Relationships between Ordovician Baltic and North American Midcontinent conodont faunas

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During most of the Early and Middle Ordovician, epicontinental seas of Laurentia, Baltica, and islands in the Iapetus Ocean between them were centers of diversification of different groups of conodonts. The most important were Phragmodontidae in Laurentia, Periodontidae in the Iapetus area, and Balognathidae in Baltica. Spectra of fossil assemblages (analyzed in terms of conodont lineages) were very stable through time in each of these biogeographic provinces. Relatively few lineages passed the biogeographic boundaries and successful immigrations were rare. An especially stable composition characterizes the Baltic faunas. A profound change in the composition of faunas in Baltica took place in the Oanduan (late Caradocian) through influx of several lineages previously confined to islands in the Iapetus. Conodont faunas of Laurentia, at times enriched by Iapetus-born lineages, evolved rather gradually until the end of the Ordovician. Diversity of Ordovician conodont assemblages seems to depend more on local ecologic factors and bathymetry than on climate. ☐*Conodonta, biostratigraphy, biogeography, evolution, Ordovician.*

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Ordovician bioprovincialism has received much attention from conodont workers and several important contributions to its recognition have been published (for review, see Jaanusson 1979; Sweet & Bergström 1974; Jaanusson & Bergström 1980; Lindström 1976 b). The profound difference between conodont faunas of the North American Midcontinent and those of the southeastern Appalachians and Europe has been recognized since the Sweet *et al.* (1959) paper. A boundary separating these two distinct biogeographic units has been traced along the Helena–Saltville fault in the southern Appalachians and corresponding structural features to the north (Bergström 1971; Jaanusson & Bergström 1980). Although changes in the distribution of particular Late Ordovician conodont taxa have been discussed in detail by Sweet & Bergström (1974) and faunal changes across the Appalachians in the Middle Ordovician have been presented by Bergström & Carnes (1976), much remains to be done regarding the pattern of distribution and shifts of Early and Middle Ordovician conodont lineages in Europe as well as precisely tracing relationships of those lineages that are thought to be typical of provinces. It must be stated, however, that data are still far from complete, and numerous key faunas (for example those from the Middle Ordovician of Great Britain and the Sudeten Mountains) have not yet been described in terms of multielement taxonomy. Accordingly, this paper is just a preliminary report on a study that remains to be completed.

Terminology

Choice of the best element-notation system begins to be a difficult task for conodontologists. Among several proposed systems of terminology for elements in the conodont apparatus (for review, see Sweet 1981b; also Barnes *et al.* 1979 and Dzik & Trammer 1980) two seem to be applicable for most apparatuses. Those are Jeppsson's (1971) and Sweet's (1981b) systems. When applied to sextimembrate apparatuses they are easily transferable to each other.

For the purpose of the present paper Jeppsson's notation has been chosen. It was originally introduced as a tool for expressing homology of elements. Symbols of all types of elements are derived by abbreviations of former form–taxonomic generic names, which seems to be in good agreement with tradition in biological terminology. In the same way terms for, say, larval stages (echinospira, pilidium, calyptopis, zoëa, etc.), or organs (stigmaria, helens, aptychi, etc.) have been introduced, all being based on names of former taxa. This does not leave a place for uncertainty regarding reference for homologization. Particular types of elements are identified in any apparatus by homologization with particular elements of the *Ozarkodina* apparatus. There is no assumed *a priori* order in arrangement of the types of elements in the apparatus, therefore no trouble appears when insertion of a new type of element into the transition series appears necessary.

The apparatus of *Amorphognathus* is proposed here as a homologization standard for septimembrate apparatuses. The complete set of elements in such apparatuses contains, according to this notation (in supposed order), sp, oz, tr, pl, ke, hi, and ne types. Sweet (1981b) and Bergström (1981) proposed to consider the keislognathiform element of *Amorphognathus* as pl (Sb) and consequently created 'location' Sd for tetraprioniodontiform elements. There are, however, analogous tetraramous elements in the pl (Sb) location in apparatuses other than those of the Balognathidae (for example

Microzarkodina and *Paraprioniodus*), while it has been asserted that the keislognathiform element is a homologue of one of the Sc elements in those Balognathidae that do not have it (Dzik 1976). In the typical apparatus of the Balognathidae, Sa, tetraprioniodontiform (Sb), keislognathiform, and Sc elements form a single symmetry transition series, and a keislognathiform element should be inserted between Sb and Sc elements. This could be done either by introducing a third letter to the notation (like Sbb) or by replacing Sc elements *sensu* Sweet (1981b) to Sd location and reserving the Sc location only for homologues of the keislognathiform elements of *Amorphognathus* (which I would prefer). Kuwano (1982) proposed symbols Sa-b and Sb for homologues of pl and ke elements in the *Ozarkodina excavata* (Branson & Mehl) apparatus, respectively.

Meanings of other terms used in the text are explained in the *Treatise on Invertebrate Paleontology* (Sweet 1981 b). There also all taxonomic, auctor references that are not listed in this paper can be found.

Comments on methodology

One basic trouble in establishing a good scientific framework for a discussion of conodont provincialism is the lack of unequivocal meaning for units in paleobiogeography. Concepts of high-rank biogeographic units are usually based on more or less objectively determined differences in the composition of faunistic assemblages from different areas. This does not create special difficulties unless problems of the boundary between particular units and their change in geologic time are involved. Then any biogeographic unit appears to have a particular meaning that depends on methods used in recognizing it and the particular group of fossils used, rather than on objective factors (Jaanusson 1979). For these reasons Lindström (1976 a) has proposed to separate the territorial and faunistic aspects of provincialism, and to abandon the first one and shift the discussion toward aspects of the evolution of particular faunas. These may completely change their distribution in time. This means that he has proposed to study high-rank communities (faunas) rather than high-rank ecosystems (provinces and realms in common understanding). Data discussed below show, however, that there is no visible integration among species, either in their distribution within faunas or within particular conodont communities. This fits well with data concerning the distribution of other groups of fossils as well as with theoretical considerations (Hoffman 1979). There is also little evidence of invasion of other areas by entire groups of conodonts that form the core of particular faunas. Rather, each species seems to change the area of its distribution separately, and when all the 'fauna' is replaced by another assemblage the replacing assemblage is rarely the 'fauna' that occurred in another area before. At least some conodont species may occur alone. The concept of a conodont 'fauna' thus appears quite foggy and there is little chance to make it more objective.

For all these reasons I prefer to define biogeographic units not on the basis of their supposed internal integration but on external factors. A boundary between two such units should be drawn on the supposed discontinuity in spatial distribution of environmental factors, which may be expressed in an abrupt change in the distribution of some organisms. The concepts of island biogeography (MacArthur & Wilson 1967) are applicable to such biogeographic units. It is not difficult to find boundaries in the terrestrial environment with the features required by this definition. The marine environment is much more continuous, but discontinuities in the distribution of particular marine environments such as margins of the continental shelf, areas of convergence of warm and cold water, thermoclines, a range of uplifts of oceanic currents carrying biogenes, etc., can be used to delineate boundaries between marine ecosystems. All these factors may separate oceanic water into discrete cells that are different in the composition of their faunal and floral assemblages. Features of these cells may change with the evolution of climate and even more profoundly with the tectonic evolution of continents (Williams 1976). In the present paper the Ordovician epicontinental seas of Laurentia (the Midcontinent province), Baltica (the Baltic province), and islands in the Iapetus Ocean between them (the North Atlantic province) are considered to be paleobiogeographic units of this kind (Fig. 1).

Four main kinds of faunal processes may be connected with the evolution of biogeographic units defined above: (1) Phyletic evolution of particular species. (2) Change in the distribution of particular species within boundaries of the unit. (3) Immigrations of species from other ecosystems, which displace local species from their niches, but do not change the state of faunal equilibrium. (4) Immigrations of species that occupy previously uninhabited niches, or destruction of the previous distribution of niches, in both cases changing faunal equilibrium.

How can one recognize these basically different processes from the limited fossil record? It would be especially important to have a tool that permits distinction between rebuilding of the fossil assemblage caused by a local environmental change and immigration of extrinsic faunal elements. Solution of this problem seems to be the first step to the serious considerations of bioprovincialism (see discussion in Sweet & Bergström 1974; Barnes *et al.* 1973; Bergström & Carnes 1976). A strict distinction between species of different lineages coexisting at the same time and chronospecies being part of the same (monospecific at any time) lineage must be made in any analysis of this kind. Because of objective limitations of the fossil record, particular fossil assemblages must be analyzed in terms of lineages rather than particular chronospecies. Similarly, a direct comparison of the same paleoenvironments in different provinces seems to be outside the possibilities provided by sedimentological analysis. Fossils alone seem to be the most sensitive environmental indicators. A consideration of the entire spectrum of environments within two provinces would be a way to reach these objectives; but rarely, if ever, are enough data available to reconstruct such spectra for particular time units. Some support is fortunately given by Walther's law. One may assume that vertical changes in the composition of conodont assemblages, which reflect the influence of changing environments through time, are characteristic for each biogeographic unit, for in such units different parts of the ecospace are inhabited by organisms that represent lineages specific to it. Different provinces are thus expected to have different dynamics of fossil assemblages in relation to environmental changes.

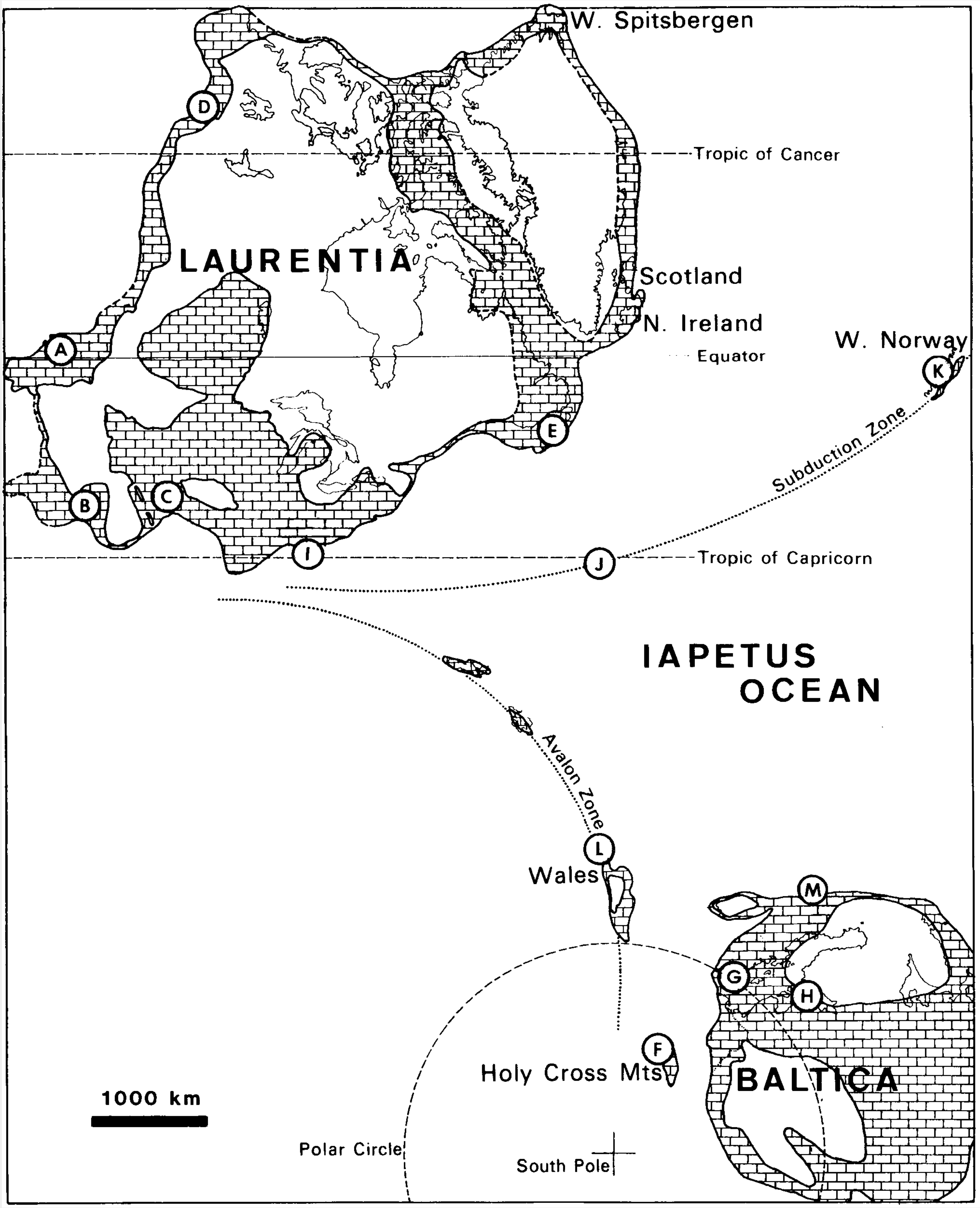


Fig. 1. Presumed geographic position of main localities discussed in the text in the late Early and early Middle Ordovician according to Bergström (1979) and Bruton & Bockelie (1980). ☐A. Ibex area of Utah and Basin Ranges of Nevada (Ethington & Clark 1981; Harris *et al.* 1979). ☐B. Marathon area of Texas (Bergström 1978). ☐C. Arbuckle Mountains of Oklahoma. ☐D. Sunblood Range of the District of Mackenzie (Tipnis *et al.* 1979). ☐E. Western shore of Newfoundland (Fåhraeus & Nowlan 1978; Stouge in press). ☐F. Holy Cross Mountains (Dzik 1978). ☐G. Island of Öland (van Wamel 1974). ☐H. Estonia (Viira 1974). ☐I. Southeastern Appalachians (Bergström & Carnes 1976). ☐J. Central Newfoundland (Fåhraeus & Hunter 1981). ☐K. Trondheim area of Norway (Bergström 1979). ☐L. Type section of Llandeilo, Wales (Bergström 1971). ☐M. Kalkberget and Gammalhodberget sections, Jämtland (Löfgren 1978).

Logs of contribution of particular conodont lineages (species) in samples plotted against time (rock thickness) are used here as a practical tool for recognition of the dynamics of assemblages (Fig. 11). This method of presentation of quantitative data on conodont distribution has been extensively used for biostratigraphic correlation and environmental analysis (Bergström & Sweet 1966; Sweet 1979a, b; Jeppsson 1979). This kind of logs may also show whether a new species that appears in the assemblage is invading an unoccupied niche or displacing some earlier species from its niche. In the first case the appearance of a new species is accompanied by a proportionate reduction of the contribution of all other species, without a change in the relations among them. The same effect may also be produced by a relative increase in productivity by some species, however. Ecologic competition between new and old species has an effect only on that part of the assemblage affected by it (for examples see Fig. 11).

Sources of data

The present article owes its origin to the fortunate opportunity to compare data on the Baltic and Polish Ordovician conodonts I collected as a member of the Zakład Paleobiologii PAN in Warsaw, Poland, with extensive collections of Midcontinent conodonts gathered during many years by Walter C. Sweet, Stig M. Bergström, and their students at The Ohio State University in Columbus, Ohio. It should be noted that I have had free access at Ohio State University to all available collections, including several that have not been described in the literature. Many of these collections, as noted below, were carefully sorted before I saw them, and components of the individual species were arranged in different parts of the slides to reflect the taxonomic judgment of the sorter. These have been of great help to me. Other collections were not sorted when I examined them and are currently under study by others. My judgement as to the assemblages of species represented in the unsorted samples or as to the quantitative relations between particular species is thus no more than an approximation and may well be different from the one expressed when the collections have been completely prepared. The following sources of data have been particularly useful:

Midcontinent conodonts. – The main source of data concerning Midcontinent conodonts used here is a collection of samples from the Lower and Middle Ordovician of the Arbuckle Mountains, Oklahoma (see Sweet & Bergström 1973). Two long sections were sampled by Walter C. Sweet, Valdar Jaanusson, and Stig M. Bergström in 1972 and subsequently processed in the Department of Geology and Mineralogy of The Ohio State University. These include samples from the upper 234 feet (71.3 m) of the West Spring Creek Formation, the entire Joins, Oil Creek, McLish, Tulip Creek, and Mountain Lake formations at a locality along Interstate Highway 35 north of Ardmore, Carter County; and samples from the McLish, Tulip Creek, and Bromide formations from a section along Oklahoma Highway 99, south of Fittstown. The major part of the collection has apparatuses of particular species separated on the slides. This means that most of the apparatuses have been reconstructed by Walter C. Sweet and Stig M. Bergström.

