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Ordovician conodonts and the Tornquist Lineament

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ABSTRACT

The Holy Cross Mts. in southern Poland are generally believed to be split by a tectonic dislocation into two separate parts, a NE one being a part of the Baltic Craton and a SW part belonging to the Małopolska Terrane of a complex geotectonic history connected with the Trans-European Suture Zone (Tornquist Lineament). Unexpectedly, conodont assemblages of earliest Middle Ordovician (early Darriwilian) age from Pobroszyn in the northeastern Łysogóry region and from Szumsko in the southwestern Kielce region show virtually identical species composition. One of the dominant species both in Pobroszyn and Szumsko, *Trapezognathus pectinatus* sp. n., characterized by denticulated M elements, occurs elsewhere only on the northern margin of Gondwana. Separation of the Małopolska microcontinent from Baltica continued after the disappearance of *Trapezognathus* and an apparently allopatric speciation process was initiated by a population of *Baltoniodus*. Also in this case, denticulation developed in the M elements of the apparatus but the process of speciation of *B. norrlandicus denticulatus* ssp. n. was truncated by re-appearance of the Baltic lineage of *Baltoniodus*. Later conodont faunas from the region are of Baltic affinities, but remain distinct in showing a relatively high contribution from exotic species of *Sagittodontina*, *Phragmodus*, and *Complexodus*. The periodic North American Midcontinent tropical influences observable in the Baltic region did not reach the Holy Cross Mts. The Ordovician conodont faunas from the Holy Cross Mts. can be fit into a transect extending from Baltica to Gondwana, with several intermediate terranes. This new evidence disproves the long-held concept that the Łysogóry and Kielce regions had separate early Palaeozoic fates and that the Małopolska Terrane was unified with Baltica already in the earliest Ordovician. The Trans-European Suture Zone truly marks the presence of a wide Tornquist Sea in the early Palaeozoic.

1. Introduction

The tectonic units corresponding to the early Palaeozoic continents of Baltica and Gondwana are separated by several central European terranes located in-between. The most prominent geological discontinuity that exposes disparity of these tectonic units is the Tornquist Lineament. It is usually interpreted as the Trans-European Suture Zone, a subject of repeated rifting, compression and strike-slip movement since the latest Precambrian (e.g., Antonowicz et al., 1994; Pharaoh et al., 2006), although the geophysical evidence is equivocal and may be also interpreted as a result of local subsidence (Mazur et al., 2015). The only place in the central section of the Tornquist Lineament where the possible suture is accessible at the surface, is the boundary between two tectonic units of the Holy Cross Mountains. A dislocation parallel to the SW margin of the Tornquist Lineament separates the northern Łysogóry unit from the southern Kielce unit, which represents the northern margin of the mostly subsurface Małopolska Massif. The Łysogóry facies development indicates an open-sea environment extending northward. Because of their different early Palaeozoic sedimentary regimes it is generally believed that these were parts of separate terranes (recently reviewed by Walczak and Belka, 2017).

Palaeomagnetic data from the Ordovician Mójcza Limestone in the Kielce region plot well on the coeval Darriwillian to Katian segment of the polar wander path for Baltica (Schätz et al., 2006). According to Nawrocki et al. (2007), the Małopolska Terrane developed near the present southern edge of Baltica and was dextrally relocated for a relatively small distance along the Trans-European Suture Zone. The juxtaposition of the Małopolska Massif against the Łysogóry area could have been a result of its detachment from the margin of Baltica due to right-lateral strike-slip movement in the late Silurian (Narkiewicz, 2002). This would mean that both the Holy Cross Mts. units were parts of the East European Craton. However, although data on detrital mineral sources appeared inconclusive (Valverde-Vaquero et al., 2000), the provenance of clastic material in Cambrian time inferred from K-Ar cooling ages show that the blocks of Łysogóry, Małopolska, and Upper Silesia are crustal fragments derived from the Gondwana margin, not

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displaced parts of the East European Craton. Walczak and Belka (2017) used Sm-Nd isotope signature to identify sources of clastic material to these units. It has appeared that Małopolska was supplied from Amazonian, not Baltic, sources during the early and middle Cambrian. Instead, the Łysogóry late Cambrian material shows a close similarity to the Baltic crust. This has allowed to posit a hypothesis that the Małopolska Terrane migrated during this time span along more or less the same latitude from its original position near the South American part of Gondwana to its present position near Baltica. In result, the Małopolska Massif was the first Gondwana-derived microplate that accreted to the margin of Baltica (Belka et al., 2000).

These conflicting geotectonic scenarios call for a test. Usually, palaeobiogeography is used for such purposes but few groups of early Palaeozoic organisms include species distributed widely enough to show connections between former continents and restricted enough in their distribution to expose differences between particular terranes. The early Middle Ordovician pelagic conodonts are especially predisposed for such purposes because of distinct provincialism. In the Ordovician, biogeographic distinctions between faunas were the most prominent in the whole Palaeozoic. Fortunately, a few new sites with Ordovician conodonts located between the central European transition from Gondwana to Baltica are available. Although not as stratigraphically complete as those studied previously, they offer crucial biogeographic evidence. Altogether, the set of conodont fossil assemblages extends geographically from the Prague basin (Dzik, 1984; Ferretti, 1998), Thuringia (Dzik, 1990; Ferretti and Barnes, 1997), the Sudetes (Dzik, 1999b), Kielce region of the Holy Cross Mountains (Dzik, 1978, 1994, 1999b; Dzik and Pisera, 1994), the Łysogóry region (Dzik, 1999a; Trela et al., 2001), Podolia in Ukraine, Bornholm (Stouge and Rasmussen, 1996) and many Baltic localities (e.g., Viira et al., 2001, 2006; Männik and Viira, 2012; Hints et al., 2012; Rasmussen and Stouge, 2018), some of them from areas previously not considered. The new evidence on conodont faunas from the Podolian locality Kytaihorod, the Łysogóry locality Pobroszyn, and the Kielce region locality Szumsko is presented below (Fig. 1).

2. Methods

The conodont elements were extracted from carbonate rocks with standard techniques. The samples were disintegrated with dilute formic acid. In case of the Szumsko material, this usually resulted in a large amount of dolomitic "sand" with various contribution from quartz grains. Fortunately, the dolomite crystals were easily removed in Franz electromagnetic separator and heavy liquid was used to enrich samples from Szumsko and Kytaihorod with high quartz sand contents. Composition of newly reconstructed conodont apparatuses was identified by tracing homology of particular element types. Terminology of element sides refers to their inferred position in the apparatus (Dzik, 1994, 2015).

There are various approaches to describing and interpreting geographic distribution of organisms. The traditional biogeography counts number of shared species or higher rank taxa between ecosystems or particular sites to develop a hierarchical system of their classification. It is an approach analogous to phenetics in taxonomy but the obtained picture of relationships is static in respect to the geological time. The cladistic approach refers rather to sharing of species by ecosystems, as an analogy to character distribution among taxa. "The use of temporal data is avoided in cladistic biogeography because of the risk of incorporating ideas about unobserved processes into the interpretation of biogeographic patterns" (Cecca et al., 2016, p. 4). The opposite attitude is chosen here, exploiting the spatio-temporal coordinates of fossil populations and tracing their hypothesised ancestor-descendant relationships across ancient environments (Dzik, 1983, p. 60).

3. Conodonts from Kytaihorod in Podolia

The sampled section in Podolia is located below the village Kytaihorod. The strata there exposed consist of about 0.5 m of calcareous sandstone representing the Molodovo Formation and 0.7 m of sandy limestone with thin clay intercalations of the Subich Formation (Drygant et al., 1982). Above an erosional discontinuity, a few centimetre thick conglomerate of the Teremcy bed marks the beginning of

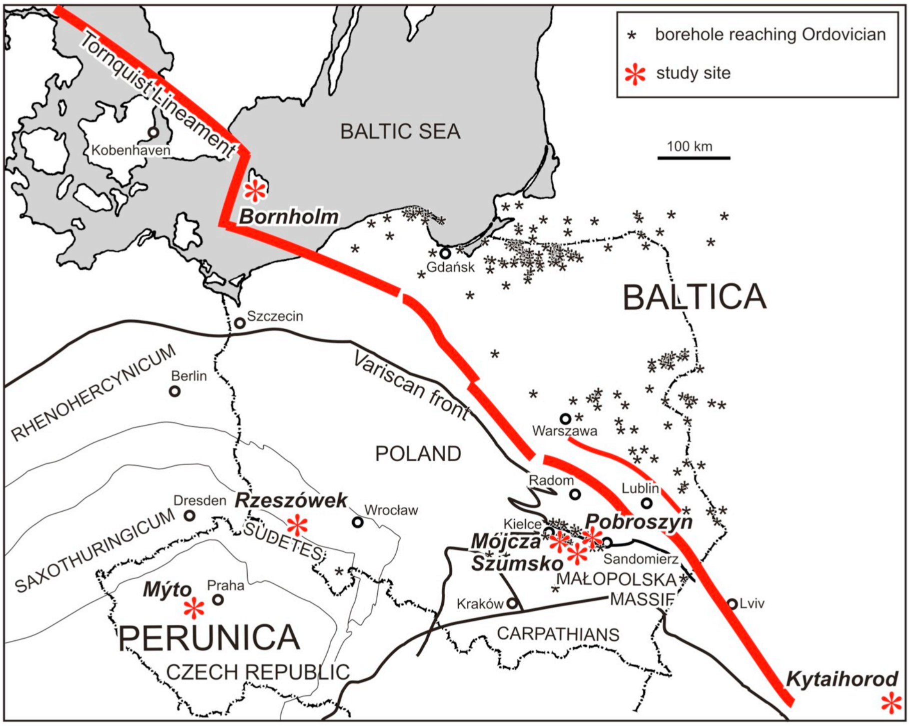

Fig. 1. Location of Central European exposures and drill-holes referred to in the text (larger asterisks) and those reaching the Ordovician strata in proximity to the Tornquist Lineament. Names in large block letters refer to Palaeozoic terranes.

