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Conodont Evolution in High Latitudes of the Ordovician

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Abstract

Distribution of conodonts in temperate and cold-water regions of the Ordovician was much less punctuated by migrations than in the equatorial zone of that time. This enables stratophenetic studies of lineages in particular sections and to trace splitting of them and migrations. Time and space distribution of conodont faunas in Early Paleozoic terranes incorporated into the Variscan belt of central Europe and bordering the SW margin of the East European Platform is analysed in this way. Prior to, and even despite of, introduction of a rather uniform Late Ordovician *Hamarodus* fauna the studied area was a place of gradual evolution of several local conodont lineages which were that time restricted to the cold-water climatic zone, although some of them later have adapted to quite different climatic conditions. The oldest known parts of the lineages of *Phragmodus* have been traced in the Holy Cross Mts., *Plectodina* in the Sudetes, and *Icriodella* in Thuringia. The oldest *Amorphognathus* s. s. appeared in the latest Llanvirn of the Holy Cross Mts. and there is a gap in record of its supposed derivation from Early Llanvirn "*A.*" *variabilis*. It is suggested that Welsh "*A.*" *inaequalis* represents the closely related but distinct lineage of *Rhodesognathus*, characterized by secondary gradual reduction of the platform. It appears thus that the most characteristic members of the Late Ordovician equatorial faunas had their origin in subpolar or even polar regions. An attempt to connect peculiarities in distribution of conodonts with the Ordovician paleogeography is presented.

Introduction

Geological history of the part of Europe bordering the SW margin of the East European Platform is still poorly understood. The area, delimited by the Tornquist-Teysseyre line (the boundary of the Platform) and the margin of the Carpathian and Alpine flysch nappes (Fig. 1), is composed of several small terranes accreted to the Platform during the Paleozoic. Later deformations and a thick cover of younger sediments have obliterated much of geological records of tectonic events that caused the consolidation of this part of Europe. Paleobiogeographic evidence is thus of high value in testing geotectonic hypotheses concerning the region.

The terranes of the Central European Variscan belt are generally believed to be connected with the African margin of Gondwana during the Early Paleozoic (SCOTESE et al., 1985; LIVERMORE et al., 1985), being thus located close to the South Pole of that time. This is consistent with the paleontological evidence (see DZIK, 1983, for review) at least regarding the Bohemian and Thuringian Ordovician faunas. There are, however, also some inconsistencies in the present distribution of conodont faunas, the most important being supposed presence of the Midcontinent-type *Phragmodus* fauna in the Sudetes (BARANOWSKI & URBANEK, 1972; LINDSTRÖM, 1976), located precisely in between three supposedly cold-water faunas of the Holy Cross Mts., Thuringia, and Bohemia (KNÜPFER, 1967; DZIK, 1978, 1983).

The present paper is aimed to elucidate some of these apparent paleobiogeographic discrepancies starting from an analysis of evolutionary connections among conodonts of particular central European terranes. The picture of the distribution of particular lineages in time and space will then be compared with paleogeographic interpretations of the area inferred from presumed Variscan and Caledonian movements of respective blocks.

A brief review of the geology of the studied area seems necessary at the beginning, because the data crucial for its understanding are dispersed in regional geological literature. For brevity, references to only the most recent papers are given, in which an interested reader may find more complete review of published data.

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Geotectonic background

The SW margin of the East European Platform is marked by a change from marginal platform deposits of marly limestones (during the Early Ordovician) or black bituminous shales (during the Middle Ordovician) to deep-water graptolite shales and flysch. A belt of highly folded Early Paleozoic rocks separates the Platform from the massives of Małopolska (MODLIŃSKI, 1981). The latter is an area in SE Poland of quite different sedimentary regime which emerged that time from surroundings of rocks presumably oceanic in origin. Facies distribution in the Early Paleozoic supports its subdivision into three blocks: the Małopolska, Jędrzejòw, and Upper Silesia Massives. The Ordovician crops out at the NW tip of the region in the Holy Cross Mountains and was traced by several deep boreholes (TOMCZYK, 1962; JURKIEWICZ, 1975), although most of the Early Paleozoic was removed from the area by subsequent erosion.

In the axial part of the Holy Cross Mountains (Kielce facies region of the Małopolska Massif) carbonate platform sedimentation was preceded by deposition of thick clastic formations of Cambrian to Early Ordovician ages, being probably a product of denudation of elevated parts of the Małopolska Massif that was still active tectonically at that time. The major deformations took there place between the Late Cambrian and the latest Tremadoc (the Sandomirian orogeny).

In the Kielce facies the first thin carbonate intercalations appeared within the Bukòwka Sandstone. Both the macrofossils (brachiopods, bellerophonts and rare trilobites) known from the sandstones and a diverse assemblage of acrotretid brachiopods and conodonts extracted from the limestone intercalations (BEDNARCZYK & BIERNAT, 1978) are of Baltic type. Regarding the age of the formation two stratigraphically indicative conodont species of *Paroistodus*, *P. amoenus* (LINDSTRÖM) and *P. parallelus* (PANDER), diagnostic of different zones of the Latorpian, and Volkhovian *Baltoniodus navis* (LINDSTRÖM) have been listed. However, I was not able to trace in the collection of Dr. WIESŁAW BEDNARCZYK, kindly provided for examination by him, any specimen of *Paroistodus*, while few specimens of *Baltoniodus* really indicate, as long as it can be judged from development of denticulation and elongation of processes (unfortunately the most diagnostic ke element was not found), the Late Volkhovian age of the assemblage. It is evident that the whole sequence of the Bukówka Sandstone was deposited in a brief period of the Late Arenigian (Late Volkhovian to earliest Kundan).

Beginning from the early Kundan a continuous sedimentation of the stratigraphically highly condensed Mòjcza Limestone took place. This formation is known from several localities distributed along a line connecting Kielce with Sandomierz (NNW-SEE).

The area of platform sedimentation in the Holy Cross Mts. is bordered by regions of deeper water sedimentary regime both to the north (the Łysogòry facies region) and to the south (Brzeziny belt) (TOMCZYK & TURNAU-MORAWSKA, 1966). The Ordovician is represented there by thick sequences of claystones and mudstones with thin carbonate intercalations. No conodont studies have been undertaken there but, judging from graptolites, one may expect that the main carbonate bed in these sections corresponds to the hiatus in deposition of the Mòjcza Limestone in the Kielce facies region. The southern belt of deep water sediments, best known from the borehole in Brzeziny (TOMCZYK & TURNAU-MORAWSKA, 1964) separates the Holy Cross Mts. from the Jędrzejòw Massif (JURKIEWICZ, 1975).

The Mòjcza Limestone can be identified in virtually all borehole cores both in the Małopolska and Jędrzejòw Massives, which are complete enough, from the Książ Wielki IG 1 borehole on SW to the Uszkowce 4 borehole on the NE margin of the Massif (TOMCZYK, 1962; JURKIEWICZ, 1975). Its base is probably of approximately the same age in the whole area (though there are some arguments in favor of its slightly higher position in localities of Międzygòrz and Koziel) but it is uncertain whether its top is coeval or not. In the Mòjcza section the organodetrital Mòjcza limestone is overlain by limy marls while in the outcrop at Zalesie Nowe, as well as in several outcrops and boreholes of the Łysogòry facies region, the Late Caradocian and Ashgillian are developed as a more or less thick claystone series.

The Devonian of the Jędrzejòw Massif was of the same carbonate platform development as in the rest of the Małopolska Massif, which indicates that the consolidation and full accretion of these blocks was completed much earlier. Perhaps even in the Ordovician they were not completely isolated, with the Brzeziny belt of deeper sedimentation being a remnant of a former separation.

An area of folded Early Paleozoic rocks separates the Jędrzejòw Massif from the massif of Upper Silesia, which was already consolidated and peneplained before the Early Cambrian. Most of the Early Paleozoic rocks had been removed by erosion and the Late Carboniferous coal formations were subsequently deposited, reaching more than 3 000 m in thickness. The Ordovician is now known only in the marginal parts of the Upper Silesia Massif, in vicinities of Myszkòw, where it was recovered in several deep boreholes. It starts from a thin layer of basal conglomerate, overlying folded Cambrian rocks, followed by relatively thick sequence of weakly folded limestones. The strata are

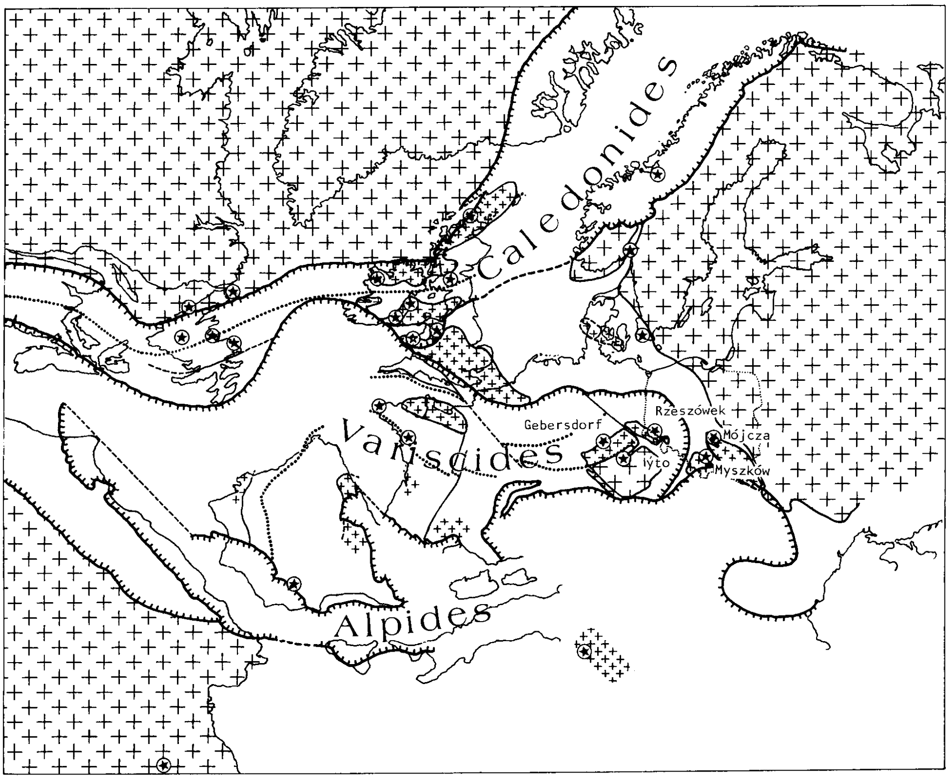


Fig. 1. Locations of the most important Ordovician conodont faunas within the Caledonian, Variscan, and Alpine orogenic belts, the boundaries of which are superimposed on the Pangean paleogeography of the North Atlantic region.

currently studied by Dr. M. NEHRING-LEFELD and Mrs. A. SIEWNIAK-MADEJ of the Geological Survey of Poland. A light coloured organodetrital limestone represents there at least the time span from the topmost Arenigian (early Kundan) to the early Caradocian, the brownish micritic limestone topping the sequence contains late Caradocian and/or Ashgillian conodonts. Unlike sections in the Małopolska Massif sandstones are evidently lacking in the Upper Silesian Ordovician. It is consistent with decreasing from NE to SW thickness of clastic formations within the Małopolska and Jędrzejòw Massives; perhaps the source of quartz sand was the Cambrian folded along the northern margin of the massif in the Sandomirian orogeny.

A wide belt of the Variscan flysch is located between the Upper Silesia Massif and the Sudetes. Greywackes and shales of deep-water origin are the oldest rocks reached by boreholes in the Opole Silesia. By analogy with the Lower Carboniferous exposed in the eastern Sudetes they are supposed to be of late Visean age. There is no reason to assume that this area was consolidated before the late Carboniferous Variscan orogeny and one may suppose that the Sowie Gòry Massif, possibly the oldest part of the Sudetes, was separated in the Ordovician by oceanic floor from the Upper Silesia Massif (GROCHOLSKI, 1987).

The most eastward exposures of the Early Paleozoic in the Sudetes are these in the Kłodzko Depression. In its eastern part the whole Silurian and the Early Devonian is developed in the graptolite shale facies. The underlying sandstones are believed to represent the Ordovician. Quite different is the development of the Silurian in the western part of the Kłodzko depression where coral limestones of this age were found (GUNIA & WOJCIECHOWSKA, 1971). This may suggest a proximity of an elevated pre-Silurian massif.

It was not the Sowie Gòry Massif, which now contacts the area from the north. The Massif, composed mostly of gneisses being a result of pre-Frasnian metamorphism of supposedly Proterozoic greywackes and arkoses (Żelaźniewicz, 1987) is structurally isolated from the Kłodzko Depression and its presence did not influence sedimentation on its southern proximities till the late Tournaisian, although on its northern margin a thick sequence of conglomerates was deposited during the Late Devonian indicating intense erosion. Among pebbles pieces of rocks have been found which do not occur in the Sowie Gòry but are known from the Gòry Izerskie, more than fifty kilometers westward. Slates, gneisses and granites of the Gòry Izerskie originated also in result of metamorphism of greywacke-arkose sediments (ŻABA, 1984). One may wonder whether these two ancient regions of the Sudetes did not form a single massif during the Early Paleozoic, split and dislocated during the Late Devonian (see HOLDER & LEVERIDGE, 1986). Nevertheless, the true relationship between the Sowie Gòry and other pre-Caledonian massifs of the Sudetes, as well as number and geographic extent of them, during the Ordovician is still obscure.