I have also examined samples from the Tumbez and Elway-Eidson formations of the Lay School section, Grainger County, Tennessee, collected and arranged by species on his slides by Carnes (1975) and the collection of Blackriveran conodonts from the Pan American Davidson core from a borehole in Richland County, Ohio, collected, arranged and tabulated by Votaw (1971). Neither Carnes nor Votaw has yet published his ideas about these samples. During a short stay in Washington, D. C., I saw samples from the Whiterockian of Nevada that form the basis of the Harris *et al.* (1979) paper. Some previously unpublished data concerning Nevada conodonts have also been supplied to me by Anita G. Harris (U. S. Geological Survey) and Stig M. Bergström, who also made available to me some of his samples from Marathon, Texas. John E. Repetski (U. S. Geological Survey) allowed me to examine his collection of conodonts from the Dutchtown Formation of Missouri. Published data used here are from sections in Nevada (Ethington & Schumacher 1969), Utah (Ethington & Clark 1981), the District of Mackenzie (Tipnis *et al.* 1979), the Melville Peninsula (Barnes 1977), Quebec (Barnes & Poplawski 1973), Scotland (Higgins 1967) and several other localities.

North Atlantic conodonts. – The section of the Mójcza Limestone at Mójcza, Holy Cross Mountains, Poland, which has been preliminarily described elsewhere (Dzik 1978), was fully sampled in 1979 and is currently under study at the Zakład Paleobiologii PAN. Szaniawski (1980) has published a description of Tremadocian conodonts from the same area. I saw the collection of Dr. Zdzisława Urbanek (University of Wrocław) from the Sudeten Mountains (see Baranowski & Urbanek 1972) in 1978. A description of some Bohemian conodonts is currently in press (Dzik 1983). Welsh conodont faunas have been partially described and reviewed by Bergström (1964, 1971) and I have seen some of his samples. Additional published data concern Newfoundland (Fåhraeus & Nowlan 1978; Fåhraeus & Hunter 1981; Stouge 1982 and in press), the Appalachians (Sweet & Bergström 1962; Bergström *et al.* 1972; Bergström & Carnes 1976; Landing 1976), the Armorican Massif (Lindström *et al.* 1974), and western Norway (Bergström 1979).

Baltic conodonts. – Baltic conodonts have been described in great detail in several papers summarized by Lindström (1971), Bergström (1971), van Wamel (1974), Viira (1974), Dzik (1976), and Löfgren (1978). Along with samples from erratic boulders of Baltic origin from northern Poland, I base my knowledge of Baltic faunas on samples from some Estonian and Swedish sections. Several samples were taken in 1977 from the Sukhrumägi section near Tallin. In 1980 I also sampled the upper part of the Langevoja and Hunderum substages at Hälludden, Öland, as well as the Ceratopyge Beds and Latorpian at the Ottenby cliff, Öland; the section partially described by Fåhraeus (1966) at Gullhögen quarry, Skövde, Västergötland, and a few other localities in Västergötland. Stig M. Bergström has shown me his collection of conodonts from the Gullhögen quarry, which covers the upper part that was not sampled by me. During a few days stay in

Tallinn I had an opportunity to study collections of conodonts from several boreholes described by Viive Viira (Geological Institute, Tallin; see Viira 1974). Especially important were cores from the Ohesaare and Kaagvere boreholes, which present a good record of the evolution of *Amorphognathus*. A detailed description of the conodont succession within the latter borehole has not been published.

Correlation

Although Baltic and Midcontinent Ordovician conodont faunas are basically different, several influxes of populations belonging to quickly evolving lineages took place between them, thus allowing some time correlation between them. These correlation horizons are discussed briefly below in stratigraphic order. The zonation proposed by Lindström (1971) and Bergström (1971), with a few additions by Dzik (1978), based on the evolution of Baltic lineages, is used here as a reference standard. A few zones previously proposed are omitted, namely the *Baltoniodus triangularis* and *Microzarkodina parva* Zones. The first is based on a species that is hard to identify (see Dzik 1984); the second is defined as an assemblage zone. In addition, the *Prioniodus alobatus* Zone, which may partially represent the *P. gerdae* Zone, is omitted because it is based on a species of unknown time of origin. No comparable zonation of the Midcontinent Ordovician has been proposed yet (see, however, Ethington & Clark 1981 and Stouge in press). Several Midcontinent conodont chronospecies have well-recognized phylogeny and their appearances supply several useful correlation horizons. These horizons are used here provisionally only for the purpose of having reference to some Midcontinent evolutionary events, not exactly correlated with the Baltic zones (see Figs. 11, 12). They are not intended to be boundaries of an established zonal scheme, which remains to be defined.

(1) *Glyptoconus*(?) *asymmetricus* (Barnes & Poplawski 1973) probably evolved from *G.* (?) *striatus* (Graves & Ellison 1941) at the time of deposition of the upper Fillmore Formation of the Ibex area, Utah (see Ethington & Clark 1981). The Joins Formation of Oklahoma, the Hølonda Limestone of Norway, and the *A. raniceps* Limestone of Öland are thus younger than, or at least contemporary with, the upper Fillmore.

(2) *Microzarkodina flabellum* (Lindström 1955) occurs in the highest Wah Wah and the lower half of the Juab Formation in the Ibex area (Ethington & Clark 1981). Because periodontids presumably originated in *Prioniodus elegans* Zone time and evolutionarily advanced *Microzarkodina* cannot be older than the top of the *Oepikodus evae* Zone, the uppermost Wah Wah is not older than upper *O. evae* Zone.

(3) *Histiodella holodentata* Ethington & Clark 1981 originated from *H. sinuosa* (Graves & Ellison 1941) in the upper part of the Lower Table Head Formation of Newfoundland (Stouge in press), in the middle of the Lehman Formation of the Ibex area, Utah (Ethington & Clark 1981), in the uppermost Antelope Valley Limestone at Steptoe, Nevada, and in the middle of the same formation in the Toquima Range, Nevada (Harris *et al.* 1979) It appeared in the Baltic area (Viira 1974) and the Holy Cross Mountains, Poland (Dzik 1976, 1978), in the early Kundan, where it occurs together with *Amorphognathus variabilis* Sergeeva 1963. This means that the Baltic *A. variabilis* Zone is not older than the upper Lehman Formation of Utah and other occurrences of *H. holodentata*.

(4) *Eoplacognathus suecicus* Bergström 1971 occurs with the biostratigraphically probably very diagnostic *Phragmodus* sp. n. of Harris *et al.* (1979) in Nevada (Harris *et al.* 1979), below the first occurrences of *Phragmodus flexuosus* Moskalenko 1973.

(5) Early *P. flexuosus* is known to occur together with *Eoplacognathus reclinatus* (Fåhraeus 1966) (R. L. Ethington, personal communication).

(6) Advanced *P. flexuosus* (having a more prominent gradient in the size distribution of denticles on the pl element than earlier forms) occurs in the Kukrusean of Estonia with *Baltoniodus variabilis* (Bergström 1962) (Bergström 1971). Several co-occurrences of *Baltoniodus*, *Phragmodus*, and the *Polyplacognathus friendsvillensis–sweeti* lineage are known from the Appalachians (Bergström & Carnes 1976; Fåhraeus & Hunter 1981).

(7) *P. sweeti* Bergström 1971 appears in the Uhakuan of Volhynia (Drygant 1974).

(8) *Baltoniodus gerdae* (Bergström 1971) occurs in the Mountain Lake Formation of Oklahoma with typical *Phragmodus inflexus* Stauffer 1935 (Sweet & Bergström 1973).

(9) *Amorphognathus tvaerensis* Bergström 1962 occurs with *Phragmodus undatus* Branson & Mehl 1933 in the Bromide Formation of Oklahoma in the section south of Fittstown as well as in several other localities (Bergström & Sweet 1966). *P. undatus* is known also in the Oanduan of Estonia (Viira 1974) and the Mjøsa Limestone of Norway (Bergström 1971).

Patterns in the distribution of conodont lineages

Presumed relationships between Midcontinent and Baltic lineages and their connections with conodonts of other areas are discussed below. The groups have been arranged in family-rank taxa according to the supposed pattern of relationships among them. They may be arranged into four larger groups, which differ in the ground plan of the apparatus and of particular elements. The first such group is formed by conodonts included here in the family Chirognathidae, which are characterized by hyaline elements with strongly developed denticulation and with morphologically rather continuous transition between all elements of the apparatus. They are supposed to have evolved directly from the Cambrian Westergaardodinidae. The second group comprises the families Fryxellodontidae, Panderodontidae, Protopanderodontidae, and Ulrichodinidae, which have apparatuses of coniform elements but do not have a geniculate ne element; the Distacodontidae, with a geniculate ne element but a tr element without lateral processes; and possibly the Cordylodontidae and Multioistodontidae, whose relationships are inadequately known. the third and fourth groups include conodonts with rather highly differentiated apparatuses, originally with nondenticulated elements, ne being geniculate and tr with lateral processes. They differ in the number of processes developed in particular elements. The third group, consisting of the Prioniodontidae, Phragmodontidae, Balognathidae, Icriodontidae, and perhaps the Distomodontidae, has apparatuses with triramous sp, oz, and tr elements and a tetraramous (rarely triramous) pl element. The fourth one, including Oistodontidae, Periodontidae, and most of the post-Middle Ordovician conodonts, originally had biramous sp and oz elements and triramous tr and pl elements. Dzik (1976) proposed to include the first group in the suborder Westergaardodinina Lindström 1970, the second and third in the Prioniodontina Dzik 1976, and the fourth in the Ozarkodinina Dzik 1976.

Chirognathidae Branson & Mehl 1944

Chosonodina Müller 1964, which is widespread but never numerous in the North American Midcontinent (Mound 1965, 1968; Ethington & Clark 1981; Harris *et al.* 1979), seems to have evolved during deposition of the Joins and Oil Creek formations of Oklahoma from its original *Westergaardodina*-like shape toward a morphology similar to that of *Chirognathus* Branson & Mehl 1933. Typical *Chirognathus* occurs much higher, above the *B. gerdae* Zone (Webers 1966) and may belong to the same lineage, which seems to be confined to the Midcontinent. *Bergstroemognathus* Serpagli 1974 and *Appalachignathus* Bergström, Carnes, Ethington, Votaw & Wigley 1974 may be related to this group. They occur in the American part of the North Atlantic province and the Midcontinent, but, although having almost worldwide distribution (Serpagli 1974; Bergström & Carnes 1976; Cooper 1981), have not been recorded from the Baltic area. Juvenile specimens of Whiterockian *Leptochirognathus* Branson & Mehl 1943, different from older *Chosonodina* only in very robust denticulation, have a base with an acute outer side, which may be a remnant of the small lateral process of *Tripodus laevis* Bradshaw 1969 from the West Spring Creek Formation of Oklahoma. A similar process occurs in *Jumudontus gananda* Cooper 1981 with an almost worldwide occurrence (except the Baltic region), and in unnamed species of the same genus from the Joins Formation of Oklahoma (see McHargue 1975). All these conodonts are supposed to be indicative of warm, shallow-water environments (Barnes *et al.* 1973; Bergström & Carnes 1976).

Multioistodontidae Bergström 1981

I provisionally assemble here, following Bergström (1981), genera with apparatuses composed of hyaline, gently curved ramiform elements that bear some similarity to those of the Tremadocian *Cordylodus* Pander 1856. Among them, *Multioistodus* Cullison 1938 s.s. (restricted to species that lack a geniculate ne element and with rather little distinction between elements of the apparatus) and *Erismodus* Branson & Mehl 1933 (together with related forms) are almost exclusively Midcontinent lineages (Sweet 1982). *Erraticodon* Dzik 1978, which appeared briefly two times in the Baltic area (Dzik 1978), is more common on the American side of the North Atlantic province (Sweet & Bergström 1962; Stouge in press), and in the Midcontinent (Harris *et al.* 1979; Ethington & Clark 1981) but it is a lineage that is rather typical of the Australian province (Bergström 1971; Cooper 1981). *Spinodus* Dzik 1976 may have originated from *Erraticodon* through some transitional forms that occur in the Midcontinent (see Bradshaw 1969, Pl. 137:7–11) and North Atlantic provinces (Landing 1976; Stouge in press). It occurs subordinately in the North Atlantic part of the Appalachians (Sweet & Bergström 1962; Bergström & Carnes 1976), central Newfoundland (Fåhraeus & Hunter 1981), Scotland and Wales (Bergström 1971), the Holy Cross Mountains, Poland, and the Baltic area (Dzik 1976).

Fryxellodontidae Miller 1981 (Fig. 2)

Discovery of two more specimens of *Nericodus* Lindström 1955 in the *P. proteus* Zone of Ottenby, Öland (Fig. 2 B, C), which appear to be morphologically similar to *Polonodus* Dzik 1976 (Fig. 2 A, D), suggests to me that these genera, together with *Fryxellodontus* Miller 1969, which shares a widely conical shape and lacks a well-defined cusp, represent a group of closely related lineages. Even if the Öland specimens represent a species intermediate between Tremadocian *Nericodus* and Late Arenigian *Polonodus*, this does not necessarily mean that *Polonodus* originated in the Baltic area. This genus, before its brief appearance in the Kundan of the Holy Cross Mountains and the Baltic area (Dzik 1976), seems to have been rather widespread in Texas, Nevada (Harris *et al.* 1979; Bergström 1978, 1979), and western Newfoundland where it is well represented in the Table Head Formation (Stouge in press). Although very variable, and exhibiting morphologic change during ontogeny, *Polonodus* does not seem to have had a differentiated apparatus, or to have been represented by many species.

Panderodontidae Lindström 1970 (Fig. 3)

This group (taken to include the Belodellidae Khodalevich & Tschernich 1973) is characterized by species whose skeletal elements have a very deep basal cavity and whose apparatuses have low morphologic diversification. Little is known about its early evolution. The most generalized morphology of elements is shown by *Scalpellodus* Dzik 1976, which is known to occur in the Baltic area from the end of the early Volkhovian (Löfgren 1978) but does not have any known Baltic ancestry. There is little morphologic difference between *S. latus* (van Wamel 1974), the oldest, and *S. cavus* (Webers 1966), the youngest species of this genus (Fig 3: 22, 27) and originally they were considered to belong to the same chronospecies (Dzik 1976). Löfgren (1978) has shown, however, that during the Early Ordovician some evolutionary transformation occurred in this lineage in the Baltic area, which was expressed mostly in the smoothing of the surface of elements and simplification of the apparatus. Elements of the *Scalpellodus* apparatus are difficult to distinguish from particular elements of Gen. n. B ('Ordovician *Belodella*') and the '*Paltodus*' *jemtlandicus* Löfgren 1978 group, therefore it is not easy to trace distribution of this genus on the basis of data in the literature. *Macerodus dianae* Fåhraeus & Nowlan 1978 from the Cow Head and St. George groups of Newfoundland (Stouge 1982), may represent the 'scandodontiform' element of *S. latus* or a related species (see

Löfgren 1978; Pl. 5:6). On the other hand elements of *Scalpellodus striatus* Ethington & Clark 1981 from the Fillmore Formation of Utah (Ethington & Clark 1981) may well belong to other genera with generalized morphology of elements of the apparatus. Certain *Scalpellodus* occurred in the Midcontinent from the time of the *E. suecicus* Zone (Harris *et al.* 1979), was also not uncommon in the Appalachians (Bergström & Carnes 1976) and lasted there even after its disappearance in the Baltic area. Possibly this lineage reappeared briefly in the Baltic area in the Ashgillian (Viira 1974).

Panderodus Ethington 1959, which differs from *Scalpellodus* in possessing a fissure on the lateral side of the elements, is known to occur in the *O. evae* Zone of Argentina (Serpagli 1974; Fig. 3:11 and possibly in Australia ('*Protopanderodus primitus* Druce' of Cooper 1981). It did not appear in the Baltic area before the middle Kundan (Dzik 1976) and appeared in the Midcontinent even later, the oldest ones there being known from the Crystal Peak Dolomite of Utah (Ethington & Clark 1981). It shows a scattered but wide distribution in both these provinces. Several other conodont lineages with elements bearing a lateral fissure may be derived from *Panderodus*, all of them being typical representantives of shallow-water communities. Among them *Dapsilodus* Cooper 1976 (Fig. 3:16), has very wide distribution, but *Scabbardella* Orchard 1980 (Fig. 3:19) seems to be confined mostly to Wales and the Holy Cross Mountains before the Ashgillian.

The most typical of the North American Midcontinent group of conodonts with coniform elements are robustly denticulated panderodontids, which were represented in the late Middle Ordovician by at least two lineages of the genera *Pseudobelodina* Sweet 1979 (Fig. 3:21), and *Belodina* Ethington 1959 (Fig. 3:17, 18), which in the Late Ordovician were supplemented by several lineages of *Culumbodina* Moskalenko 1973, *Plegagnathus* Ethington & Furnish 1959, and *Parabelodina* Sweet 1979 (Sweet 1979 b). The oldest known species of this group, *B. monitorensis* Ethington & Schumacher 1969, appears in the middle part of the McLish Formation of Oklahoma and initiated a lineage that became widespread in the Midcontinent (Sweet 1981 a; see also Nowlan 1979) but did not enter the Baltic area until the latest Caradocian (Viira 1974; Dzik 1976; S. M. Bergström, personal communication). Precise place of origin and ancestry of *Belodina* is unknown, although the ancestor was almost certainly some species of *Panderodus* (Sweet 1981a). The oldest known serrated *Panderodus*-like conodonts have been described from the Late Llanvirnian of the Baltic area (Dzik 1976) as *Belodella serrata* Dzik 1976 (Fig. 3:20). Its direct relationship to the Silurian *Belodella* is questioned (Ethington & Clark 1981) and it may rather be related to *Pseudobelodina*, which has more elaborated denticulation but still a low degree of diversification of elements in the apparatus (Sweet 1979 b). Because of the rarity of *B. serrata* in Baltic assemblages it can hardly represent a Baltic lineage. Roots of the *Belodina* group are to be looked for elsewhere.

