Spontaneous Article

Faunal dynamics and evolution of Ordovician conodonts on the Baltic side of the Tornquist Sea

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ABSTRACT: Continental drift of Baltica from the Tremadocian subpolar latitudes to subtropical latitudes in the Katian was the main factor controlling the succession of the Ordovician Baltic conodont communities. These faunas were gradually enriched during the Floian as a result of immigrations from the regions experiencing warmer climate. Reinterpretation of quantitative data in terms of population approach to fossil assemblages shows how some of these immigrants evolved anagenetically in place, changing their contribution to the secondary productivity of the ecosystem. The composition of the fauna became surprisingly uniform, at least since the numerical domination by the presumably indigenous *Baltoniodus* lineage was established during the Dapingian. *Baltoniodus* was supplemented by another indigenous lineage of *Trapezognathus-Lenodus-Eoplacognathus*, which continued its subordinate occurrence during the Darriwilian. The early Sandbian transgression resulted in immigration of the *Amorphognathus* lineage that emerged allopatrically in an unknown region but then began evolving anagenetically until the end of the Ordovician. Conodonts with coniform apparatus elements added complexity to the general picture of immigrations and disappearances, but only the lineage of *Protopanderodus rectus* seems to have differentiated geographically its contribution to the biological productivity. Several brief cooling and warming episodes did not result in any long-term transformations of the conodont communities. Most intriguing was the immigration of the *Yaoxianognathus* lineage that probably gave rise to all of the post-Ordovician ozarkodinids. By that time, *Yaoxianognathus* had its close relative in the tropical North American Midcontinent, but the source area was probably in the Darriwilian of the Argentinian part of Gondwana. Forms with thin P_1 elements of basal cone walls, like *Scabbardella* or *Hamarodus*, are indicators of glacial Gondwanan influences. The lineage of *Sagittodontina*, associated with these in the Małopolska microcontinent (with Gondwanan affinities), was subordinate in Baltica until it had been influenced by the Hirnantian glaciation that ended the Baltic conodont fauna.

KEY WORDS: Baltica, concept of species, Gondwana, methodology, oral apparatuses, palaeobiogeography, palaeobiology, phylogeny.

The Ordovician was an epoch of the highest diversity of conodonts in their long geological history. This aspect of the period stimulated development of the most advanced methodologies of biostratigraphy and palaeobiology (Bergström 1971; Lindström 1971; Bergström & Ferretti 2017). In particular, the Baltic region provided opportunity to perfect the population and apparatus approach to Ordovician conodonts with reliable stratigraphic control. Faunas inhabiting the ancient continent of Baltica were mainly under control of its drift from the subpolar location in the Cambrian to the equatorial in the Silurian (Bergström 1990; Torsvik & Cocks 2017). Episodic global temperature fluctuations, as well as short-term eustasy, which to some degree influenced the climate (Edward *et al.* 2022), were superimposed on the gradual regional warming resulting from changing palaeogeography (Rasmussen & Stouge 2018; Stouge *et al.* 2020). Even the latest Ordovician conodont community in Baltica (Bergström & Bergström 1996) was dominated by species typical of the temperate climatic conditions.

The general pattern of Ordovician conodont succession and evolution can be deciphered using a classic faunistic approach to the fossil record. The spatial distribution of Ordovician conodont communities has been addressed in several papers, starting from Barnes & Fåhraeus (1975) and Bergström & Carnes (1976). While presenting the results of previous research I refer to the fates of individual species rather than their role as parts of living communities, the structures of which are inferred from fossil assemblages. Such an approach prevents controversies connected with the generally low integration within communities (*inter alia*, Hoffman 1979; Hubbel 2005).

The fossil record of conodont species succession in the Ordovician of the Baltic region is probably one of the most complete for any taxonomic group. Thousands of samples have yielded millions of specimens and it is now no longer easy to discover any new species not already reported in the literature. Based on this unusually rich material, the pattern of immigrations of conodonts to the Baltic region has been repeatedly addressed in several papers in attempt to understand their faunal history (e.g., Dzik 1983; Bagnoli & Stouge 1996; Stouge *et al.* 2020). The methodology applied in this work, based more on palaeobiology than biostratigraphy, will hopefully help to decipher the faunal history of conodonts.

1. Material

Quantitative data on the distribution of 838,822 conodont elements were available for the purpose of the present work. They range in age from the late Tremadocian (Hunneberg age in Baltic regional geochronology) to the late Katian (Pirgu age). Conodont zones referred to in the text are informally understood as chronological units diagnosed on evolutionary origins of eponymous species. They are not necessarily identical, with the widely used biostratigraphic zones based on First or Last Appearance Datums, which were ecologically controlled and unavoidably diachronous in geographic space. No distinction is made between zones and subzones.

1.1. Boreholes and exposures

The research was focused on the evidence obtained from boreholes drilled in the Polish part of the East European Platform (55,875 specimens). The most complete core of the borehole Lesieniec IG 1 (21°30′03.17″E 54°11′25.16″N; drilled in 1970 by Oil Exploration Company in Wołomin) provided 64 samples. They have been supplemented by six samples from the borehole Gałajny IG 2, 11 samples from the Jezioro Okrągłe IG 1 (Podhalańska *et al.* 2019), and four samples from the Bartoszyce IG 1, all representing the same tectonic unit that approximately covers the Warmia (Ermland) and Masuria regions (Fig. 1). Some literature data are also available in Bednarczyk (1979), who illustrated Floian conodonts from boreholes drilled nearby at the northernmost tip of Poland.

The Mazury elevation, where Triassic rocks cover directly the Precambrian crystalline basement (Modliński 1973; Barmuta *et al.* 2017; Golonka *et al.* 2019), separates the Peribaltic syneclysis from another area of the preserved subsurface Ordovician in NE Poland, located southward in the Podlasie region. It is represented by three samples from the Widowo and two samples from the Niwa boreholes. Some conodonts of Floian to Katian age were already described from there by Nehring-Lefeld (1987). The boreholes Kovel-1 (Saadre *et al.* 2004) and Pishcha-16 (Drygant 1974) in Volhynia provide qualitative data from the same geotectonic unit in Ukraine. Further south there are exposures in Podolia, which I sampled at the locality of Kytaihorod (Dzik 2020).

The newly obtained, unavoidably limited evidence from boreholes and a few Swedish, Estonian and Russian exposures can be merged with numerical literature data on the Baltic Ordovician conodonts (591,296 specimens). Their taxonomy is here revised according to present understanding of the apparatus species (supplementary Tables 1–68 available at https://doi.org/10.1017/S1755691024000070). I also had the opportunity to sample Ordovician exposures at Sukhrumägi in Estonia, as well as at Ottenby, Hälludden, Varvboholm, and the Gullhögen Quarry in Sweden. This supplemented data from literature sources with 18,823 specimens. Quantitative data on conodonts from the Volkhov age strata at Putilovo Quarry in Ingria come from Tolmacheva *et al.* (2001a). A few samples were taken by me in the same region at the Lynna River, the section described in detail by Lindskog et al. (2020), who gave also a qualitative description of the conodont succession. Probably the most complete qualitative data on the Mid and Late Ordovician conodont succession is available from Estonia (i.e., Hints *et al.* 2012; Mellgren *et al.* 2012; Männik 2017). The meaning of all these materials can be understood owing to the meticulous work published in classical papers by students of the Scandinavian and East Baltic Ordovician (Löfgren 1978, 1985, 1993, 1994, 1995, 1997a, 2003; Bagnoli *et al.* 1988; Stouge & Bagnoli 1990; Bagnoli & Stouge 1997; Zhang & Sturkell 1998; Rasmussen 2001; Tolmacheva & Fedorov 2001; Tolmacheva *et al.* 2001a, 2001b; Tolmacheva & Purnell 2002; Stouge & Nielsen 2003; Viira *et al.* 2006b).