Northward of the Sowie Gòry and Gòry Izerskie the Early Paleozoic is represented by greenstones with lenses of the Wojcieszòw crystalline limestones which are interpreted as products of small carbonate platforms topping basaltic seamounts (LORENC, 1984). The only reliably identified fossils from the Wojcieszòw limestones are archeostracans and spicules of hexactinellid sponges. They cannot be used to age determinations. In the Radzimowice slates, believed to underly the limestones or being coeval with them, specifically undeterminable but definitely Ordovician conodonts have been found (URBANEK & BARANOWSKI, 1986). Even farther to the north in the central part of the Gòry Kaczawskie the whole Early Paleozoic is developed in deep-water facies and there, in sericitic slates, a few rich assemblages of Early to Middle Ordovician conodonts have been found (BARANOWSKI & URBANEK, 1972). The uniform sedimentation conditions continued in this region till the Early Carboniferous (URBANEK et al., 1975).

The nature of the southern boundary of the Sudetes and the area of the Elbe lineament, separating them from the Moldanubian Massif is even less clear although presence of metamorphosed deep water sediments in the area in between the massives of the Sudetes and the shallower area of the Barrandian may suggest that during the Early Paleozoic these areas were separated by oceanic floor. The closest to the Moldanubicum fossiliferous Early Paleozoic rocks occur in Thuringia and South Saxony. The Ordovician strata occur there over a large area and are accessible in several exposures. Clastics of the Early Orodovician *Phycodes* Beds and "pencil slates" (Griffelschiefer), as well as the Late Ordovician glacio-marine Lederschiefer, which are not suitable for preservation of extractable conodont elements, contribute the most to the thickness of the Ordovician in the area. Despite of it these strata cover only a small part of the Ordovician time span. The most of the Ordovician period in Thuringia is represented by highly condensed iron ore formation of the Gräfenthaler Series as indicated by distribution of conodonts.

Owing to the pioneer work by KNÜPFER (1967) it was possible to date both the base and the top of the upper iron ore horizon of the Gräfenthaler Series. Accomodating his results to later established ranges of particular species it appears that the change from fine clastic sedimentation of the pencil slates to conditions enabling formation of phosphatic and chamosite ooids and oncoids took place in Kundan times (top of the Arenigian) while the thin limestone layer topping the iron ore formation was deposited in the latest Caradocian.

The older conodont assemblage of KNÜPFER (1967), from the base of the upper iron horizon in Gebersdorf, is represented by innumerous and poorly preserved conodonts (partially in effect of using a harsh method of extraction with hydrochloric acid). Its oldest possible age can be estimated on the basis of occurrence of elements of an early species of the *Eoplacognathus (Lenodus)* lineage. Forms of this kind are unknown before the beginning of the Kundan (DZIK, 1983). In Baltic localities they are also unknown above the Kundan and, although their longer persistence in Thuringia cannot be excluded, it seems unlikely that the base of the iron ore horizon is younger than the Kundan.

In the next chapter the distribution of conodonts in these regions will be analyzed and compared with literature data concerning other Early Paleozoic faunas of western Europe and the Mediterranean region.

Conodont assemblages

General aspects of the distribution of Late Ordovician conodonts in Europe have been discussed by SWEET & BERGSTRÖM (1984). Here their review is supplemented by data on conodont localities from Polish and East German parts of the Variscan orogenic belt.

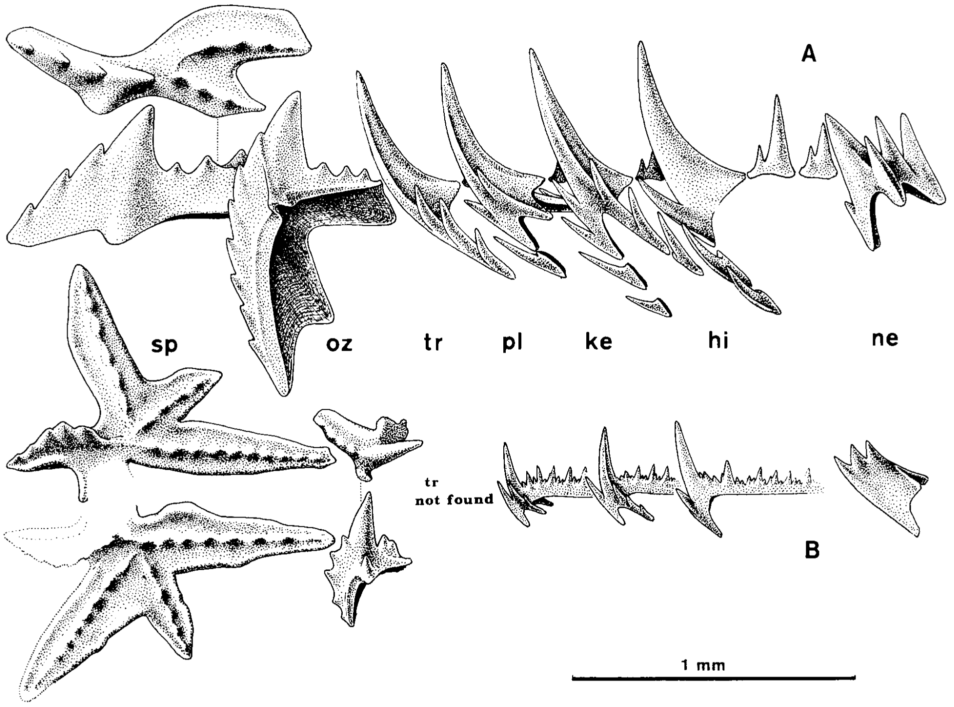


Fig. 2. Most important ramiform conodont apparatuses from the Kalkbank of the Obere Erzhorizont of Thuringia. Composite drawings based on KNÜPFER's (1967) materials. — A. *Sagittodontina bifurcata* KNÜPFER, 1967. — B. *Amorphognathus superbus* (RHODES, 1953).

Thuringia

Of special interest is the presence of an early species of *Icriodella* in the older Thuringian assemblage from the base of the upper iron ore horizon of the Gräfenthaler Series of Thuringia. The species, an available name for which is *I. cerata* (KNÜPFER), is probably the same which occurs in the Sudetes (see below) and may be ancestral to *I. praecox* LINDSTRÖM, HENRY & RACHEBOEUF (LINDSTRÖM et al. 1974) from the Llandeilian of the Armorican Massif. Later evolution of the lineage was recognized by BERGSTRÖM & ORCHARD (1985) and BERGSTRÖM et al. (1987) in the Welsh Caradoc.

It is remarkable that no coniform element was identified in this horizon by KNÜPFER (1967). This is almost certainly a result of the applied technique of preparation. Owing to courtesy of Professor JÖRG SCHNEIDER of the Bergakademie Freiberg I had occasion to sample the section of the Gräfenthaler Series in an abandoned mine at Wittmansgereuth. Only a single sample, treated with hydrofluoric acid, appeared to be productive (though still very poor), namely that from the base of the upper iron ore horizon. Among three generically identifiable elements the two represent most probably oz elements of *Icriodella* but the third one is a *Drepanodus*, unfortuanately not identifiable specifically.

Much better represented in his collection is the younger assemblage of KNÜPFER (1967) from the silicified limestone layer crowning the ore horizon. There are many samples from now not accessible localities, some containing hundreds of elements. No apparent difference in numerical contribution of particular species between samples or localities has been noted therefore it has to be concluded that the Kalkbank was deposited synchroneously in the area. Although all specimens are more or less fragmentary they are numerous enough to allow apparatus identifications. Because only a provisional synonymy list of the form-taxa names applied to morphologic types of elements by KNÜPFER (1967) was presented by SWEET & BERGSTRÖM (1984: p. 85) it seems reasonable to precise it.

Species from the base of the Upper Iron Ore Horizon:

1. *Lenodus* cf. *variabilis* (SERGEEVA, 1963), includes: sp - *Priomorphognathus alata* KNÜPFER; oz - *Prioniodus ferrarius* KNÜPFER, *P. alatus* HADDING, *Haddingodus serra* (HADDING), *?Disparodus bergstroemi* KNÜPFER, *D. simplex* KNÜPFER; tr - *Roundya pyramidalis* SWEET & BERGSTRÖM; pl - *Tetraprioniodus lindstroemi* SWEET & BERGSTRÖM, *T. asymmetricus* BERGSTRÖM, *Roundya? laticosta* KNÜPFER; hi - *Paracordylodus* cf. *lindstroemi* BERGSTRÖM.

2. *Icriodella cerata* (KNÜPFER, 1967), includes: sp - *Dichognathus* cf. *typica* BRANSON & MEHL; oz? - *Sagittodontus?* sp.; tr - *Sagittodontus? muelleri* KNÜPFER, *S. posteroconvexus* KNÜPFER; pl? - *Hertzina? acuta* KNÜPFER; ke - *Belodus solidus* KNÜPFER; hi? or ne? - *Cordylodus ceratus* KNÜPFER.

3. "*Carniodus*" *antiquus* KNÜPFER 1967, here probably also the poorly preserved specimens belong identified as *Chirognathus* sp., *Carniodus antiquus* KNÜPFER, *Prioniodina* sp., *Multioistodus* sp., *Lonchodus* sp.

4. Quite undeterminable and perhaps not even conodonts: *Drepanodus* sp., *Oneotodus* sp., *Proacodus alienus* KNÜPFER.

Conodonts of the Kalkbank:

1. *Scabbardella altipes* (HENNINGSMOEN, 1948). There is a gradual transition between particular morphologic types of elements in this species and if even there are any differences between the Thuringian and Baltic populations I am not able to indicate them without biometrics. Names applied by KNÜPFER: *Acodus inornatus* ETHINGTON, *A. similaris* RHODES, *Acontiodus altipes* HENNINGSMOEN, *Drepanodus similaris* RHODES, *D. flagellus flagellus* KNÜPFER, *D. f. pseudoaltipes* KNÜPFER, *Acodus flagellus flagellus* KNÜPFER, *A. f. compactus* KNÜPFER.

2. *Sagittodontina bifurcata* KNÜPFER, 1967 (Fig. 2A). BERGSTRÖM (1983) was the first who appreciated unusual character of this superficially *Amorphognathus*-like species and reconstructed its apparatus on the basis of Libyan materials. In addition to his interpretations, which are wholly supported by analysis of the Thuringian materials, I have noted surprisingly wide range of variability in number of denticles in elements of the symmetry transition series. It seems that in these elements bars connecting bases of denticles were weakly calcified and the processes were actually represented by isolated denticles connected by a weakly mineralized tissue (perhaps like in Devonian *Icriodus*; see NICOLL, 1982). It seems thus that numerous loose groups of denticles and supposed minute cusps, included by SWEET & BERGSTRÖM (1984) into multielement *Istorinus erectus* KNÜPFER, belong actually to *Sagittodontina*. The most characteristic feature of the species is the acutely pointed wider side of the "anterior" process of the oz element (see Fig. 3C). The apparatus includes thus: sp - *Sagittodontina robusta* KNÜPFER, *S. bifurcata* KNÜPFER, *S. unidentata* KNÜPFER, *S. separata* KNÜPFER, *Sagittodontus dentatus* ETHINGTON, *S. robustus robustus* RHODES, *S. r. flammeus* KNÜPFER, *Lonchodus* sp.; oz - *Ambalodus triangularis indentatus* RHODES; tr - *Trichonodella* n. sp.; pl - *Tripodontus compactus* KNÜPFER; *I. muelleri* KNÜPFER: *?Distacodus stola* LINDSTRÖM; ke - *Zygognathus? atypica* KNÜPFER, *Z. asymmetrica* KNÜPFER, *Roundya gebersdorfi* KNÜPFER, *?Acodus deltatus altior* LINDSTRÖM; hi - *Strachanognathus thuringensis* KNÜPFER, *Ligonodina?* sp., *?Istorinus recurvus* KNÜPFER, *I. postdentatus* KNÜPFER, *I. erectus* KNÜPFER, *?Drepanodus suberectus* (BRANSON & MEHL), *D. humilis* KNÜPFER, *D. disymmetricus* KNÜPFER, *?Clavohamulus* n. sp. 1 & 2; ne - *Goniodontus ordovicicus* KNÜPFER, *Goniodontus* n. sp., *?Acodus abnormis* KNÜPFER.

3. *Amorphognathus superbus* (RHODES, 1953) (Fig. 2B).
Identification of the species is based on an assumption that the single ne element found by KNÜPFER (1967: p. 30, Pl. 3: 14) belongs to it and not to associated *Rhodesognathus*. This assumption is also supported by relatively large size of platform elements, a feature of *A. superbus* rather than *A. ordovicicus*. SWEET & BERGSTRÖM (1984) have chosen different interpretation of the Thuringian species and included in it also elements here interpreted as representing *Rhodesognathus* apparatus. According to the present apparatus identification the following form-species belong to it: sp - *Amorphognathus ordovicica* BRANSON & MEHL; oz - *Ambalodus triangularis triangularis* BRANSON & MEHL (only Pl. 9: 3-4; not 2, which belongs to *Rhodesognathus*); pl - *Tetraprioniodus superbus* (RHODES); ke - *Keislognathus gracilis* RHODES; hi - *Ligonodina delicata* (BRANSON & MEHL), *?Carniodus* sp. WALLISER; ne - *Holodontus* sp.

4. *Hamarodus europaeus* (SERPAGLI, 1967), includes: sp-oz elements not identified by KNÜPFER but present in his collection; slide Nos. 244, 433, 325, 146 (9 specimens); tr - *Roundya* n. sp. KNÜPFER; pl - *Gothodus excavatus* KNÜPFER; hi - *Cordylodus delicatus* BRANSON & MEHL; *?C. d. proclinus* KNÜPFER; ne - *Oistodus abundans* BRANSON & MEHL.