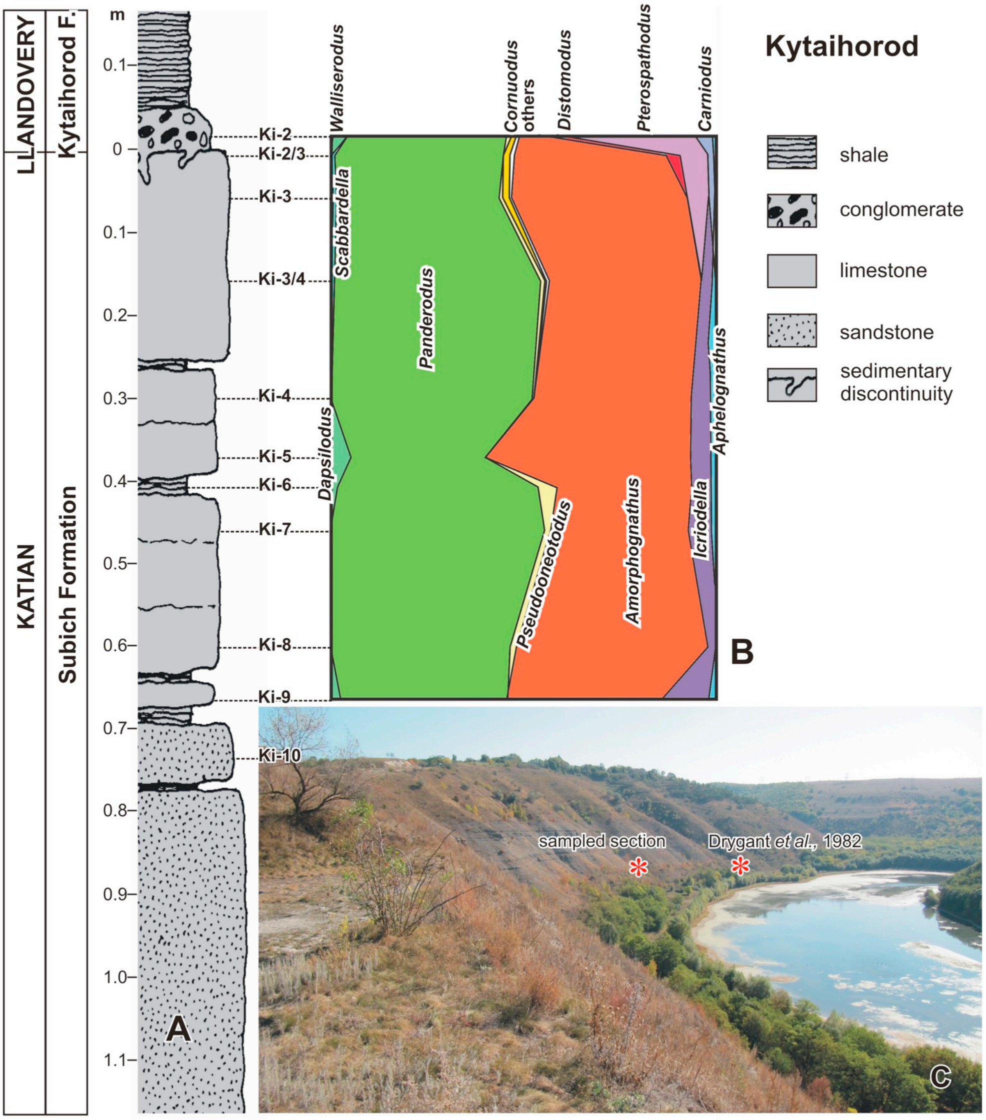

Fig. 2. Rock column of the Late Ordovician (late Katian) strata exposed at Kytaihorod in Podolia, Ukraine (A), percent contribution of elements of particular genera to samples (B) and photograph of the exposure with the collecting site indicated (photo of Daniel Drygant, Lviv).

the Silurian Kytaihorod Formation (Fig. 2A). Only the Subich Formation limestone has yielded Ordovician conodonts. Their fossil assemblage is virtually uniform throughout the section (Fig. 2B), being dominated with *Panderodus* and *Amorphognathus*. A species of *Icriodella* is also common, other conodont species being subordinate. *Hamarodus*, so common in the coeval strata of Holy Cross Mts. and the regions of Gondwanan affinities is virtually lacking. *Scabbardella*, another typical component of high-latitude Late Ordovician assemblages, is represented only by a few specimens in sample Ki-3, contributing only 0.6% to the sample (Supplementary material Table 1).

In sample Ki-3, about 5 cm below the top of the Ordovician limestone, a minor addition of Silurian (Late Llandovery) conodonts emerges, including *Pterospathodus amorphognathoides* and species of its assemblage (*Pseudooneotodus tricornis*, *Distomodus* sp., *Carniodus* sp., *Ozarkodina* sp.) known from the Baltic region. Most probably they come from the filling of vertical burrows in the limestone from the overlaying Teremcy or Restiv beds of the Kytaihorod Formation (Drygant, 1984; Racki et al., 2012). The contamination ranges as deep as 18 cm (to sample Ki-3/4), where a single *Pterospathodus* specimen has been found. Only the most important indigenous Ordovician species are commented on below.

The most characteristic element M of the *Panderodus* apparatus from Kytaihorod (Fig. 3AI–AL) fits the morphology of homologous element of *P. gracilis* (Branson and Mehl, 1933) as illustrated by Nowlan and Barnes (1981). The P_1 specimens of *Icriodella* from Kytaihorod (Fig. 3AD–AH) differ from those of the type population of *I. prominens* Orchard, 1980 from the lower Keisley Limestone of England (Orchard, 1980; Bergström and Ferretti, 2015) in a shorter dorsal process usually counting only a couple of denticles, instead of 4–5. The latter is probably of *A. ordovicicus* Zone age, as *A. duftonus* is present in the upper Keisley Limestone (Orchard, 1980, p. 13). The M elements of *Amorphognathus* from Kytaihorod with a transverse denticle (spur), diagnostic for *A. duftonus* (Rhodes, 1955), are relatively well represented in the material (altogether 69 specimens). Although biometrics is not possible, because most specimens are incomplete, the range of variability in the morphology of the element can be estimated. It is expressed mostly in the prominence of the spur, ranging from its complete lack in rare specimens to extreme development, being longer than the cusp (Fig. 3H–Q). Taxonomic implications of this variability require a comment.

According to Ferretti et al. (2014a, p. 806) rare specimens of *A. superbus* morphology co-occur with *A. ordovicicus* in the lower portion of the Sholeshook Limestone in Wales. The same sequence of events expressed in gradual disappearance of denticulation of the ventral

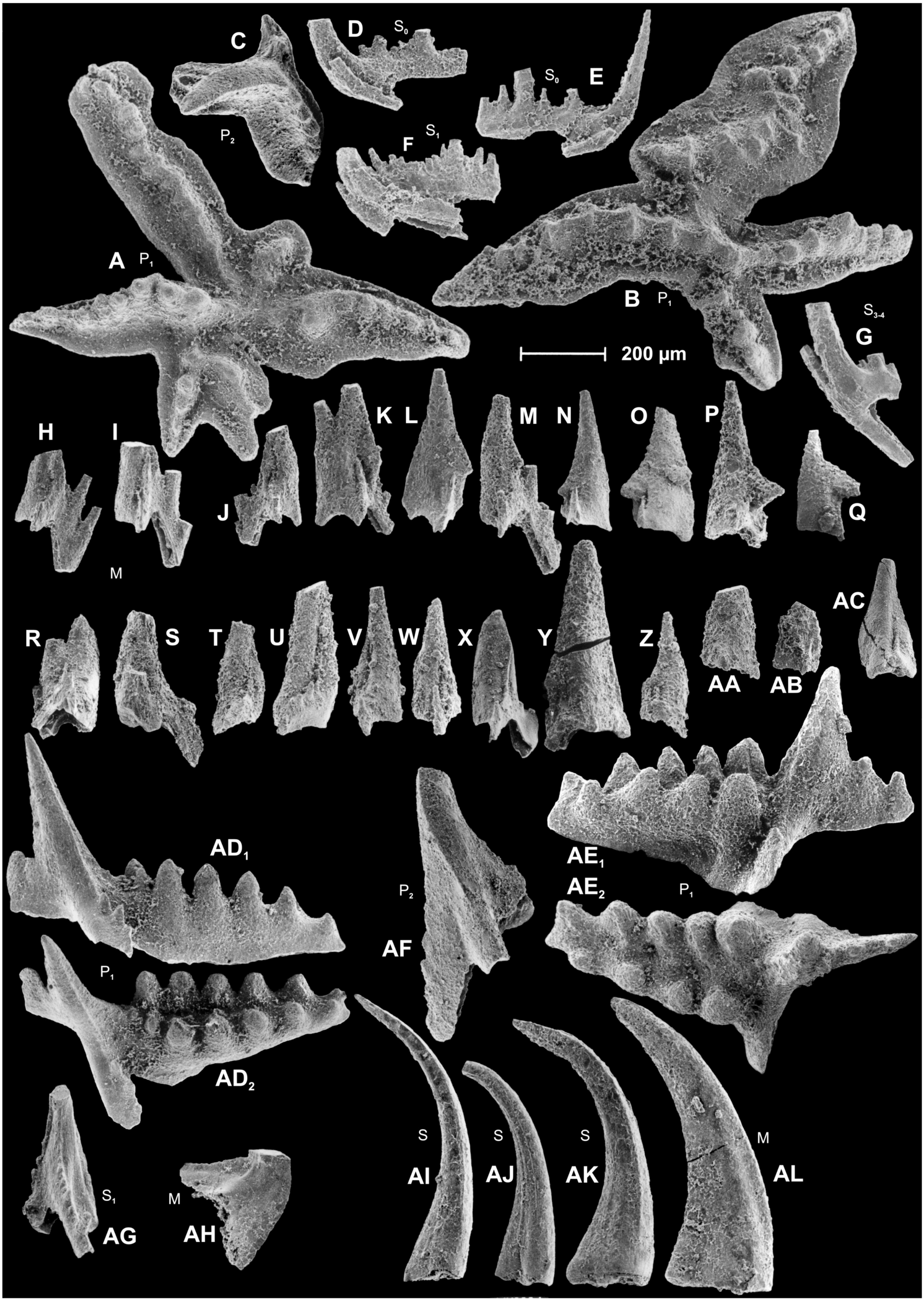

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Fig. 3. Conodonts from the Late Ordovician (late Katian) of Kytaihorod in Podolia, Ukraine (all from sample Ki-3, except for E that is from sample Ki-5 and AI – AL from sample Ki-3/4) compared with related species from the Holy Cross Mountains, Poland and Carnic Alps, Austria. Location of elements in the apparatus are indicated on this and following figures. A–Q. *Amorphognathus duftonus* Rhodes, 1955, specimens ZPAL cVI/960 and 958 (A, B; elements P_1), ZPAL cVI/961 (C; element P_2), ZPAL cVI/962 and 953 (D, E; elements S_0), ZPAL cVI/963 (F; element S_1), ZPAL cVI/964 (G; element $S_{3–4}$), ZPAL cVI/969, 968, 967, 965, 970, 966, 971, 974, 972, and 973 (H–Q; elements M arranged according to size of the dorsally oriented denticle on the cusp; H, I, M, P, Q are sinistral, J, N, O are dextral). R–AC. *A. ordovicicus* Branson and Mehl, 1933, elements M from Mójcza sample Ma-174, specimens ZPAL cVI/981, 980, 978, 975, 982, 977, 979, 983, and 976 (R-Z; R, T, U, V, W, Y, Z are dextral, S and X sinistral) are compared with those from Zalesie sample Za-5, specimens ZPAL 986 and 985 (AA – AB; dextral and sinistral, respectively), and from the Uqua Formation at Cellonetta Lavinerinne sample Cr-8A, specimen ZPAL cVI/984 (AC; sinistral). AD – AH. *Icriodella* sp. aff. *I. prominens* Orchard, 1980, specimens ZPAL 958 and 957 (AD and AE; elements P_1), ZPAL cVI/956 (AF; element P_2), ZPAL cVI/955 (AG; element S_1), and ZPAL cVI/954 (AH; element M). AI-AL. *Panderodus* sp.; specimens ZPAL cVI/990, 989, 988, and 987 (elements P?, S_0, $S_{1–4}$, and M).

process in M element in the *A. superbus-ordovicicus* lineage is recorded in the lower part of the Zalesie Formation at Mójcza (Dzik, 1994, 1999a, fig. 3). The M element of the type population of *Amorphognathus ordovicicus* Branson and Mehl, 1933 at the Ozora Quarry in southeastern Missouri has its ventral process reduced and undenticulated (Bergström and Leslie, 2010, fig. 4:1). This chronospecies has a wide geographic distribution (e.g., Nowlan and Barnes, 1981; Nowlan, 1983; Ferretti and Serpagli, 1999). Rare specimens of such morphology have been recovered by myself also from the Zalesie in the Holy Cross Mts. sample Za-5 (Fig. 2R–Z) and sample Cr-8A of the Uqua Formation (previous 'Uggwa Limestone') at Cellonetta Lavinerinne in the Carnic Alps (Fig. 2AC).