1.2. Glacial erratic boulders

It is necessary to keep in mind that, during the Pleistocene, the continental ice motion removed most of the sedimentary rock cover from Scandinavia and East Baltic, and deposited it over the central European plain, locally accumulating more than 200 metres of glacial deposits. The sedimentary rocks survived glacial erosion only locally, where early Palaeozoic strata were protected under Permian volcanic caps or preserved within meteoritic craters (Fig. 1). Some rock formations are no longer represented in exposures. This makes glacial erratic boulders an important source of evidence for the conodont succession in the Baltic region (Wolska 1961; Dzik 1976). The Ordovician boulders collected in the Pleistocene drift in Poland yielded 55,875 specimens. The large number of specimens in particular samples enabled tests of the apparatus reconstructions based on less numerous samples from boreholes. This is exemplified by the large sample E-360 (of 46,499 specimens; Figs 2–4; supplementary Table 41) assembled in an attempt (not quite successful) to identify discrete classes of coniforms and identify their position in the apparatus.

The routes of glacier tongues have been inferred mostly by identification of source areas of crystalline rocks represented by erratic boulders (e.g., Viiding *et al.* 1971; Overweel 1977; Hall & van Boeckel 2020). However, limestone boulders significantly contribute to the till, too. Glacial erratics of Ordovician limestone are known as far northward as central Sweden (Löfgren & Laufeld 2007). They were transported southward mostly along the middle of the present-day Baltic Sea (Hall & van Boeckel 2020), but it is difficult to connect precisely the distribution of particular rock types with the source outcrops. Unlike specific kinds of igneous rocks identified in the Scandinavian crystalline basement, formations of sedimentary rocks were once widely distributed in the Baltic area. The material at my disposal is too scarce to determine precisely occurrences of particular kinds of limestone boulders in moraines representing specific glacial episodes. Nevertheless, it is apparent that some characteristic lithologies differ in frequency between western and eastern Poland. For instance, the red cephalopod limestone is common on the Baltic seashore in the west, whereas glauconitic limestone of the same age is common in the east. This refers to occurrences of glacial drift deposited in the last glaciation about 20 ka, and in the preceding one about 140 ka, but also during the most extensive glacier expansion up to the Sudetes about 340 ka (Mokrzeszów). Therefore, I subdivided the conodont assemblages from glacial erratics in two groups, covering the eastern and western halves of Poland.

1.2.1. Erratics from eastern Poland. Mochty: E-079, E-080, E-081, E-085, E-103, E-190, E-211, E-213, E-214, E-215, E-216, E-291, E-294, E-303, E-305, E-307, O-461; Wieżyca: E-087, E-231, E-237, E-239, E-240; Rozewie: E-111, E-116, E-130, E-252, E-320, E-323, E-335, E-348, E-349; Zgierz: E-089, E-090, E-096, E-112, E-113, E-173, E-182, E-189, E-201, E-204, E-207, E-295, E-204; Jóźwin: E-314, E-315, E-317, E-330, E-334, E-336; Orłowo: E-117, E-134, E-135, E-137, E-194, E-195, E-196, E-224, E-225, E-226, E-227, E-254, E-255, E-319, E-322; Chłapowo: E-119, E-124, E-197; Wieżyca?: E-232, E-236; Kartuzy: E-326.

1.2.2. Erratics from western Poland. Miedzyzdroje: E-104, E-138, E-140, E-141, E-142, E-143, E-144, E-145, E-148, E-149, E-154, E-157, E-181, E-186, E-222, E-228, E-229, E-230, E-251, E-259, E-260, E-261, E-262, E-263, E-266, E-267, E-268, E-270, E-271, E-273, E-274, E-276, E-279, E-282, E-283, E-285, E-350, E-351, E-352, E-353, E-354, E-355, E-356, E-357, E-358, E-359, E-360, E-361, E-362,
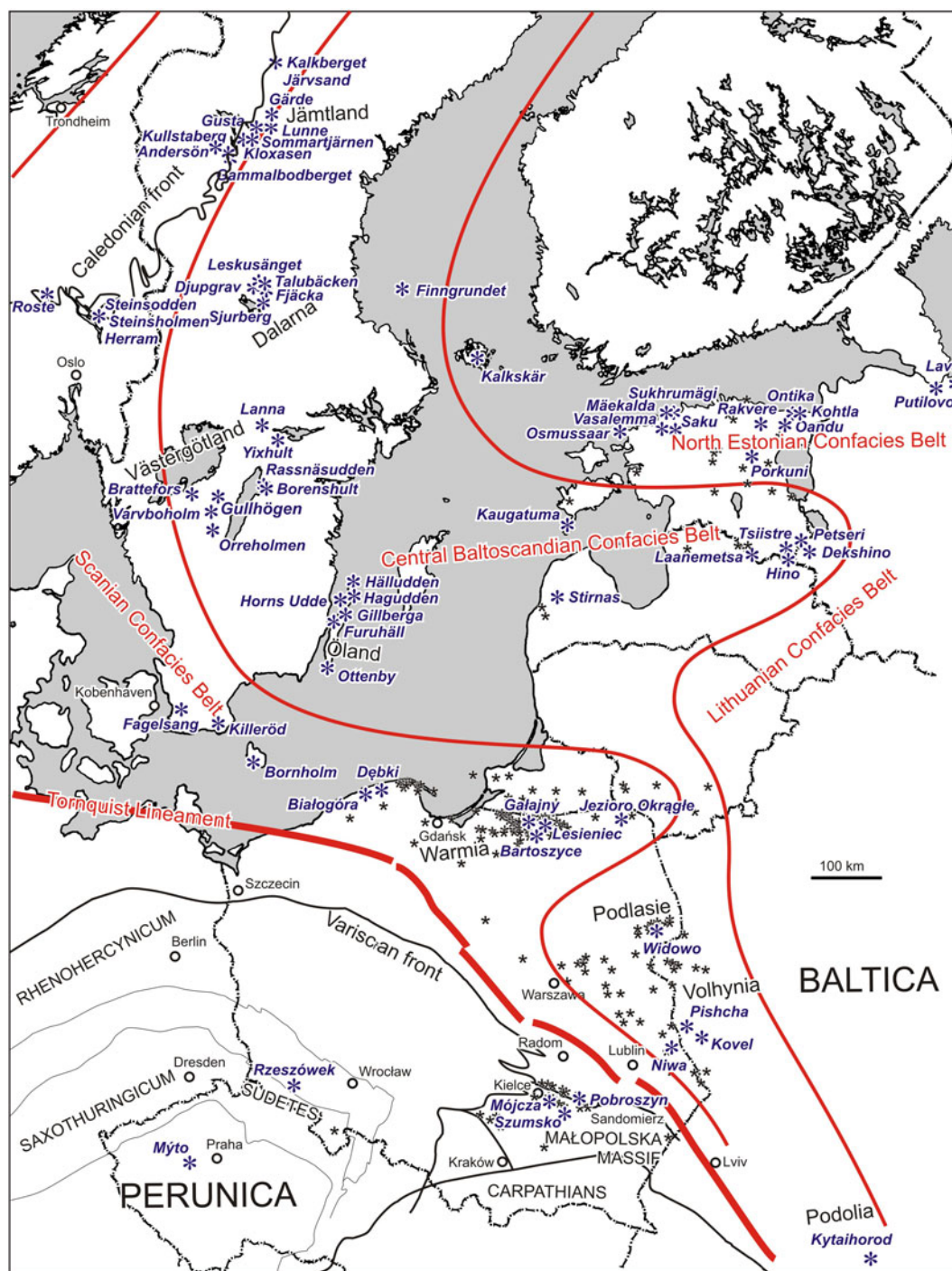
Figure 1 The exposures and boreholes mentioned in the text (marked with larger blue asterisks) and other boreholes that reached the Ordovician rocks (marked with small black asterisks) shown on a non-palinspastic map of north-central Europe.