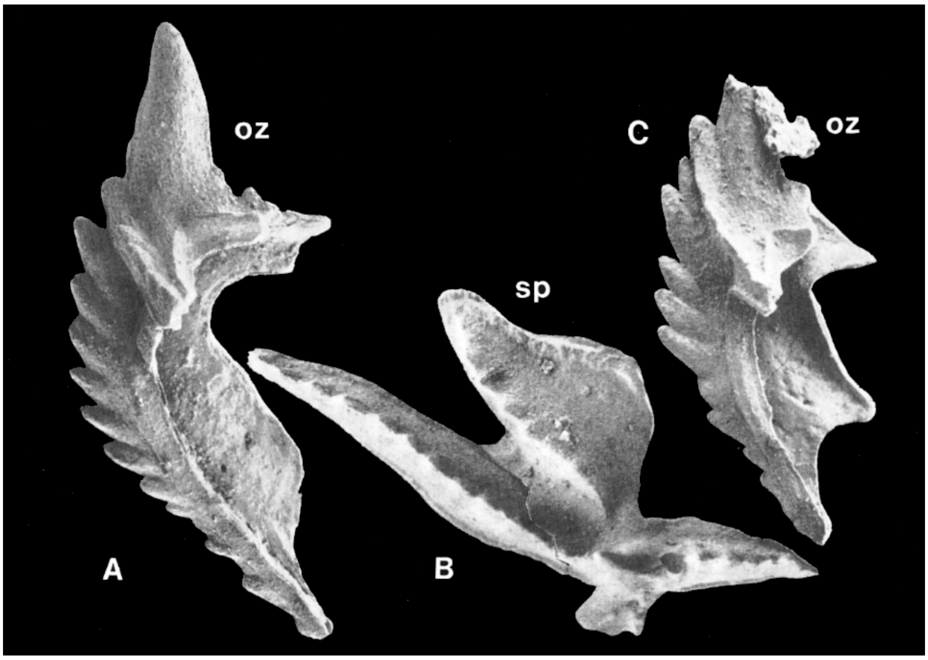
5. *Rhodesognathus* sp., includes: sp - *Ambalodus robustus* RHODES; oz - *A. triangularis triangularis* BRANSON & MEHL (only KNÜPFER, 1967, Pl. 9: 2, not 3-4); ke - ?*Roundya* cf. *inclinata* (RHODES); hi? - *Cordylodus delicatus proclinus* KNÜPFER (not the holotype).

6. *Walliserodus* sp., includes: sp-hi - *Panderodus intermedius* (BRANSON, MEHL & BRANSON); ne - *Drepanodus* cf. *latus* LINDSTRÖM.

7. *Dapsilodus* sp., includes *Acanthodus* cf. *arcuatus* LINDSTRÖM.

The Sudetes

Determinable Ordovician conodonts are known in this area only from a single locality near Rzeszòwek (Reichenwalde of German authors) in the Kaczawa Mts., (Gòry Kaczawskie, Bober-Katzbachgebirge) where they have been extracted from slightly metamorphosed sericitic slates by means of hydrofluoric acid (BARANOWSKI & URBANEK, 1972). Although preservation of elements is generally poor (they are crushed and etched by the acid: Fig. 5) samples are so productive that it is possible to reconstruct more or less safely their original appearance and even arrange them into apparatuses (Figs. 5-7). Most regrettably, because of very complicated microtectonics it appears impossible to establish precisely spatial relationships among samples in the rock column (URBANEK, 1975). It is evident, however, that they represent at least three distinct time horizons. Materials collected by Dr. Zdzisława Urbanek (Wrocław University) were subject to a joint apparatus restudy (DZIK & URBANEK, 1983) which has not been finished yet. The comments below are the result of an examination of her collection containing 7,260 identifiable specimens.



3. Diagnostic features of two chronospecies of *Sagittodontina* from the Mòjcza Limestone as shown by their platform elements. — A-B. *Sagittodontina kielcensis* (DZIK, 1967): A. Element oz ZPAL CVI/424, sample MA-54, x 75. B. Element sp ZPAL CVI/413, sample MA-60, x 70. C. *Sagittodontina* aff. *bifurcata* KNÜPFER, 1967, element oz ZPAL CVI/427, sample MA-91, x 70. Note angulation at the base.

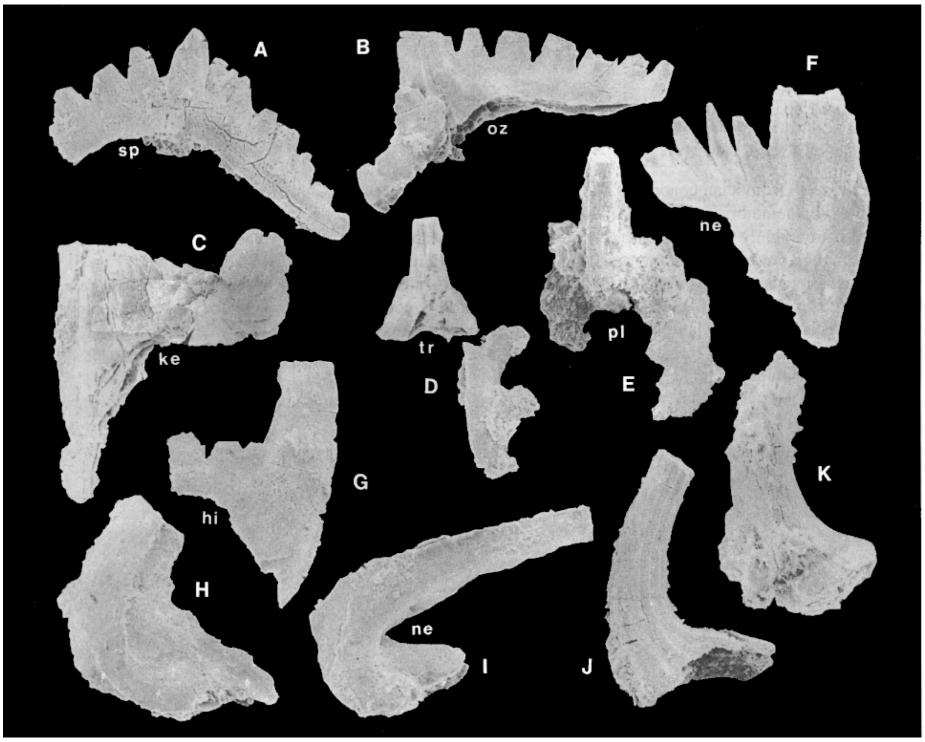


Fig. 4. Representative conodont elements from the older assemblage from Rzeszòwek slates, sample 202/7-3 (collection of Dr. Zdzisława Urbanek housed at Wrocław University). — A-G. *Plectodina* aff. *flexa* (Rhodes, 1953); elements sp (A) and hi (G) x 80, oz (B) x 85, ke (C) x 100, tr (D) and pl (E) x 105, ne (F) x 160. H-I. *Paroistodus parallelus* (Pander, 1856), x 80. J. *Scolopodus rex* Lindström, 1955, x 80. K. *Cornuodus longibasis* (Lindström, 1955), x 80.

Among six of the most productive samples from the locality in the bottom of the Kamieniec creek near Rzeszòwek five (202/7-2,3, 10a, 11, 12a) contain from 6.6 to 9.8 per cent elements of *Paroistodus* with costate sides diagnostic for *P. parallelus* (Pander) (Fig. 4H-I). The species is known to occur in the Late Latorpian and earliest Volkhovian of the Baltic region, where it evolved into acostate *P. originalis* (Sergeeva) (Lindström, 1971). Cooccurrence of *Microzarkodina flabellum* (Lindström) (2.4 to 12.8 per cent; (Fig. 5B), having a similar range of occurrence in the Baltic area, and simple cones *Scolopodus rex* Lindström (0.7 to 2.2 per cent; Fig. 4J), *Drepanodus arcuatus* Pander (0.0 to 2.8 per cent), *Cornuodus longibasis* (Lindström) (0.7 to 2.2 per cent), *Protopanderodus rectus* (Lindström) (13,7 to 35,3 per cent), and *Drepanoistodus* sp. (9.0 to 20.1 per cent) is consistent with such an age determination. Presence of an early form of *Baltoniodus* (10.0 to 28.8 per cent; (Fig. 50), similar to its earliest Baltic representatives traditionally named *B. triangularis* (Lindström), suggests the earliest Volkhovian rather than a Late Latorpian age. Another similar, but certainly more primitive form of *Baltoniodus* is *B. bohemicus* Dzik from the Kla-

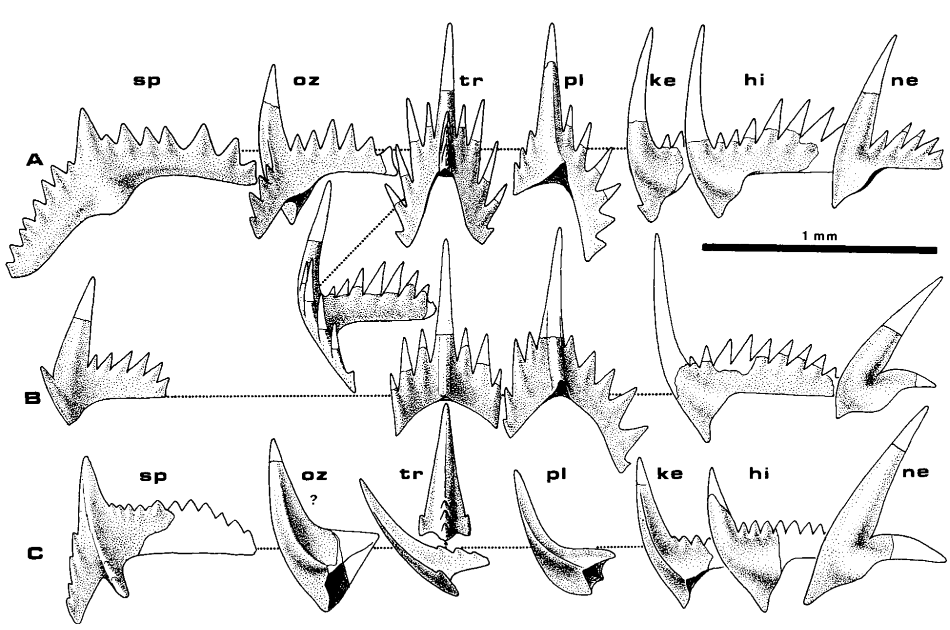


Fig. 5. Ramiform conodont apparatuses from the older assemblage of the Rzeszòwek slates. Composite drawings based on materials of Urbanek (1975). — A. *Plectodina* aff. *flexa* (Rhodes, 1953). B. *Microzarkodina flabellum* (Lindström, 1955). C. *Baltoniodus* aff. *bohemicus* Dzik, 1984.

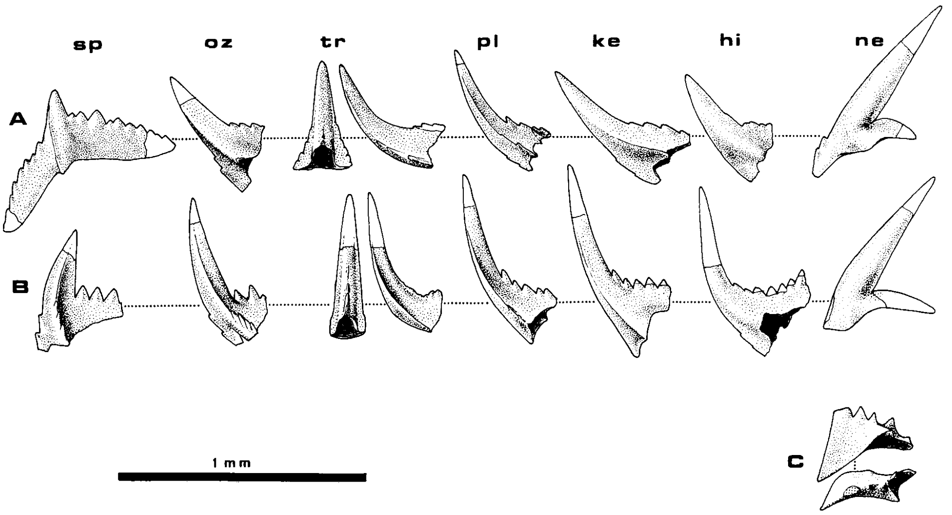


Fig. 6. Ramiform conodont apparatuses from sample 202/7-2 that do not occur in other samples of the older assemblage from Rzeszòwek. Composite drawings based on data of Urbanek (1975). A. *Baltoniodus* aff. *triangularis* (Lindström, 1955). B. "*Prioniodus*" aff. *crassulus* (Lindström, 1955). C. Undetermined ne? element.

bava Formation of Bohemia, which is associated with closely similar assemblage of simple cones (see DZIK, 1984). A single sample (202/7-2) contains also unnumerous specimens (3.7 per cent) possibly representing a species close to Baltic "*Prioniodus*" *crassulus* (LINDSTRÖM) (Fig. 6B; see also DZIK, 1984).

The most unusual feature of the assemblage represented by these five samples is the presence of a species of *Plectodina* (17.6 to 38.4 per cent) closely similar to *P. flexa* (RHODES) (Figs. 4A-G, 5A) from the Llandeilian of Wales and the Armorican Massif (LINDSTRÖM, 1979; LINDSTRÖM et al., 1974; SAVAGE & BASSETT, 1982). This and supposed presence of *Phragmodus* led BARANOWSKI & URBANEK (1974) to conclude that the assemblage contains mixed Early and Middle Ordovician faunas. An ancestor of *Plectodina* has not been identified yet but it is expected to be similar to the Early Arenigian *Microzarkodina* (DZIK, 1983). The oldest safely dated species of the genus is *Plectodina*? sp. A of STOUGE (1984; erroneously named *P. polonica* in DZIK, 1983: Fig. 5: 10) from the Late Arenigian Table Head formation of Newfoundland. There is thus nothing contradictory in a somewhat earlier presence of *Plectodina* in the Sudetes, even if it represents more advanced lineage with cyrtoniodontid ne elements. The only difference between the population from Rzeszòwek and the Late Llanvirnian to Llandeilian Welsh *P. flexa* is the presence of a long medial process in at least some tr elements (Fig. 5).