Protopanderodontidae Lindström 1970 (Fig. 3)

This highly diversified group of conodonts (taken to include the Scolopodontidae Bergström 1981, Oneotodontidae Miller 1981, and Teridontidae Miller 1981) includes species having robust elements with a relatively shallow basal cavity and usually a distinct coniform tr element in the apparatus.

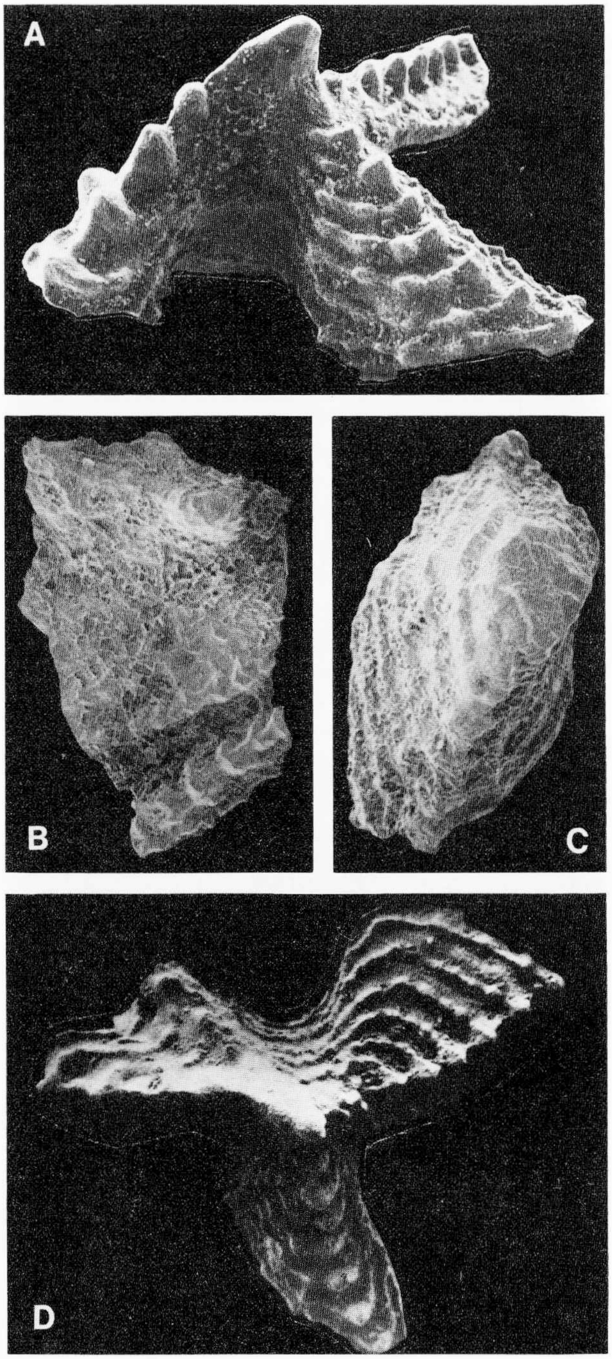
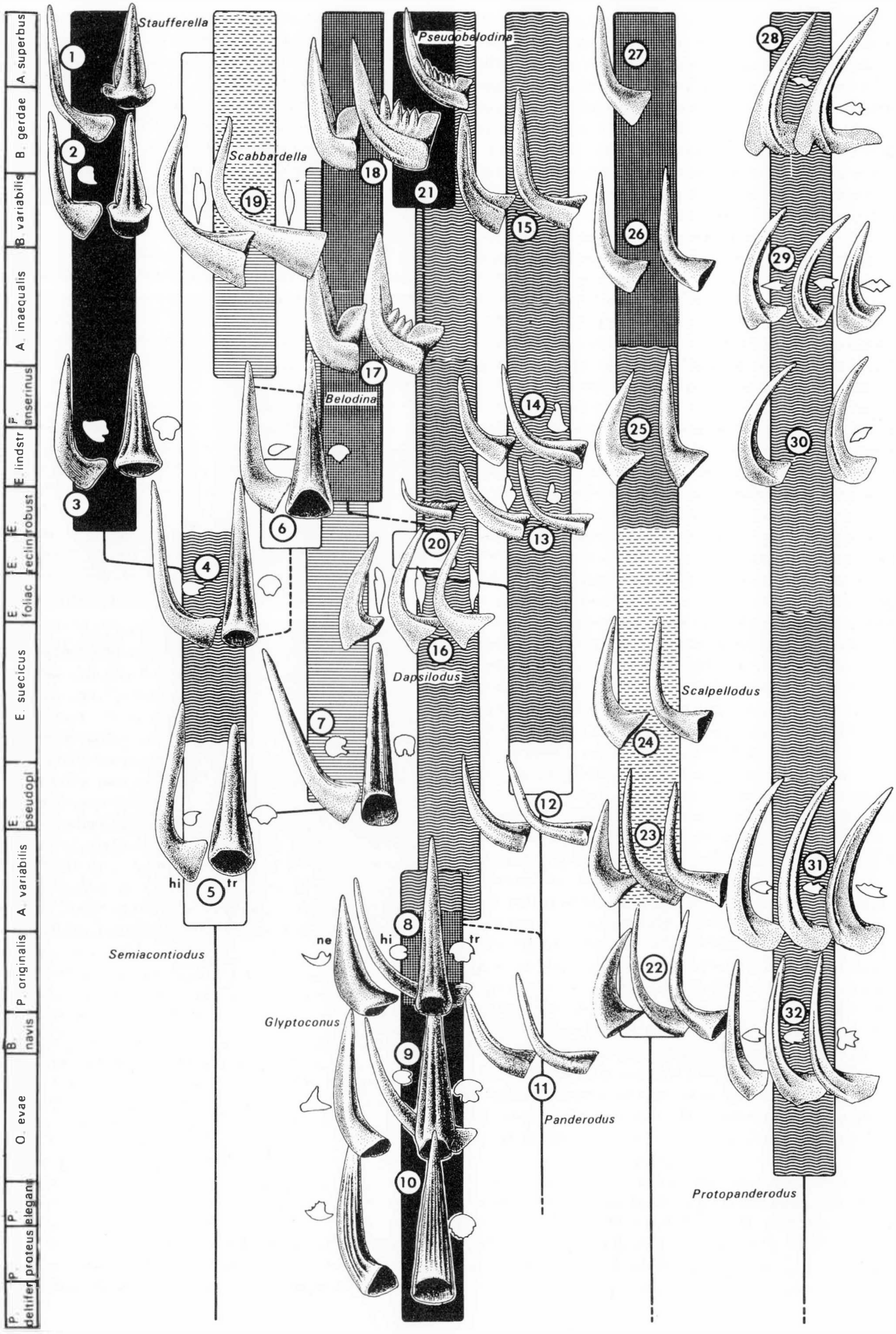


Fig. 2. □A, D. *Polonodus clivosus* (Viira 1974), erratic boulder of glauconitic limestone E-080, early *E. pseudoplanus* Zone as indicated by associated *Baltoniodus*, Mochty near Warsaw, Poland; specimen ZPAL CVI/217, oblique lateral and oral views to compare with *Nericodus*(?) sp.; ×100 and 95, respectively. □B, C. *Nericodus*(?) sp., Ottenby, southern Öland, sample Ot-7, 95 cm above the base of limestone sequence, *P. proteus*(?) Zone, Early Latorpian. □B. Specimen ZPAL CVI/381, oral view, ×48. □C. Specimen ZPAL CVI/382, ×88.

Although no species intermediate in age between the Tremadocian *Semiacontiodus nogamii* (Miller 1969) from the Notch Peak Formation of Utah and *S. cornuformis* (Sergeeva 1963) from the Baltic late Volkhovian and Kundan has been described (however, '*Scalpellodus latus*' of Cooper 1981 may belong here) there is no significant difference in morphology and composition of the apparatus that would substantiate


A. superbus
B. gerdae
B. variabilis
A. inaequalis
F. anserinus
E. lindstr
E. reclin
E. robust
E. foliac
E. suecicus
E. pseudopl
A. variabilis
P. originalis
B. navis
O. evae
P. elegans
P. proteus
P. deltifer
Staufferella
Scabbardella
Pseudobelodina
Belodina
Dapsilodus
Scalpellodus
Semiacontiodus
Glyptoconus
Panderodus
Protopanderodus
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their generic distinction (Dzik 1976). *S. cornuformis* occurred in the Baltic area until the end of the Caradocian without significant change in morphology. A similar form occurs in the Antelope Valley Limestone of Nevada together with *Eoplacognathus suecicus*, but it is unclear whether it represents an influx of the Baltic lineages or is a continuation of a Tremadocian Midcontinent lineage of the genus. Certainly the Midcontinent population of *Semiacontiodus* evolved separately from the Baltic one later, in the time span between the deposition of the Tulip Creek and Mountain Lake formations of Oklahoma (Fig. 3:1–3), and developed a very characteristic incision of the lateral carinae close to the base (*Staufferella* Sweet, Thompson & Satterfield 1975). This feature seems to develop further (Webers 1966; Bergström & Sweet 1966; Sweet *et al.* 1975) and has some biostratigraphic potential. An opposite direction in evolution is represented by *S. longicostatus* (Drygant 1974) from the Holy Cross Mountains and Volhynia (Fig. 3:7), which lost lateral carinae on the tr element (Dzik 1976).

Another lineage of conodonts similar to *Semiacontiodus*, but having two types of symmetrical elements with *Panderodus*-like fissures, helps to link Midcontinent and Baltic conodont faunas (Fig. 3:8–10). Bergström (1979:303) has noted the common occurrence of asymmetrical, wide elements originally described as *Protopanderodus asymmetricus* Barnes & Poplawski 1973, with symmetrical prominently striated and costate elements in several localities, and suggested that they belong to the same apparatus. This species seems to have a very wide, but time–restricted occurrence, being known from the lower part of the Joins Formation of Oklahoma, the upper Fillmore to Juab formations of Utah (Ethington & Clark 1981), the Antelope Valley Limestone of Nevada (Harris *et al.* 1979), the Mystic Conglomerate of Quebec (Barnes & Poplawski 1973), the Catoche, Port au Choix, and Table Head Formations of Newfoundland (Stouge 1982, and in press), the Hølonda Limestone of Norway (Bergström 1979), and the Kundan of Öland and Jämtland, Sweden (Löfgren 1978). Gracile striated elements of the same type occur throughout the Ibex section of Utah; however, below the range of *P. asymmetricus* they are associated with more elongate asymmetrical elements, which together may represent another part of the same assemblage for which the name *Glyptoconus*(?) *striatus* (Graves & Ellison 1941) is available (see Ethington & Clark 1981). Some hyaline symmetrical elements from the lowermost Fillmore Formation of Utah (*'Scolopodus' cornutiformis* Branson & Mehl 1933 and. *S. paracornutiformis* Ethington & Clark 1981), the Jefferson City Formation of Missouri (Kennedy 1980) and the West Spring Creek Formation of Oklahoma may represent roots of this lineage, which then appears to be very typical of the Midcontinent Early Ordovician faunas.

Until now the evolution of *Protopanderodus* Lindström, 1971 has been recognized in only very general terms (see Dzik 1976; Löfgren 1978; Bergström 1978; Harris *et al.* 1979; Kennedy *et al.* 1979) and connections between Midcontinent and Baltic populations cannot be traced exactly. It is not clear if Whiterockian *Protopanderodus* from Oklahoma (Fig. 3:31–32), is conspecific with contemporaneous Baltic populations. Some differences can be found between samples from the Oil Creek and McLish formations where a few *Protopanderodus* elements with a flat anterior side (Fig. 3:32) have been found.

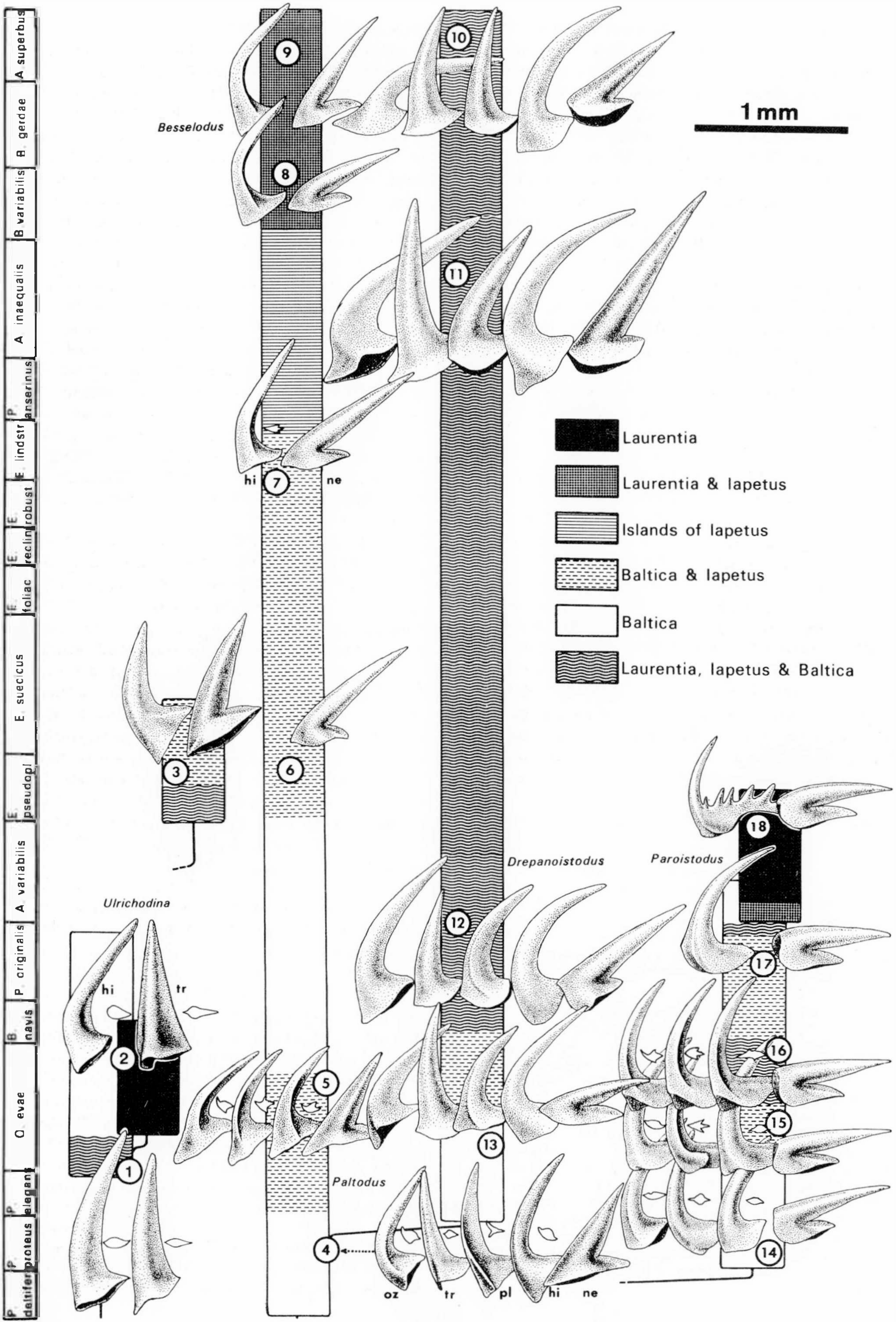
Fig. 3. Proposed interrelationships among selected Baltic and Midcontinent lineages of Panderodontidae and Protopanderodontidae. For explanation of column symbols, see Fig. 4. (1) *Staufferella falcata* (Stauffer 1935); apparatus reconstruction of Sweet *et al.* (1975). (2) *Staufferella* sp. n., Mountain Lake Formation, Oklahoma. (3) *Semiacontiodus* sp. n., McLish Formation, Oklahoma. (4, 5) *S. cornuformis* (Sergeeva 1963), after Dzik (1976). (6) *S. carinatus* Dzik 1976; after Dzik (1976). (7) *S. longicostatus* (Drygant 1974); after Dzik (1976). (8) *Glyptoconus*(?) *asymmetricus* (Barnes & Poplawski 1973); apparatus reconstruction of Bergström (1979). (9) *G.*(?) *striatus* (Graves & Ellison 1941); data from Ethington & Clark (1981). (10) *G.*(?) *cornutiformis* (Branson & Mehl 1933); after Kennedy (1980) and Ethington & Clark (1981). (11) *Panderodus* sp.; after Serpagli (1974). (12, 13) *P. sulcatus* (Fåhraeus 1966); after Löfgren (1978) and Dzik (1976). (14) *P.* sp. McLish Formation, Oklahoma. (15) *P.* sp., Mountain Lake Formation, Oklahoma. (16) *Dapsilodus viruensis* (Fåhraeus 1966); after Dzik (1976) and Löfgren (1978). (17) *Belodina monitorensis* Ethington & Schumacher 1969, McLish Formation, Oklahoma. (18) Same species, Mountain Lake Formation, Oklahoma. (19) *Scabbardella altipes* (Henningsmoen 1948); after Dzik (1976). (20) *Pseudobelodina*(?) *serrata* (Dzik 1976); after Dzik (1976). (21) *P.* sp., Mountain Lake Formation, Oklahoma. (22) *Scalpellodus latus* (van Wamel 1974); after van Wamel (1974). (23) *S. gracilis* (Sergeeva 1974); after Löfgren (1978). (24) *S. viruensis* Löfgren 1978; after Löfgren (1978). (25) *S.* sp.; after Dzik (1976). (26) *S. cavus* (Webers 1966), Mountain Lake Formation, Oklahoma. (27) Same species after Webers (1966). (28) *Protopanderodus liripipus* Kennedy, Barnes & Uyeno 1979; after Dzik (1976), Harris *et al.* (1979). (29) *P. varicostatus* (Sweet & Bergström 1962), Tulip Creek Formation, Oklahoma. (30) *P.* sp., McLish Formation, Oklahoma. (31) *P. gradatus* Serpagli 1974; after Dzik (1976). (32) *P.* sp., Oil Creek Formation, Oklahoma.