E-364, E-367, E-368, E-369, E-370, E-371, E-383; Szczecin: E-275; Rewal: E-328, E-338, E-339; Złocieniec: E-342, E-344; Mokrzeszów: E-374, E-375.

2. Methods

A troublesome aspect of the apparatus approach to conodonts is that in the case of closely related sympatric species some elements of their apparatuses do not exhibit taxonomically diagnostic characters. They cannot be determined at the species level. In such cases I attribute them to both species, splitting the counted specimens roughly in the proportion shown by those elements that are taxonomically determinable.

Regrettably, almost all conodont researchers apply the vertical (typologic) concept of species. Conodonts are not different in this respect from other organisms that have a fossil record complete enough to substantiate recognition of chronospecies. From the biostratigraphic point of view, the methodological differences between vertical and horizontal approaches are seemingly just subtleties. However, this is a truly relevant issue. It has to be remembered that because of the Gaussian nature of population variability, specimens representing any vertically defined chronospecies are very rare at the beginning and at the end. This makes the stratigraphic range of such species strongly dependent on the sample size. Admittedly, boundaries of biostratigraphic units based on horizontally defined species are foggy as well. The biological evolution is slow, its path is crooked and unpredictable. The evidence is never quite convincing, despite numerous biometrically studied examples of the Ordovician conodonts (e.g., *Baltoniodus* in Dzik 1994, 2020; *Microzarkodina* in Löfgren & Tolmacheva 2008).
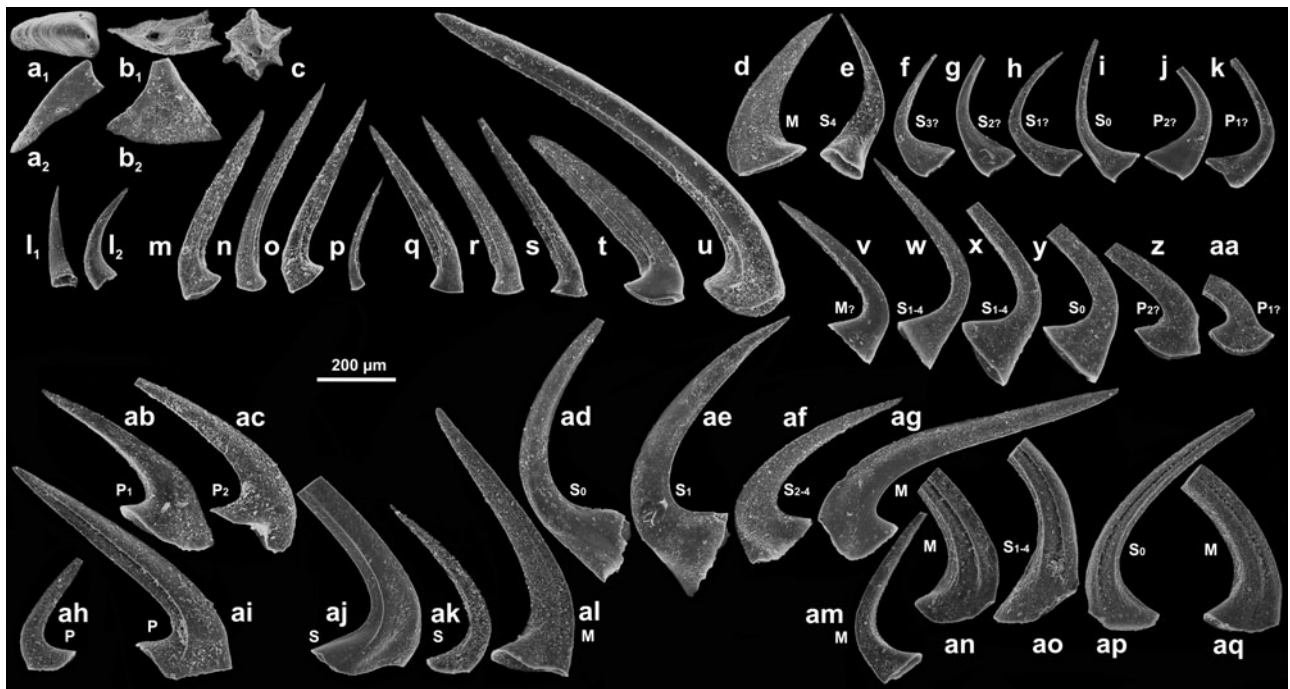
Figure 2 Composition of conodont apparatuses with coniform elements identified in sample E-360 from Miedzyzdroje, Baltic coast of Poland. (a) *Pseudooneotodus mitratus* (Moskalenko 1973) specimen ZPAL cVI/1104 in occlusal and lateral views. (b, c) *Nericodus capillamentum* Lindström 1955a? specimens ZPAL cVI/1183 and 1181 in occlusal (b_1, c) and lateral (b_2) views. (d–k) *Scalpellodus latus* (van Wamel 1974) early form, specimens ZPAL cVI/1114–1116, 1118, 1119, 1121, 1117 and 1120, respectively (d; element M). (l) 'Oneotodus' sp.; specimen cVI/1110 in medial and lateral views. (m–t) *Decoriconus peselephantis* (Lindström 1955a); specimens ZPAL cVI/1112, 1109, 1106, 1113, 1107, 1108, 1110 and 1111, respectively. (u) *Protopanderodus*? sp.; specimen 1105. (v–aa) *Cornuodus longibasis* (Lindström 1955a); specimens ZPAL cVI/1122–1127, respectively. (ab–ag) *Drepanodus arcuatus* Pander 1856; specimens ZPAL cVI/1128–1133, respectively. (ah–am) *Protopanderodus rectus* (Lindström 1955a); specimens ZPAL cVI/1135, 1134, 1136, 1137–1139, respectively. (an–aq) *Protopanderodus sulcatus* (Lindström 1955a); specimens ZPAL cVI/1141–1144, respectively.

The major concern with diagnosing chronospecies refers especially to the biological implications of such a procedure. Obviously, ranges of vertically understood (typologic) species overlap by definition, even when they are parts of a continuous phyletic lineage (e.g., Albanesi & Barnes 2000; Pyle & Barnes 2002, figs 12–14; Stouge *et al.* 2020, fig. 3). Application of

Figure 3 Composition of conodont apparatuses with coniform P and S elements but geniculate M element identified in sample E-360. (a–g) *Triangulodus brevibasis* (Sergeeva, 1963) specimens ZPAL cVI/1145–1150, respectively. (h) *Paroistodus parallelus* (Pander 1856) specimen ZPAL cVI/1153. (i–m) *Paroistodus originalis* (Sergeeva 1963a) specimens cVI/1154–1158, respectively. (n–p) *Drepanoistodus forceps* (Lindström 1955a) specimens ZPAL cVI/1151, 1152 and 1200, respectively. (q–v) *Drepanoistodus basiovalis* (Sergeeva, 1963) specimens ZPAL cVI/1159–1164, respectively.