The sample deviating from others in composition (202/7-7) lacks *Paroistodus* and any true *Plectodina* containing instead platform elements associated with ramiforms (4.5 per cent) closely resembling the apparatus of Baltic *Lenodus variabilis* (SERGEEVA) (Fig. 7D). Such a shape of the platform developed in the Baltic lineage in the latest Volkhovian and the oldest representatives of the Balognathidae, still similar to the ancestral *Baltoniodus navis* (LINDSTRÖM) occur in the borehole Lesieniec 1 in *Paroistodus originalis* Zone. This strongly suggests the earliest Kundan age of the discussed assemblage which is supported by morphology of associated, well denticulated species of *Baltoniodus* (53.4 per cent), perhaps a late form of *B. navis* (Fig. 7C). Presence of a species of *Scalpellodus* (6.2 per cent) similar to *S. gracilis* (SERGEEVA), *Drepanoistodus basiovalis* (SERGEEVA) (1.5 per cent), and especially *Dapsilodus viruensis* (FÅHRAEUS) (17.3 per cent) at least does not contradict such an age determination.

The assemblage contains also a species representing possibly a new genus related to *Plectodina* (12.5 per cent; Fig. 7A) and, especially interesting, a very primitive *Icriodella* (4.6 per cent) most probably conspecific with *I. cerata* (KNÜPFER) from Thuringia (Fig. 7B).

The Upper Silesia Massif

Numerous and relatively well preserved conodonts occur in Ordovician limestones in cores of deep boreholes drilled in vicinities of Myszkòw (NEHRING-LEFELD & SIEWNIAK-MADEJ in preparation). The oldest well represented assemblages are dominated by early species of *Baltoniodus* and *Eoplacognathus* lineages associated by several coniform conodonts and, most interestingly, by "*Prioniodus*" *crassulus - Phragmodus polonicus* transition series. They are thus close to be the same as in the basal parts of the Mòjcza Limestone in the Holy Cross Mts. (see below).

Also in the Llandeilo, like in the Mòjcza faunas, *Amorphognathus inaequalis* occurs followed by abundant *Complexodus*. Higher up a shallow-water assemblage with *Panderodus* of yet undeterminable age has been found, perhaps corresponding to parts of the Mòjcza section rich in representatives of this lineage. In the micritic limestone close to the top of the sequence a *Hamarodus* fauna was identified, judging from innumerous specimens of the same composition as in the coeval strata of the Holy Cross Mts. The conodont assemblages from the Upper Silesia Massif differ thus from the Baltic ones in that they lack the species which are also lacking in the Holy Cross Mts. and contain these which, being lacking (or very rare) in the Baltic region, are abundant in the Holy Cross Mts. (like earliest *Phragmodus* and *Complexodus*).

The Jędrzejòw Massif

Ordovician conodonts are known from the borehole Książ Wielki IG 1 from the depth of 1277.2-1270.2 m. BEDNARCZYK (in JURKIEWICZ, 1975) lists a few form-species representing most probably the multielement species *Scabbardella altipes* (HENNINGSMOEN), which is very common in the Late Caradocian of the Mòjcza Limestone being the most numerous member of the *Hamarodus* fauna.

The Holy Cross Mountains

The oldest conodonts of the area have been found in a thin layer of unconsolidated glauconitic sand just above the basal conglomerate in Chojnòw Dòł. It contains broken coniform elements, among them a primitive oistodontiform ne element suggesting latest Tremadocian age of the assemblage. Better preserved specimens were extracted from overlying chalcedonites, well exposed in Wysoczki for which also latest Tremadocian age was attributed (SZANIAWSKI, 1978).

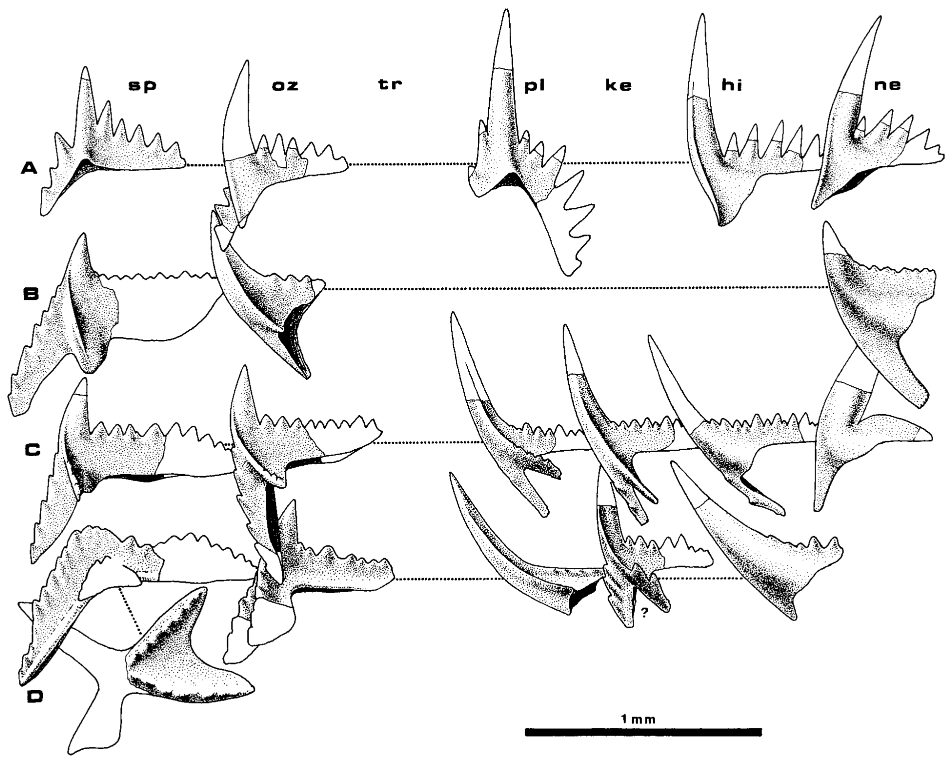
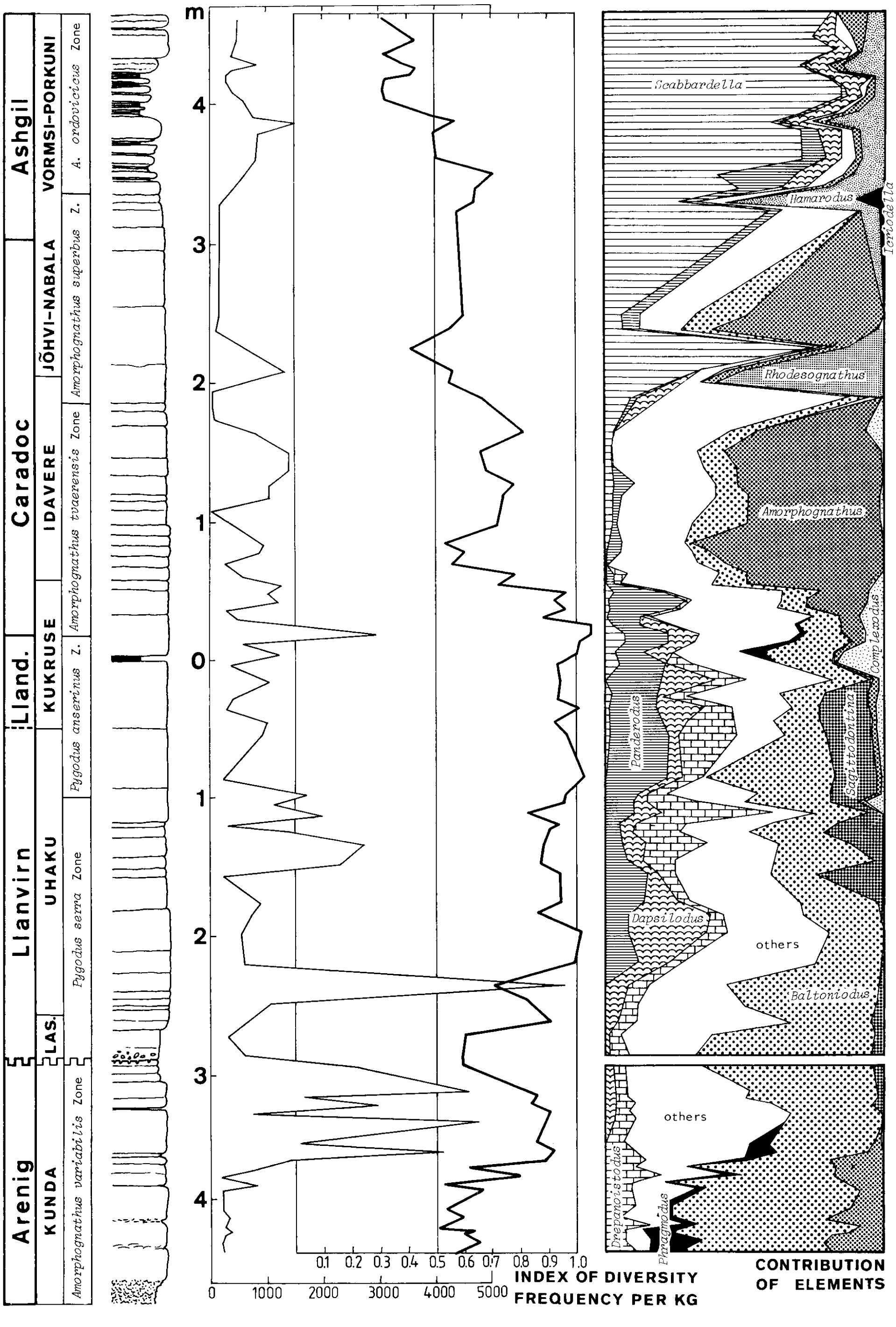


Fig. 7. Ramiform conodont apparatuses from the younger assemblage from Rzeszòwek, sample 202/7-7. Composite drawings based on data of URBANEK (1975). — A. *Plectodina*(?) sp. B. *Icriodella cerata* (KNÜPFER, 1967). C. *Baltoniodus parvidentatus* (SERGEEVA, 1963). D. *Eoplacognathus* (*Lenodus*) cf. *variabilis* (SERGEEVA, 1963).

Arenigian conodonts occur in thin limestone intercalations within the Bukòwka sandstone. A faunule from a single thin layer of red marly limestone exposed once in the Bukòwka quarry and recovered by the borehole Bukòwka IG 1 within a depth interval of 83.5-84.0 m was listed by BEDNARCZYK & BIERNAT (1979) and discussed above. The samples do not differ in generic composition from slightly younger assemblages from the basal sandy layers of the Mòjcza Limestone.

Conodonts occur in the Mòjcza limestone in all its localities. They are best known from the Mòjcza (Fig. 8) and Międzygòrz quarries, the latter being difficult to be precisely sampled because of tectonically complex situation of the limestone sequence. Frequencies of elements in samples from Mòjcza range generally from 200 to 1000 per kilogram of the rock, sometimes reaching 6000 (Fig. 8). Diversity of the assemblage is generally high being somewhat lower in the basal sandy part of the sequence and gradually dropping during the Caradocian and Ashgillian. The assemblage is dominated by typically Baltic species though in the basal part *Phragmodus* (Fig. 11), believed to be typical rather for the North American Midcontinent and Siberian faunas and extremely rare in the Baltic region, contributes significantly to it. The topmost strata contain the *Hamarodus* fauna, which is typical also for coeval Baltic rocks, but in Mòjcza it lacks species of North American affinities being also much less diverse.

Unlike most of Baltic sections of the Llanvirnian and Llandeilian, showing rather high contributions of *Eoplacognathus* and *Pygodus*, in Mòjcza these conodonts are innumerous (Fig. 9), while the *Sagittodontina* lineage, rare in the Baltic area that time, is very well represented there (Fig. 11). Judging from compositions of samples collected in different kinds of rocks (dolomites in Międzygòrz, black claystones in Zalesie Nowe), these differences were not controlled so much by facies differences but rather by climatic distinction of the area. The difference between the carbonate platforms of the Małopolska Massif and the East European Platform was not deep so much to support separation


Arenig
Llanvirn
Lland.
Caradoc
Ashgil
KUNDA
LAS.
UHAKU
KUKRUSE
IDAVERE
JÕHVI-NABALA
VORMSI-PORKUNI
Amorphognathus variabilis Zone
Pygodus serra Zone
Pygodus anserinus Z.
Amorphognathus tvaerensis Zone
Amorphognathus superbus Z.
A. ordovicicus Zone
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INDEX OF DIVERSITY
0 1000 2000 3000 4000 5000
FREQUENCY PER KG
Scabbardella
Hamarodus
Icriodella
Rhodesognathus
Amorphognathus
Complexodus
Sagittodontina
Panderodus
Dapsilodus
others
Baltoniodus
Drepanoistodus
Phragmodus
others
CONTRIBUTION OF ELEMENTS