Ulrichodinidae Bergström 1981 (Fig. 4)

For a long time *Ulrichodina* Furnish 1938 has been considered to have had a monoelemental apparatus (Sweet & Bergström 1972; Kennedy 1980; Ethington & Clark 1981), and to be an exclusively Midcontinent genus without known ancestry. In most of its known occurrences (never in great number) its symmetrical elements occur with asymmetrical elements of identical coloration and somewhat similar shape (Fig. 4:2). Such an association is also recorded in a sample from the top of the West Spring Creek Formation of Oklahoma, which includes asymmetrical elements that are similar to, or identical with, *Eucharodus parallelus* (Branson & Mehl 1933) (see Kennedy 1980). This is exactly the type of association typical of *Scandodus furnishi* Lindström 1955 (see Bergström 1981), occurring, among other localities, in the Latorpian of Ottenby cliff, Öland (Fig. 4:1). Below the range of typical *Ulrichodina*, in the House Formation of Utah, Ethington & Clark (1981) have found several elements which they identified as '*Scandodus*' sp. n. 5, that are very similar to *S. furnishi* and may represent a Midcontinent population of this species before its divergent evolution into *U. abnormalis* (Branson & Mehl 1933). This species has a tr element with a characteristic, but not unique, undulation of the base, which is known to occur also in *Paltodus* (see Szaniawski 1980). *Ulrichodina* (incl. *Scandodus*) did not develop a geniculate ne element, which separates it from *Paltodus*, and it may be a successor of *Utahconus* Miller 1980, which has a similar apparatus composition and element morphology (Miller 1980).

Distacodontidae Bassler 1925 (Fig. 4)

The oldest known representative of this group (taken to include the Drepanoistodontidae Bergström 1981), *Paltodus*


A. superbus
B. gerdae
B. variabilis
A. inaequalis
P. anserinus
E. lindstr
E. robust
E. reclin
E. foliac
E. suecicus
E. pseudopl
A. variabilis
P. originalis
B. navis
O. evae
P. elegans
P. proteus
P. deltifer
Besselodus
1 mm
Laurentia
Laurentia & Iapetus
Islands of Iapetus
Baltica & Iapetus
Baltica
Laurentia, Iapetus & Baltica
Drepanoistodus
Paroistodus
Ulrichodina
Paltodus
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deltifer Lindström 1955, from the *Ceratopyge* Limestone of Sweden and time-equivalent strata in Estonia and the Holy Cross Mountains (see Szaniawski 1980) still has ne elements of a very primitive shape, with indistinct geniculation, and tr elements of *Ulrichodina* shape (Fig. 4:4). Subsequent evolution of *Paltodus, Drepanoistodus,* and *Paroistodus* has been discussed by Lindström (1971) and Dzik (1976). With the possible exception of *Drepanoistodus* these lineages are confined in their phyletic evolution to the Baltic area, with several brief appearances in the Midcontinent (see Barnes & Poplawski 1973; Ethington & Clark 1981). It has been suggested by Stouge (in press) that element-species '*Cordylodus*' *horridus* Barnes & Poplawski 1973 was associated in the same apparatus with an ne element of *Paroistodus originalis* (Sergeeva 1963) shape. My study of material from Nevada described by Harris *et al.* (1979) supports this idea (Fig. 4:18). It seems that *P. horridus* is a Midcontinent offshoot of the Baltic *Paroistodus* lineage, which developed denticulation on the posterior process of non-ne elements in the same way as in *Protopanderodus insculptus* (Branson & Mehl 1933) (see Bergström 1978).

Lindström (1971) has distinguished two chronospecies of Baltic *Drepanoistodus*, which represent subsequent steps in relative elongation of the cusp of the ne element. Although such an evolutionary transformation obviously took place, it is obscured by high variability of this element within Baltic populations (van Wamel 1974; Dzik 1976; Löfgren 1978). There is no problem finding a distinction between the older of these chronospecies, *D. forceps* (Lindström 1955) (Fig. 4:13), and Midcontinent *D. angulensis* (Harris 1962) from the Joins and overlying formations of Oklahoma (Fig. 4:12) and contemporaneous strata of Utah (Ethington & Clark 1981). *D. angulensis* seems to be more advanced in morphology of the ne element than the second Baltic chronospecies, *D. basiovalis* (Sergeeva 1963), and there is a problem of distinction between *D. angulensis* and the younger *D. suberectus* (Branson & Mehl 1933). It remains also to be determined to what degree evolution of *Drepanoistodus* was independent in the Midcontinent and Baltic area.

Fig. 4. Proposed interrelationships between Baltic and Midcontinent lineages of Ulrichodinidae and Distacodontidae. (1) *Ulrichodina* (*Scandodus*) *furnishi* (Lindström 1955); after Bergström (1981). (2) *Ulrichodina abnormalis* (Branson & Mehl 1933), West Spring Creek Formation, Oklahoma. (3) '*Paltodus*' *jemtlandicus* Löfgren 1978; after Löfgren (1978). (4) *Paltodus deltifer* (Lindström 1955), Ceratopyge Beds of Öland. (5) *P. subaequalis* Pander 1856, Latorpian of Öland. (6) Gen. n. of Löfgren (1978). (7) *Besselodus semisymmetricus* (Hamar 1966); after Dzik (1976). (8) *B.* sp., Mountain Lake Formation, Oklahoma. (9) *B. variabilis* (Webers 1966); data from Webers (1966); see also Aldridge (1982). (10) *Drepanoistodus suberectus* (Branson & Mehl 1933); after Bergström & Sweet (1966) and Webers (1966). (11) Same species, McLish Formation, Oklahoma. (12) *D. angulensis* (Harris 1962), Oil Creek Formation, Oklahoma. (13) *D. forceps* (Lindström 1955); after Dzik (1976). (14) *Paroistodus numarcuatus* (Lindström 1955), Ceratopyge Beds of Öland. (15) *P. proteus* (Lindström 1955), Latorpian of Öland. (16) *P. parallelus* (Pander 1856), Latorpian of Öland. (17) *P. originalis* (Sergeeva 1963); after Dzik (1976). (18) *P.*(?) *horridus* (Barnes & Poplawski 1963), Antelope Valley Limestone, Nevada.

Oistodontidae Lindström 1970 (Fig. 5)

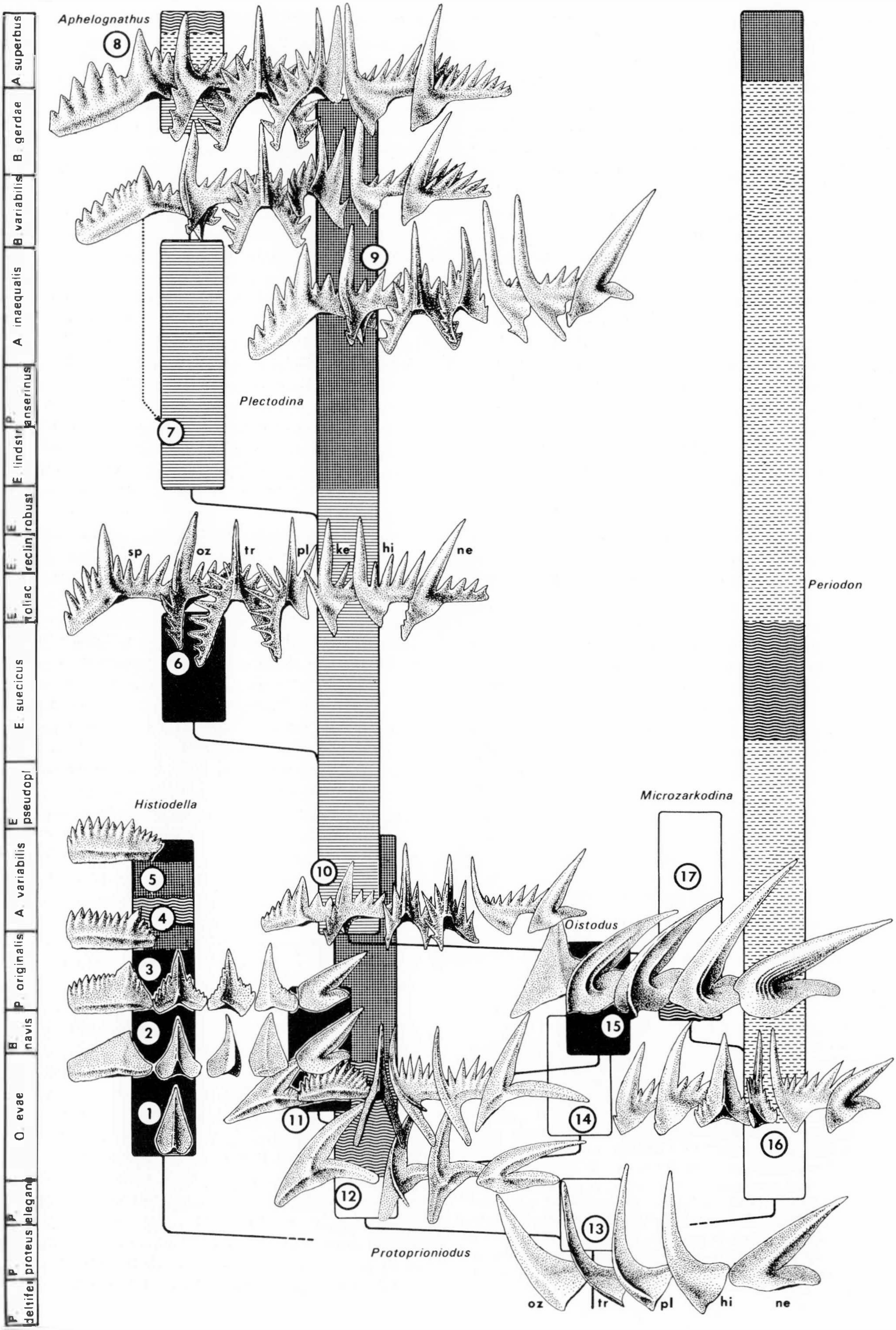
The oldest well-known species of this group (tentatively taken to include the Juanognathidae Bergström 1981) is '*Triangulodus*' *subtilis* van Wamel 1974, which appeared in the Baltic area in the *P. proteus* Zone (van Wamel 1974; Fig. 5:13). Having very primitive morphology of elements, the apparatus of this species differs from similar apparatuses of the Distacodontidae in triramous tr and pl elements and from *Eoneoprioniodus* (= *Triangulodus*) in biramous oz and triramous pl, as well as in albid, instead of hyaline, elements. It may be considered an ancestor of several lineages of *Protoprioniodus* McTavish 1973, which developed mostly in Australia (McTavish 1973; Cooper 1981) but occasionally invaded the Midcontinent (Ethington & Clark 1981) and the Baltic area (van Wamel 1974; Cooper 1981). To this genus may be assigned a lineage typical of the Midcontinent represented by '*Gothodus*' *marathonensis* Bradshaw 1969 (Fig. 5:11), which may be a direct successor of Australian '*Microzarkodina*' *adentata* McTavish 1973. It has a highly diversified apparatus, with denticulated ramiform elements, and was widely distributed from the District of Mackenzie (Tipnis *et al.* 1979), Utah (Ethington & Clark 1981), through Texas (Bradshaw 1969), Oklahoma (Mound 1965; McHargue 1975), to Scotland (Higgins 1967).

Histiodella Harris 1962 developed from a *Juanognathus*-like ancestor (Ethington & Clark 1981) that probably differed from '*T*'. *subtilis* only in the reduced posterior processes of tr and pl elements. The *Histiodella* lineage (Fig. 5:1–5), was typical of marginal areas of Laurentia, and is known to have occurred during the Early Whiterockian in the American part of the North Atlantic province (including the Hølonda Limestone of Norway; Bergström 1979) and in the Midcontinent (Barnes & Poplawski 1973; Landing 1976; Harris *et al.* 1979; Ethington & Clark 1981). Its advanced species, *H. holodentata* Ethington & Clark 1981, briefly invaded the Baltic area and the Holy Cross Mountains in the Kundan (Viira 1974; Dzik 1976, 1978). Evolution of denticulation in the *Histiodella* lineage provides an excellent tool for time correlation of the Midcontinent Early Whiterockian (McHargue 1982; Stouge in press).

The Midcontinent and Baltic lineages of *Oistodus* Pander 1856 differ from each other in the width of lateral processes of tr elements and they may have had an independent origin from *Protoprioniodus* (Fig. 5:14, 15).

Periodontidae Lindström 1970 (Fig. 5)

The group is tentatively taken to include the Cyrtoniodontidae Hass 1959 (see confusion with *Cyrtoniodus* in Bergström 1981). The oldest, still unnamed species of *Periodon* appears in the *P. elegans* Zone or slightly earlier (van Wamel 1974). It differs from contemporaneous Oistodontidae in the ramiform appearance of all elements except ne ones (Fig. 5:16). Even in the *O. evae* Zone some sp elements can be found with undenticulated blades. Tr and pl elements have well-developed lateral processes (Serpagli 1974; Landing 1976; Dzik 1976), which puts the species close to *Microzarkodina flabellum* (Lindström 1955), its supposed derivative (see Löfgren 1978). *Microzarkodina* has reduced posterior processes in these types of elements and in the Kundan developed denticulation on the anterior process of the sp element, being


A superbus
B gerdae
B variabilis
A inaequalis
P. anserinus
E lindstr
E robust
E reclin
E foliac
E suecicus
E pseudopl
A variabilis
P originalis
B navis
O evae
P elegans
P proteus
P deltifer
Aphelognathus
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Plectodina
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Periodon
Histiodella
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Microzarkodina
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Oistodus
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Protoprioniodus
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in these respects similar to the oldest species of *Plectodina* (see Sweet 1981a:246), *'Phragmodus' polonicus* Dzik 1978, which, however, has an oz element with an anterolateral process (Dzik 1978; Stouge in press; Fig. 5:10). Evolution of all these lineages seems to be concentrated in the North Atlantic province, but they differ in their distribution, and *Microzarkodina* very rarely invaded the Midcontinent (Ethington & Clark 1981) while *Plectodina* is unknown in the Baltic area.

The evolution of *Plectodina* has great importance for the later history of conodont faunas but it is not possible to reconstruct it now in detail. Presumably several independent lineages evolved in the seas of the Welsh Massif, the Appalachians, and the western margin of the Midcontinent. These are distinguishable mostly in the development of denticulation on the ne element. Welsh *P. flexa* (Rhodes 1952) (Fig. 5:7) may be an ancestor of younger *Aphelognathus rhodesi* (Lindström 1959) from the Crug Limestone (Orchard 1980; Sweet 1981a) which differs from it only in the complete reduction of the anterior ('lateral') process of the oz element (Fig. 5:8). This species was the most characteristic among non-Baltic forms that appeared in the Oanduan of the Baltic area (Fig. 10A–G; Viira 1974) and destroyed the climactic Baltic conodont community evolving there since the Arenigian (Fig. 11). The *Aphelognathus* lineages appeared in the Midcontinent somewhat later, the oldest species being *A. kimmswickensis* Sweet, Thompson & Satterfield 1975 of Kirkfieldian age (Sweet 1981a), which may even be an independent derivative of *P. aculeata* (Stauffer 1935) (Sweet 1981a).