Figure 4 Composition of conodont apparatuses with denticulated ramiform elements identified in sample E-360. (a–h) *Baltoniodus navis* (Lindström 1955a) specimens ZPAL cVI/1165–1168, 1203, 1169–1171 respectively. (i–q) *Trapezognathus diprion* (Lindström 1955a) specimens ZPAL cVI/1174, 1173, 1172, 1175–1180, respectively. (r) Unidentified platform element ZPAL cVI/1182. (s) Unidentified juvenile M element (possibly *Periodon*) ZPAL cVI/1184. (t–z) *Microzarkodina flabellum* (Lindström 1955a) specimens ZPAL cVI/1185–1187, 1189, 1188, 1198, 1190 and 1191 respectively. (aa–af) *Periodon flabellum* (Lindström 1955a) specimens ZPAL cVI/1192–1197, respectively.

such methodology gives a false support to biased views on evolution: as the evidence of sudden origin of species, evolution proceeding exclusively by 'speciation' or even as a result of 'species selection'. There is no doubt that 'vertical taxonomy' results in a misrepresentation of data. Potentially, it is possible to 'translate' the hard palaeontological evidence into something of use to evolutionary biology, but it is not an easy task.

This is why in this work the 'horizontal' (population) approach to taxonomy is followed. This requires that a species discrimination is done on each sample separately, irrespective of whether it belongs to a continuous stratigraphic succession or not. This enables biologically meaningful quantitative description of lineages, making it possible to estimate the numerical contribution of particular species to fossil assemblages.

2.1. Standing crop versus biological productivity

Frequency of a particular species in a time-averaged fossil assemblage reflects its contribution to the biological productivity of an ecosystem, not to the standing crop (Dzik 1979), which is a truth usually overlooked by palaeontologists (e.g., Kranz 1977; Kidwell & Flessa 1996; Dietl *et al.* 2015). This is why juvenile individuals are seemingly underrepresented and adults overrepresented in most fossil assemblages. Exceptions are assemblages that originated by catastrophic events, but this hardly refers to minute conodont elements deposited continuously together with mineral grains to the sediment. It is thus tempting to interpret the conodont fossil assemblages in terms of palaeoecology and to estimate quantitatively their contribution to the flow of living matter in the Palaeozoic sea. Several factors may prevent this. The most obvious of them is taphonomy (Von Bitter & Purnell 2005) that results not only in distorting the contribution

of particular apparatus elements but also in deformation of the actual proportions of species. Remarkably, the imbalance is much more significant in the late Palaeozoic conodont fossil assemblages than in the Ordovician ones, presumably as a result of increased predation on conodonts (*inter alia*, Zatoń *et al.* 2017). Delicate S and M elements are more prone to fragmentation in the predator's intestine than massive P elements. Still, the percentage contribution of apparatus elements of particular species is a meaningful approximation to reality and also enables a presentation of changes in structure of fossil communities in geological time.

The numerical proportion of fossilised individuals does not necessarily reflect the real contribution of a species to biological productivity in an ancient community. This depends on their growth rates and mature size. The generation turnover may be much more intense in species of small size individuals and their contribution to the biological productivity much lower in terms of the standing crop. Counting and measuring rhythmic increments presumably representing Ordovician or Devonian days (Dzik 2000, 2008, 2015) may allow us to estimate these aspects of the biology of conodonts. Specimens of high quality of preservation and with unmineralised basal body tissue are then required. In any case, the conodont element size alone is a source of easily accessible important information. Potentially, also the weight (or volume) of fossils may reflect biomass of ancient organisms (e.g., Dzik 1979) but fragmentation of conodont elements due to their taphonomy, diagenesis and laboratory preparation prevents reliable measurements.

To offer at least a crude overview of particular species' contribution to the conodont community, drawings of restored apparatuses are illustrated with the same magnification (Figs 5–8
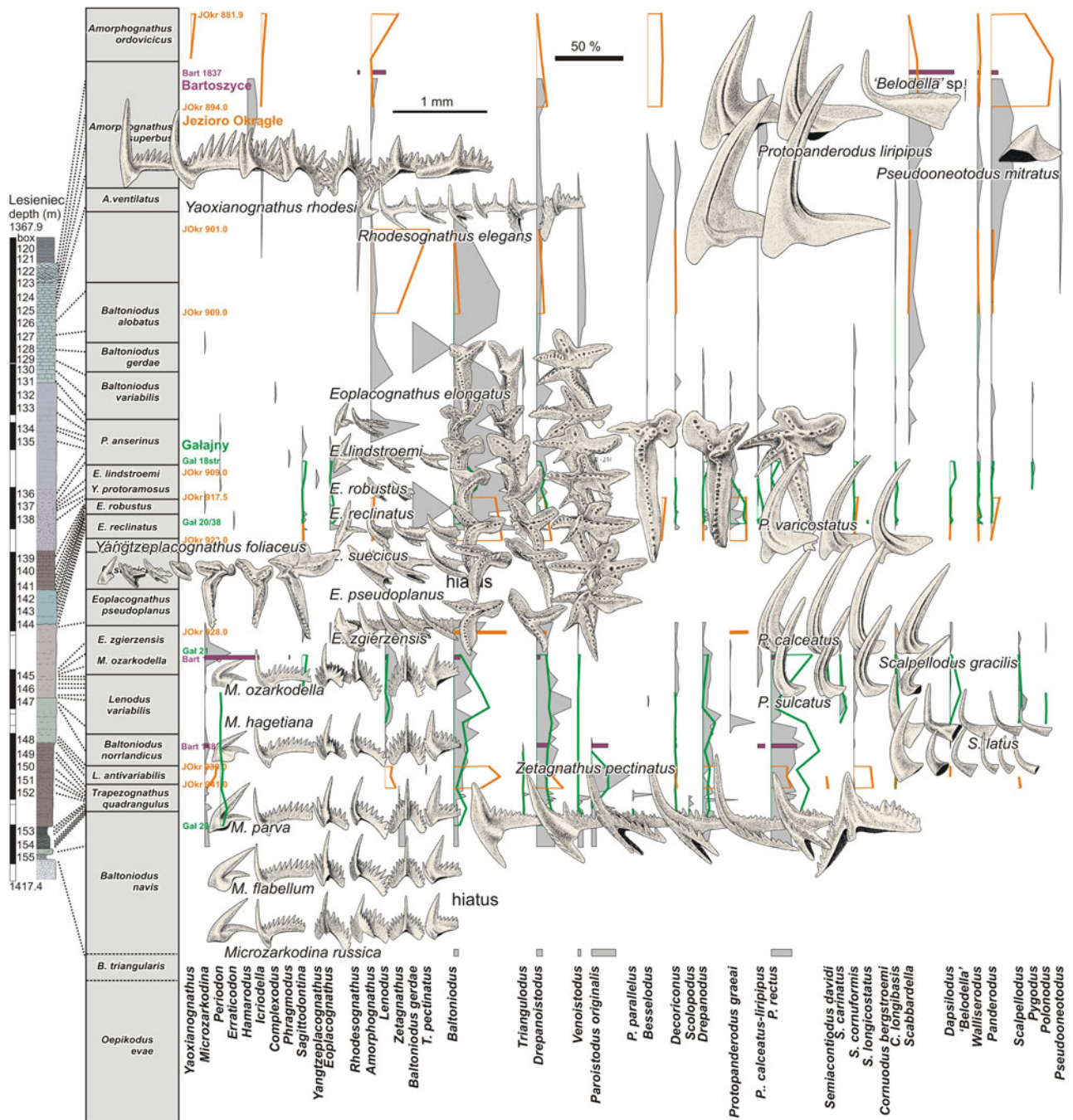
Figure 5 The Ordovician conodonts succession in the Warmia–Masuria region recorded in the boreholes Lesieniec IG 1, Gałajny IG 2, Bartoszyce IG 1 and Jezioro Okrągłe IG 1. Geological ages of biostratigraphic units in this and subsequent figures are standardised according to absolute geological ages proposed by Dronov (2005) and Nõlvak *et al.* (2006) that are comparable with ages based on data from other regions (Goldman *et al.* 2020). Ranges of informal conodont zones and biozones (without making a distinction between zone and subzone ranks) are shown here; their correspondence to international higher-rank geochronological units is shown on Fig. 8b. Drawings of conodont elements are in the same magnification to visualise the contribution of particular species to biological productivity of their communities.

and 9). These show the approximate mean size of elements in samples that depend on the population dynamics; that is, on the distribution of mortality at particular stages of ontogeny.