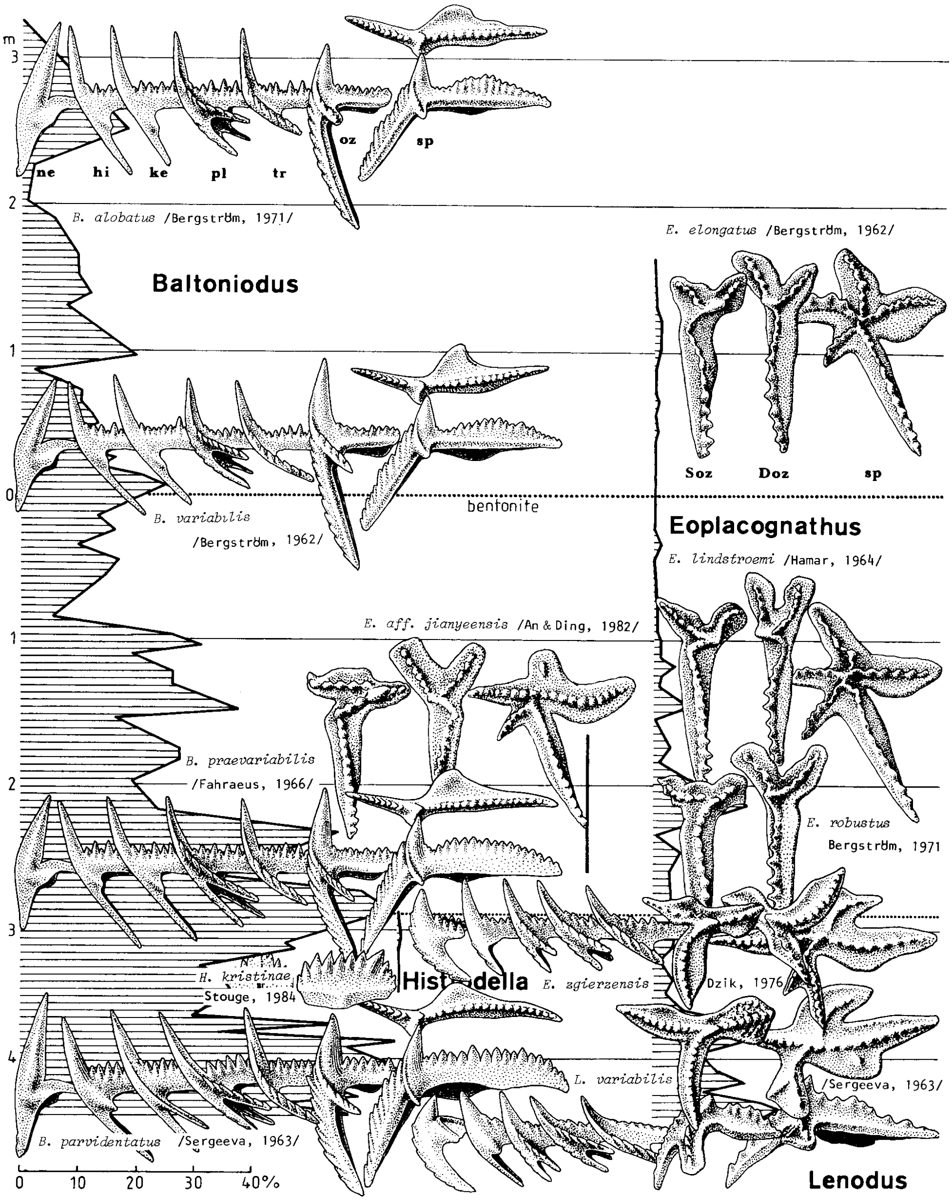


Fig. 9. Per cent contribution of elements to samples and apparatus reconstructions of conodonts characteristic for the lower parts and present at the base of the Mòjcza limestone.

◀

Fig. 8. Section of the Mòjcza Limestone at Mòjcza, Holy Cross Mts., Poland; frequency of conodont elements per kilogram of rock, Shannon's index of diversity and a log of percent contribution of the dominating species to the whole conodont assemblage in particular samples. Levels indicated at subsequent drawings correspond to meters above and below the bentonite layer; also the discontinuity surface may serve as a convenient reference horizon.

of these regions by a wide ocean or attribution to different climatic zones. Instead, some similarity between the Mòjcza assemblages and coeval assemblages from Volhynia and somewhat northerly located Podlasie and Masuria suggests proximity of the Małopolska Massif of the East European Platform, supporting the suggestion of the presence of only a hundred-kilometers wide deeper zone separating these blocks during the Ordovician (Dzik, 1978, 1983).

Although rare, representatives of *Eoplacognathus* and *Pygodus* allow strict correlation of the lower part of the Mòjcza limestone with the Ordovician of the Baltic region as well as the South China. The presence of *Histiodella* and *Phragmodus* gives some valuable suggestions regarding correlation with the North American Midcontinent. The lineage of *Amorphognathus* serves as a means of intercontinental correlation of the upper half of the section (Figs. 16, 17). The lineages are represented well enough to allow biometrical studies of uninterrupted evolution. Somewhat surprisingly in virtually all cases the evolution is gradual and almost linear in respect to the rock thickness. Paradoxically, the unusually good record of evolution in the Mòjcza Limestone hampers strict identification of zonal boundaries. For instance, the base of the *Amorphognathus tvaerensis* Zone, which is sharply cut elsewhere (Bergström, 1971), being marked by appearance (immigration) of the diagnostic species cannot be indicated precisely in Mòjcza because the lineage was there present continuously and its rate of evolution is too slow in respect to population variability to allow strict correlation (Fig. 17).

Perhaps more or less abrupt changes in diversity and composition of assemblages can be used for more precise age correlation of the Ordovician within the Baltic realm. Several such changes are apparent in the Mòjcza section. Thus, in the part of the Mòjcza Limestone below the major discontinuity surface (1.5 m in thickness) two somewhat different assemblages can be distinguished (Fig. 8). The difference is apparent owing to introduction of several new lineages at approximately the same time, both among simple-cones (*Semiacontiodus*, *Protopanderodus graei*, *P. gradatus*, *Dapsilodus*; Figs. 12, 13) and ramiforms (*Sagittodontina* and *Histiodella*). Despite of contribution of coarse quartz sand this part of the section is much condensed, too. This is clearly indicated by degree of evolutionary transformation in the *Lenodus-Eoplacognathus* and *Phragmodus* lineages (Figs. 9, 11).

Paradoxically again, the discontinuity surface itself has virtually no bearing on composition and diversity of conodont assemblages although it is evident from the morphologic gap in development of ke elements in *Baltoniodus* lineage as well as from the morphology of *Eoplacognathus* elements just above the surface that at least three conodont subzones (*Eoplacognathus pseudoplanus*, *E. suecicus*, and *E. foliaceus*) corresponding to two Baltic stages (late Kundan, Aserian and early Lasnamägian) are lacking (Fig. 9). Reworked elements of a *Baltoniodus* chronosubspecies typical for the late Kundan and Aseri present in the sample above the surface suggest that strata of this age were deposited in the area and later removed by submarine erosion. Reworking cannot be blamed for possible changes to be smoothened because the taxonomic stability continues high above the surface being followed by significant evolutionary changes in the *Eoplacognathus* lineage. The diversity did not change up to somewhat above the bentonite layer although in this part of the section some gradual rearranging of the assemblage took place. Both *Panderodus*, believed to be typical of rather warm waters of the Ordovician, and *Sagittodontina*, which occurs in polar regions of that time (thus, lineages of quite different biogeographic regimes) become more and more abundant.

The diversity dropped steeply in the zone between 0.2 and 0.7 m above the bentonite (Fig. 8). This may correspond in time to introduction of the *Amorphognathus* lineage to the Baltic region and the North American Midcontinent; in Mòjcza it appeared rather gradually, much earlier than in the Baltic, prior to the *Pygodus serra-P. anserinus* transition. With increase in abundance of the *Amorphognathus*, *Sagittodontina* disappeared (Fig. 11). It emerged again with the second drop in diversity; there *Amorphognathus* become almost lacking being replaced for some time by *Rhodesognathus*. This event corresponds approximately to the *Amorphognathus tvaerensis-A. superbus* transition. Perhaps this was the time when several foreign lineages invaded the Baltic region (Dzik, 1983).

The next two meters of the section are marked by the appearance of *Scabbardella*. Except for minute *A. ordovicicus* all the remaining representatives of the assemblage are characterized by deep and wide basal cavities, irrespective of their evolutionary relationships (*Scabbardella*, *Walliserodus*, *Hamarodus*, *Dapsilodus*). Perhaps it indicates further deterioration of the climate.

The Baltic area

Although faunal dynamics of Ordovician conodonts in the Baltic region is generally well recognized (Lindström, 1971; Bergström, 1971) the published quantitative data are available only for the Arenigian to Early Llanvirnian (Löfgren 1978, 1985) and Ashgillian (Sweet & Bergström, 1984) parts of the rock column. Assemblages of intermediate age were studied quantitatively only on the basis of glacial erratic boulders (Dzik, 1976). Along with numerous exposures in Scandinavia and Estonia there are also many deep boreholes from the marginal parts of the East European Platform available as a source of data on Ordovician conodonts. A core from one such borehole, Lesieniec 1,

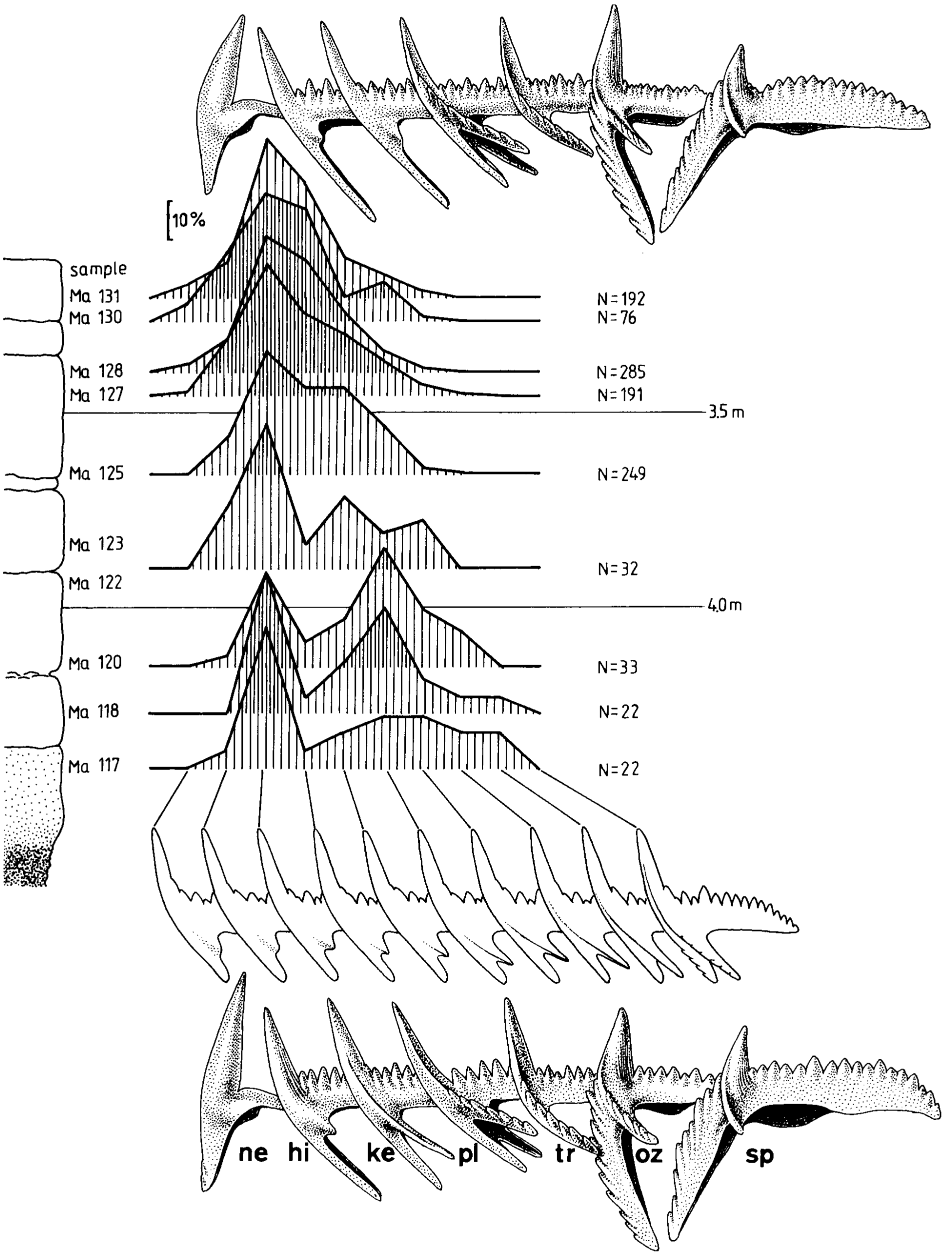


Fig. 10. Evolution of the ke element in the apparatus of *Baltioniodus* in strata below the discontinuity surface at Mòjcza. The whole range of variability of ke and hi elements in the genus was subdivided into ten morphologic classes. The diagram presents per cent contribution to the classes in samples. Note that originally bimodal frequency distribution become unimodal toward the top. Apparatuses of ancestral *B. parvidentatus* (SERGEEVA, 1963) and derived *B. praevariabilis* (FÅHRAEUS, 1964) are drawn.