Prioniodontidae Bassler 1925 (Fig. 6)

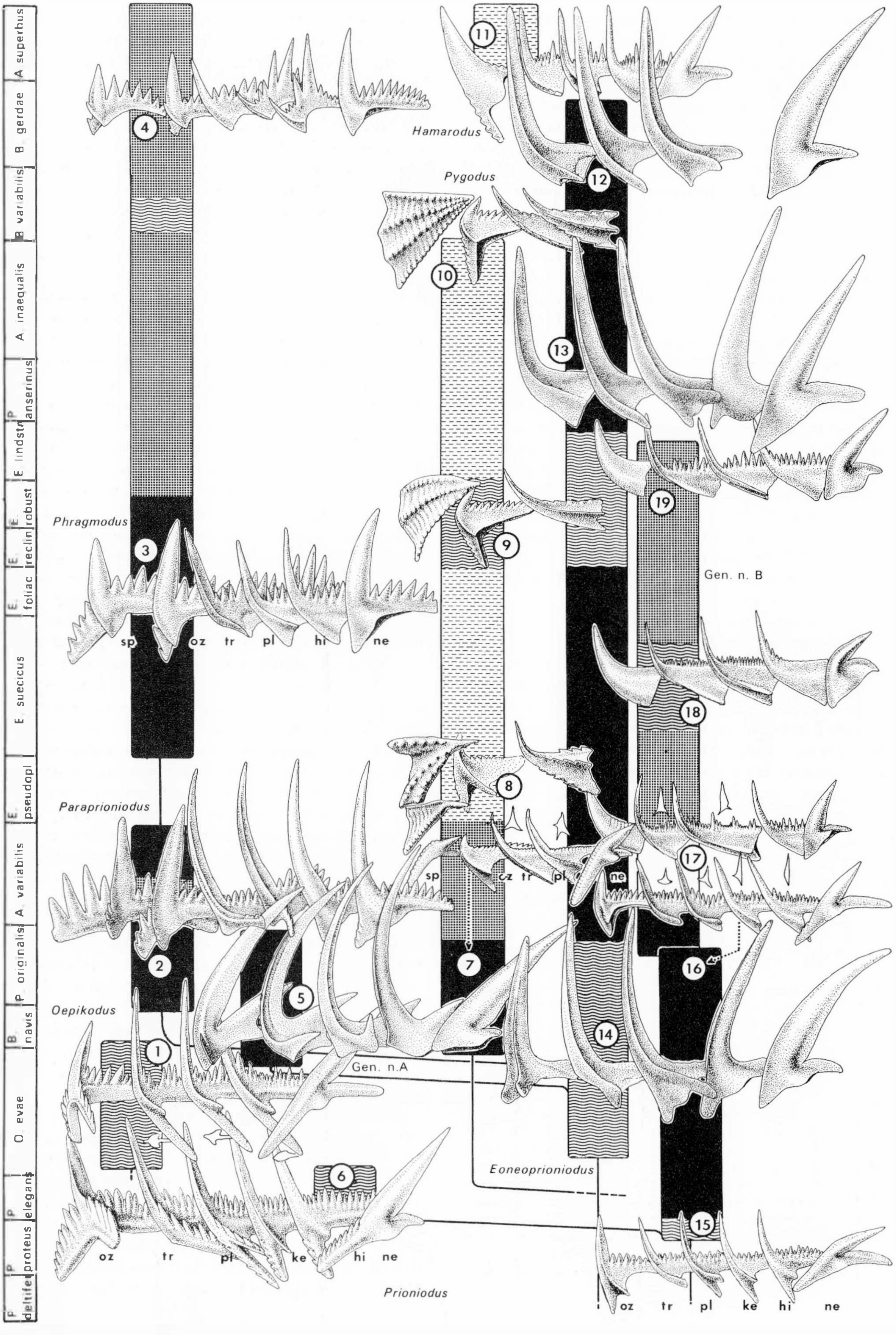
The group is taken to include the Oepikodontidae Bergström 1981 and Pygodontidae Bergström 1981. Still inadequately known species of *Acodus* Pander 1856 appearing in the Tremadocian of the Baltic area and the Holy Cross Mountains are supposed to be derivatives of *Paltodus*, and are the oldest representantives of this group. They differ from *Paltodus* in having much more prominent lateral ribs or processes of the oz, tr, and pl elements (Lindström 1971; Szaniawski 1980). Among Baltic *Acodus* s.l. are almost certainly the ancestors of both the Oistodontidae and the Prioniodontidae. Origin of the latter is marked by development of a fourth rib on the pl element. *Tripodus distortus* (Branson & Mehl 1933) (= *Diaphorodus delicatus*; see Lindström 1977; Kennedy 1980; Ethington & Clark 1981), which is closely similar to Baltic *Acodus* and possibly conspecific with one of its species, is widespread in the Midcontinent, among other localities in the upper West Spring Creek Formation of Oklahoma (Fig. 8:22). Diversification of apparatuses with ramiform elements probably took place in Australia during the deposition of the Emanuel Group (McTavish 1973) but still little is known about the origin of the most characteristic and widespread species of this family: *Prioniodus elegans* Pander 1856; *Oepikodus evae* (Lindström 1955), and *Prioniodus*(?) *communis* (Ethington & Clark 1964). In the case of the first two species this significantly undermines concepts of zones based on their occurrences.

Fig. 5. Proposed interrelationships among Baltic and Midcontinent lineages of Oistodontidae and Periodontidae. (1) *Histiodella* sp. n.; after Ethington & Clark (1981). (2) *H. altifrons* Harris 1962, Joins Formation, Oklahoma. (3) *H. sinuosa* (Graves & Ellison 1941), Oil Creek Formation, Oklahoma. (4) *H. holodentata* Ethington & Clark 1981; after Dzik (1978). (5) *H.* sp. n.; after Harris *et al.* (1979). (6) *Plectodina* cf. *joachimensis* Andrews 1967, Dutchtown Formation, Missouri. (7) *P. flexa* (Rhodes 1952), Llandeilo Limestone, Wales. (8) *Aphelognathus*(?) *rhodesi* (Lindström 1959), Oanduan of Baltic area. (9) *Plectodina* sp. n., 'Bromide' Formation, Oklahoma. (10) *P. polonica* (Dzik 1978); data from Dzik (1978) and Stouge (1980). (11) *Protoprioniodus*(?) *marathonensis* (Bradshaw 1969), Joins Formation, Oklahoma. (12) *P. elongatus* (Lindström 1955); after van Wamel (1974). (13) *P.*(?) *subtilis* (van Wamel 1974); after van Wamel (1974). (14) *Oistodus lanceolatus* Pander 1856 (not illustrated). (15) *O.*(?) *multicorrugatus* Harris 1962, Joins Formation, Oklahoma. (16) *Periodon* sp. n., uppermost Latorpian, Öland. (17) *Microzarkodina ozarkodella* Lindström 1971 (not illustrated).

Prioniodus(?) *communis* (Fig. 6:15), which may be conspecific with *'Gothodus' microdentatus* van Wamel 1974, that appears in the Baltic area before *P. elegans* (see van Wamel 1974), and evolved in the Midcontinent into a form with rather robust lateral process of the oz (incl. sp) element (Fig. 6:16). I am inclined to identify this species, which occurs in the basal part of the Joins Formation of Oklahoma, with the Argentinian *P.*(?) *intermedius* Serpagli 1974 rather than with Australian *P.*(?) *minutus* McTavish 1973, as has been done by Ethington & Clark (1981). I would consider identity of *P.*(?) *intermedius* with *P.*(?) *communis* unlikely. *O. evae* deeply differs from *P.*(?) *communis* in having tetraramous rather than triramous tr elements (Fig. 6:1; Bergström & Cooper 1973).

In the Oklahoma section supposed *P.*(?) *intermedius* is followed, with some overlap, by a prioniodontid species with a *Scalpellodus*-shaped oz(sp) element in its apparatus, and probably conspecific or closely related to *'Belodella' robusta* Ethington & Clark (Fig. 6:17). This lineage occurs without significant changes throughout almost the entire Whiterockian (Bergström 1978; Harris *et al.* 1979; Stouge in press) with very few short-lived occurrences in the Baltic area (Löfgren 1978). The Oklahoma material is too meager to test suspicion of possible *P.*(?) *intermedius* – *'B'. robusta* relationships but because of the general plan of the apparatus, a prioniodontid relationship of the discussed lineage seems indisputable. It has nothing to do with Siluro-Devonian *Belodella* Ethington 1959, which is rather an offshoot of serrated panderodontids, and there is urgent need for a generic name for the Ordovician species.

An unnamed prioniodontid that occurs in the Fillmore Formation of Utah ('?*Ruetterodus* sp.' of Ethington & Clark 1981) and in the Joins Formation of Oklahoma (*'Haddingodus'* of Mound 1965; Fig. 6:7 herein) may help in understanding the apparatus of the bizarre North Atlantic *Pygodus* Lamont & Lindström 1957. Its apparatus has a prioniodontid plan, but differs in the rather peculiar denticulation and reduction of the posterior process of sp element while the anterior and lateral processes are connected by the expanded base (Fig. 6:7). Composition of this apparatus is reconstructed very provisionally and more detailed studies may change many details; however, it seems that typical *Pygodus* apparatuses can be derived from it through intermediate forms described by Landing (1976) as *Fryxellodontus? ruedemanni* Landing 1976 (incl. *Stolodus* sp. cf. *S. stola*) from the *O. evae* Zone of New York and by Löfgren (1978) from the Kundan of Sweden. The evolution of *Pygodus* has been used as a basis for zonation of the Llandeilian of the North Atlantic and Baltic provinces


A superbus
B gerdae
B variabilis
A inaequalis
P anserinus
E lindstr
E robust
E reclin
E foliac
E suecicus
E pseudopl
A variabilis
P originalis
B navis
O evae
P elegans
P proteus
P deltifer
Hamarodus
Pygodus
Phragmodus
Paraprioniodus
Oepikodus
Gen. n.A
Gen. n. B
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Prioniodus
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(Bergström 1971); therefore the mode of its evolutionary transformations is of particular interest to geochronology. Fåhraeus & Hunter (1981) have opposed the earlier assumption that *P. serra* (Hadding 1913) and *P. anserinus* Lamont & Lindström 1957, were parts of the same evolutionary lineage, and stated that *P. anserinus* evolved allopatrically from *P. serra* with significant overlap in their time distribution. Having *a priori* nothing against such an interpretation I must note that not enough evidence for it has been presented by Fåhraeus & Hunter (1981). Their data show an increase in the contribution of sp elements with four rows and a decrease of three-row ones. Although each type of sp elements is typical of the particular species, their common occurrence in samples intermediate in age between occurrences of typical populations of both species, does not necessarily mean that two genetically isolated populations are represented by each of these samples. Biometrical evidence for a morphologic gap between *P. serra* and *P. anserinus* morphotypes occurring in the same samples is necessary to show this. Also, it must be kept in mind that the fourth row on the sp element of *Pygodus* appears in ontogeny with some delay in respect to the other rows. A simple change in the population dynamics of intermediate populations may involve changes in the numerical contribution of particular morphotypes to the samples.

Hamarodus Viira 1974, which appears in the Baltic area (Bergström 1971; Viira 1974) and the Holy Cross Mountains (Dzik 1976, 1978) in the upper part of the *A. superbus* Zone (Fig. 6:11), also present in Wales (Orchard 1980) and the Carnic Alps (Serpagli 1967), is not known from the Midcontinent. Its apparatus, which has sp and oz elements with a very deep basal cavity, as well as tr and pl elements with reduced but still denticulated lateral processes, suggests a relationship to Gen. n. B ('Ordovician *Belodella*') rather than to *Periodon* (see Bergström 1981), which differs in the pattern of denticulation. Both interpretations would lead to the same conclusion regarding its supposed North Atlantic origin.

Fig. 6. Proposed interrelationships among selected Baltic and Midcontinent lineages of Phragmodontidae and Prioniodontidae. (1) *Oepikodus evae* (Lindström 1955), Latorpian of Öland. (2) *Paraprioniodus costatus* (Mound 1965), Joins Formation, Oklahoma. (3) *Phragmodus flexuosus* Moskalenko 1973, Antelope Valley Limestone, Nevada. (4) *P. inflexus* Stauffer 1935; after Sweet (1981 a). (5) '*Multioistodus*' *compressus* Harris & Harris 1962?, Oil Creek Formation, Oklahoma. (6) *Prioniodus elegans* Pander 1856; after van Wamel (1974) and Bergström (1981). (7) *Pygodus*(?) aff. *ruedemanni* (Landing 1976), Joins Formation, Oklahoma. (8) *Pygodus* sp. n.; after Löfgren (1978). (9) *P. serra* (Hadding 1913); after Dzik (1976) and Löfgren (1978). (10) *P. anserinus* Lamont & Lindström 1957; after Bergström (1971) and Sweet & Bergström (1962). (11) *Hamarodus europaeus* (Serpagli 1967); after Dzik (1976) and Orchard (1980). (12) *Eoneoprioniodus alatus* (Dzik 1976), Mountain Lake Formation, Oklahoma. (13) Same species, McLish Formation, Oklahoma. (14) *E. cryptodens* Mound 1965, Joins Formation, Oklahoma. (15) '*Gothodus*' *microdentatus* van Wamel 1974 and *Prioniodus*(?) *communis* (Ethington & Clark 1964); after van Wamel (1974) and Ethington & Clark (1981). (16) *P.*(?) *intermedius* Serpagli 1974?, Joins Formation, Oklahoma. (17) Aff. '*Belodella*' *robusta* Ethington & Clark 1981, Oil Creek Formation, Oklahoma. (18) '*Belodella*' *jemtlandica* Löfgren 1978; after Löfgren (1978). (19) '*B.*' *nevadensis* (Ethington & Schumacher 1969), McLish Formation, Oklahoma.

Phragmodontidae Bergström 1981 (Fig. 6)

The oldest species of *Eoneoprioniodus* Mound 1965, which occurs in the *O. evae* Zone of Argentina (Serpagli 1974) and Australia (Cooper 1981), but invaded the Midcontinent somewhat later, during deposition of the Kanosh shale of Utah and the Joins Formation of Oklahoma (Mound 1965; Ethington & Clark 1981), and appearing even later briefly in the Baltic area (Lindström 1971; van Wamel 1974; Dzik 1976; Löfgren 1978), differs from *Acodus* and *Tripodus* only in having hyaline and generally much larger elements. Baltic *E. brevibasis* (Sergeeva 1963) is a direct successor of primitive Australian *E. larapintinensis* (Crespin 1941) rather than a relative of contemporaneous, alate Midcontinent *E. cryptodens* Mound 1965 (Fig. 6:14). *E. alatus* (Dzik 1976) has a Midcontinent ancestry and is common in the McLish and the Mountain Lake formations of Oklahoma (Fig. 6:13).

Conodonts that are similar in the apparatus organization pattern, but different in having processes of all except ne elements expanded into sharp-pointed blades, are known from the most of the early Whiterockian Midcontinent localities and were described by Ethington & Clark (1981) as *Multioistodus compressus* Harris & Harris 1962. Although the specific name may be appropriate (this is hard to decide without revision of the types of *M. compressus*), this apparatus (Fig. 6:5) is completely different from the apparatus of the type species of *Multioistodus, M. subdentatus* Cullison 1938, from the Dutchtown Formation of Missouri, which also occurs in the Joins Formation of Oklahoma. *M. subdentatus* has a cusp with a rounded cross-section, has weakly diversified and very variable elements of the apparatus, and lacks a geniculate ne element. It may rather be related to *Cordylodus*. In the Joins Formation a third *Multioistodus*-like species occurs, which however, has non-hyaline elements and differs from both species discussed above also in having rather short, straight and flat cusps. It seems to have no direct relation to '*M.*' *compressus* because its tr and pl elements have reduced posterior processes. Possible relationships to Oistodontidae seem to be unlikely because of the triramous oz(sp) element (Fig. 8:1). These two *Multioistodus*-like lineages require new generic names. The common occurrence of so many and such morphologically similar forms, which are unknown elsewhere, remains to be explained.

Another strange Midcontinent lineage is represented by '*Scandodus*' *sinuosus* Mound 1965, which in Utah and Oklahoma constitutes the core of most pre-*Phragmodus* assemblages (Fig. 11). Elements of its apparatus are almost homeomorphic with primitive *Eoneoprioniodus* species but, contrary to the reconstruction by Ethington & Clark (1981), the apparatus lacks geniculate ne elements. An origin from *Eoneoprioniodus* by reduction of the ne element, or from *Scolopodus*, seems equally probable.

Paraprioniodus costatus (Mound 1965) (Fig. 6:2) may have evolved from *Eoneoprioniodus cryptodens* and may have given rise to early *Phragmodus* Branson & Mehl 1933 (Sweet & Dzik in preparation). Until the end of the Ordovician *Phragmodus* was the most abundant conodont in the eastern Midcontinent. Before the appearance of *P. undatus* Branson & Mehl 1933 in the Oanduan of the Baltic area, the only Baltic record of this genus is two specimens of an advanced *P. flexuosus* Moskalenko 1973 found by Bergström (1971) in the Kukrusean of Estonia.