In the following succession of events in the evolution of the lineage leading to *A. duftonus*, the spur (a triangular transverse denticle inserted between the bases of dorsal and posterior processes) gradually developed. Its occurrence throughout the section of the Sholeshook Limestone has been reported by Ferretti et al. (2014a). This is recorded also in the upper part of the Zalesie Formation at Mójcza (Dzik, 1999a). Initial stage in the development of the spur is represented also by a single M element found in the Pernik beds near the top of the Králův Dvůr Formation in Bohemia (Ferretti, 1998). In Estonia, *A. duftonus* occurs in the Valga-10 core section at depth 324.00 m in the Bernati Member of Kuldiga Formation (Kaljo et al., 2008, fig. 8F, H) associated with *Decoriconus* sp., last *Gamachignathus* sp., and *Pseudooneotodus* aff. *Beckmanni*. It is preceded by a hiatus marked by development of redbed at the top of the underlying Kuili Formation. *Sagittodontina* (= *Noixodontus*) appears there immediately above the range of *A. duftonus* in the regressive Edole Member of Kuldiga Formation (Kaljo et al., 2008, fig. 7). This may suggest that either the Bernati Member corresponds to the horizon with *Mucronaspis* (lacking conodonts) or the Hirnantian cooling reached Baltica somewhat later than the Perunica microcontinent.

Both *A. ordovicicus* and *A. duftonus* occur in 'Calcaire des Vaux' in Normandy, a unit delimited by erosional surfaces from below and above. Illustrated M elements of the former come from level 4, the latter from level 6 but they may represent extremes of population variability as well (Ferretti et al., 2014b). They are associated with *Scabbardella* and *Sagittodontina*, but *Panderodus* and *Hamarodus* are also present. This Armorican fauna appears thus closely similar to those in Thuringia and Bohemia of Gonwanan provenance.

I suggest that *A. superbus*, *A. ordovicicus*, and *A. duftonus* are successive chronospecies in a monospecific lineage, with variable morphology of M elements within populations, their diagnostic morphology being expressed only by most specimens in the community, but not all of them. Ferretti et al. (2014a; Bergström and Ferretti, 2015) interpreted them as sympatric species partially or continuously co-occurring through the Sholeshook Limestone. Apparently, to resolve the taxonomy of the late *Amorphognathus* species one needs to determine the range of within-population variability in each sample separately. In case of the Kytaihorod section, there seems to be a continuity in the series of morphotypes and I consider the whole set of *Amorphognathus* samples conspecific. Only one *Amorphognathus* species, that is *A. duftonus*, occurs at Kytaihorod. The apparatus of *Amorphognathus duftonus* was asymmetric, like that of its ancestor, *A. ordovicicus*. This is mostly expressed in development of posterior processes in P_1 elements (Fig. 3A, B). In all sinistral elements examined, they bifurcate immediately after formation of the set of posterior processes and the dorsal one develops almost always two denticles and a distinctly separated platform lobe. In dextral elements, bifurcation is delayed and the dorsal branch consists usually of only one denticle. In some cases no separate process emerges and the bifurcation is expressed only in the sinuosity of the ventral branch. The most variable aspect of the P_1 elements is size of the anterior process. It is broken in most specimens, but among those more or less completely preserved the process is prominent and almost undivided (Fig. 3B). No specimen of *A. ventilatus* morphology has been found at Kytaihorod, which may mean that this species had a restricted stratigraphic and/or geographic distribution.

The tropical component of North American Midcontinent affinity is represented at Kytaihorod by rare elements of *Aphelognathus* similar to *A. rhodesi* (Lindström, 1959) known also from older strata (Oandu stage, early Katian) in the Baltic area (Dzik, 1983). Only one M specimen of juvenile *Hamarodus brevirameus* (Walliser, 1964), associated with possible P_1 one, has been found in sample Ki-2/3. Stouge and Rasmussen (1996) suggested that more than one species of *Hamarodus* can be distinguished, the Canadian *H.* cf. *H. europaeus* of Nowlan (1983) being different in having "lamellar cavities". Actually these are regular growth increments visible in any conodont element if the basal cavity is not filled with a mineralised tissue (e.g., Dzik, 2000, 2008).

4. Conodonts from Pobroszyn in the Łysogóry region

The "Łysogóry facies region", named by Tomczyk (*in* Tomczyk and Turnau-Morawska, 1967), differs profoundly from the Kielce facies zone in the lack of coarse clastic sedimentation in the Early Ordovician. The complete succession of the Ordovician strata in this region is documented by the Jeleniów IG 2 and several other boreholes (Tomczykowa, 1968; Biernat and Tomczykowa, 1968).

The only exposure of the Ordovician in the Łysogóry region with a conodont record is at Pobroszyn near Opatów. In 1998 Wiesław Trela and Sylwester Salwa dug three trenches at Pobroszyn, which exposed almost the entire Ordovician succession and its contacts with Cambrian and Silurian strata (Fig. 4). The Klonówka Shale Formation exposed there yielded acritarchs *Acanthodiacrodium*, *Dasydiacrodium*, *Cymatiogalea*, and *Stelliferidium* suggestive of late Cambrian to Tremadoc ages (Trela et al., 2001). The limestone and phosphorite intercalation in the shale above may correspond to the subsurface (known only from boreholes) Bukowiany limestone formation.

I sampled the exposed strata for conodonts, but only three samples yielded identifiable specimens (Dzik, 1999a). Acritarchs identifiable to species level were found only in one sample about 0.5 m below the sample Po-10 most productive for conodonts. The species *Cymatiogalea polygonophora* Górka, 1967, *Stelliferidium* cf. *modestum* (Górka, 1967), and the other acritarch genera *Caldariola* and *Peteinosphaeridium* may indicate late Tremadocian or perhaps Tremadocian/Floian boundary rocks (Trela et al., 2001).

In the lowest limestone horizon, in the middle part of the section (sample Po-10), conodonts of the latest Dapingian *Baltoniodus navis* Zone occur. Probably also the M element illustrated by Bednarczyk and Stempień-Sałek (2011, pl. 5:6) as representing *Oepikodus evae* (Lindström, 1955) belongs to *B. navis* (Lindström, 1955). The

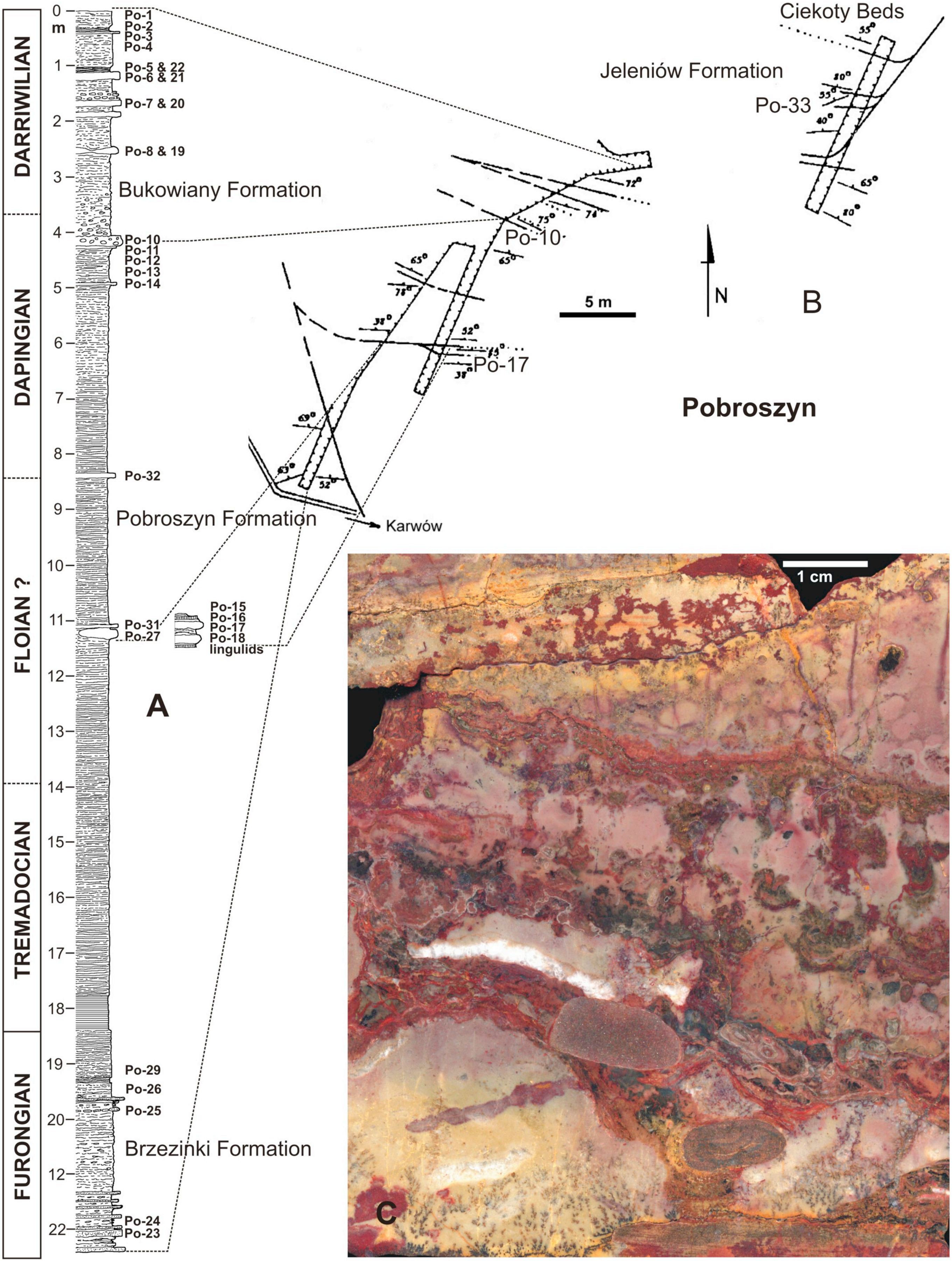

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Fig. 4. Section at Pobroszyn in the Łysogóry region of the Holy Cross Mountains, Poland. A. Rock column of strata exposed in the main trench, probably covering the whole Ordovician; sandstone (in lower portion) and limestone intercalations within shale are shown as more resistant. B. Map of trenches (modified after Trela et al., 2001). C. Polished section of the conglomerate slab (sample Po-10; orientation uncertain; for sedimentological interpretation see Trela, 2005, 2008).

assemblage is of an unusual composition as for the Baltic palaeozoogeographic province (Supplementary material Table 2). Although *Baltoniodus*, *Microzarkodina*, and coniform conodonts typical of the Baltic Dapingian and somewhat younger Kielce and Łagów assemblages are present, the dominant form is a new species of *Trapezognathus* endemic to the Holy Cross Mts. Even more surprising was to find, together with these cold-water species, some rare forms similar rather to the North American Midcontinent *Ulrichodina* and *Bergstroemognathus*. About 3 m above, in a laminated limestone bed, rare conodonts (*Baltoniodus* and *Lenodus*) suggestive of the earliest Darriwilian have been found.

