcoelodus typus*; for status of *Microcoelodus*, see above.

Pteroconus Branson & Mehl, 1933 (see *Ptiloconus*).

Pygodus Lamont & Lindström, 1957 *(P. anserinus)*. TS a pygodiform element; apparatus also with haddingodiform and possibly tetraprioniodiform, hibbardelliform elements (Bergström 1971).

Rhipidognathus Branson, Mehl & Branson, 1951 (*R. symmetricus*). TS apparatus of blade and trichonodelliform elements (Bergström & Sweet 1966; Kohut & Sweet 1968).

Rhodesognathus Bergström & Sweet, 1966 (*Ambalodus elegans* Rhodes, 1953). TS apparatus with two types of ambalodiform elements.

Rhynchognathodus Ethington, 1959 (*Rhynchognathus typicus* Ethington, 1959). TS part of apparatus of *I. superba*, TS of *Icriodella* Rhodes; jr. synonym of *Icriodella* (Bergström & Sweet 1966; Webers 1966).

Rhynchognathus Ethington, 1959 (see *Rhynchognathodus*).

Rosagnathus Rhodes, 1955 *(R. superbus)*. TS a tetraprioniodiform element of multielement *A. ordovicicus*, TS of *Amorphognathus* (Bergström 1971); jr. synonym of *A.*

Sagittodontina Knüpfer, 1967 *(S. robusta)*. T of TS a fragmentary blade; apparatus unknown.

Sagittodontus Rhodes, 1953 *(S. robustus)*. TS part of apparatus of *Icriodella superba* Rhodes, 1953 (Bergström & Sweet 1966; Kohut 1969); synonym of *Icriodella.*

Scandodus Lindström, 1955 *(S. furnishi)*. TS a bielemental apparatus of drepanodiform and scandodiform elements (Lindström 1971).

Scolopodus Pander, 1856 *(S. sublaevis)*. TS known only from Pander's description; if *S. rex* Lindström 1955 is the same, apparatus includes symmetrical and asymmetrical hyaline drepanodiform elements (Lindström 1971).

Scotlandia Cossman, 1909 (Valentia morrochensis Smith, 1907). T of TS an unrecognizable fragment; may not be conodont.

Scyphiodus Stauffer, 1935 *(S. primus)*. TS a distinctive blade with compound denticulation on one process; apparently only type of element in apparatus.

Serratognathus Lee, 1970 *(S. bilobatus)*. Bilaterally symmetrical platform-like elements; somewhat similar to *Nericodus* and *Hirsutodontus*; may not be conodont.

Spathognathodus Branson & Mehl, 1941 (TS Silurian; included in apparatus assigned to *Hindeodella* by Jeppsson, but to *Ozarkodina* by Lindström; see *Hindeodella, Ozarkodina.*

Stereoconus Branson & Mehl, 1933 *(S. gracilis)*. Monoelemental simple-cone apparatus; not well known.

Stolodus Lindström, 1971 (*Distacodus stola* Lindström, 1955). Monoelemental apparatus of costate deeply excavated simple cones; possibly related to *Coelocerodontus.*

Strachanognathus Rhodes, 1955 *(S. parvus)*. Intraspecific variation in elements of TS (Bergström 1962) suggests apparatus may be monoelemental.

Subcordylodus Stauffer, 1935 *(S. elongatus)*. T of TS a cordylodiform element; Webers (1966) regards as part of apparatus of *Phragmodus inflexus*; synonym of *Phragmodus.*

Subprioniodus Smith, 1907 *(S. paucidendatus)*. Ts of TS unassignable fragments; name should be used only for type material.

Tetraprioniodus Lindström, 1955 *(T. robustus)*. TS includes tetraprioniodiform elements of a *Prioniodus* close to *P. elegans* Pander; jr. synonym of *Prioniodus.*

Tokognathus Nieper (in Hill and others), 1969 *(T. proclinatus)*. Incompletely described, poorly figured T of TS a compound element with multidenticulate posterior process, laterally costate cusp; affinities obscure; may be related to *Phragmodus* or *Plectodina.*

Tortoniodus Stauffer, 1935 *(T. politus)*. T of TS a prioniodiniform element that Webers (1966) associates with several other blades; apparatus not well known; generic name useful now only for type material.

Trapezognathus Lindström, 1955 *(T. quadrangulum)*. T of TS part of apparatus of *Prioniodus (Baltoniodus) triangularis* (Lindström 1971); jr. synonym of *Prioniodus.*

Trichognathus Branson & Mehl, 1933 (see *Trichonodella*).

Trichonodella Branson & Mehl, 1948 (*Trichognathus primus* Branson & Mehl, 1933). TS is trichonodelliform element of *P. aculeata*, TS of *Plectodina* Stauffer, 1935, or of closely related *Plectodina* species; jr. synonym of *Plectodina.*

Tricladiodus Mound, 1965 *(T. clypeus)*. Apparatus unknown.

Trigonodus Nieper (in Hill and others), 1969 *(T. triangularis)*. T of TS a simple cone with smooth anterior margin and prominent anterolateral costae; affinities obscure; may be part of transition series including drepanodiform and costate simple cones.

Tripodus Bradshaw, 1969 *(T. laevis)*. Ts of TS fragmentary simple cones possibly related to *Stolodus* and *Walliserodus*; apparatus unknown; may include transition series.

Tripodontus Knüpfer, 1967 *(T. muelleri)*. TS apparently a tetraprioniodiform element like those of *Amorphognathus* apparatus.

Trirhadicodus Harris, 1964 (*Multioistodus tridens* Cullison, 1938). TS part of apparatus of *M. subdentatus*, TS of *Multioistodus.*

Trucherognathus Branson & Mehl, 1933 *(T. distortus)*. TS apparatus unknown; may be part of apparatus including form-species of *Curtognathus, Cardiodella, Polycaulodus.*

Tvaerenognathus Bergström, 1962 *(T. ordovicicus)*. TS a holodontiform element of *Amorphognathus tvaerensis* Bergström; jr. synonym of *Amorphognathus* (Bergström 1964, 1971).

Ulrichodina Furnish, 1938 *(U. prima)*. Simple cone; apparatus unknown; ?monoelemental.

Valentia Smith, 1907 (see *Scotlandia* Cossman).

Walliserodus Serpagli, 1967 (*Paltodus debolti* Rexroad, 1967). TS apparatus includes a transition series of prominently costate simple cones.

Zygognathus Branson, Mehl & Branson 1951 *(Z. pyramidalis)*. TS apparatus of zygognathiform and eoligonodiniform elements; perhaps others; possibly dervied from *Plectodina* by reduction in other ramiform components (Kohut & Sweet 1968).

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