Balognathidae Hass 1959 (Figs. 7, 8)

The group is taken to include the Polyplacognathidae Bergström 1981. *Baltoniodus* Lindström 1971 developed its apparatus independently of and later than *Prioniodus* (Lindström 1971; Dzik 1983), and is a derivative of the younger part of possibly the same lineage of *Acodus* (Fig. 8:21). Until the invasion of the American part of the North Atlantic province, and subsequently the Midcontinent, by *B. variabilis* (Bergström 1962) and its successors, the evolution of this genus was almost completely restricted to the Baltic and adjacent areas (Dzik 1976). Some very rare species of *Baltoniodus* with incompletely known apparatuses occurred before the appearance of *B. variabilis* in the Midcontinent and the North Atlantic provinces, however (Fig. 8:18).

The origin from *Baltoniodus*, and the early evolution of *Amorphognathus* Branson & Mehl 1933, is well marked by changes in morphology of the ne element and development of a platform on the sp element (Fig. 8:8, 9). In the Late Volkhovian of the Baltic area there was a species of *Amorphognathus* similar to *Baltoniodus navis* (Lindström 1955) in morphology of the ramiform elements and with an ne element that differed from the corresponding element of *Baltoniodus* only in a much larger angle between the cusp and posterior process – *A. falodiformis* (Sergeeva 1963) (Lindström 1977; Fig. 7A–E herein). In some populations of *B. navis* with robust elements, the sp element has in some cases a lateral ridge on the posterior process (Dzik 1976, Fig. 22 a). Fragments of similar appearance with a somewhat better developed platform have been identified in a sample 30 cm below the top of the *Asaphus lepidurus* Zone (Volkhovian) at Hälludden, Öland (Fig. 7A) associated with typical ne elements of *A. falodiformis* (Fig. 7E). A sample from the overlying, about 10 cm thick bed contains sp elements with a somewhat more prominent posterolateral process and with an initial crista on the posterolateral side of the base of the ne element that is connected with a crista on the posterior process in its proximal part. This V-shaped arrangement of cristae appears to be well developed in a sample from the top layer of the Volkhovian at Hälludden. All available specimens of the sp element from several samples of the overlying *Asaphus expansus* Zone have a very weakly developed bifurcation of the anterolateral process, with its widened posterior part of the base lacking denticulation (Fig. 8:9). This is the typical *A. variabilis* Sergeeva 1963. Subsequent samples show, however, gradual development of the platform and posterolateral process, which is always shorter than the posterior one. Profound changes in the morphology of the anterolateral process occur between samples bordering the discontinuity surface between the *A. expansus* and *A. raniceps* Zones (Bohlin 1949; Jaanusson 1957). The basal sample from the *A. raniceps* Zone contains sp specimens with well-developed denticulation on both rami of the anterolateral process, which are of approximately equal length. Later evolution of *Amorphognathus* has been discussed by Dzik (1976, 1978). It may be worth adding that the transition from *B. navis* to *B. prevariabilis parvidentatus* (Sergeeva 1963) occurs in the uppermost Volkhovian and the transition from the latter chronosubspecies into *B. p. medius* (Dzik 1976) is in the middle of the *A. expansus* Zone, while the typical population of *B. p. medius* has been recognized 190 cm above the base of the *A. raniceps* Zone.

Elongation of the posterior ramus of the anterolateral process in the sp elements marks the origin and early development of *Eoplacognathus* Hamar 1966. The oldest species known, *E. zgierzensis* Dzik 1976, which has been found 260 cm below the top of the Kundan in the Gullhögen quarry, Västergötland (the best specimen being unfortunately lost during manipulations), and in the Ohesaare borehole, Estonia, has a posterior ramus of the process only about two times longer than anterior one, while those of *Amorphognathus* are of almost equal length and all younger species of *Eoplacognathus* have a posterior ramus several times longer than the anterior one in comparable ontogenetic stages of development. *E. zgierzensis* has an almost symmetrical pair of oz elements, which, as in *E. pseudoplanus* (Viira 1974), have all processes of similar length. Asymmetry is better visible in oz elements of *E. pseudoplanus* and even more distinct in *E. suecicus* Bergström 1971, which has longer anterolateral processes of these elements. Subsequent evolution of the Baltic *Eoplacognathus* lineage has been discussed by Bergström (1971). It seems that *Eoplacognathus* was confined in its phyletic evolution to the central part of the Baltic area while *Amorphognathus* evolved during the same time in areas close to the Holy Cross Mountains, Armorican, and Welsh massifs (Dzik 1978).

The lineage typical of the North American part of the North Atlantic province and the Midcontinent, represented by *Polyplacognathus friendsvillensis* Bergström 1971 and *P. sweeti* Bergström 1971, has been considered unrelated to Baltic *Eoplacognathus* and close to later *P. ramosus* Stauffer 1935 on the basis of the presence of marginal crenulation of the platform (Bergström 1971). I propose here another orientation of oz elements of *Polyplacognathus* than that proposed by Bergström (1971) with his posterior process being anterolateral (Fig. 8:3–5). When compared in this way with *E. suecicus*, which invaded the Midcontinent before the first appearance of *P. friendsvillensis*, not many differences can be found. Early populations of *P. friendsvillensis* from the lower part of the McLish Formation of Oklahoma contain juvenile oz elements that are very similar to those of *E. suecicus*. The typical feature of the American lineage, whose later evolution has been described by Bergström & Carnes (1976), seems to be a twisted row of denticles on the anterolateral process in its proximal part in the oz elements. At least two species of *Eoplacognathus* show this feature: *E.* n. sp. A of Bergström 1971 from the Furudal Limestone of Sweden and '*E. foliaceus–reclinatus* transition' of Harris *et al.* (1979) from the Antelope Valley Limestone of Nevada. There is no way to derive *P. ramosus* from *P. sweeti*. It can quite easily be derived from *E. elongatus* (Bergström 1971), however, which invaded the Midcontinent before the first appearance of *P. ramosus*. Some specimens of *E. elongatus* from the Mountain Lake Formation of Oklahoma have crenulation of the platform margin. It appears thus that *Polyplacognathus* in its current meaning consists of two lineages that are not directly related to each other. To avoid this obviously polyphyletic grouping I would suggest including *Eoplacognathus* in synonymy with *Polyplacognathus*, as no difference in apparatus composition or element construction has been indicated. *P. sweeti* has a very wide distribution and also invaded the Baltic area (Bergström 1971; Drygant 1974).

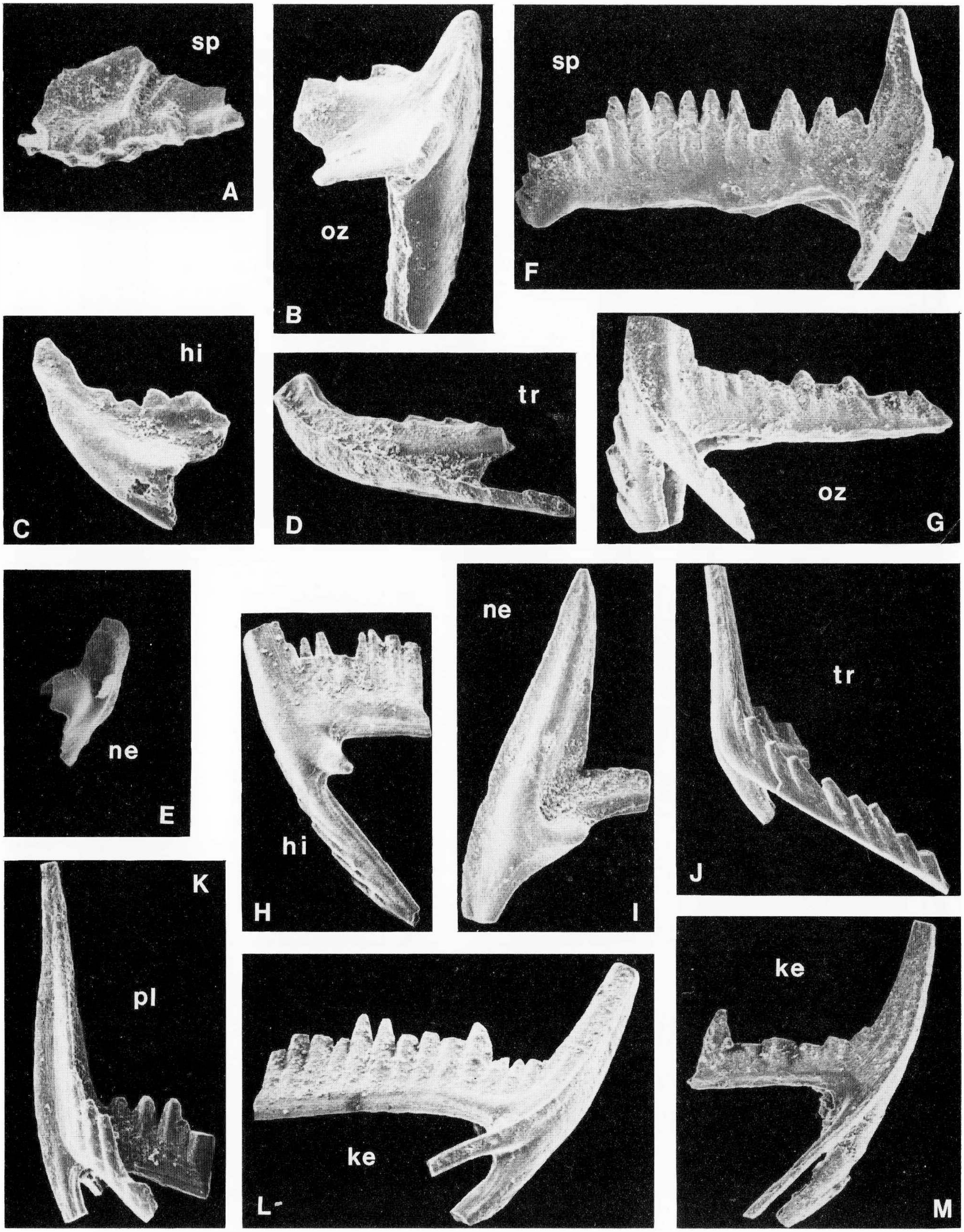
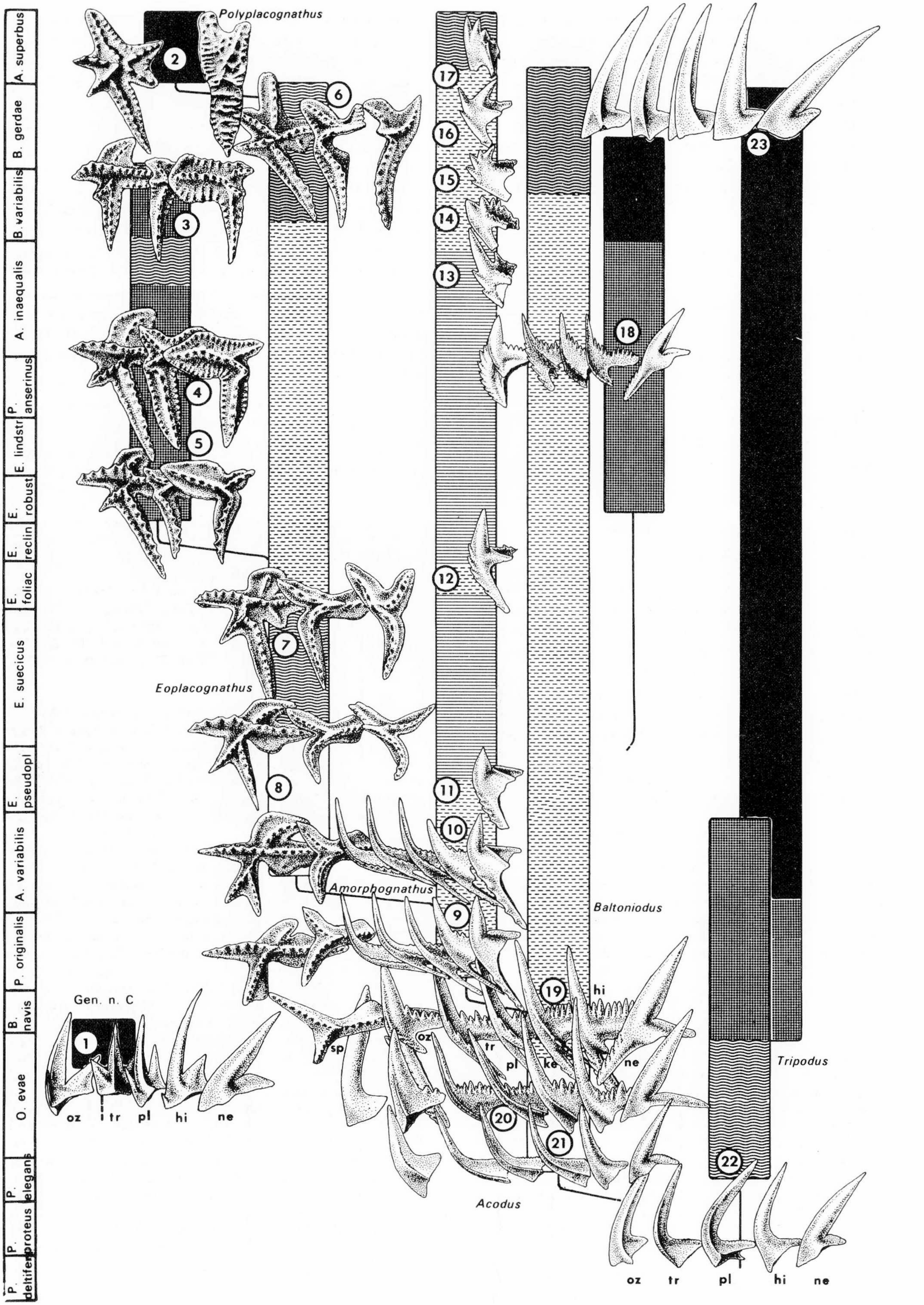


Fig. 7. □A–E. *Amorphognathus falodiformis* (Sergeeva 1963). □F–M. Associated with it *Baltoniodus navis* (Lindström 1955). Sample Ha 15, 30 cm below the top of Volkhovian, Hälludden, Öland. Specimens ZPAL CVI/383–396, respectively; all ×80.


A. superbus
B. gerdae
B. variabilis
A. inaequalis
P. anserinus
E. lindstr
E. robust
E. reclin
E. foliac
E. suecicus
E. pseudopl
A. variabilis
P. originalis
B. navis
O. evae
P. elegans
P. proteus
P. deltifer
Polyplacognathus
Eoplacognathus
Amorphognathus
Baltoniodus
Tripodus
Acodus
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Complexodus Dzik 1976, which occurs in the Holy Cross Mountains in great numbers has an unknown origin, although it has a wide distribution and is also known from China (An 1982). Similarly unknown is the origin of *Rhodesognathus* Bergström & Sweet 1966, which is represented in the Midcontinent and Wales by species distinct from that of the Holy Cross Mountains, *R. polonicus* (Dzik 1976), which has a much better-developed platform. According to Sweet (1979 a) the apparatus of *Rhodesognathus* may include ramiform elements similar to those of *Amorphognathus*.

Icriodontidae Müller & Müller 1957

The oldest well-known species of this group, *Icriodella superba* Rhodes 1953, appears rather suddenly and without known direct ancestry in the Oanduan of the Baltic region (Viira 1974; Fig. 10H–J herein) and slightly earlier in the Midcontinent (Bergström & Sweet 1966; Webers 1966). Its apparatus composition suggests a direct relationship to the Balognathidae. The occurrence of its supposed ancestor in the Llanvirnian of the Armorican Massif (Lindström *et al.* 1974) as well as earlier appearance in Wales (Bergström 1971), suggest North Atlantic provenance of the lineage.