The Jeleniów shale formation, located above the Pobroszyn formation (Fig. 4; Samsonowicz, 1934; Tomczykowa, 1968), is probably tectonically reduced or even missing at Pobroszyn. In the borehole material the thickness of this unit may reach 150 m. The lower Jeleniów beds, represented by a less than 1.5 m thick limestone intercalated with shale, contain *Hustedograptus*-like biserial graptolites, which indicates its Darriwilian age (Tomczykowa, 1968). Above the limestone there is a relatively thick succession of mostly graptolite shale (about 150 m) of the Upper Jeleniów beds, with thin limestone intercalations (Tomczyk, 1957, 1962). *Nemagraptus* occurs in the lower part of this unit, which thus corresponds to the Sandbian.

The topmost limestone intercalation in shale at Pobroszyn has yielded specimens of the conodonts *Amorphognathus*, *Hamarodus*, and *Scabbardella* indicative of the Katian. This may mean that these are already the informal Wólka siltstone formation. The pelagic trilobite *Cyclopyge kontkiewiczi* (Gürich, 1901), the first trilobite fossil described from the Ordovician of Poland (Gürich, 1901), was found probably there. The Wólka beds of possibly 100 m thickness are known mostly from artificial exposures along the Łysogóry range and yielded a diverse trilobite and brachiopod *Foliomena* assemblage of the late Katian in other localities in the region (Kielan, 1959; Cocks and Rong, 1988; Mergl, 1990).

Only the most prolific sample Po-10 provides material of some value to biogeographic considerations and taxonomic identification of particular species require comments that are given below. Although identification of element types of *Decoriconus* is difficult, the slightly constricted base and fine ribbing on the external side of the element cusp (Fig. 5A–E) seem to fit the range of variability in *D. mercurius* Löfgren, 1998, occurring in coeval Dapingian strata in Sweden Löfgren (1998). No element S_0 diagnostic for species of *Semiacontiodus* has been found at Pobroszyn but elements S (Fig. 5F) are undistinguishable from the Baltic *S. cornuformis* (Sergeeva, 1963) revised by Löfgren (1999a). The morphology of *Cornuodus* elements in the sample (Fig. 5G–K) agrees with those determined as *C. longibasis* (Lindström, 1955) by Stouge and Bagnoli (1990), Zhang (1998) and Löfgren (1999b). Elements from the Mójcza Limestone with asymmetric base attributed to this species by Dzik (1994) as M elements are missing in the Pobroszyn sample. Probably the Mójcza material represents another species. Element notation proposed by Zhang (1998) and by Löfgren (1999b) are different from that by Dzik (1994) and used here (Fig. 5G–K).

The morphology of diagnostic M elements of *Protopanderodus* (Fig. 5Q–S) seems to fit both that of *P. rectus* (Lindström, 1955) and *P. robustus*, as interpreted by Mellgren and Eriksson (2006). There is some ontogenetic change and population variability regarding the transverse section of the cusp. I do not see any discontinuity in gradation between morphs that would substantiate identification of more than one species of *Protopanderodus* in Po-10 sample.

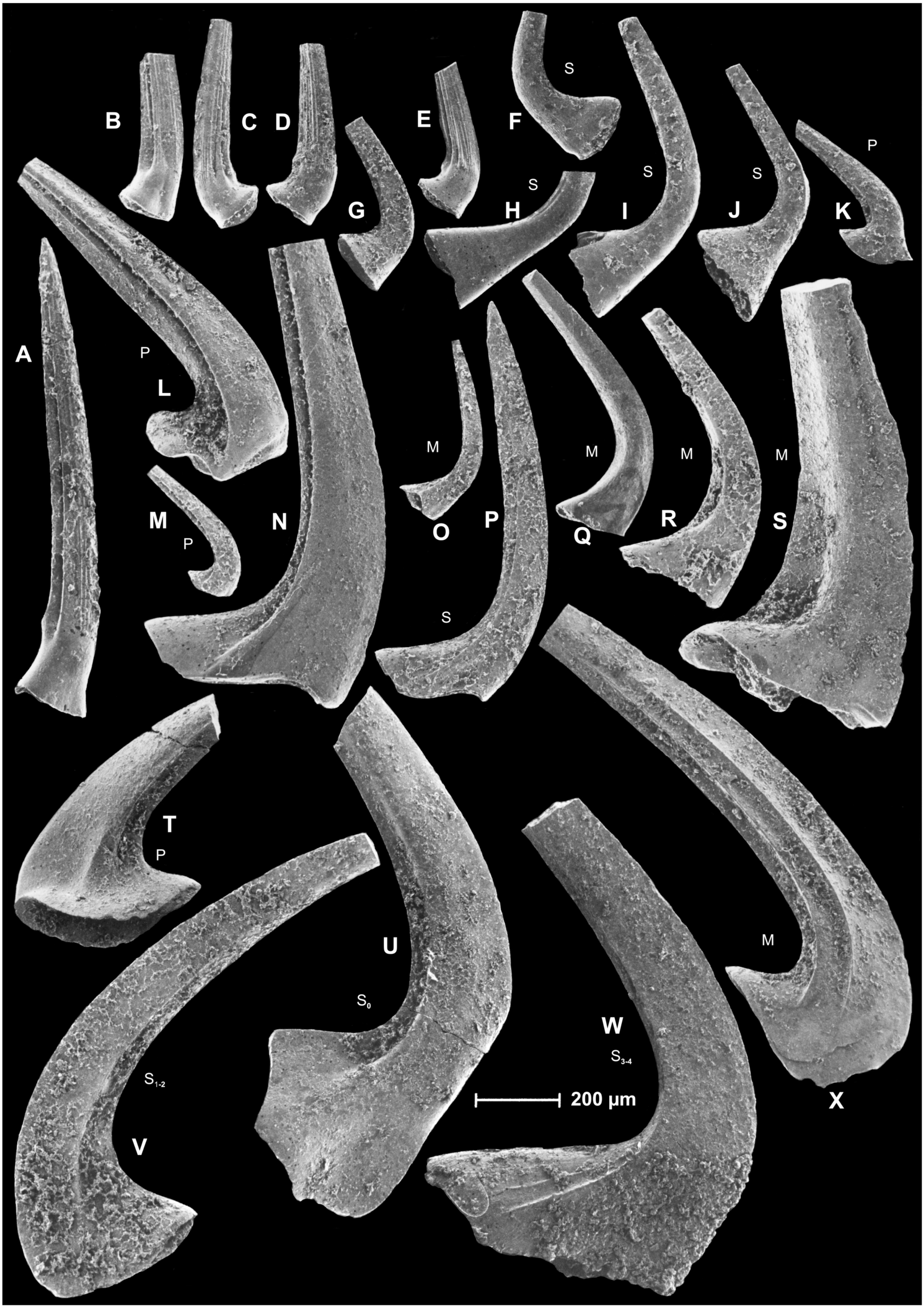
The apparatus composition of *Drepanodus arcuatus* Pander, 1856 has been determined by Löfgren (1997). It is supported by data from Pobroszyn (Fig. 6) in that all elements' surface is smooth. It seems that in Pobroszyn it co-occurs sympatrically with a species with prominent ribbing of elements cusps (Fig. 5T–X). The latter is here determined as *Drepanodus robustus* Hadding, 1913. Its lectotype from Fågelsång in Scania (Hadding, 1913, pl. 1: 5) is large for a conodont, which is a feature of *Drepanodus*. Moreover it 'possesses several small but distinct lateral costae', which is also the case with the specimen recovered from the topotype section by Bergström (2007, p. 81). Such costae are missing in the *Protopanderodus* species identified as *P. robustus* (Hadding, 1913) by Mellgren and Eriksson, 2006. This seems to confirm the species identification by Dzik (1994) but leaves open the question of its generic identity. Bergström (2007, p. 81) prefers to classify it in *Protopanderodus* because the holotype 'agrees in general morphology with species of *Protopanderodus*'. However, the presence of costae is rather of species than genus rank taxonomic value and *Drepanodus* differs from *Protopanderodus* significantly in its more complex structure of the apparatus (Dzik, 1994), with two distinct P elements and the M element having a strongly curved, almost geniculate base (in *Protopanderodus* the element is twisted, developing an oblique anterior surface delimited by sharp ridges). This is rather clearly shown by samples from the Holy Cross Mts.

The Pobroszyn specimens of *Drepanoistodus basiovalis* (Sergeeva, 1963) are generally more robust than those from coeval strata of the East European Platform, with a strong longitudinal rib along the posterior side of the cusp in M element (Fig. 7A–E; population variability has been quantified by Dzik, 1984). The holotype M element of *Oistodus basiovalis* from the upper Volkhovian at village Simonkovo in Leningrad district (Sergeeva, 1963, pl. 7: 6a-b) seems to fit the modal morphology of the Pobroszyn population although it shows some growth irregularity at the external (dorsal) tip of the base. Whether the S_0 elements in the type population are also of the kind attributed by myself to the same species in the Pobroszyn sample remains to be determined.

To find at Pobroszyn two sympatric species of *Drepanoistodus*, *D. basiovalis* and *D. contractus* (Lindström, 1955), so similar to each other is surprising. The most characteristic for *D. basiovalis* is the symmetrical element S_0, with its triangular profile and a very wide cusp (compare Fig. 7D and L, that is ZPAL cVI/883 and 930). The M elements of *D. contractus* differ usually in having wider external edge of the cusp and weaker longitudinal rib. In fact, all other elements of the apparatus of *D. contractus*, as interpreted here, differ from *D. basiovalis* in being more flattened (contrary to interpretation of Stouge and Bagnoli, 1990).

The apparatus of *Paroistodus originalis* (Sergeeva, 1963) was reconstructed by Löfgren (1997). The diagnostic aspects of elements is their flattening and a wide zone of inverted basal cavity on their external sides (Fig. 8C, D). A gradual transition into *Paroistodus horridus* is documented in Argentina by Albanesi and Barnes (2000). Near the top of the Lower Gualcamayo Formation they recovered a succession of samples, in which undenticulated *Paroistodus* elements are associated with those bearing single denticle, then in an even higher sample specimens with two or three denticles join them and in the Middle Gualcamayo Formation only specimens with four denticles occur. One would interpret such pattern as a gradual change in population variability but these authors preferred to see a punctuated emergence of sympatric species. According to Zhang (1998) P elements of *P. horridus* are undenticulated, so it is potentially possible, although unlikely, that the rare Pobroszyn specimens represent this species, known from the Andes, Newfoundland (Stouge, 1984), Scandinavian Caledonides (Rasmussen, 2001), Kazakstan (Tolmacheva, 2014), south China (Zhang, 1998), and Australia (Zhen and Percival, 2004).