2.2. Between-orders homology of conodont elements
The number of element types has hardly any correspondence to the number of locations in the apparatus and descriptives referring to it are not used here. Most probably, the same number of elements characterise apparatuses in high rank conodont taxa. Still, it is a matter of continued controversy how many elements were present in them.

Geniculation of the M elements in the basal members of the ozarkodinid, prioniodontid and distacodontid apparatuses

makes homology of the remaining locations in the apparatus rather easy despite the profound changes in the apparatus composition (Dzik 2015). This is much more problematic in respect of the panderodontid and protopanderodontid apparatuses, interpreted in contradictory ways. Fortunately, there are two findings of almost complete apparatuses of *Panderodus unicostatus* (Branson & Mehl 1933) from Podolia and Wisconsin, which are informative enough to solve the problem.

The fused cluster from Podolia consists of 13 elements and was interpreted as coprolithic in origin. The lack of one asymmetric element was attributed to its loss during preparation of the specimen, whereas that of the symmetrical element to the evolutionary reduction. Such interpretation is substantiated by the general
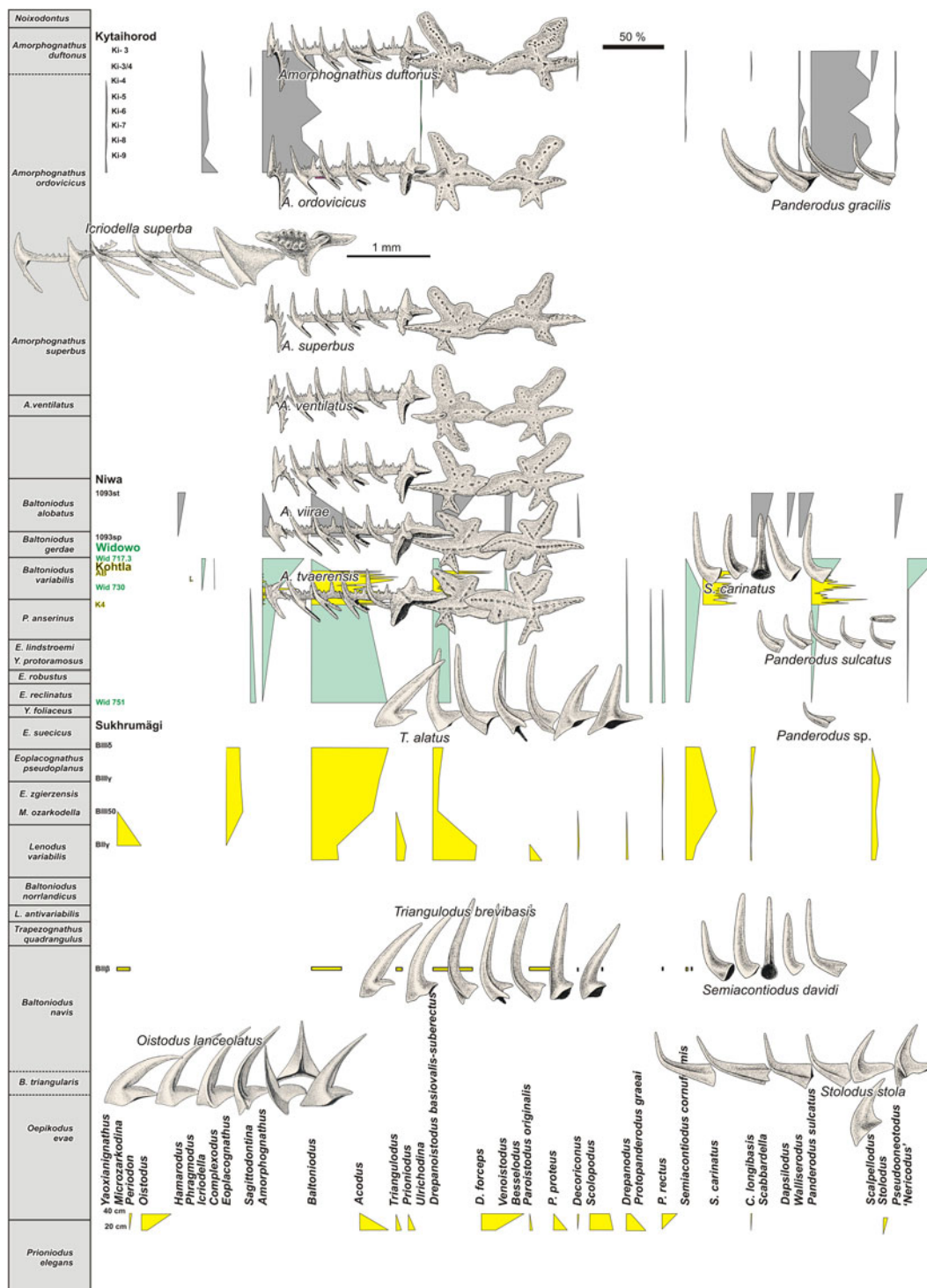
Figure 6 The Ordovician conodonts succession in the Podlasie region recorded in the boreholes of Niwa and Widowo, supplemented by data from exposures at Kytaihorod in Podolia, Ukraine (Dzik 2020), Kohtla (data from Viira et al. 2006a; supplementary Table 64) and Sukhrumägi in Estonia.

lack of symmetrical elements in fossil assemblages of loose *Panderodus* elements in the Silurian. As a result of attempted reconstruction of the deformation of the apparatus in the stomach of a predator, the apparatus was restored as composed of 14 elements showing the size gradient, with the largest elements pair in anterior position, representing the M location (Dzik & Drygant 1986).