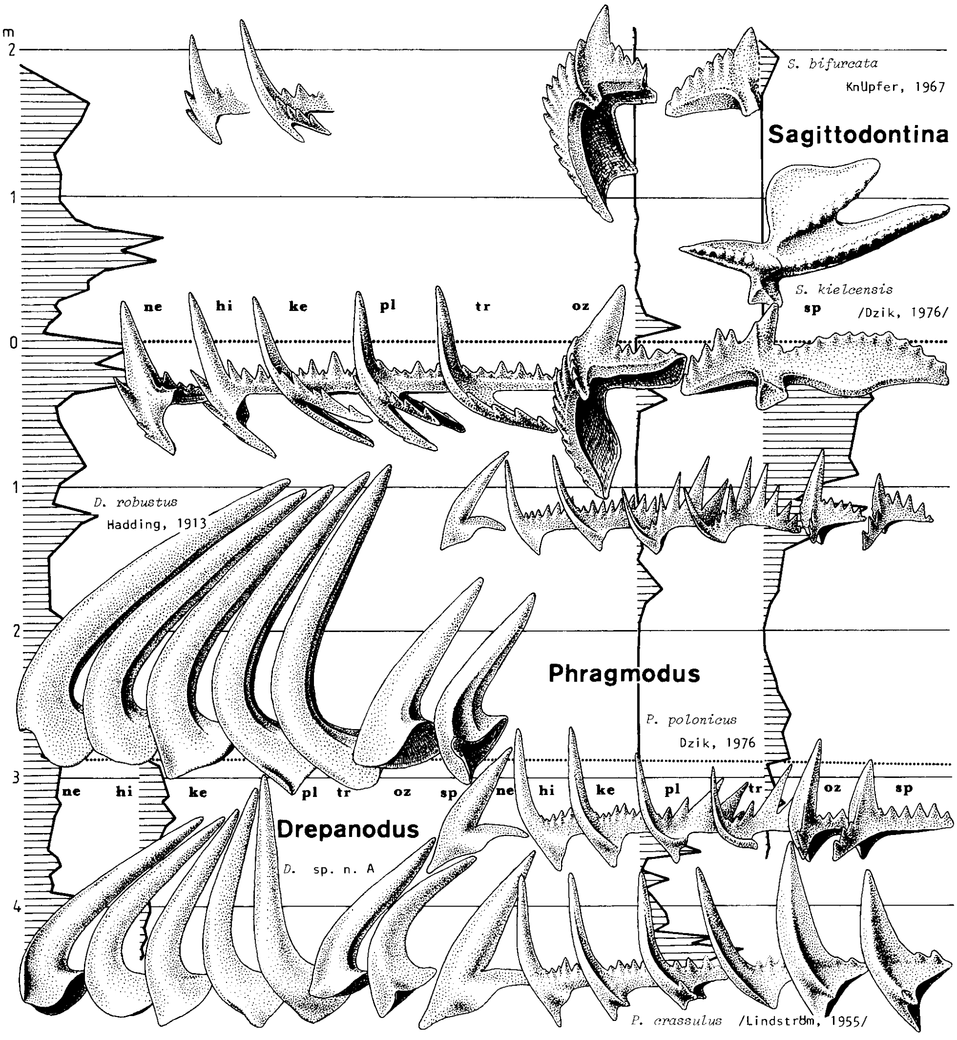


Fig. 11. Per cent contribution of elements to samples and apparatus reconstruction of conodonts typical for the lower part but introduced somewhat above the base of the Mójcza Limestone.

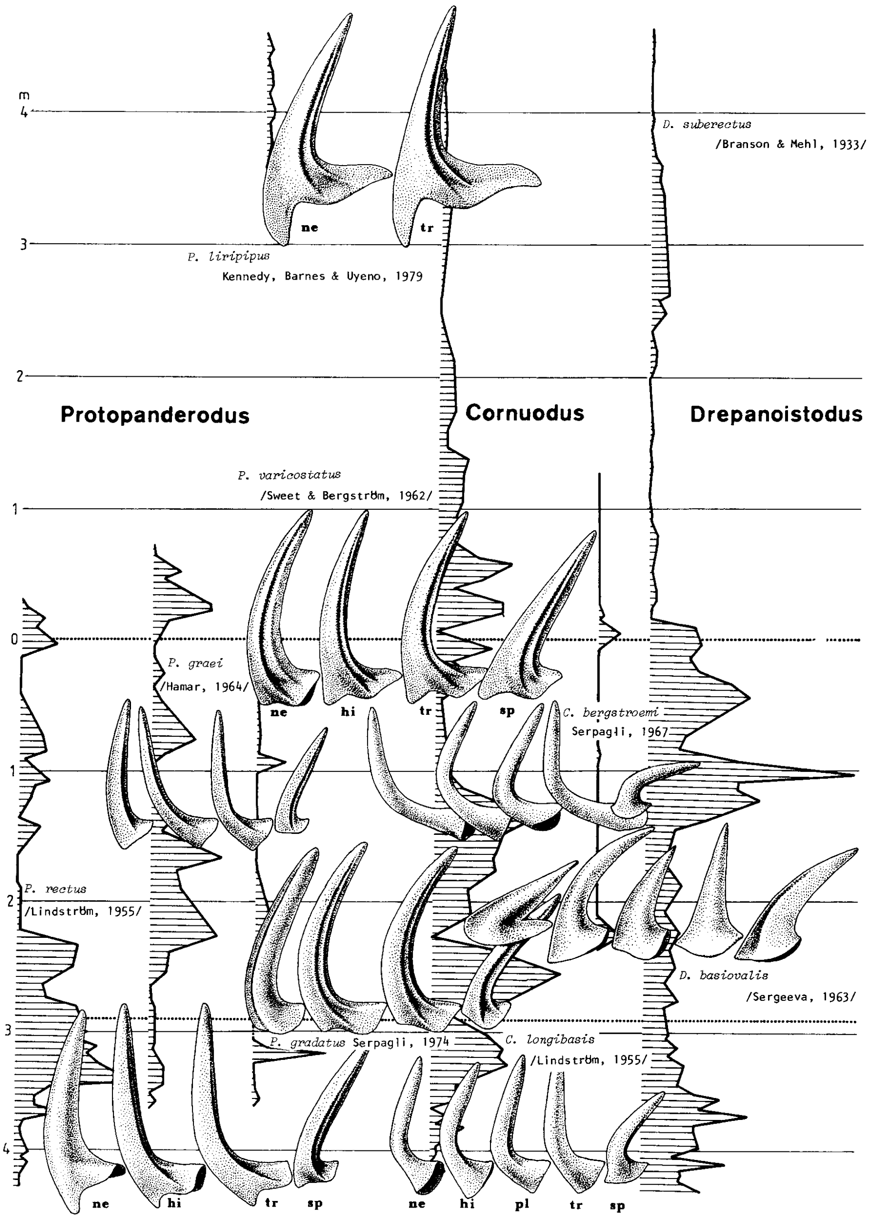


Fig. 12. Per cent contribution of elements to samples and apparatus reconstructions of long-ranging coniform conodonts which are typical for the lower half of the Mójcza Limestone.

with almost complete limestone section of the Ordovician, was provided for study to me by the petroleum exploration enterprises (Przedsiębiorstwo Poszukiwań Naftowych, Wołomin, Poland). Along with other sampled cores it allows close comparison of marginal Baltic assemblages with those from the Holy Cross Mts. The main difference between the Baltic and the Małopolska-type conodont assemblages is the dominance of *Sagittodontina* during the Llanvirnian in the latter and some Midcontinent influences in the Baltic faunas which do not reach the Małopolska Massif. In the Late Ordovician it is the invasion of "*Aphelognathus*" *rhodesi* (LINDSTRÖM) (DZIK, 1983) and *Belodina*. Another such event took place in the Early Kundan when *Parapanderodus asymmetricus* (BARNES & POPLAWSKI) was briefly occurring in the Baltic area (LÖFGREN, 1985) but, unlike the associated foreign lineages of *Histiodella* and *Polonodus*, it did not reach the Małopolska Massif.

Patterns of evolution

Although the best preserved and the most numerous materials of Ordovician conodonts are known from then equatorial regions of the North American Midcontinent and Siberia they can rarely be used for studies of long-term evolutionary processes because the dominating factor controlling their distribution there is migration. Virtually all lineages appear suddenly in the Midcontinent sections and, after more or less prolonged persistence, they disappear do not showing easily recognizable evolutionary transformations (see SWEET, 1979).

Quite different is the fossil record of conodont evolution in temperate (perhaps even cold-water) faunas of the Baltic region (BERGSTRÖM, 1971), the Małopolska Massif (DZIK, 1976, 1978), and South China (CHEN & ZHANG, 1985). Many lineages persisted there long enough without significant shifts in spatial distribution to allow profound evolutionary transformations to be recorded even in a single section. Whenever a stable carbonate sedimentation occurred for a longer period, resulting in high frequency of well preserved conodont elements in rocks, the evolution can be recognized with ease. The Mòjcza locality, presented above, is one of the best owing to virtually continuous sedimentation of organodetrital limestone during almost 50 milion years. Despite of a high stratigraphic condensation only a single biostratigraphically recognizable gap in the sequence was identified.

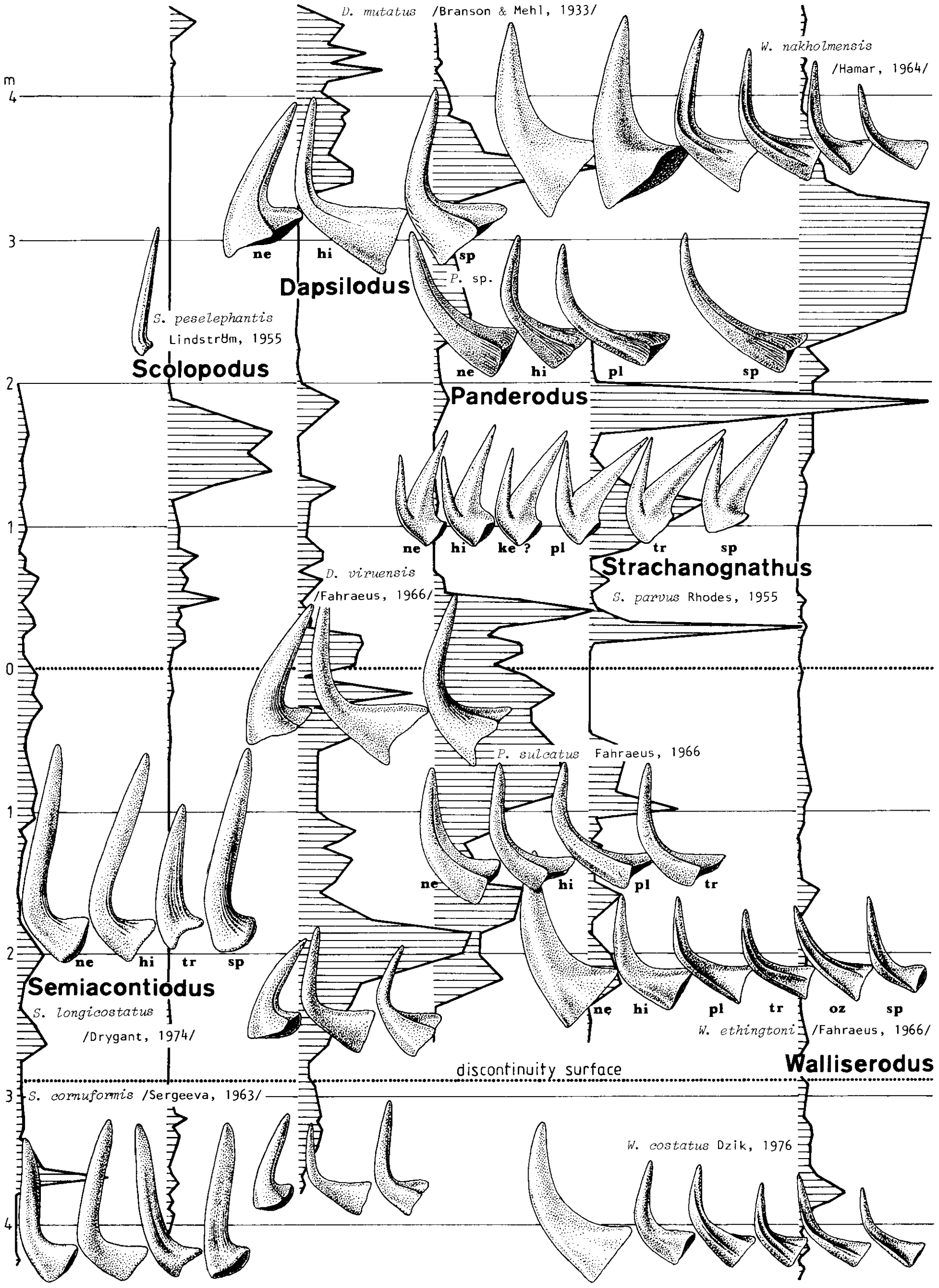
Certain conodont lineages represented in the Mòjcza section differ both in persistence and rates of their evolution. No obvious correlation between these factors has been noted. Although a few more or less abrupt rebuildings of the fauna, reviewed above, took place during the Middle Ordovician of the Holy Cross Mts., they did not have any obvious influence on rates and directions of the evolution. Somewhat surprisingly, they also have little to do with immigrations and extinctions (rather disappearances in the area) of lineages. With a few exceptions (*Histiodella*, *Rhodesognathus*, and *Icriodella*) lineages were introduced more or less gradually, also gradually their contribution to the productivity of the assemblage increased and they used to disappear in the same way. This suggests that the fossil record expresses smooth changes in spatial position of centers of highest productivity in a geographical range of particular species which was moving in relation to the locality.

Several lineages appear in the Mòjcza limestone close to its base and continue throughout much of the section. The most numerous is *Baltoniodus* occurring without breaks till the Middle Caradocian though its contribution more or less steadily decreased. In the part of the section below the discontinuity surface the evolutionary transformations of the *Baltoniodus* lineage are expressed in reduction of the "lateral" process in the ke elements. This phenomenon of a gradual disappearance of originally distinct element type was already noted in Baltic materials (DZIK, 1976) and is supported by quantitative analysis of frequency distribution of particular morphologic types of ke elements in successive samples from the Mòjcza Limestone (Fig. 10).