The S elements (including the incomplete but apparently strongly curved S_0) referred to as *Drepanoistodus*? sp. closely resemble those of *Drepanodus* (Fig. 8F, G) except for being more compressed (like those of *Paroistodus*, but lacking inversion of the basal cavity). Associated



(caption on next page)

Fig. 5. Coniform conodont elements from the Pobroszyn sample Po-10. A–E. *Decoriconus mercurius* Löfgren, 1998, specimens ZPAL cVI/900 (A), ZPAL cVI/902 (B), ZPAL cVI/901 (C), ZPAL cVI/903 (D), and ZPAL cVI/906 (E). F. *Semiacontiodus* sp., specimen ZPAL cVI/910. G–K. *Cornuodus longibasis* (Lindström, 1955), specimens ZPAL cVI/904 (G; element P), ZPAL cVI/909 (H; element S_0), ZPAL cVI/908 (I; element $S_{1–2}$), ZPAL cVI/907 (J; element $S_{3–4}$), ZPAL cVI/905 (K; element M). L–S. *Protopanderodus rectus* (Lindström, 1955), specimens ZPAL cVI/899 and 897 (L, M; elements P), ZPAL cVI/894, 896, and 895 (N–P; elements S), and ZPAL cVI/893, 892, and 891 (Q–S; elements M). T–X. *Drepanodus robustus* Hadding, 1913, specimens ZPAL cVI/924 (T; element P), ZPAL cVI/926 (U; element S_0), ZPAL cVI/927 (V; element $S_{1–2}$), ZPAL cVI/925 (W; element $S_{3–4}$), and ZPAL cVI/928 (X; element M).

weakly geniculate M element of primitive morphology may or may not belong to the same apparatus (Fig. 8H–J). It is not certain that two elements of unidentified genus (Fig. 8A–B) represent the same species, although this is suggested by the widely triangular outline of their bases. The S_1 element is unusual in having its base deeply incised. Unless this is a pathology, the material represents a new genus. A single abraded specimen found in Pobroszyn (Fig. 8E) resembles elements of *Bergstroemognathus extensus* (Graves and Ellison, 1941) from the Factory Cove Member of Shallow Bay Formation at Cow Head Peninsula of Newfoundland (Stouge and Bagnoli, 1988, pl. 1:8).

Specimens of *Microzarkodina* from Pobroszyn (Fig. 8K–Q) probably are conspecific with *M. parva* Lindström, 1971. The species differs from the ancestral *M. flabellum* (Lindström, 1955) in smaller external denticle and more regular denticulation of the inner process (Löfgren and Tolmacheva, 2008).

The most unusual conodont species in sample Po-10 is *Trapezognathus pectinatus* sp. n. Its P_1 element differs from that of associated *Baltoniodus navis* only in its more robust, pyramidal appearance, that is in a deep and wide basal cavity and weakly denticulated sharp-edged anterior process. Other processes are well-denticulated, but shorter than those of *B. navis*. These aspects are even more apparent in P_2 element, except for the anterior process being long and well-denticulated. S elements are more robust than those of *B. navis*, resembling elements of *Lenodus*, but with a more prominent denticulation. Noteworthy is the morphology of probable S_1 elements, which differs from S_0 only in a slight asymmetry. Such gradation in asymmetry is also the feature of *Sagittodontina kielcensis* (Dzik, 1976) that makes possible relationship, not necessarily contradictory, to less derived species of *Trapezognathus* having the S_1 elements of the same morphology (Stouge and Bagnoli, 1990). Elements M with prominent denticulation of the dorsal (inner) process of variable length are the most characteristic for the Holy Cross Mts. species. The external process may develop a weak denticulation in some specimens.

Although the M element of *T. pectinatus* sp. n. closely resembles the S_2 element of *Barrandegnathus bohemicus* (Dzik, 1984), homology of these elements is unlikely. Instead, this species is rather a continuation of the *Trapezognathus* lineage, initiated by *T. quadrangulum* (Lindström, 1955) with undenticulated P elements in the *Baltoniodus navis* Zone and represented by *T.* sp. in the *Microzarkodina parva* Zone of Sweden, with these elements bearing prominent denticulation. Also the M element of the latter species is incipiently denticulated on its both processes (Stouge and Bagnoli, 1990).

Probably most of the balognathid specimens reworked to the Silurian strata at Khemis-n'Ga in Moroccan Meseta (Bultynck and Sarmiento, 2003) belong to *T. pectinatus* sp. n. The diagnostic denticulation of M elements is expressed in specimens determined as *Baltoniodus navis*, *Lenodus* sp., *Trapezognathus* sp., *Lenodus* sp., and *Trapezognathus quadrangulum* (Bultynck and Sarmiento, 2003, pl. 1:2, 2:11–13, 3:1, 9, 4:12). A complete series of the apparatus of *T. pectinatus* elements can be assembled based on illustrations in Bultynck and Sarmiento (2003) but it remains unknown whether the whole fossil assemblage was reworked from a single bed or, as the authors claim, they represent several stratigraphic units.

Rare robust S elements from sample Po-10 (Fig. 10Q, R) resemble those of *Lenodus*, but complete lack of platform P elements makes this not likely. Perhaps this is an end-member of population variability of *Trapezognathus*, which is suggested by a robust appearance of some its M elements (Fig. 9R). All *Baltoniodus* elements from Pobroszyn (Fig. 10A–P) fit well those illustrated as representing *B. navis* (Lindström, 1955) by Bagnoli and Stouge (1996). This is a rather subordinate balognathid species at Pobroszyn, unlike coeval strata in Baltica.

5. Conodonts from Szumsko in the Kielce region

The borehole Szumsko Kolonia 2a was drilled by the Holy Cross Mts. branch of the State Geological Institute near the village Szumsko in the southern part of the Holy Cross Mts. near Łagów (50°41′55.18″ N, 21°07′00.42″ E) in 1966. The Ordovician was penetrated from depth 28.2 m and continued to the depth of 67.8 m (Fig. 11). The strata dip at the angle approximately 45°, which means that the actual thickness of the Ordovician rocks is about 28 m. The borehole was only partially cored. Position of productive conodont samples is indicated with various precision.

The oldest sample from 53.5–54.1 m of the core is dominated with *Scolopodus striatus* Pander, 1856 (Fig. 12J–N), with the apparatus structure consistent with that recognized by Tolmacheva (2006). The *Protopanderodus rectus* (Lindström, 1955) population from there seems identical to that of coeval strata in Baltica (Mellgren and Eriksson, 2006) being different from those of younger age from Mójcza classified in the same species by Dzik (1994) in a more elaborate profile of the M elements. Associated *P. graei* (Hamar, 1966) is represented by a single M element with sharp inner ridge, which makes identification rather certain. Associated P and S elements differ from those of *P. rectus* only in a less sinuous profile of the base, but the variability makes distinction difficult to apply to particular specimens. The M elements of *Drepanoistodus* show a rather acute ventral tip diagnostic for *D. basiovalis* (Sergeeva, 1963). Less numerous specimens of *Baltoniodus* are too incomplete to be determined at the species level although the denticulated anterior process in the single S_3 element suggests *B. navis*. In samples with mostly incompletely preserved specimens, the number of P_1 elements of *Baltoniodus* is underestimated because it is not easy to recognize such elements if processes are not preserved well enough.

Trapezognathus pectinatus sp. n. (Fig. 12O–V) described above on the basis of material from roughly coeval strata at Pobroszyn occurs at Szumsko as well. Relatively complete M element in sample taken from 52.15 m of the core marks its oldest occurrence at Szumsko. Near the depth 43.0 m a bed of conglomerate with dolomite pebbles in a calcareous sandstone matrix occurs. Probably from the pebbles comes the most numerous fossil assemblage of conodont elements from Szumsko (Supplementary material Table 3).

Although relatively large samples from depth 42.8–43.0 and 42.0–42.5 are available, *Cornuodus* from there is probably the most troublesome Szumsko conodont regarding reconstruction of its apparatus (Fig. 12E–I). Distinctions between element locations remain difficult to demarcate. The elements with widely gaping base and the cusp bent immediately above of it probably represent the P_2 locations but they grade into the dominating morphology with variably expanded conical base and the cusp bent high above at gentle right angle. These are probably elements representing hard to delimit S_0 to S_4 locations. They are very variable and there is a gradation to knee-like elements with angular bending of the cusp that probably represent the M location. Another poorly delimited morphological class is represented by elements with relatively erect cusp having its dorsal margin sharp. They may represent the P_1 location. This does not fit the morphological classes distinguished in the Mójcza material (Dzik, 1994), especially in

Fig. 6. Elements of *Drepanodus arcuatus* Pander, 1856 from the Pobroszyn section sample Po-10, specimens ZPAL cVI/923, 911, and 917 (A–C; elements P_1), ZPAL cVI/912 and 918 (D, E; elements P_2), ZPAL cVI/910 and 913 (F, G; elements S_0), ZPAL cVI/920 and 914 (H, I; elements S_{1-2}), ZPAL cVI/921 and 915 (J, K; elements S_{3-4}), and ZPAL cVI/922 and 916 (D, E; elements M).

respect to obliquely cut bases of some element types, which are missing both in Pobroszyn and in Szumsko. Löfgren (1999b) attempted to solve such problems in respect to the Baltic samples by proposing that there was only a single species of *Cornuodus*, *C. longibasis* (Lindström, 1955) with variable populations and lacking M element in the apparatus. She proposed also to place *Cornuodus* in the family Protopanderodontidae as a relative of *Drepanodus*, which seems a reasonable choice.