The bedding plane natural assemblage from the Waukesha Shale of Wisconsin consists of 13 elements preserved with the crown tissue plus one described as 'entirely mouldic'. This set of elements was interpreted as representing a 17-elements apparatus, with two asymmetric elements lost (their 'symmetry pair are absent') although both part and counterpart of the apparatus

are available. A single element in the middle of the apparatus is symmetric, unquestionably identified as the S_0 element. The smallest elements in the apparatus were interpreted as representing the P locations, consistent with interpretation of the Podolian cluster. The most significant difference, as proposed by (Murdock & Smith 2021), is the place for the compressed 'falciform' element, proposed to occupy P_3 instead of the M location. This elements pair covers all remaining elements of the apparatus in the composite picture (elements 8 and 9 in Murdock & Smith 2021, fig. 4c). The apparatus is preserved in an occluded position and I propose that these elements were originally above (or rather below in life position) the S_3 elements pair (elements 1 and 2 in Murdock & Smith 2021, fig. 4c). This removes the main
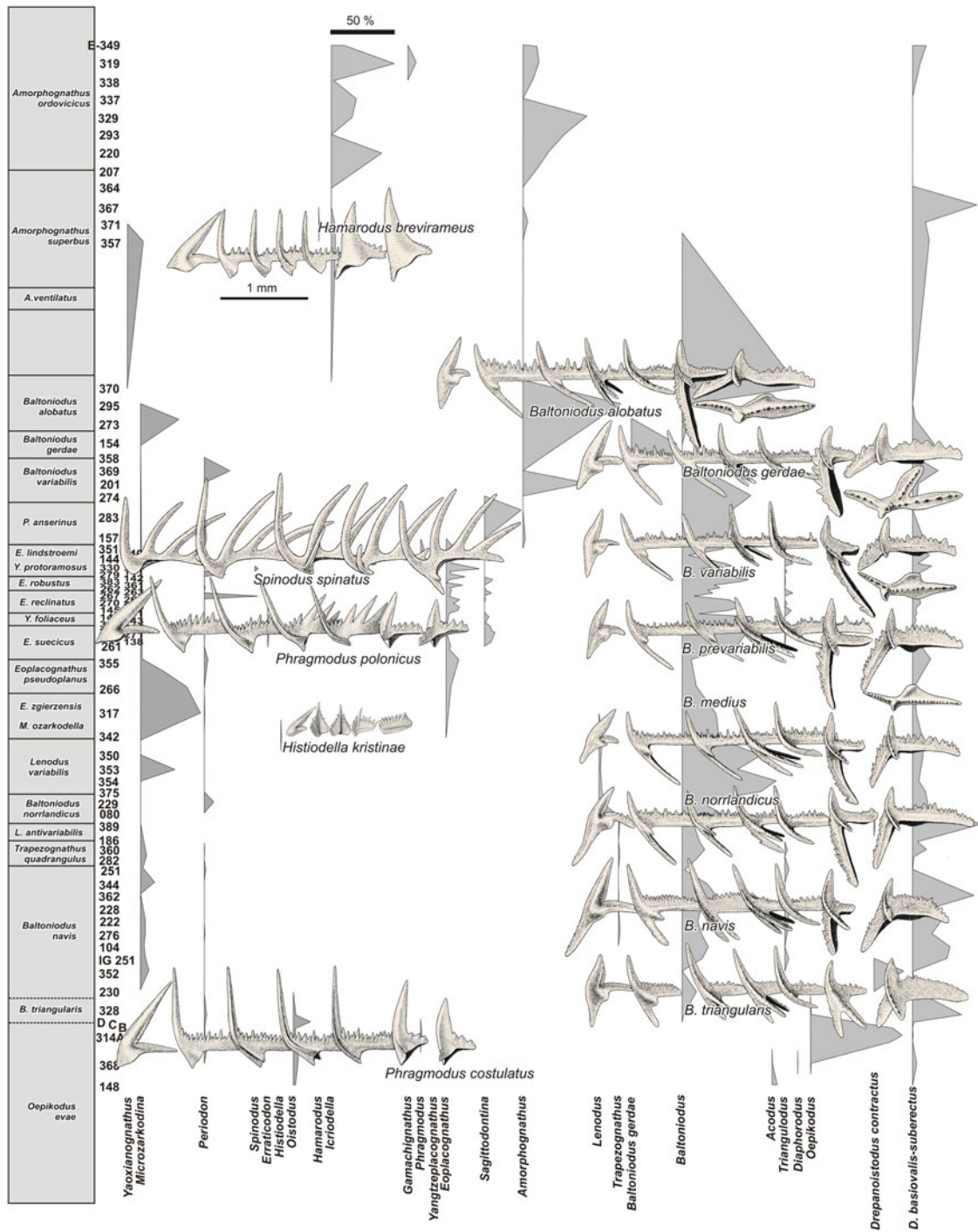
Figure 7 The Ordovician conodonts succession recorded in glacial erratic boulders from eastern Poland. The order of samples within particular zones is arbitrary.

discrepancy between interpretations of the cluster and natural assemblage of *Panderodus*.

Attempts to arrange M, S and P locations into evolutionary series linking the protopanderodontids with those of the ozarkodinids are guided only by their general morphology: M elements are expected to be characterised by a sharp cusp and curved base, S elements to be represented by a symmetry-transition series of several morphologies, and at least two types of P elements should have a robust appearance with a short cusp. On such basis I proposed interpretation of the apparatus of *Drepanodus* (Dzik 1994). Löfgren & Tolmacheva (2003) contested it and proposed the opposite order of the element morphologies, with the short-cusped element representing the M location and that with the longest sharp cusp ('pipaform') being the P element. Until

complete natural assemblage is available, this controversy will remain hard to solve.

Despite undoubtedly convergent development of geniculation in *Belodina*, it may truly be a homologue of that in the ozarkodinid and prioniodontid M elements. Then, the orientation of apparatus is such as that proposed by Dzik & Drygant (1986) and Murdock & Smith (2021) for *Panderodus*; that is, the smallest elements pair is the posteriormost one, being homologous to P_1.

2.2.1. Descriptives of conodont elements sides. The orientation of elements in conodont apparatuses representing various high-rank taxa may be different (Sweet 1988; Sweet & Donoghue 2001). This makes application of anatomical terminology to apparatuses restored on the basis of isolated elements difficult.
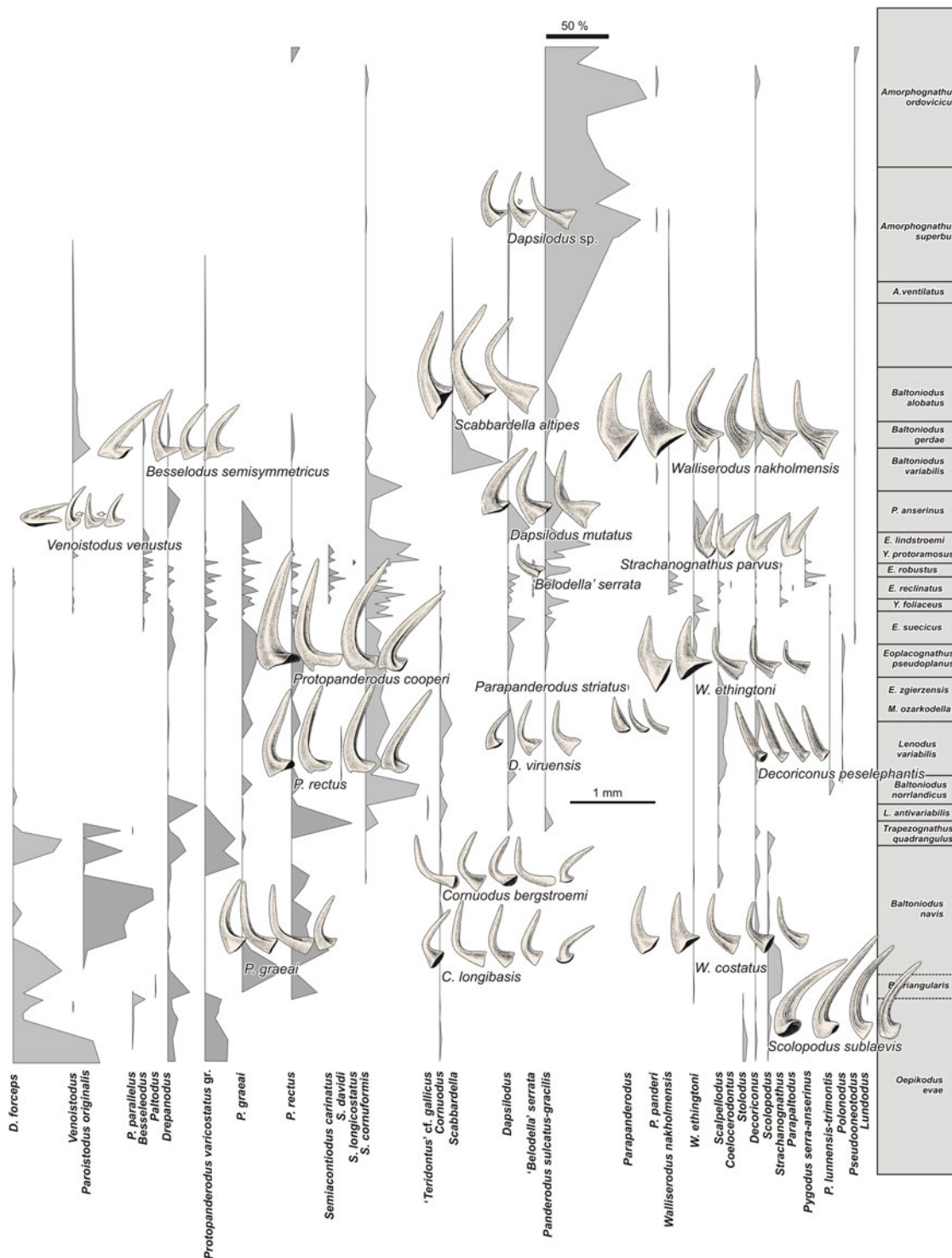
Figure 7 Continued.