Ordovician paleobiogeography of the Baltic, Midcontinent, and adjacent areas

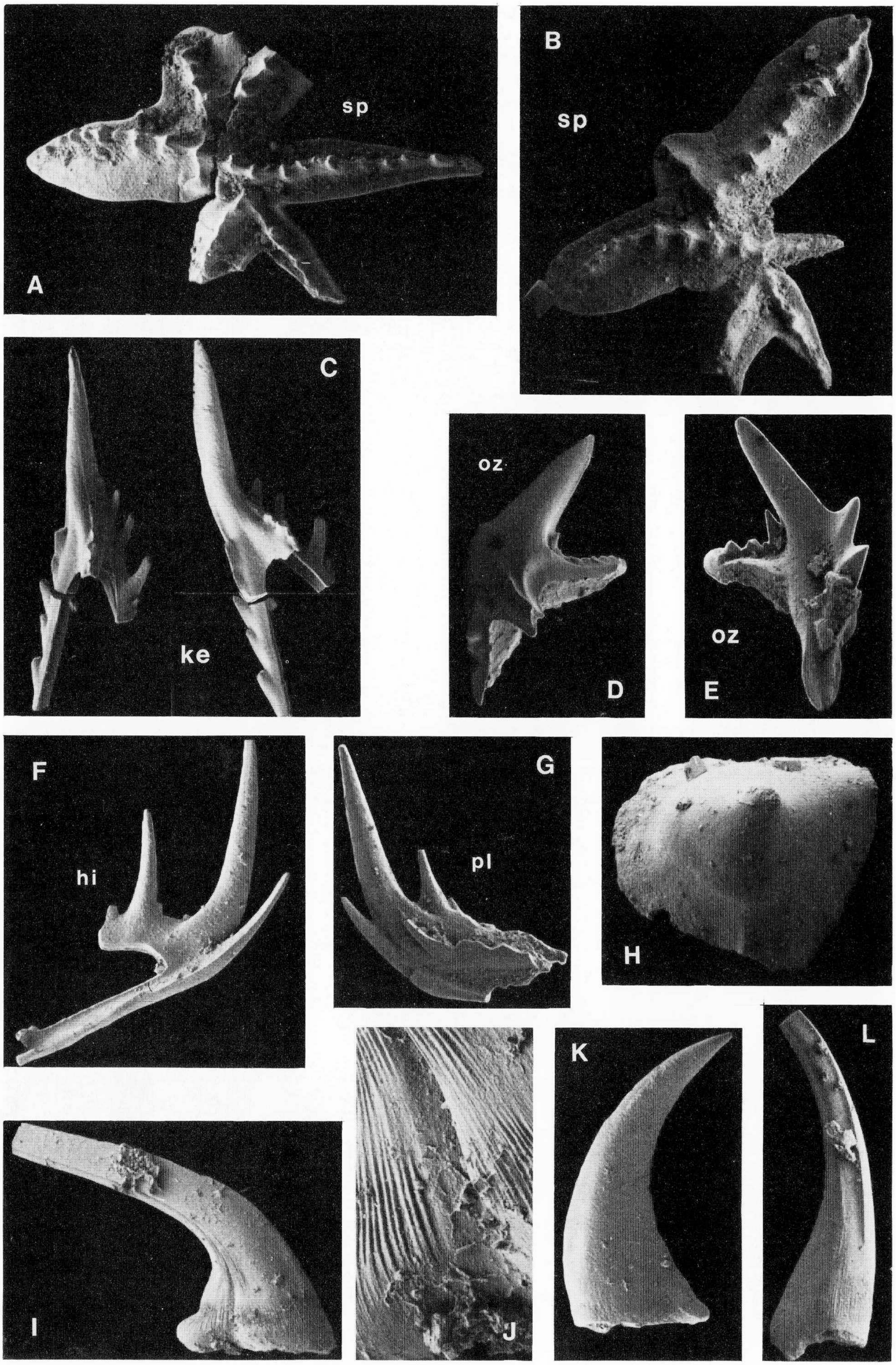
According to paleomagnetic data from the early Middle Ordovician of the Midcontinent area, the latter was part of the continental block of Laurentia, which was located close to the equator, while the latitude of the Baltic area at that time was approximately 60° S (Fig. 1; Bergström 1979). Few paleomagnetic data are available regarding the Early Paleozoic massifs in between, which were incorporated into larger continental blocks during the Caledonian and Hercynian orogenies. Probably, most of them originated as parts of island arcs bordering subduction zones of diverse ages. Their presumed position in the Ordovician may be reconstructed with some degree of confidence on the basis of knowledge of their geological history (e.g., Bergström 1979; Dzik 1978, 1984; Bruton & Bockelie 1980). Epicontinental seas associated with each of these continental blocks certainly formed their own ecosystems, which were separated from other shelf-water ecosystems by extended areas of oceanic environment (Fig. 1). Therefore, they can be treated as distinct biogeographic units in terms of island biogeography (see MacArthur & Wilson 1967). Available quantitative data on the distribution of conodont assemblages in particular areas support such a view. It is well shown on logs of the contribution of the common conodonts that form the cores of particular assemblages, when high-rank taxonomic assignment of a particular conodont lineage is indicated (Fig. 11). Relative stability in the composition of conodont assemblages in time has been documented in many cases previously (Sweet 1979 a, b; Jeppsson 1979) and it is not especially surprising to find it also

Fig. 8. Proposed interrelationships among Baltic and Midcontinent lineages of Balognathidae and possibly related forms. (1) '*Acodus*' *auritus* Harris & Harris 1962?, Joins Formation, Oklahoma. (2) *Polyplacognathus ramosus* Stauffer 1935; after Bergström (1981). (3) *P. sweeti* Bergström 1971, early form, Mountain Lake Formation, Oklahoma. (4) *P. friendsvillensis* Bergström 1971, late form, Tulip Creek Formation, Oklahoma. (5) Same species, early form, McLish Formation, Oklahoma. (6) *Eoplacognathus elongatus* (Bergström 1962), Mountain Lake Formation, Oklahoma. (7) *E. suecicus* Bergström 1971; after Harris *et al.* (1979). (8) *E. zgierzensis* Dzik 1976, Ohesaare borehole, depth 509.78–510.35 m, Estonia. (9) *Amorphognathus falodiformis* (Sergeeva 1963), uppermost Volkhovian of Öland. (10) *A. variabilis* Sergeeva 1963, Lower Kundan of Öland. (11) Same species, Upper Kundan of Västergötland. (12) *A. kielcensis* Dzik 1976, Vikarby Limestone, Västergötland. (13) *A. inaequalis* Rhodes 1952?, Kaagvere borehole, depth 312.8 m, Estonia. (14–16) *A. tvaerensis* (Bergström 1962), Kaagvere borehole, depth 293.8–303.4 m, Estonia. (17) Same species, Bromide Formation, Oklahoma. (18) *Baltoniodus* sp. n., Mountain Lake Formation, Oklahoma. (19) *B. navis* (Lindström 1955); after Dzik (1976). (20) *B. crassulus* (Lindström 1955), uppermost Latorpian of Öland. (21) *Acodus deltatus* Lindström 1955, Latorpian of Öland. (22) *Tripodus distortus* (Branson & Mehl 1933), West Spring Creek Formation, Oklahoma. (23) *T.* sp. n., Mountain Lake Formation, Oklahoma.

Fig. 9 (p. 78). Oanduan conodonts with possibly Baltic or cosmopolitan provenance. All specimens from the erratic boulder E-305, Mochty near Warsaw, Poland. ☐A–G. *Amorphognathus superbus* (Rhodes 1952), specimens ZPAL CVI/361–367, respectively; A, B: ×67, C–E: ×90, F, G: ×117. ☐H. *Pseudooneotodus* sp., ZPAL CVI/368; ×180. ☐I, J, L. *Panderodus panderi* (Stauffer 1935), ZPAL CVI/369, 371; I, L: ×120, J: ×540. ☐K. *Panderodus* sp., ZPAL CVI/370, ×120.

Fig. 10 (p. 79). Oanduan conodonts with North Atlantic provenance. All specimens from the erratic boulder E-305, Mochty near Warsaw, Poland. ☐A–G. *Aphelognathus rhodesi* (Lindström 1959), ZPAL CVI/372–378, respectively; A: ×60, B, D, E, G: ×80, C: ×120, F: ×96. ☐H–J. *Icriodella superba* Rhodes 1952, ZPAL CVI/379, 380; H: ×80, I: ×240, J: ×60.

Fig. 11 (pp. 80–81). Logs of relative percent contribution of the most important lineages in the Early and Middle Ordovician of North America (left) and Europe (right). Family assignments of particular lineages indicated by patterns. Presented localities: ☐A. Woods Hollow Shale, Marathon, Texas, data from Bergström (1978). ☐B–H. Crystal Peak, Watson Ranch, Lehman, Kanosh, Juab, Wah Wah, and Fillmore Formations from selected localities in Ibex area, Utah (Ethington & Clark 1981). ☐I–L. Mountain Lake, Tulip Creek, McLish, and continuous section of Oil Creek and Joins Formations from Arbuckle Mountains, Oklahoma. ☐M. Jefferson City Formation, Missouri (Kennedy 1980). ☐N. Lenoir Limestone, Tennessee (Bergström & Carnes 1976). ☐O. Table Head Formation, Newfoundland (Stouge 1980). ☐P. Cow Head Group, Newfoundland (Fåhraeus & Nowlan 1978). ☐Q. Mójcza Limestone, Holy Cross Mountains, Poland (Dzik 1978). ☐R. Wysoczki chalcedonite, Holy Cross Mountains, Poland (Szaniawski 1980). ☐S–U. Gullhögen Formation (courtesy of Stig M. Bergström), Vikarby Limestone, and Kundan of Gullhögen quarry, Skövde, Sweden. ☐V. Uppermost Volkhovian and Lower Kundan of Hälludden, Öland. ☐W. Ceratopyge beds and Latorpian of Ottenby cliff, Öland. ☐X–Y. Gammalbodberget and Kalkberget sections of Jämtland, Sweden (Löfgren 1978). Conodont lineages: (1) *Erismodus*. (2) *Erraticodon*. (3) '*Scandodus*' *sinuosus*. (4) *Eoneoprioniodus*. (5) Gen. n. A. ('*Multioistodus*'). (6) *Paraprioniodus*. (7) *Phragmodus*. (8) *Histiodella*. (9) *Periodon*. (10) *Microzarkodina*. (11) *Plectodina*. (12) *Prioniodus*. (13) *Oepikodus*. (14) *Protoprioniodus*. (15) *Pygodus*. (16) Gen. n. B ('*Belodella*'). (17) *Protopanderodus*. (18) *Semiacontiodus*. (19) *Glyptoconus*. (20) *Belodina*. (21) *Panderodus*. (22) *Dapsilodus*. (23) *Scabbardella*. (24) *Paltodus*. (25) *Drepanoistodus*. (26) *Paroistodus*. (27) *Ulrichodina*. (28) *Acodus* and *Tripodus*. (29) *Baltoniodus*. (30) *Amorphognathus*. (31) *Eoplacognathus*. (32) *Polyplacognathus* sensu Bergström 1971. (33) *Complexodus*. (34) *Rhodesognathus*. (35) *Drepanodus*. (36) *Scalpellodus*. (37) *Cornuodus*. (38) *Multioistodus*. (39) *Hamarodus*.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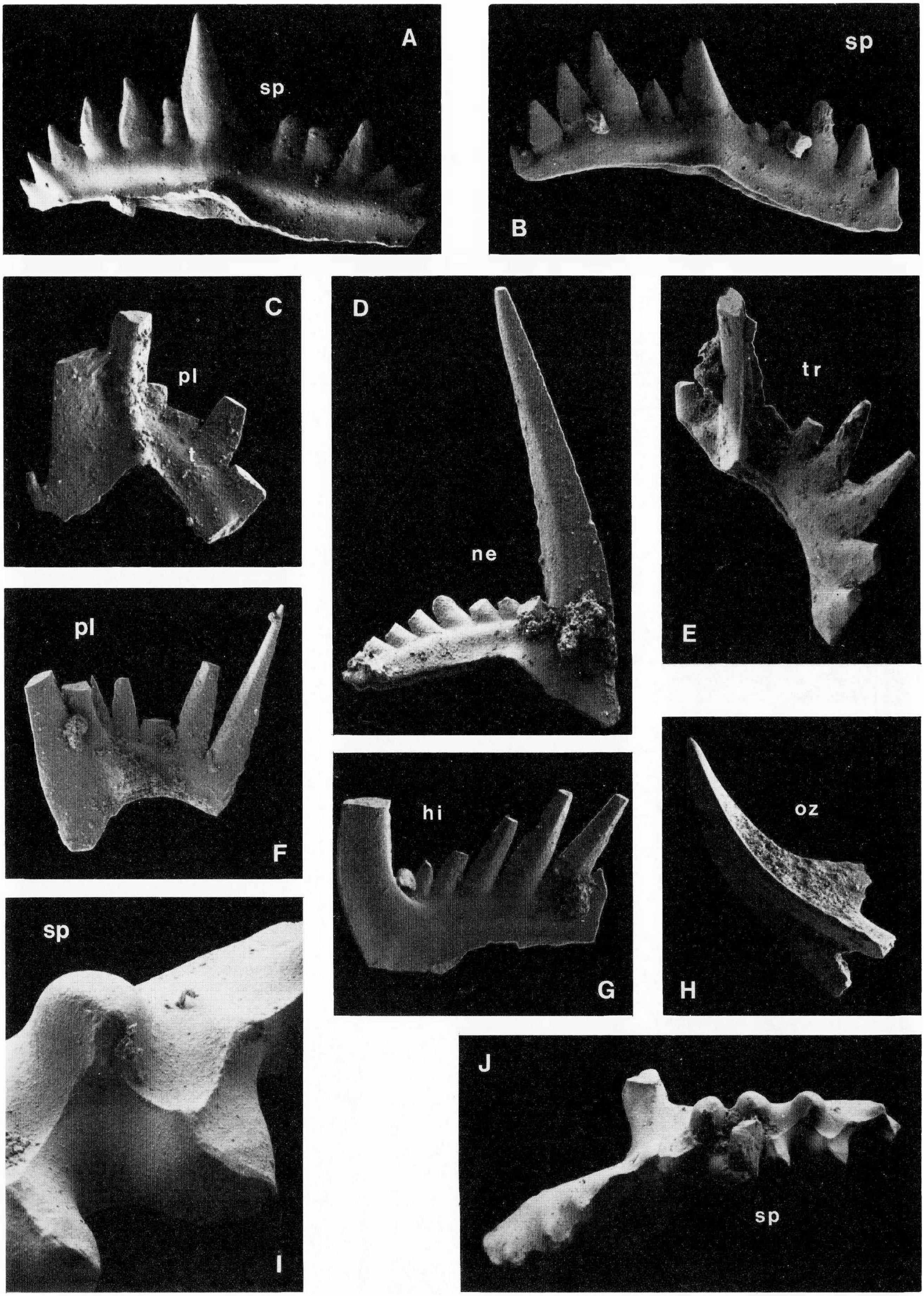
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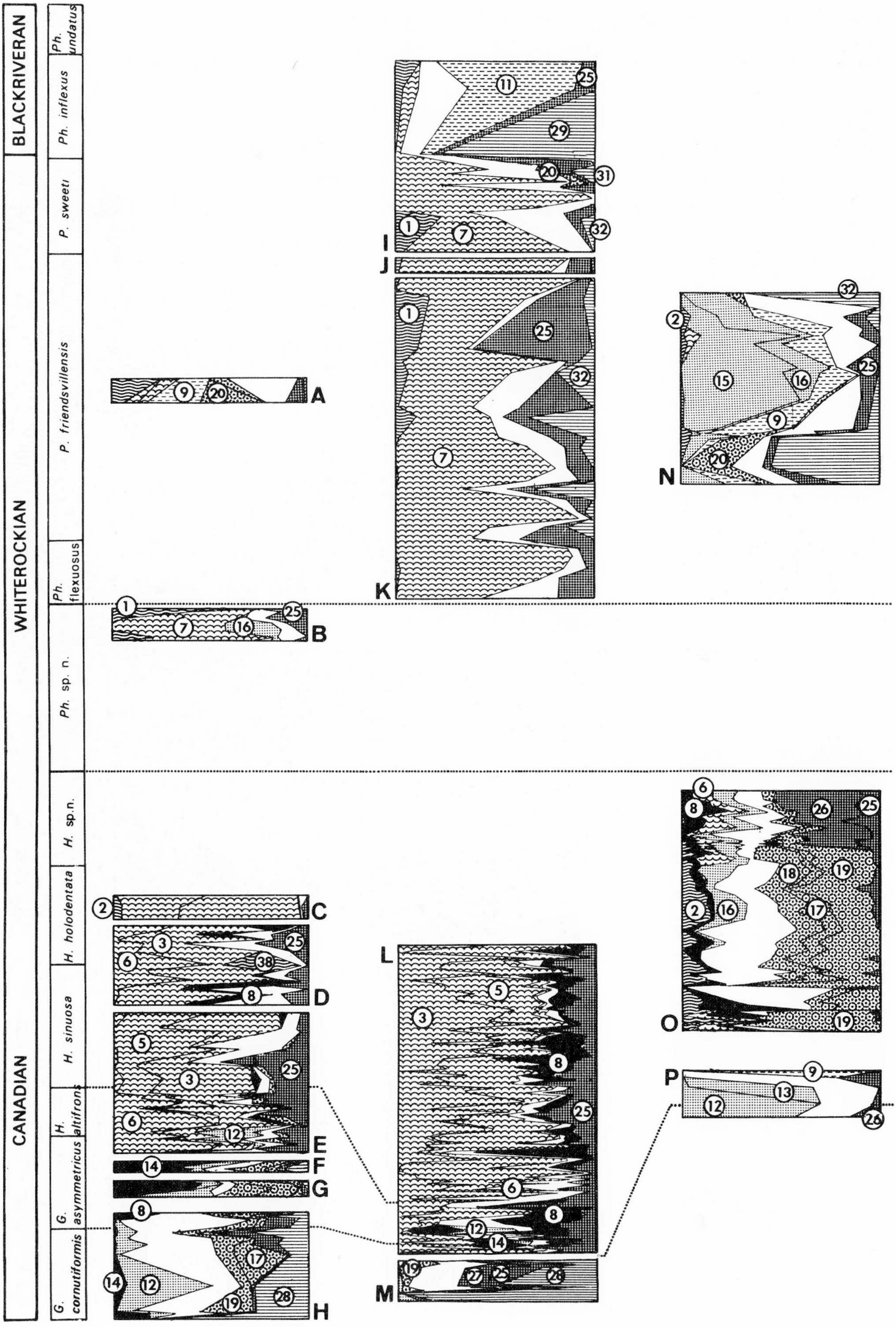
BLACKRIVERAN
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CANADIAN
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P. sweeti
P. friendsvillensis
Ph. flexuosus
Ph. sp. n.
H. sp.n.
H. holodentata
H. sinuosa
H. altifrons
G. asymmetricus
G. cornutiformis
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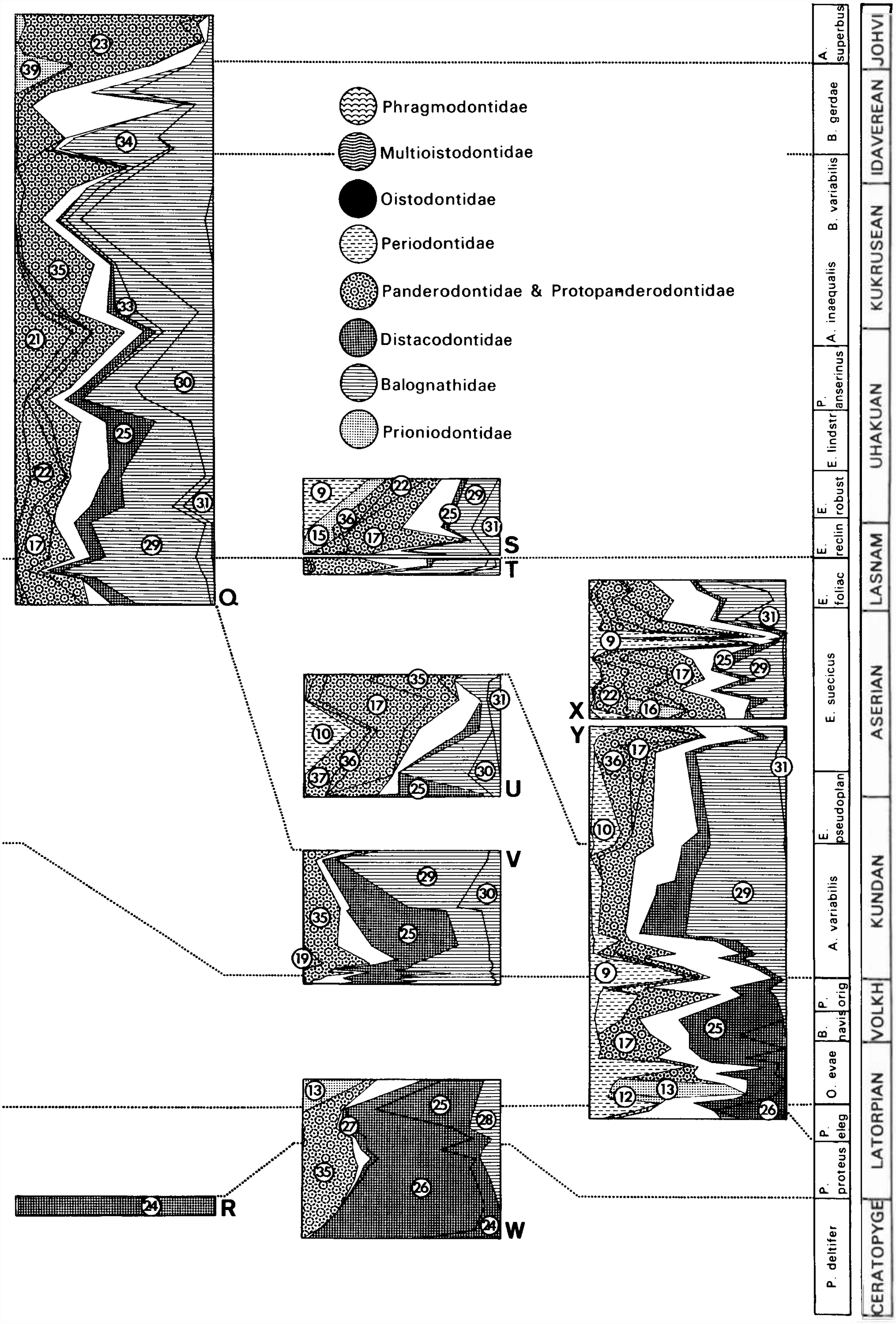
Phragmodontidae
Multioistodontidae
Oistodontidae
Periodontidae
Panderodontidae & Protopanderodontidae
Distacodontidae
Balognathidae
Prioniodontidae
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A. superbus
B. gerdae
B. variabilis
A. inaequalis
P. anserinus
E. lindstr
E. robust
E. reclin
E. foliac
E. suecicus
E. pseudoplan
A. variabilis
B. navis
P. orig
O. evae
P. eleg
P. proteus
P. deltifer
JOHVI
IDAVEREAN
KUKRUSEAN
UHAKUAN
LASNAM
ASERIAN
KUNDAN
VOLKH
LATORPIAN
CERATOPYGE