The sample taken from core at depth 42.8–43.0 yielded rather

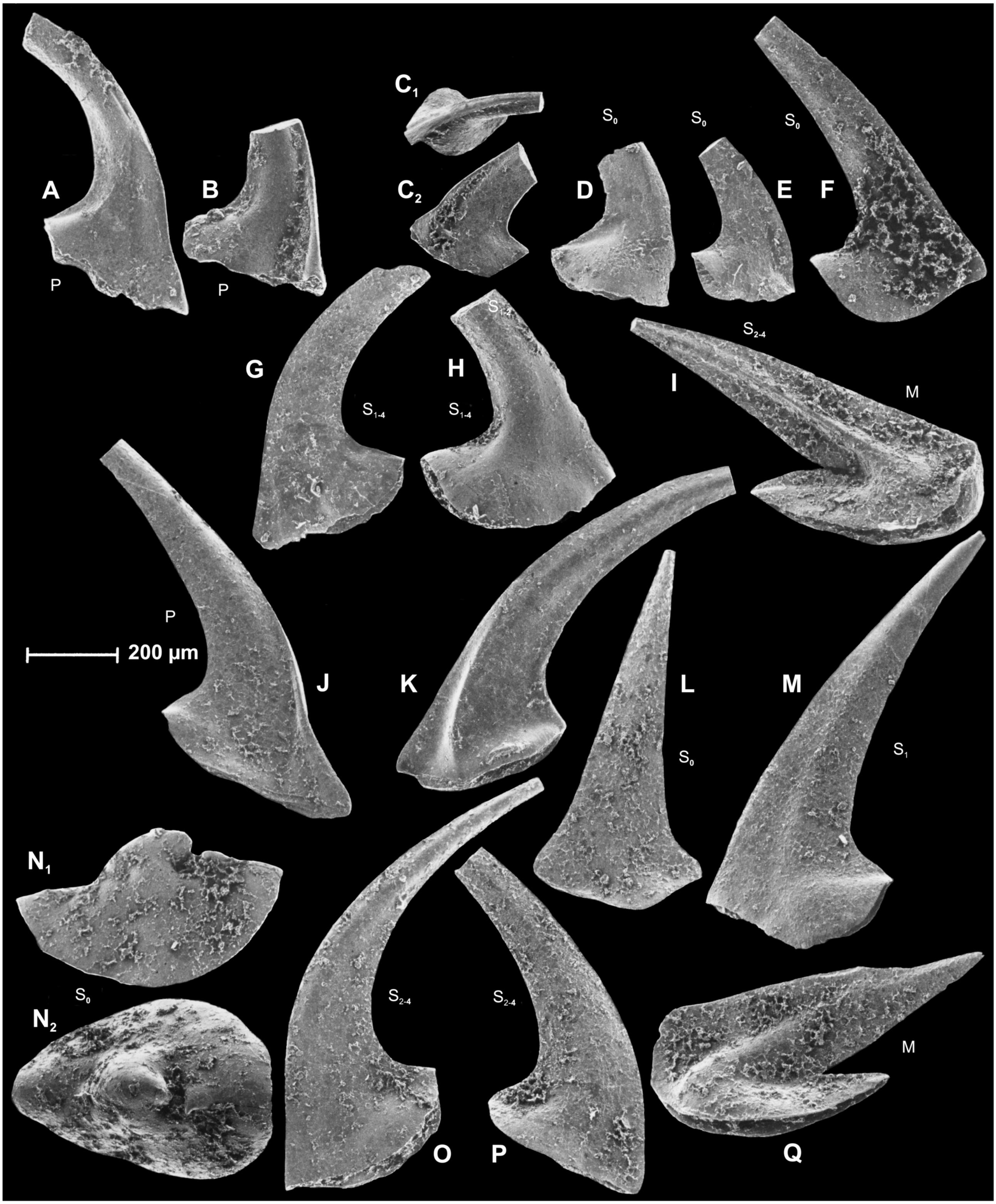


Fig. 7. Elements of the distacodontid *Drepanoistodus* from the Pobroszyn sample Po-10. A–E. *Drepanoistodus basiovalis* (Sergeeva, 1963), specimens ZPAL cVI/885, 884, and 886 (A–C; elements P), ZPAL cVI/883, 888, and 887 (D–F; elements S_0), ZPAL cVI/889 and 890 (G, H; elements S_{1-4}), and ZPAL cVI/882 (I; element M). J–Q. *Drepanoistodus contractus* (Lindström, 1955), specimens ZPAL cVI/932 and 933 (J, K; elements P), ZPAL cVI/930 (L; element S_0), ZPAL cVI/931 (M; element S_1), ZPAL cVI/874 (probably a regenerating broken element S_0), ZPAL cVI/935 and 934 (O, P; elements S_{2-4}), and ZPAL cVI/929 (Q; element M).

numerous specimens of *Drepanoistodus*. Each of its elements is very variable. Proportions of the M element change in its ontogeny. Gracile juveniles have their bases relatively elongated in respect to the cusp and an acute ventral tip. Mature specimens are of robust appearance and their ventral margin is cut transversely, with a tendency to reversal of the relatively shallow basal cavity. Such course of the ontogeny and pattern of population variability was biometrically shown in a Baltic sample of the *P. originalis* Zone age by myself (Dzik, 1984, fig. 8).

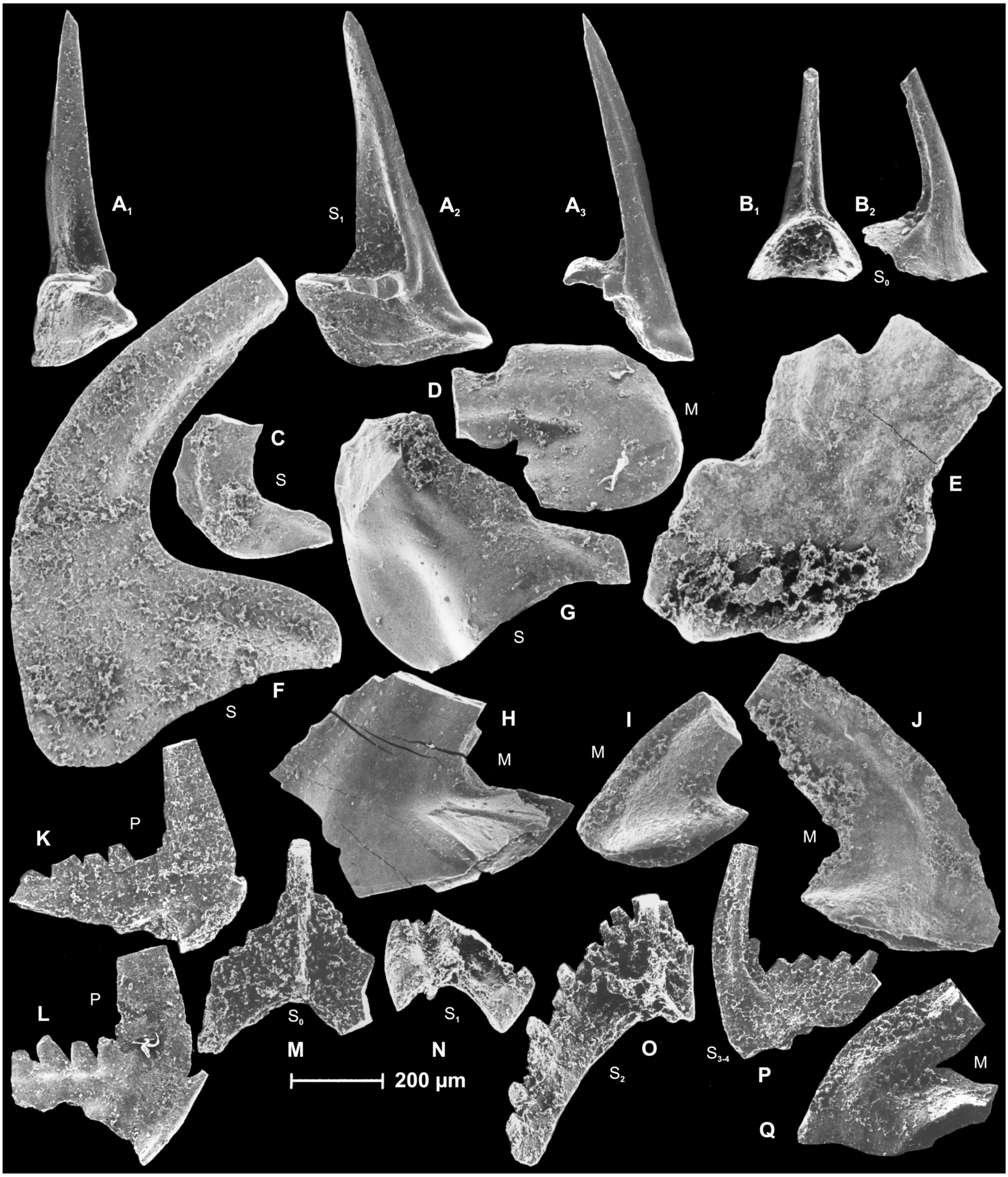


Fig. 8. Elements of subordinate conodonts species from the Pobroszyn sample Po-10. A–B. Gen. et sp. indet. 1 specimens ZPAL cVI/873 and 872, elements S_1 and S_0. C, D. *Paroistodus originalis* (Sergeeva, 1963), specimens ZPAL cVI/879 and 880, elements S and M. E. *Bergstroemognathus*? sp., specimen ZPAL cVI/871. F–J. *Drepanoistodus*? sp.; specimens ZPAL cVI/877, 878 (F, G; elements S), ZPAL cVI/881, 875, and 876 (H–J; elements M). K–Q. *Microzarkodina parva* Lindström, 1971, specimens ZPAL cVI/936 and 937 (K, L; elements P), ZPAL cVI/938 (M; element S_0), ZPAL cVI/940 (N; element S_1), ZPAL cVI/939 (O; element S_2), ZPAL cVI/941 (P; element $S_{3–4}$), and ZPAL cVI/942 (Q; element M).

Probably the name *Drepanoistodus contractus* (Lindström, 1955) is appropriate for the Szumsko material. Unlike the slightly older Pobroszyn sample, the S_0 and S_1 elements from this sample do not show co-occurrence of sympatric species of the genus. Admittedly, most specimens from Szumsko are juveniles whereas those from Pobroszyn are mature, which hampers comparison.

The same sample has yielded numerous specimens of *Phragmodus polonicus* Dzik, 1978. As pointed out in Dzik (2015, p. 41), the type species of the genus *Phragmodus* had an undenticulated M element, which makes inclusion of the Holy Cross Mts. species in this genus

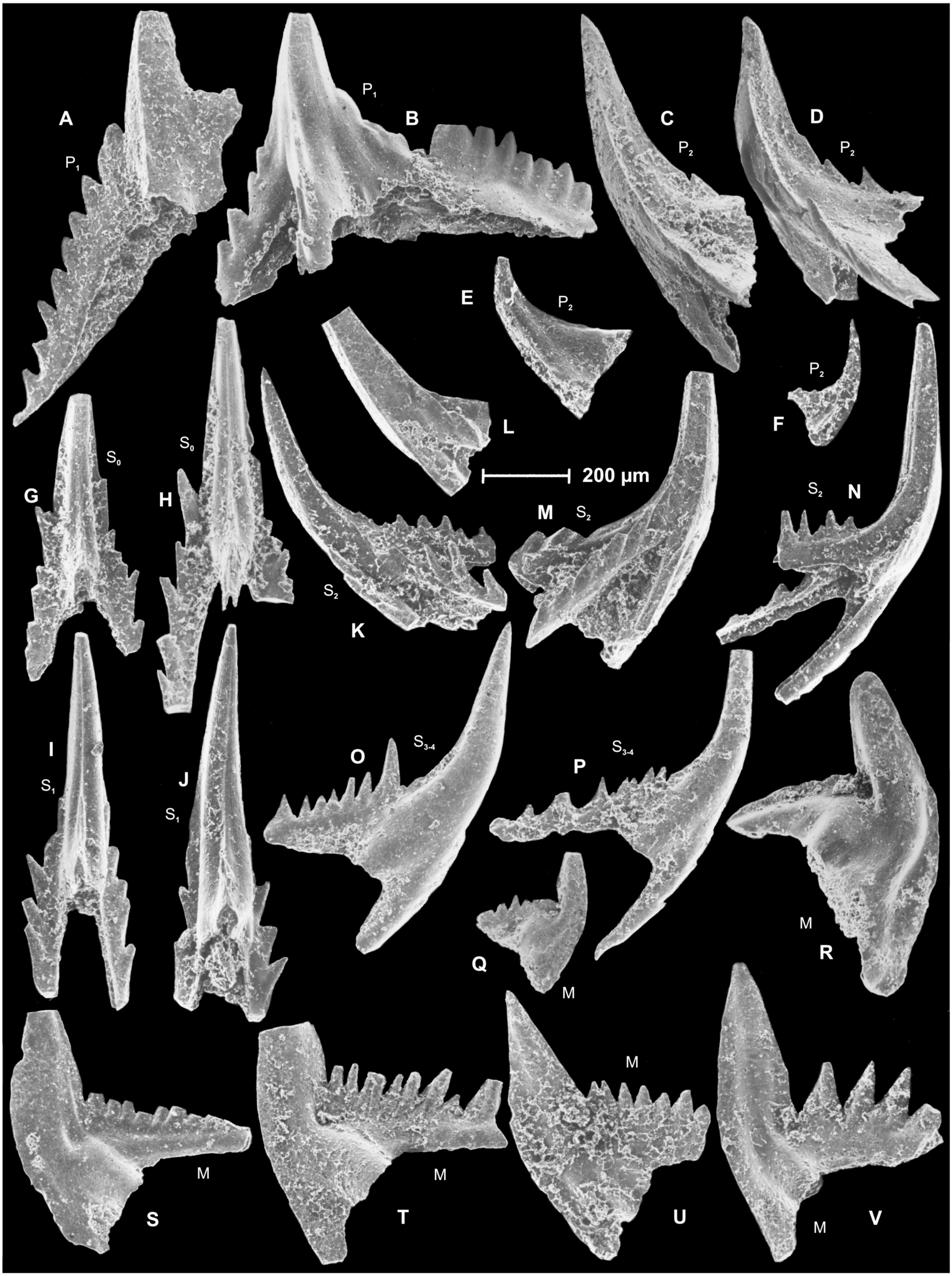


Fig. 9. Elements of the balognathid *Trapezognathus pectinatus* sp. n. from the Pobroszyn sample Po-10, specimens ZPAL cVI/851 and 850 (A, B; elements P_1), ZPAL cVI/859, 858, 864, and 865 (C–F; elements P_2), ZPAL cVI/853 and 862 (G, H; elements S_0), ZPAL cVI/855 and 854 (I, J; elements S_1), ZPAL cVI/862, 863, 861 and 860 (K–N; elements S_2), ZPAL cVI/857 and 858 (O, P; elements $S_{3–4}$), ZPAL cVI/846, 847, 869, 870, 868, and 867 (Q–V; elements M, T holotype).