To avoid inconsistency, while describing elements I refer to homology of various apparatuses with the late Palaeozoic ozarkodinids as well as to serial homology to P elements within the apparatus. They are visualised as if their processes were directed transversely to the body axis. Thus, in all elements the convexity in the course of carina is considered to correspond to the anterior side, the bulging basal cone denotes the posterior side, whereas the cusp and denticles are bent dorsalwards.

3. Taxonomy of Baltic Ordovician conodonts

Ordovician conodonts were first recognised in the Baltic region by Pander (1856) and elements of some of them were illustrated by Hadding (1913) adequately enough to identify currently understood species (Lindström 1955b; Bergström 2007). They became high-quality guide fossils owing to the seminal papers by Lindström (1971) and Bergström (1971). A lot has been done since that time, but the status of many species remains poorly established. Below I comment on them arranged according to the Linnean evolutionary suprageneric systematics.

3.1. Order *Panderodontida* Sweet 1988, family *Fryxellodontidae* Miller 1980

3.1.1. *Pseudooneotodus mitratus* (Moskalenko 1973). The type horizon of this species, the morphological simplicity of which is misleading, is the late Sandbian Baksan formation of
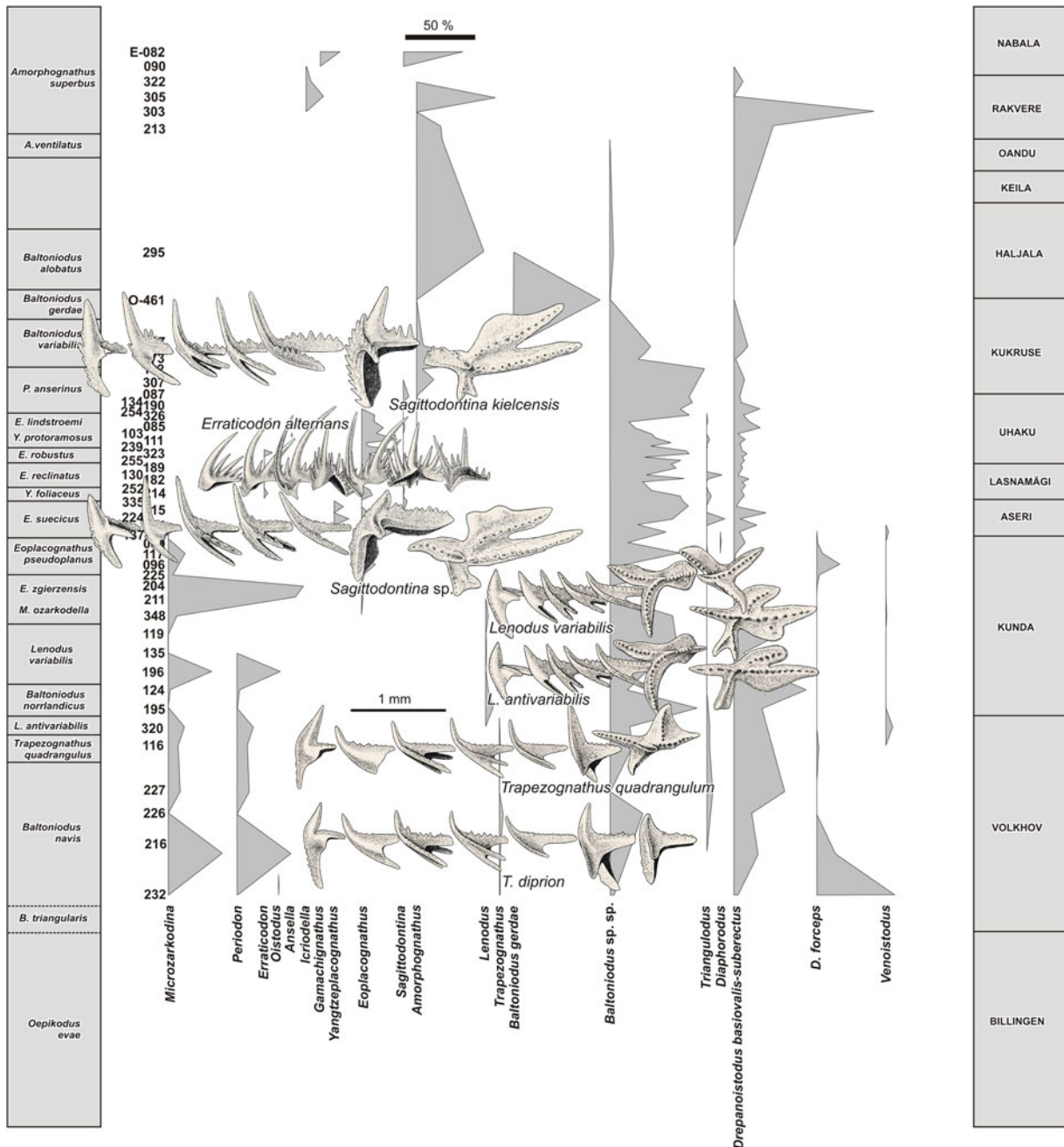
Figure 8 The Ordovician conodonts succession recorded in glacial erratic boulders from western Poland. The order of samples within particular zones is arbitrary. Correspondence to the Baltic and international geochronological units after Männik & Viira (2012).

Siberia (Moskalenko 1973). Its probable ancestor *P. nostras* (Moskalenko 1973) comes from the underlying early Sandbian Chertovo formation. It differs from *P. mitratus* in a rounded T-outline, one of the lobes having incipient denticulation (Moskalenko 1973, pl. 17:12–15). Moskalenko (1973, pl. 17:16) also illustrated and described in open nomenclature a possibly congeneric specimen from the late Darriwilian Kirensk formation with all lobes prominently tuberculated. This suggests proximity to *Polonodus* as probable relative.