The stratigraphic gap corresponds to the segment of evolution of the lineage which is known from the Baltic region as *B. praevariabilis medius* (DZIK). Rare reworked elements of this chronosubspecies were found just above the discontinuity surface but otherwise the ke elements do not undergo any easily recognizable changes throughout the remaining part of the section. Instead, the shape of the base of the "posterior" process in sp elements was evolving. A triangular platform developed there gradually but, unlike Baltic and Appalachian sections (BERGSTRÖM & CARNES 1976), no sign of development of additional process in this place are noted in Mòjcza. Instead, the platform becames more and more robust and its outline slightly irregular. It is suggestive of a direct evolution from *B. variabilis*

▶

Fig. 13. Per cent contribution of elements to samples and apparatus reconstructions of long ranging conodonts which are typical for the central and upper parts of the Mòjcza Limestone. — Note: Apparatuses of *Walliserodus ethingtoni* and *W. nakholmensis* are misplaced and should be interchanged.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D. mutatus /Branson & Mehl, 1933/
W. nakholmensis
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sp
Dapsilodus
P. sp.
S. peselephantis
Lindström, 1955
Scolopodus
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Panderodus
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Strachanognathus
D. viruensis
/Fahraeus, 1966/
S. parvus Rhodes, 1955
P. sulcatus Fahraeus, 1966
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Semiacontiodus
S. longicostatus
/Drygant, 1974/
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W. ethingtoni
/Fahraeus, 1966/
Walliserodus
discontinuity surface
S. cornuformis /Sergeeva, 1963/
W. costatus Dzik, 1976

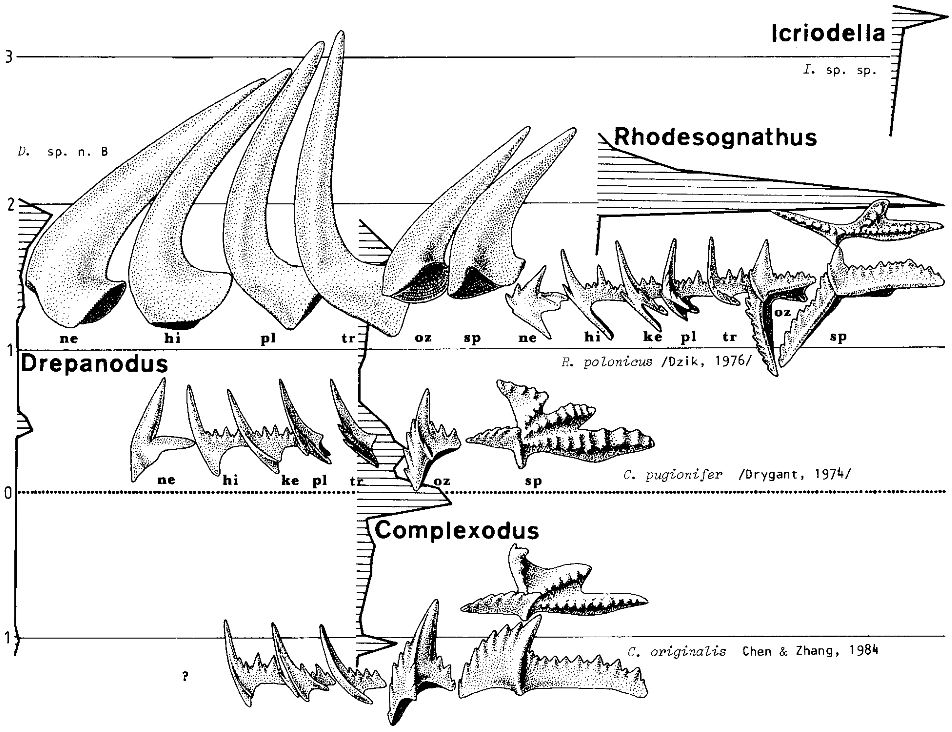

Fig. 14. Per cent contribution of elements to samples and apparatus reconstructions of conodonts with short ranges and exotic for the Małopolska Massif region.

(BERGSTRÖM) to *B. alobatus* (BERGSTRÖM), which implies a phenomenon of allopatric speciation, i. e. separation of the lineage into two separately evolving branches, the other being the North Atlantic branch of *B. gerdae* BERGSTRÖM. If it is true the appearance of *B. alobatus* in the Baltic fauna would be an effect of migration (not evolution), thus the base of the nominal zone may be diachronous in different regions. In sections with continuous evolution of the *B. prevariabilis-B. alobatus* lineage it is practically impossible to indicate precisely boundaries between particular chronospecies because of great population variability and ontogenetic changes of the diagnostic features.

The oldest conodonts with platform sp elements represented in the Mòjcza section are conspecific with Baltic *Lenodus variabilis* (SERGEEVA). Like in the Baltic region they are replaced somewhat above by *Eoplacognathus zgierzensis* DZIK. As long as it can be inferred from available data these chronospecies are connected by gradual evolutionary transformation which concern mostly elongation of a bifid "lateral" process in the sp element and development of denticulation in the ne element (Fig. 9). The series is broken by the discontinuity surface but it is now well established that in the Baltic sections the trend continued further toward *Eoplacognathus pseudoplanus* (VIIRA). No ramiform element is atributed to this and younger species of *Eoplacognathus* and it is not clear whether their apparatuses contained them. Immediately above the discontinuity surface two species of *Eoplacognathus* occur in Mòjcza, probably representing separate lineages. The more common is *E. robustus* BERGSTRÖM, which higher up is transformed into *E. lindstroemi* (HAMAR) and *E. elongatus* BERGSTRÖM. Another form, represented by innumerous and fragmentary specimens superficially similar to *E. foliaceus* (FÅHRAEUS), which differ from this species in acute angularity in bending of the main process in the left oz element (Fig. 9). It was identified with *E.* sp. A BERGSTRÖM 1971, a successor of *E. foliaceus*, by BERGSTRÖM (1983). The same lineage is better known from China (CHEN & ZHANG, 1987).

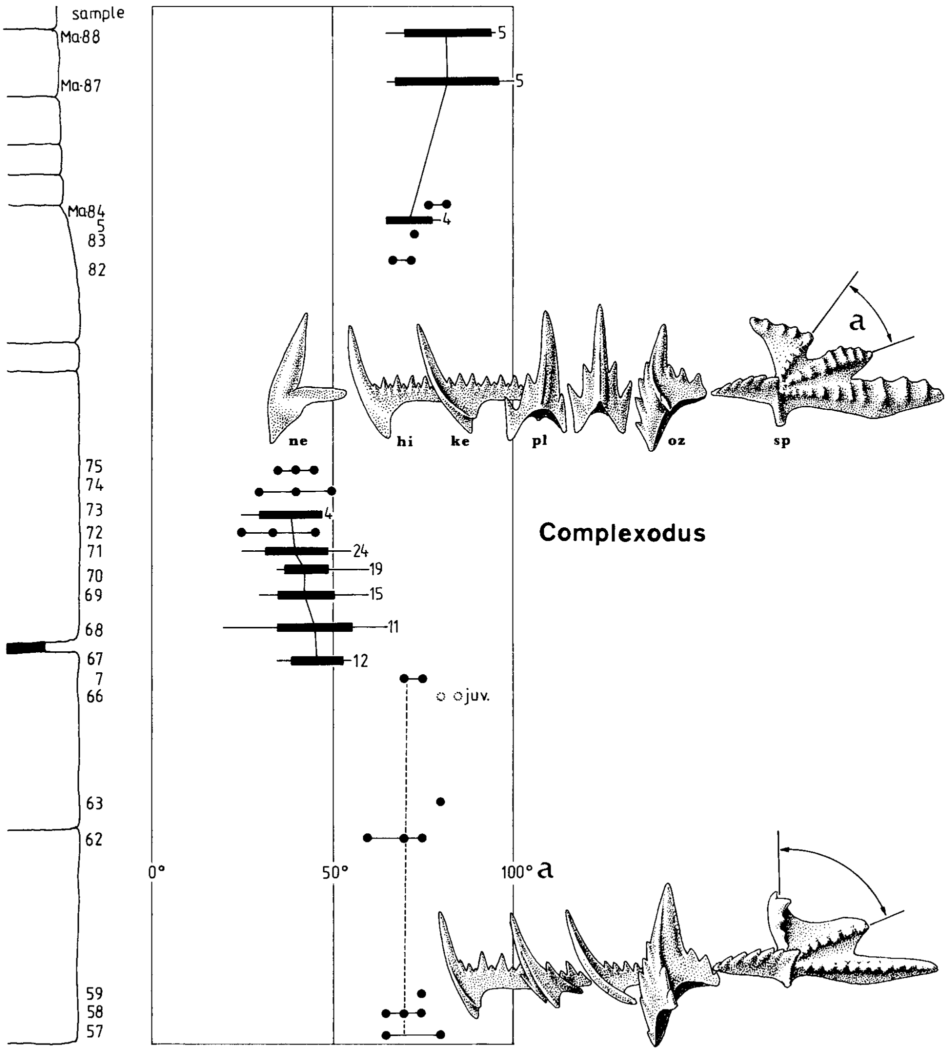

Fig. 15. Morphologic variability of *Complexodus* in the Mòjcza Limestone. The angle between processes was measured; black horizontal bars represent standard deviation ranges, thin lines the total range, points refer to single measurements.

Like the Baltic conodont assemblages the Mòjcza ones are also dominated, in terms of number of species, by coniforms. Evolutionary changes, rather poorly documented, were identified in the lineage of *Walliserodus* (Fig. 13), which probably originated from *Scalpellodus*, allopatrically evolving in the Baltic region at the same time and later replaced by *Walliserodus* (see LÖFGREN, 1978). Another evolving lineage was probably represented by the series of *Semiacontiodus cornuformis* (SERGEEVA) and *S. longicostatus* (DRYGANT) (Fig. 13), unfortunately punctuated by the discontinuity in sedimentation. Some changes, difficult to discern and possibly complicated by migration events, may be noted also in the *Dapsilodus* lineage.

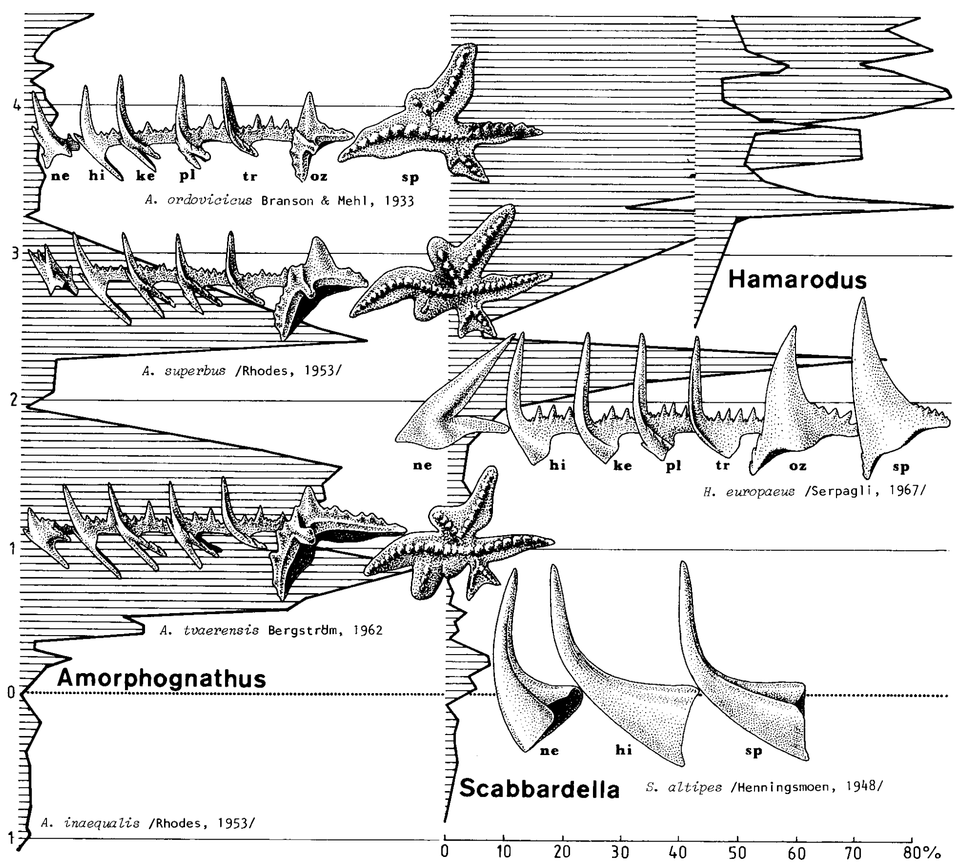

Fig. 16. Per cent contribution of elements to samples and apparatus reconstructions of conodonts typical for the upper part of the Mòjcza Limestone.

No apparent evolutionary transformation was identified in other lineages, although some of them are very long ranging. Of some interest is the occurrence of three distinct species of *Drepanodus* in the section, partially sympatric (Fig. 11, 14). Like *Cornuodus* species, they appear to have rather complex apparatus architecture which makes difficult the identification of species unless precise homologization of elements is undertaken.

It may be concluded thus that the rate of evolution is generally stable in a lineage. Coniform apparatuses are, actually by definition, the most conservative ones. More derived morphologies are obviously results of higher rates of evolution. Apparently, even if the evolution changes its subject from a one element location to another (like in *Baltoniodus*) the general rate remains high or low. It would be interesting to know how the quickly evolving lineages originate from their conservative ancestors but the available evidence does not provide any adequate example.