Fig. 10. Elements of balognathids from the Pobroszyn sample Po-10. A–P. *Baltoniodus navis* (Lindström, 1955), specimens ZPAL cVI/831 and 832 (A, B; elements P_1), ZPAL cVI/833 and 841 (C, D; elements P_2), ZPAL cVI/835 and 834 (E, F; elements S_0), ZPAL cVI/836 and 837 (G, H; elements S_{1-2}), ZPAL cVI/839 and 838 (I, J; elements S_3), ZPAL cVI/840 and 842 (K, L; elements S_4), ZPAL cVI/866, 845, 844, and 843 (M–P; elements M). Q-R. *Lenodus* sp., specimens ZPAL cVI/846 (Q; element S_0), ZPAL cVI/847 (R; element S_{3-4}).

reasonable. The name *Nordiora* proposed by Rasmussen (2001) for early members of this lineage is thus redundant and the difference between the type population of *P. polonicus* from the *Eoplacognathus lindstroemi* Zone and populations coeval with *Histiodella holodentata* is too small to make practical their species rank separation as *Nordiora torpensis* Rasmussen, 2001. They differ from each other slightly in the robustness and size of presumably mature elements, which may be difficult to distinguish from ontogenetic change.

Specimens of *Eoplacognathus* were recovered from a series of samples ranging from depth 42.1–42.3 m up to 39.0 m. Those from the upper part of the sequence possibly represent *E. lindstroemi*, those from below definitely *E. reclinatus*. Both conodonts and the rock lithology rather strictly correspond to the main part of the Mójcza Limestone at its type locality, located about 25 km to NW (Dzik, 1994). The quartz sand contribution increases gradually near this level to change the rock to a calcareous sandstone.

Microzarkodina ozarkodella occurs in samples of dolomitized limestone from 42.1–42.3 to 40.0–41.3 m. *Lenodus* seems to be gradually

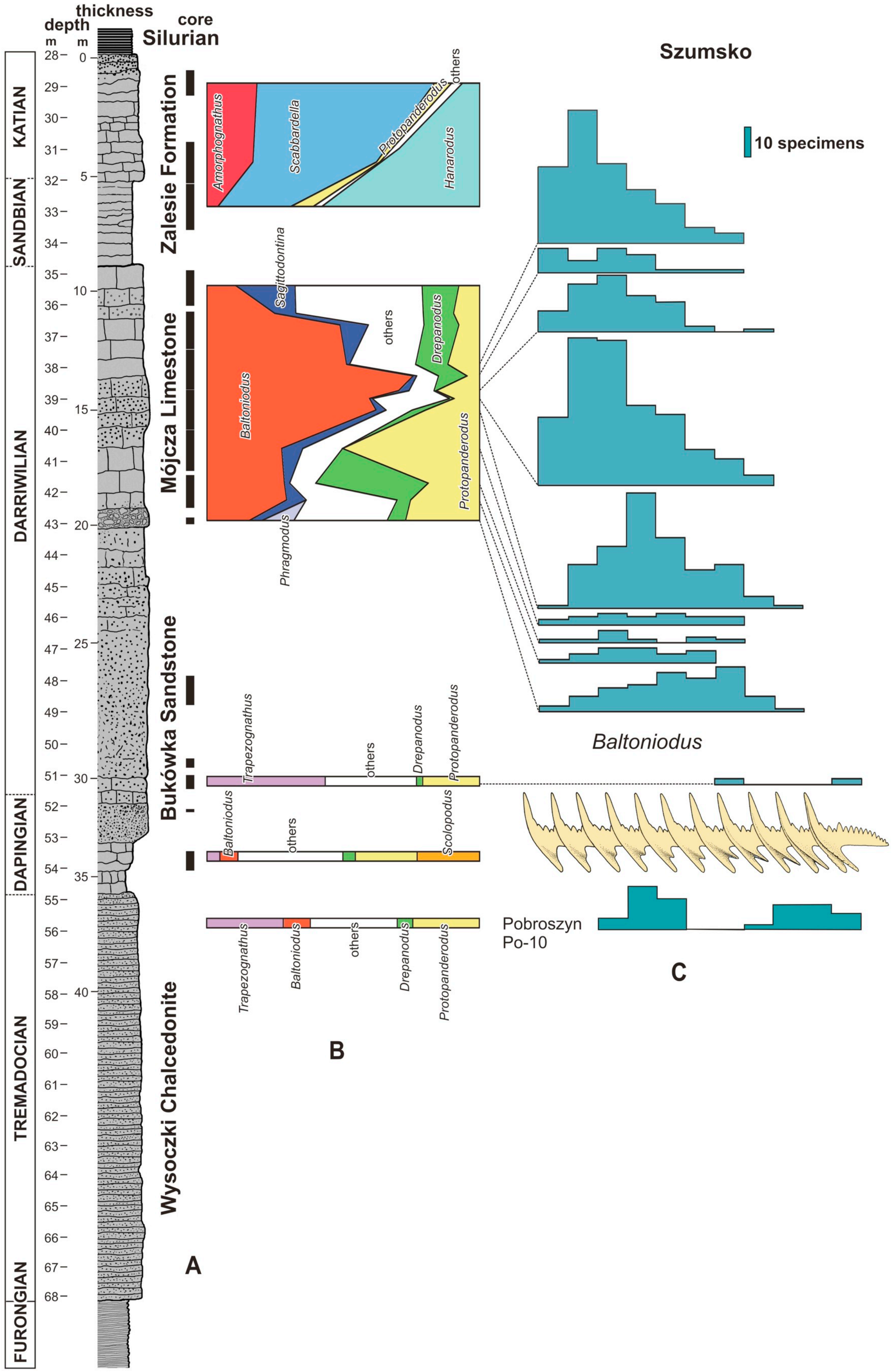


Fig. 11. Ordovician part of the Szumsko borehole with the actual depth of cored parts and estimated thickness of the rock units (A), logs of percent contribution of conodont elements from productive samples (Darriwilian and Katian in age), compared with that in Pobroszyn sample Po-10 (B), and stratophenetic presentation of changes in the length of anterior process in S3–4 elements of *Baltoniodus norrlandicus denticulatus* ssp. n., with number of elements from each sample attributed to eleven morphologic classes (C). Dots indicate quartz sand, brick-like pattern limestone, horizontal lines refer to shale.

Fig. 12. Conodonts from the lower part of the Szumsko borehole. A–C. *Decoriconus mercurius* Löfgren, 1998, specimens ZPAL cVI/1079, 1072, and 1071 from depth 42.8–43.0 m. D–I. *Cornuodus longibasis* (Lindström, 1955), specimens ZPAL cVI/1078 and 1079 (E, F, elements P), ZPAL cVI/1073 and 1076 (G, H, elements S), and ZPAL cVI/1075 (I, element M) from depth 42.8–43.0 m. J-N. *Scolopodus striatus* Pander, 1856, specimens ZPAL cVI/1081, 1080, and 1083(J, K, M elements $S_{1–4}$), ZPAL cVI/1084 (L, element S_0 in medial and lateral views), and ZPAL cVI/1082 (N, element M) from depth 53.5–54.7 m. O–V. *Trapezognathus pectinatus* sp. n., specimens ZPAL cVI/1085 (O, element P_1), ZPAL cVI/1086 (P, element P_2), ZPAL cVI/1087 (Q, element S_0), ZPAL cVI/1088 (R, element S_1), ZPAL cVI/1089 (S, element S_2), ZPAL cVI/1091 and 1090 (T, U, elements $S_{3–4}$), and ZPAL cVI/1092 (V, element M) from depth 51.05–51.5 m. W-AG. *Baltoniodus norrlandicus denticulatus* ssp. n., specimens ZPAL cVI/1093 (W, element P_1), ZPAL cVI/1094 (X, element P_2), ZPAL cVI/1095 (Y, element P_3), ZPAL cVI/1096 (Z, element S_0 in medial and lateral views), ZPAL cVI/1097 (AA, element S1–2), ZPAL cVI/1098 and 1099 (AB, AC, elements S_3), ZPAL cVI/1100 (AD, element S_4), and ZPAL cVI/1101–1103 (AE-AG, elements M; AF holotype) from depth 38.7–40.0.

replaced in these samples with *Sagittodontina* or there is an evolutionary transition between these balognathid conodonts. Unfortunately, the material is too crushed to enable reliable taxonomic identifications.

As in the nearby Mójcza and more distant Baltic sections (those near the Polish part of the east European Platform being now about hundred kilometres to NE) there is an apparent evolutionary change in the *Baltoniodus* lineage at Szumsko (Fig. 11C). The sample from 42.8–43.0 m roughly corresponds to the oldest one known from Mójcza, with characteristic acute anterior process of S_3 element, classified as *Baltoniodus norrlandicus*. The *B. prevariabilis medius* chronosubspecies, distinct in having strongly reduced homologous process, has been identified in sample from 42.0–42.5 m depth.

Rather surprisingly, specimens of S_3 elements with long anterior process re-emerge in sample 41.5–42.1. All *Baltoniodus* elements from this sample and those from samples above up to 36.0 m depth are of a rather robust appearance (Fig. 12W–AG). The change is associated with an increase of quartz sand contribution to the limestone. This may suggest a taphonomic factor contribution, as a result of sorting in transport, or selective destruction. This does not seem a sufficient explanation as the elements from successive samples differ also in a less prominent denticulation in P elements. Instead, the dorsal process of M element in many specimens became denticulated. A surprising aspect of the Holy Cross Mts. conodont succession is that denticulation of M elements in a balognathid clade apparently took place twice. The occurrence of *Baltoniodus* with M element denticulation at Szumsko is separated from the above discussed succession of *Trapezognathus pectinatus* sp. n. by a sequence of sandy dolomite and glauconitic sandstone that were not cored. No such elements occur in Baltic samples. This makes introduction of *Baltoniodus norrlandicus denticulatus* ssp. n. for this probable geographic race (subspecies) reasonable. Denticulation of M elements is prominent in many specimens from 38.7–40.0 m, 38.7–38.8 m, and 37.9–38.7 m, but they are rare in sample 39.0 and 37.9 m. It disappeared above this series of samples, although P elements remained robust and S_3 elements show relatively long and pointed anterior process even at the levels of 37.4–38.7 and 36.1–37.4 m. Such S_3 elements are lacking in sample 36.3 m and the size of largest elements is typical for *B. prevariabilis* from Mójcza and Baltic sections.