in the sections studied here. It appears, however, that during long time spans the cores of assemblages in particular areas continue to be formed by the same high-rank taxonomic units despite changes in contribution of particular evolutionary lineages belonging to these units, and that almost all areas have their own typical taxonomic units, which diversified mostly in only that area.

For instance, the evolution of the Balognathidae, with the exception of a single lineage, is confined exclusively to Baltica and adjacent islands in the Iapetus Ocean. Some lower-rank compartmentalization is visible in the case of the evolution of the *Amorphognathus* and *Eoplacognathus* lineages. The first evolved phyletically outside the central part of Baltica, with the best record on the island of the Małopolska Massif (Holy Cross Mountains; see Bergström 1971; Dzik 1976, 1978). The *P. friendsvillensis–sweeti* lineage, a supposed continuation of the *E. suecicus* lineage, underwent rapid phyletic evolution in the marginal seas of Laurentia and carbonate platforms possibly separated from them which were introduced later into the Appalachians (Bergström & Carnes 1976). This lineage did not appear in the Baltic area until the Uhakuan (Bergström 1971; Drygant 1974). The Phragmodontidae, a possibly Gondwana-born group, since its introduction occurred almost exclusively in the seas of Laurentia, where they underwent significant diversification. Some of their populations had areas of distribution that extended to islands in Iapetus and rarely expanded even to Baltica. The most successful branch of the Periodontidae had its evolution concentrated around the Iapetus islands. Each of its several lineages had somewhat different areas of distribution, some entering into the seas of Baltica (early *Periodon*, *Microzarkodina*), others tending toward Laurentia (*Plectodina–Aphelognathus* lineages). Similar patterns can be observed in the evolution of the Distacodontidae and the Panderodontidae, the latter developing to the originally(?) Midcontinent branch of *Belodina* and related genera. A few successfully developing lineages had extrinsic provenance, like *Protoprioniodus*(?) *marathonensis* of Laurentia with a probably Australian origin and *Complexodus pugionifer* of the Małopolska Island, known elsewhere only from China and Wales (S. M. Bergström, personal communication).

An independent evolution of conodont lineages confined to particular Middle Ordovician marine ecosystems involved also relative stability in the composition of particular ecologic groups of conodonts in each of the areas discussed. The pattern of vertical changes in the contribution of large groups of conodonts (Fig. 11), as well as other available data, suggest that different couples of high-rank taxa contributed to the total ecologic spectrum in each of the provinces. In Baltica (Fig. 11S–Y) this spectrum was represented mostly by shallow-water Panderodontidae and rather open-sea Balognathidae; in Laurentia (Fig. 11A–M) by Multioistodontidae and Phragmodontidae; in island areas of Iapetus (Fig. 11N–Q) by Protopanderodontidae and Periodontidae (with a significant contribution by *Amorphognathus*), and in equatorial Gondwana (Australia) probably by Multioistodontidae (*Erraticodon*) and Oistodontidae, respectively.

Among appearances of extrinsic lineages and interchanges of lineages developing in discussed areas two distinct classes can be recognized:

(1) Brief and numerically low contributions to the assemblage by appearances of species known in great numbers of specimens from other areas. Such are occurrences of *Histiodella holodentata* in the Małopolska Island and Baltica (Dzik 1978), *Glyptoconus*(?) *asymmetricus*, *Polonodus clivosus*, *Eoneoprioniodus alatus*, and *P. sweeti* in Baltica, all genuine lineages of Laurentia, as well as *Microzarkodina flabellum* and *Paroistodus parallelus*, both Baltic or Iapetus lineages, which appeared in the Midcontinent. Appearances of *Erraticodon* in discussed regions are of the same nature. No significant rebuilding of the assemblage is associated with appearances of this kind. They can be interpreted as effects of regional changes in the area of distribution of particular lineages observed close to their margins. Such populations, close to the margin of distribution of a species, must be more sensitive environmentally than highly productive populations in the center of the distribution area. Frequency-distribution data suggest that each conodont species had its own area of distribution with high productivity in the center (several species are known to contribute more than 90 % to samples from some areas) which decreases toward the margins. Rarely several species have the same center of distribution. No evident positive correlation in the distribution of different species has been observed, despite attempts to recognize persistent conodont associations (Bergström & Carnes 1976).

(2) Another class of 'migration' phenomena is represented by introductions of lineages that thereafter start to contribute significantly to the assemblages of some areas and to develop local phyletically evolving lineages, This is well exemplified by the introduction of *Eoneoprioniodus*, *Protoprioniodus* (?) *marathonensis*, *Paroistodus*(?) *horridus*, *Belodina*, *Eoplacognathus suecicus*, *E. elongatus*, and several other lineages into the Midcontinent. This is usually associated with the replacement of some previously occurring lineage or at least a significant rebuilding of the assemblage. Few events of this kind are observed in the Baltic area.

Generally Midcontinent and Baltic assemblages behaved in different ways. While Midcontinent faunas underwent rather gradual rebuilding during the Ordovician with several new lineages becoming permanent parts of communities (like Iapetus-born *Plectodina*, possibly Australian *Erismodus*, Baltic *Polyplacognathus* and *Amorphognathus*) the Baltic communities were much more conservative in their composition. Profound remodelling of them occurred in the Oanduan, when several lineages of the Iapetus provenance, represented by *Aphelognathus*, *Icriodella*, and *Phragmodus* (originally a Midcontinent form), were introduced. Although this assemblage has superficially a Midcontinent appearance, that is because of the approximately synchronous introduction of similar forms to the Midcontinent area, where they are not so distinct from local elements as they are in Baltica (see Bergström & Sweet 1966; Kennedy *et al.* 1979). Probably no direct Midcontinent to Baltic 'migration' took place at that time. Subsequent evolution of the Baltic assemblage with introduction of the numerically dominant conodonts *Hamarodus* and *Scabbardella* did not make it similar to that of Laurentia.

Sweet & Bergström (1974) suggested that rebuilding of the Baltic conodont fauna in *B. gerdae* Zone time was caused by a shift of the warm-water zone toward the pole accompanied by an expansion of the warm-water Midcontinent fauna. In terms of the continental drift concept this effect may be reached by moving the Baltic continental plate toward the equator. Because it is generally believed that warm-water animal communities are more diverse than cold-water ones one may attempt to test this idea by measuring changes in diversity in both areas during the Ordovician. Among several proposed, the measure of diversity based on Shannon's formula of information content (Berry *et al.* 1979) seems to be one of the simplest and has relatively easily understood ways of inference. The formula may be written in the following way:

$$D = -\sum_{s=1}^{n} C_s \log C_s.$$

Where D=diversity of the assemblage; C_s=relative contribution (decimal fraction) of particular species s to total sample. This is a measure of improbability of a particular composition of the assemblage. The largest value of D characterizes samples with large numbers of equally contributing species, the smallest one samples in which a single species dominates the assemblage.

Index of diversity is calculated here for Oklahoma, Utah (data from Ethington & Clark 1981), Jämtland (data from Löfgren 1978), the Holy Cross Mountains, Västergötland and Öland sections. Data are plotted against time scaled by appearances of zonally (or potentially zonally) diagnostic species (Fig. 12). Results are quite opposite to those expected (Dzik 1984). During the Early Ordovician the diversities of Baltic and Midcontinent assemblages do not differ significantly; both are relatively high. During the Middle Ordovician, plots for studied sections from both areas diverge somewhat, with higher (sic!) diversity in supposedly cold-water Baltic assemblages. In all cases, a significant decrease in diversity is usually connected with shallowing of basins. The difference between Baltic and Midcontinent assemblages may be partially caused by differences in bathymetric characters of the studied sections. Still remaining to be explained is the lack of any significant difference between other, bathymetrically more comparable parts of the sections, which may suggest that conodonts preserved in the sediment represent only a small fraction of the trophic group to which they belonged.

Acknowledgements. – Several Swedish sections of the Ordovician were sampled by me and some samples were processed during a two-month stay at the Department of Palaeobiology, University of

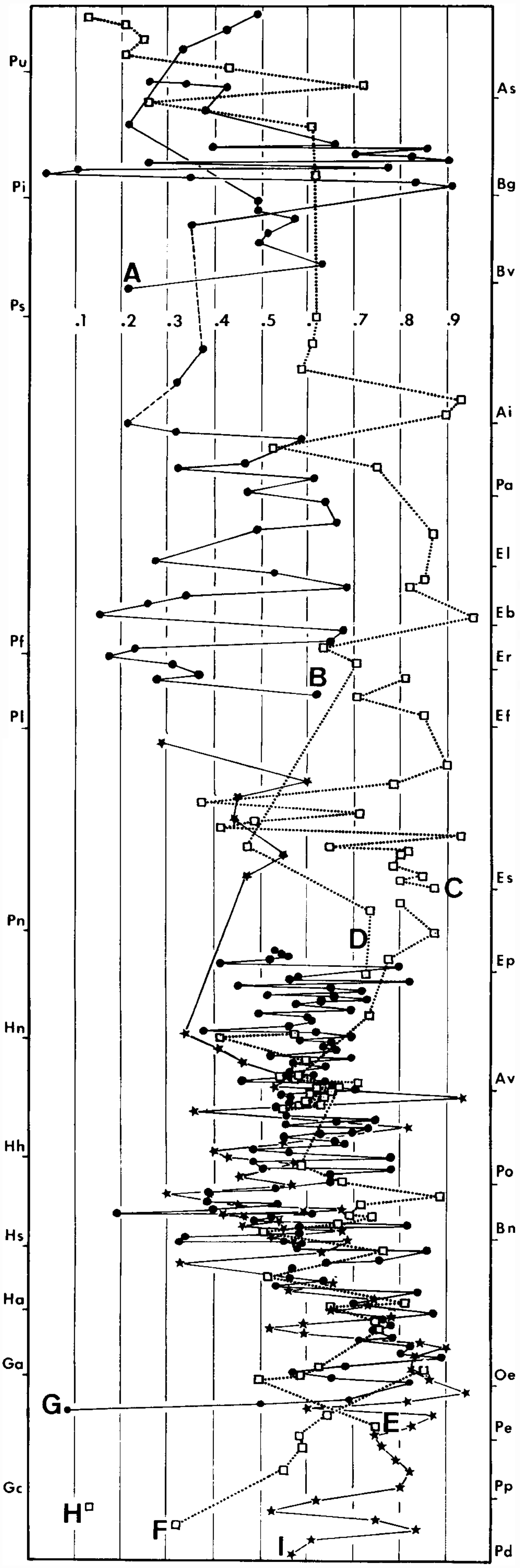

Fig. 12. Index of diversity plotted against time for sections representative of the Baltic and Midcontinent provinces. Appearances of zonal (or potentially) zonal species (same as on Fig. 11) indicated by initials left and right of the diagram. □A. Section of the 'Bromide' Formation near Fittstown, Oklahoma. □B. McLish to Mountain Lake Formations north of Ardmore, Oklahoma. □C. Gammalbodberget section, Jämtland (data from Löfgren 1978). □D. Mójcza Limestone, Holy Cross Mountains, Poland (Dzik 1978). □E. Kalkberget section, Jämtland (Löfgren 1978). □F. Ottenby cliff section, Öland. □G. Top of West Spring Creek to Oil Creek Formations north of Ardmore, Oklahoma. □H. Wysoczki chalcedonite, Holy Cross Mountains, Poland (Szaniawski 1980). □I. Top of House to Crystal Peak Formations from selected outcrops of the Ibex area, Utah (Ethington & Clark 1981).

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Baltic and Polish samples were processed at the Institute of Paleobiology of the Polish Academy of Sciences (Zakład Paleobiologii PAN, abbreviated ZPAL) and photographed specimens are housed there. Micrographs other than those enumerated above were taken at the Nencki's Institute of Experimental Biology in Warsaw. Drawings of conodont elements presented in the text are reconstructions based on camera lucida sketches of specimens housed either at the Department of Geology and Mineralogy of The Ohio State University in Columbus, Ohio, USA, or at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland.

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