Among lineages of unknown foreign origin the most important is that of *Complexodus* (Figs. 14, 15). It is represented in the Mòjcza section by at least two distinct chronospecies. The oldest one is *C. originalis* Chen & Zhang, known also from China (Chen & Zhang, 1987) and Wales (see Bergström & Orchard, 1987), which differs from the younger *C. pugionifer* (Drygant), known also from the Ukrainian part of the East European Platform, in gaping, sharply denticulated "lateral" processes. Although these species evidently represent successive stages in the evolution of the lineage their distribution in Mòjcza was probably controlled by migration. A transition between

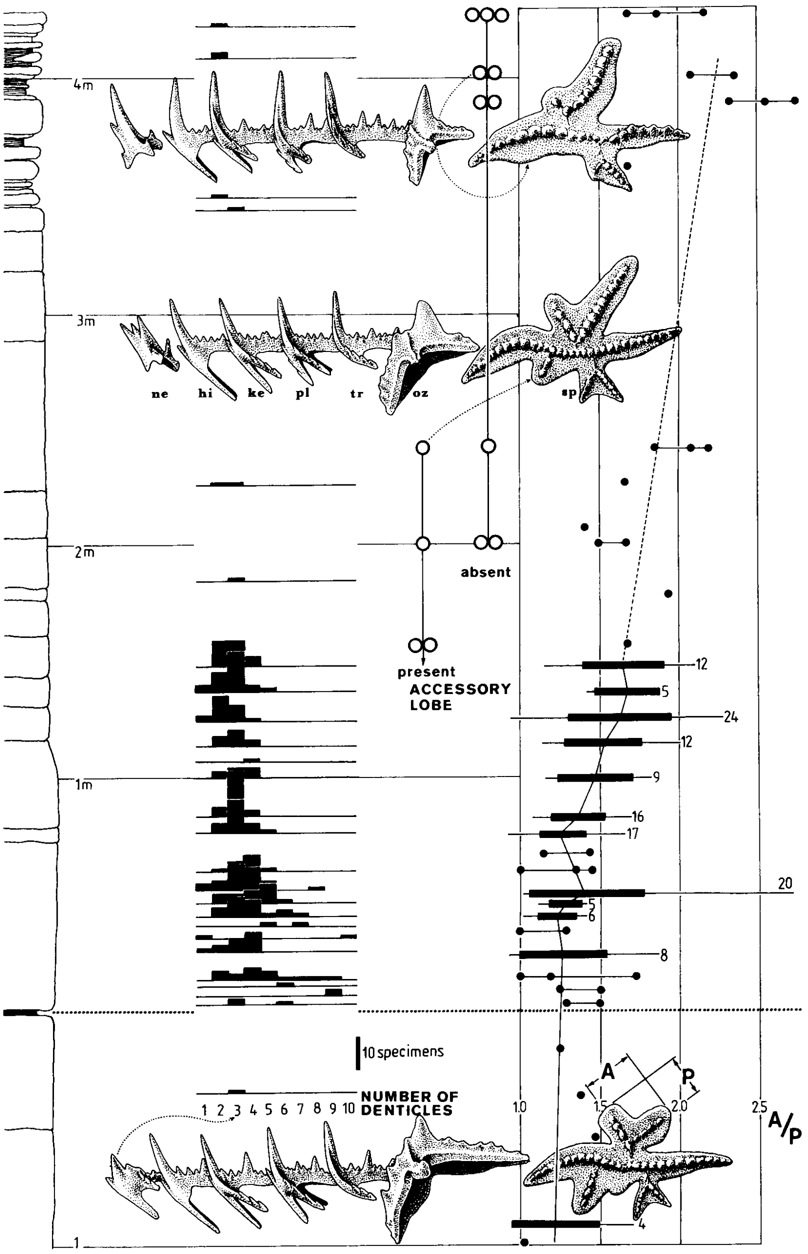

Fig. 17. Evolution of *Amorphognathus* in the Mójcza Limestone. Number of denticles in front of the "posterior" bifurcation in the ne elements and ratio in length between branches of the "posterolateral" process of both sinistral and dextral sp elements was counted. Also, at the *A. tvaerensis-A. superbus* transition also presence or lack of accessory lobe is indicated (circles).

them remains unproven despite of some apparent evolutionary changes in the part of the lineage where contribution of elements is high (Fig. 15), of a direction consistent with expectations. There is no continuity in the distribution of morphologies between underlying and overlying parts of the range of the lineage. This is provisionally interpreted as an effect of three independent successive migrations of *Complexodus* to Małopolska.

The best example of evolution in Mòjcza is provided by the *Amorphognathus* lineage (Fig. 17). The lineage was introduced to the area just before the *Pygodus serra-P. anserinus* transition, thus much earlier than in the Baltic region. Temporally it corresponds to the occurrence of *A. inaequalis* Rhodes in Wales and the Armorican Massif (LINDSTRÖM et al., 1974; SAVAGE & BASSETT, 1982; BERGSTRÖM & ORCHARD, 1986; BERGSTRÖM et al., 1987), but the Mòjcza population, if even conspecific, apparently differs from the Welsh one in much beter developed platform in the sp elements. Although supposed origin of the *Amorphognathus* lineage from *Sagittodontina kielcensis*, which remains the best canditate for direct ancestry, suggests such an appearance of platform in transitional forms, this is not consistent with the observed stratigraphic order of morphologies. It is suggested thus that the Polish-Baltic lineage leading to *A. tvaerensis* BERGSTRÖM is representative of a biospecies allopatric to the contemporaneous Welsh *A. inaequalis* RHODES. While in Mòjcza the sp elements become more and more complicated in outline, in Wales they seem to simplify gradually becoming more and more *Rhodesognathus*-like. It is remarkable that in *R. polonicus* (DZIK), which for a brief time invaded Mòjcza in the Late Caradocian, the shape of the platform in the sp elements is unusually variable and in later populations of the same genus lateral processes associated with the platform disappeared completely. The apparatus of *Rhodesognathus*, both in *R. polonicus* (Fig. 14) and *R. elegans*, occurring abundantly in the Lesieniec 1 borehole, is closely similar to that of *Amorphognathus*.

The collection of elements of *Amorphognathus* from the Mòjcza Limestone is large enough to enable quantitative studies of the evolution. Practically in every case when particular character is studied it appears that the change is very smooth and prolonged in time. When combined with great population variability it makes any arbitrary boundaries between chronospecies very foggy (Fig. 17). This means that also boundaries of zones based on these chronospecies can be identified only if large samples are available and even then the limits of uncertainty must have significant time dimensions.

Patterns of migration

Numerous conodont localities are known now within and around the Variscan orogenic belt of Europe (see SWEET & BERGSTRÖM 1984 for review). Unfortunately, in most of them conodonts are known only from some time horizons, do not allowing reconstruction of the faunal dynamics and do not providing enough certainty that a sample is representative for a whole fauna. Outside the Baltic Region and the North American Midcontinent more or less representative series of samples are known only from the Holy Cross Mts., Wales and England. In some cases this allows tracing, with more or less certainty, processes of allopatric speciation. For instance, as it was already noted above, at the time when in the Holy Cross Mts. the *Walliserodus* lineage was developing, most probably from a *Scalpellodus*-like ancestor, in the Baltic region *Scalpellodus* persisted to occur, producing a series of chronospecies (LÖFGREN, 1978) until it has been replaced by the immigrant *Walliserodus* lineage. Similar patterns of divergent allopatric evolution can be found in lineages of *Amorphognathus*, *Rhodesognathus*, *Eoplacognathus*, and *Baltoniodus*, already commented above. Application of the same way of reasoning to the area well within the Variscan belt is more risky, but some results are promising.

The occurrences in the Early Ordovician rocks of the area, believed to be located in high latitudes of that time, of several lineages, which are typical rather for equatorial faunas of the Middle and Late Ordovician are of special interest. The origin of the oldest representative of *Phragmodus*, *P. polonicus* DZIK, recorded in the basal part of the Mòjcza Limestone, a species which later expanded to Siberia and the North American Midcontinent, is symptomatic (Fig. 11). Rare specimens of *P. polonicus* are known also from the East European Platform (borehole Lesieniec 1; BERGSTRÖM & ORCHARD, 1986), but at that time the lineage was already split into several different forms developing in the equatorial regions. The best known one of these is *P. flexuosus* MOSKALENKO, that has well denticulated ne elements.

Interestingly, although the *Plectodina* lineage had a similar biogeographic history to *Phragmodus*, occurring initially only in the Sudetes and somewhat later in Newfoundland, the Armorican Massif and Wales, and finally during the Caradocian and Ashgillian diversified into several lineages in England and the Midcontinent, it never occurred in the Baltic area. Only its advanced derivative "*Aphelognathus*" *rhodesi* (LINDSTRÖM) invaded briefly the area in the late Caradocian together with other warm-water British species (see DZIK, 1983; SWEET & BERGSTRÖM, 1986). *Plectodina* was followed in its changes of distribution by the lineage of *Icriodella* which was typical for a quite different facies (see BERGSTRÖM, 1983). These and several other lineages cannot be fit together into a linear pattern of changes in distribution from south to north or back. Rather, the simplest pattern of biogeographic processes is a trifid one

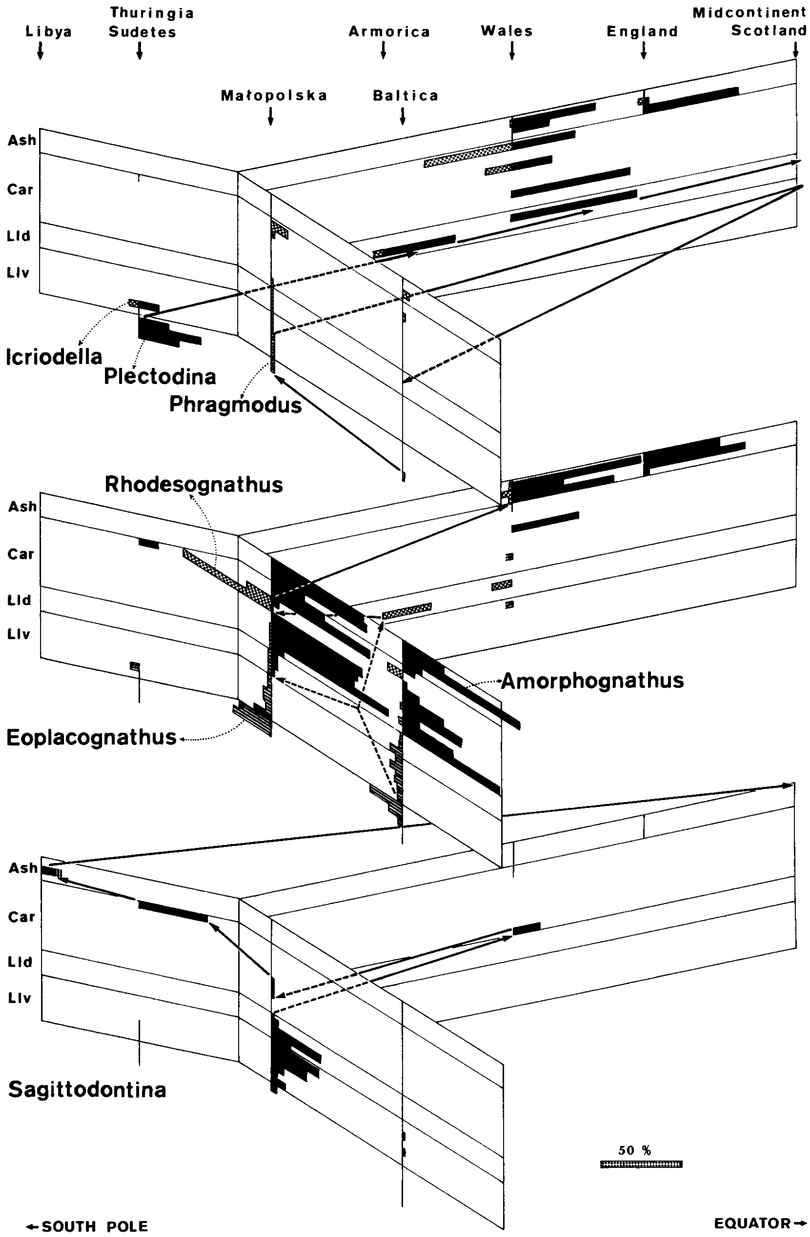

Fig. 18. Diagram illustrating order of appearance of particular species of conodonts in the best known regions of the Variscan orogenic belt of Europe. Simplified patterns of percent contribution for composite sections are added based on data of SWEET & BERGSTRÖM (1984), BASSETT & SAVAGE (1982), LÖFGREN (1985), and ORCHARD (1980). Suggested direction of expansion of geographic ranges or migrations are indicated by arrows.

(Fig. 18), with Gondwana, Laurentia, and Baltica at the ends. *Phragmodus* and *Plectodina* are the best to exemplify northward routes of migration (which dominate), *Sagittodontina* is a rare example of the opposite direction. It originated somewhere close to the Małopolska Massif, probably from a Baltic ancestor (*Lenodus*), known from brief appearances also in the Llanvirnian of the Baltic region and the Early Caradocian of Wales (*"Prioniodus deani"* Savage & Bassett, 1984 clearly conspecific with *S. kielcensis*), and abundant in the Late Caradocian of Thuringia and the Ashgillian of Libya (Bergström & Massa, 1987).

The pattern of distribution of conodont lineages, rather regular during the Middle Ordovician, become complicated in the Late Ordovician. In the Late Caradocian several warm-water lineages invaded the Baltic area, and faunas containing rather unusual combinations of species developed in the Ashgillian (Sweet & Bergström, 1984). The most surprising is the appearance of *S. bifurcata* (*"Noixodontus girardeauensis"* of McCracken & Barnes, 1982) in the Midcontinent, possibly indicating a world-wide cooling of the climate at the Ordovician-Silurian boundary.

Conclusions

The trifid pattern of displacements of conodont lineages during their Middle and Late Ordovician evolution is hardly consistent with the Early Paleozoic paleogeography inferred from the assumption that the closure of Iapetus preceded similarly directed collision of microcontinents with Laurasia during the Variscan orogeny (i. a. Baird et al., 1980; Livermore et al., 1985; Scotese et al., 1985; Holder & Leveridge, 1986). If this would be the case,- than the Baltic faunas of the Ordovician, being geographically closer to the Midcontinent should not deviate so much from the latitudinal gradient well established within the British Caledonides and the central European Variscan belt. Rather, it seems that during the Ordovician the terranes now incorporated into the Variscan belt occupied longitudes not much different from these of Laurentia while Baltica was located much to the East (as suggested in Dzik, 1984: Fig. 7). The paleomagnetic data concerning the discussed area, suggestive of rather close to the Equator positions of the Moldanubian Massif and Baltica in the Early and Middle Ordovician (see Bylund, 1986; Krš et al., 1987) are also inconsistent with the observed biogeographic gradients.

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