Among P elements of *Baltoniodus norrladicus denticulatus* ssp. n. with wide disposition of processes, which are generally interpreted as P_1, there are specimens with gently narrowing and relatively short dorsal process as well as specimens with this process elongated and with the basal cavity expanded in proximity of the cusp (Fig. 12W–Y). Possibly there are thus three morphological classes and corresponding locations in the P series. Unfortunately, most specimens in the material are incomplete, with detached dorsal process, which prevents statistically significant analysis of the distribution of variability.

There is an apparent tectonic(?) discontinuity above 34.9–36.0 m of the core, which corresponds to a sudden change from shales to phosphate-rich oolitic limestone. An advanced *Sagittodontina kielcensis* and early *Amorphognathus tvaerenensis* are present in the latter.

Single M specimen of *Amorphognathus* in the topmost sample from the core segments 28.5–29.3 m, although incomplete, is of *A. ordovicicus* morphology. The assemblage represented by fragmented specimens is apparently of low diversity. *Scabbardella*, *Amorphognathus* and *Hamarodus*, typical for the Late Ordovician high latitudes dominate but *Protopanderodus* cf. *liripipus* is a warm-water element. The same assemblage was recovered from samples taken from 30.8 to 32.4 m and 32.1–33.6 m core segments.

6. Conodont faunal dynamics between Baltica and Gondwana

Some ties between the marginal Gondwanan Perunica microcontinent and at least marginal environments of the Baltic area are evidenced by the occurrence of the seemingly endemic Bohemian *Barrandegnathus bohemicus* (Dzik, 1984), originally described from the late Dapingian Klabava Formation near Mýto near Prague (Dzik, 1984), in the earliest Darriwilian of the Baltic Bornholm Island (Stouge, 2005). Conodonts of this age, probably slightly preceding the Pobroszyn record, are unknown in the Holy Cross Mts., which prevents comparison.

The Małopolska Terrane between Perunica and Baltica and the new evidence on Darriwilian conodonts from there supports their transitional location also on biogeographic grounds. Rather surprisingly, it has appeared that the Łysogóry and Kielce regions, traditionally considered to be different geotectonic units in the Ordovician, show virtually identical conodont faunas. Moreover, like chitinozoans from the same locality (Wrona, 2002, 2004), they are basically different from the coeval conodonts of the Baltic region. *Trapezognathus pectinatus* sp. n., one of the dominant species in both faunas, is known elsewhere in Morocco, that is in northern Gondwana (cf., Bultynck and Sarmiento, 2003). Also the prioniodontid *Aldridgeognathus* from Oman, well within Gondwana (Miller et al., 2018), apparently represents the *Trapezognathus* clade as shown by morphology of its S_1 elements. This supports a high-latitudinal origin of the whole *Trapezognathus-Lenodus-Sagittodontina* clade. *T. pectinatus* apparently represents a continuation of the *Trapezognathus* lineage initiated a little earlier in the latest Dapingian of Sweden by *T. quadrangulum* (Stouge and Bagnoli, 1990). It is possible that the change from *Lenodus* (or from *Trapezognathus*) to *Sagittodontina* took place also at Szumsko, although the material is too fragmentary to be sure of this.

The Darriwilian sub-polar cold-water icriodellid *Omanognathus* probably encompasses not only the Oman's type species (Miller et al., 2018) but also the roughly coeval Thuringian and Sudetes species *O. ceratus* (Knüpfer, 1967). The subsequent evolution of the lineage is marked by gradual geographic expansion to low latitudes, but being confined to shallow-water environments (Dzik, 1990, 2015).

Additional evidence of isolation of the Małopolska microcontinent from Baltica is offered by apparently allopatric speciation process initiated somewhat later by the population of *Baltoniodus*. A possible interpretation of their morphological disparity is that the *Baltoniodus* population from the Małopolska microcontinent was isolated for a while from that of the Baltic region. The process of speciation was apparently not completed and interbreeding after re-joining re-established the preceding status. Prominently denticulated M elements and the anterior process in S_3 elements delayed in reduction make the Szumsko population different from those from the Baltic region. It deserves the geographic race (subspecies) rank as *Baltoniodus norrlandicus denticulatus* ssp. n. The alternative interpretation is that the difference resulted from temporary change in population dynamics, with lowered juvenile mortality at Szumsko and with most individuals attaining large mature size. This would mean that denticulation is a result of domination of mature specimens unknown from any Baltic sections, which seems unlikely. It is disproved by the high contribution from S_3 elements with acute anterior process, which in the Baltic sections disappeared much before the *E. reclinatus* Zone. The series of samples with the fossil record of this uncompleted speciation event, that have been uncovered by the borehole at Szumsko in the southern part of the Kielce region of the Holy Cross Mts. probably correspond to the sedimentary gap in other Ordovician localities in the area. As suggested above, the speciation was truncated by immigration of a population of the Baltic *Baltoniodus prevariabilis*. Until its immigration, the Szumsko populations not only allopatrically developed denticulated M elements, but continued earlier initiated evolution towards reduction of the anterior process in S_3 elements (although it was somewhat delayed in this respect to its Baltic relatives). The conodont assemblages from the part of the Mójcza limestone at Mójcza above the discontinuity and at Szumsko are of generally Baltic appearance, but remain somewhat distinct by relatively high contribution from *Sagittodontina*, *Phragmodus*, and *Complexodus*. The periodic North American Midcontinent influences observable in the Baltic region (e.g., immigrations of *Erraticodon* and *Cahabagnathus*) did not reach the Holy Cross Mts. (e.g., Dzik, 1983).

Unlike the Darriwilian and the remaining Middle Ordovician, the Late Ordovician conodont assemblages in Europe are much less biogeographically discriminative. This is probably connected with the global climate cooling and migration of Gondwanan faunal elements to low latitudes. Anyway, the Late Ordovician Gondwanan conodont fauna from Libya was composed mostly of conodonts characterized by very deep basal cavities of their elements, like *Scabbardella* and *Sagittodontina* (Bergström and Massa, 1992). That is with thin crowns probably in result of shortage of calcium in high-latitude cold seas. The conodont assemblage from the Upper Djeffara Formation of Libya (in stratigraphic proximity to glacial deposits) is dominated with *Sagittodontina* (45%), *Scabbardella* (23%), and *Amorphognathus* (21%) (Bergström and Massa, 1992).

In the famous Kalkbank of Thuringia located immediately below the glacigenic Lederschiefer (Dzik, 1990; Fuchs, 1990; Ferretti and Barnes, 1997), the dominant conodonts are as well *Sagittodontina* (41% of identifiable elements), *Scabbardella* (34%), and *Amorphognathus* (12%). Possibly less sub-polar position of the region is marked by *Hamarodus*, another conodont (of unknown origin) with a deep basal cavity contributing about 4% to the sample. Quite similar conodont assemblage was recovered from the Bohemian Králův Dvůr Formation of Bohemia, representative for the Late Ordovician of the Perunica microcontinent, with Ordovician faunas of generally Gondwanan affinities. These strata are separated from the diamictites of the overlying Kosov Formation only by beds with the *Mucronaspis* fauna. The conodont fossil assemblage is dominated by *Scabbardella altipes* (30% of conodont elements), *Sagittodontina* cf. *robusta* (22%), and *Amorphognathus* (19%) (Ferretti, 1998). In addition, an important contributor to the assemblage is *Hamarodus* (7%).

Sagittodontina is virtually missing in the Late Ordovician conodont faunas from regions located at lower latitudes until its almost global expansion as the Hirnantian *Noixodontus*. This refers to assemblages from the middle part of the Zalesie Formation at Mójcza in the Kielce Region of the Holy Cross Mts. (Dzik, 1999a). In the uppermost part of the sequence *Hamarodus* is replaced as one of the dominant elements with *Dapsilodus*. Sample Po-33 from Pobroszyn the Łysogóry Region of the Holy Cross Mts. is too small to be statistically significant, but apparently *Scabbardella*, *Hamarodus* and *Amorphognathus* are its most important components.

This unusual stability of composition among high-latitude conodont faunas and smooth transition to faunas of temperate-seas is noteworthy. One may argue that this is a result of the lack of thermal stratification in cold-water seas resulting in uniform distribution of pelagic organisms. In the temperate seas of Baltica, particular conodont species clearly show different geographic distribution (Rasmussen and Stouge, 2018). This is well exemplified also by the conodonts from the Subich Formation at Kytaihorod in Podolia on the SW margin of Baltica. Coniform elements with a thin crown are of little significance there. Instead, relatively robust *Panderodus* elements dominate, together with *Amorphognathus*. Another shallow-water species indicating a shallow-water environment is that of *Icriodella*. A warm-water species of *Aphelognathus* is subordinate. Also the Late Ordovician conodont faunas from the Alps, located between Bohemia and the African shore of Gondwana, lack *Sagittodontina* among important faunal contributors. Instead, they include *Plectodina*, a rather warm-water element in the late Ordovician (e.g., Flajs and Schönlaub, 1976; Bagnoli et al., 1998; Ferretti and Serpagli, 1999). This is apparently a result of late insertion of Alpine terranes between the margin of Gondwana and the early Palaeozoic terranes bordering it.

7. Taxonomic nomenclature

Subphylum Conodonta Sweet, 1988.
Class Conodonta Eichenberg, 1930.
Order Prioniodontida Dzik, 1976.
Family Balognathidae Hass, 1959.
Genus *Baltoniodus* Lindström, 1971.
Type species: *Prioniodus navis* Lindström, 1955.

Baltoniodus norrlandicus denticulatus ssp. n.

Holotype: element M ZPAL cVI/1102 (Fig. 12AF).

Type horizon and locality: Late Darriwilian *Eoplacognathus reclinatus* Zone, Mójcza Limestone at Szumsko, borehole depth 38.7–40.0, Holy Cross Mts., Poland.

Diagnosis: Elements M with weakly developed denticulation of the inner process, elements S_3 with a relatively long undenticulated anterior process.

Material: 4086 specimens (Supplementary material Table 3).

Genus *Trapezognathus* Lindström, 1955.

Type species: *Trapezognathus quadrangulum* Lindström, 1955.

Trapezognathus pectinatus sp. n.

Holotype: element M ZPAL cVI/870 (Fig. 9T).

Type horizon and locality: earliest Darriwilian *Microzarkodina parva* Zone, the Bukowiany limestone formation at Pobroszyn section, sample Po-10, Holy Cross Mts., Poland.

Diagnosis: Elements M with erect cusp and prominent denticulation of the medial process; elements P well denticulated.

Material: 1093 specimens from Pobroszyn and 72 specimens from Szumsko (Supplementary material Tables 2 and 3).

8. Conclusions

It appears thus that particular Ordovician conodont species show different geographic ranges along the transect from Baltica to Gondwana. An unexpected discontinuity in biogeographic gradients between the Łysogóry region of the Holy Cross Mts. and the East European Platform has been revealed. This indicates that the Tornquist Lineament marks a wide sea separating the Małopolska microcontinent (with the Holy Cross Mts. at its northern tip) from Baltica in the early Palaeozoic.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2019.04.013.

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