P. mitratus appeared in Baltica in the *Baltoniodus navis* Zone (boulder E-360, supplementary Table 41; Fig. 2a) and continued its occurrence to the *Amorphognathus ordovicicus* Zone (Fig. 5), usually being represented by a single element per sample. An exception is the borehole Lesieniec IG 1 with a sample of *E. robustus* Zone (Les-1371/3; supplementary Table 56) that yielded seven elements and similar occurrences in the *A. superbus* Zone (supplementary Table 66). This does not allow reasonable restoration of the apparatus but it is likely that it consisted of only one pair of elements. The Silurian species of the genus are represented by elements with a virtually circular outline (e.g., Sansom 1996).

3.1.2. *Lundodus gladiatus* (Lindström 1955a). The species occurs in Baltica in the *Prioniodus elegans* and *Oepikodus evae* Zones. Bagnoli & Stouge (1997) proposed its apparatus reconstruction with denticulated S elements slightly resembling those of *Stolodus*, but this is based on a small material and requires verification. Five P elements in the Ottenby section sample Ot-10 (supplementary Table 2) in my material do not add anything to its knowledge.

3.1.3. *Nericodus capillamentum* Lindström 1955a. The ancestry of *Polonodus* was proposed by me to be in a species illustrated from Ottenby as *Nericodus* (?) sp. (Dzik 1983) but apparently conspecific with *Polonodus*? *lofgreni* Stouge & Bagnoli 1988. Löfgren (1985, fig. 4aab; also Löfgren 1990, fig. 4p) illustrated its S elements and noticed (Löfgren 1990, p. 256) that 'these ramiforms are much less *Baltoniodus*-like than the ramiforms' attributed by her to *Polonodus*. Moreover, there was a
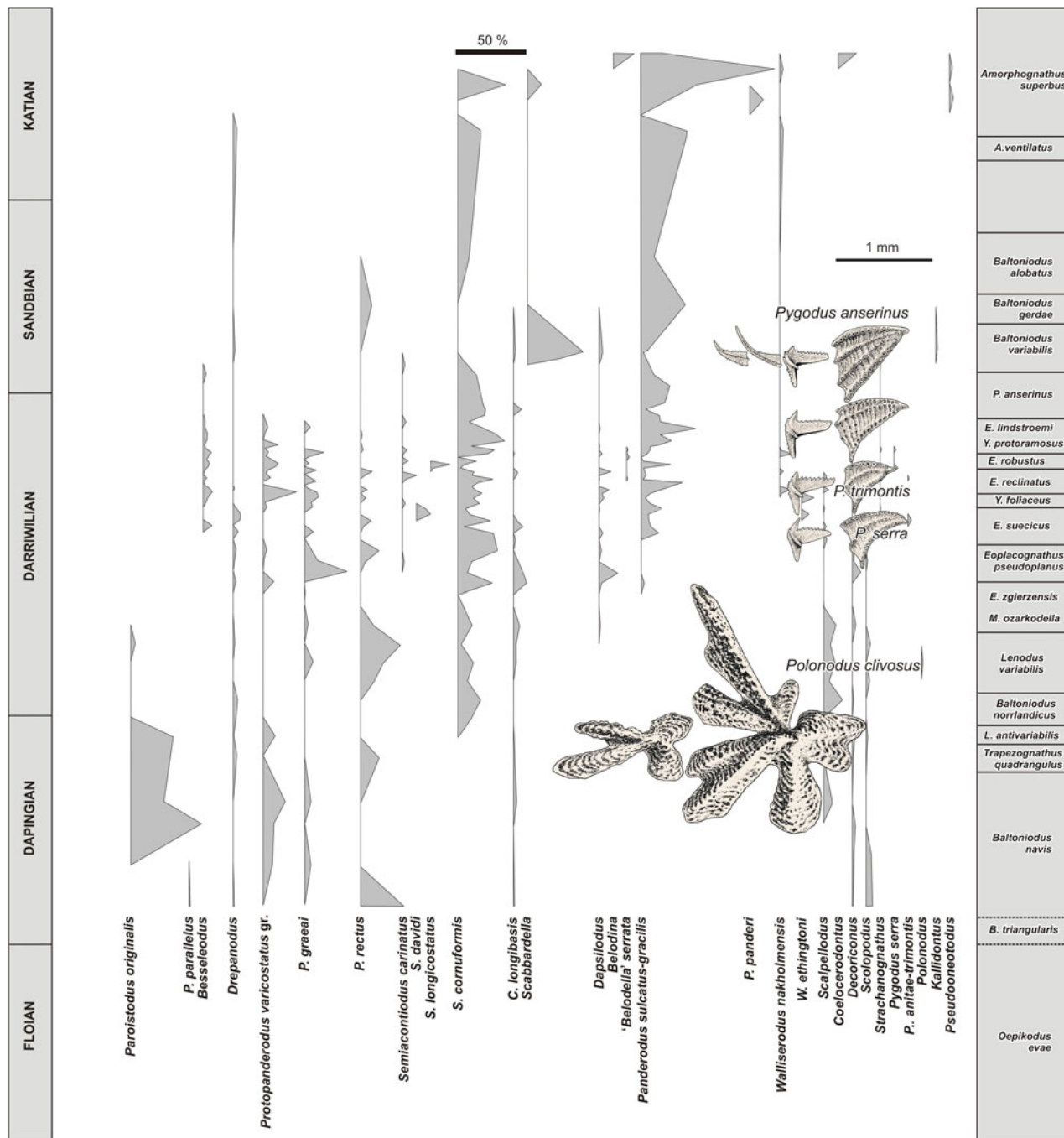
Figure 8 Continued.

large gap in the fossil record between these chronospecies. It has to be pointed out that they are very rare in the Baltic region and appeared there as immigrants from elsewhere, being abundant in Newfoundland and South America. Possibly the lineage can be traced back to the earliest Floian and latest Tremadocian in the succession of species of *Kallidontus* (Pyle & Barnes 2002) from British Columbia. In the course of evolution of this lineage, P elements developed ramification similar to that in *Polonodus* and S elements became gracile and denticulated like homologous elements of *Pygodus*. '*Polonodus*' *corbatoi* (Serpagli 1974) from Argentina may belong to the same lineage (Lehnert 1993; Albanesi 1998). Probably *Nericodus* Lindström 1955a, with *N. capillamentum* Lindström 1955a from the late Volkhov age Lower Limbata Limestone of Yxhult as its type species (Miller 1980), has nomenclatorial priority over *Kallidontus*. Fragmentary elements from sample E-360, as well as some other samples, may be conspecific with it (Fig. 2b, c).

3.1.4. *Polonodus clivosus* (Viira 1974). The holotype of *Ambalodus clivosus* Viira 1974 from the Ohesaare borehole depth of 510.35 m of the late Kunda age was originally interpreted as a sinistral element with bifurcated processes (probably P₁). It co-occurs in the same sample as another specimen (probably P₂) interpreted as a dextral element named *Ambalodus*? sp. n. The illustrated paratype of *P. clivosus* comes from coeval strata at the Ab'ya borehole. Another late Kunda age sample from the Ohesaare borehole (depth 510.12 m) yielded specimens closely similar to the holotype of *P. clivosus*, described as *Amorphognathus*? sp. n. This set of elements provides enough evidence to substantiate attribution of specimens from the *Histiodella kristinae* Zone of Newfoundland to the same species (Stouge 1984). It co-occurs with the more derived *Polonodus tablepointensis* Stouge 1984, in respect to bifurcation of processes. I suggest that these are extreme morphotypes within the same population and that the Newfoundland assemblage of *Polonodus*
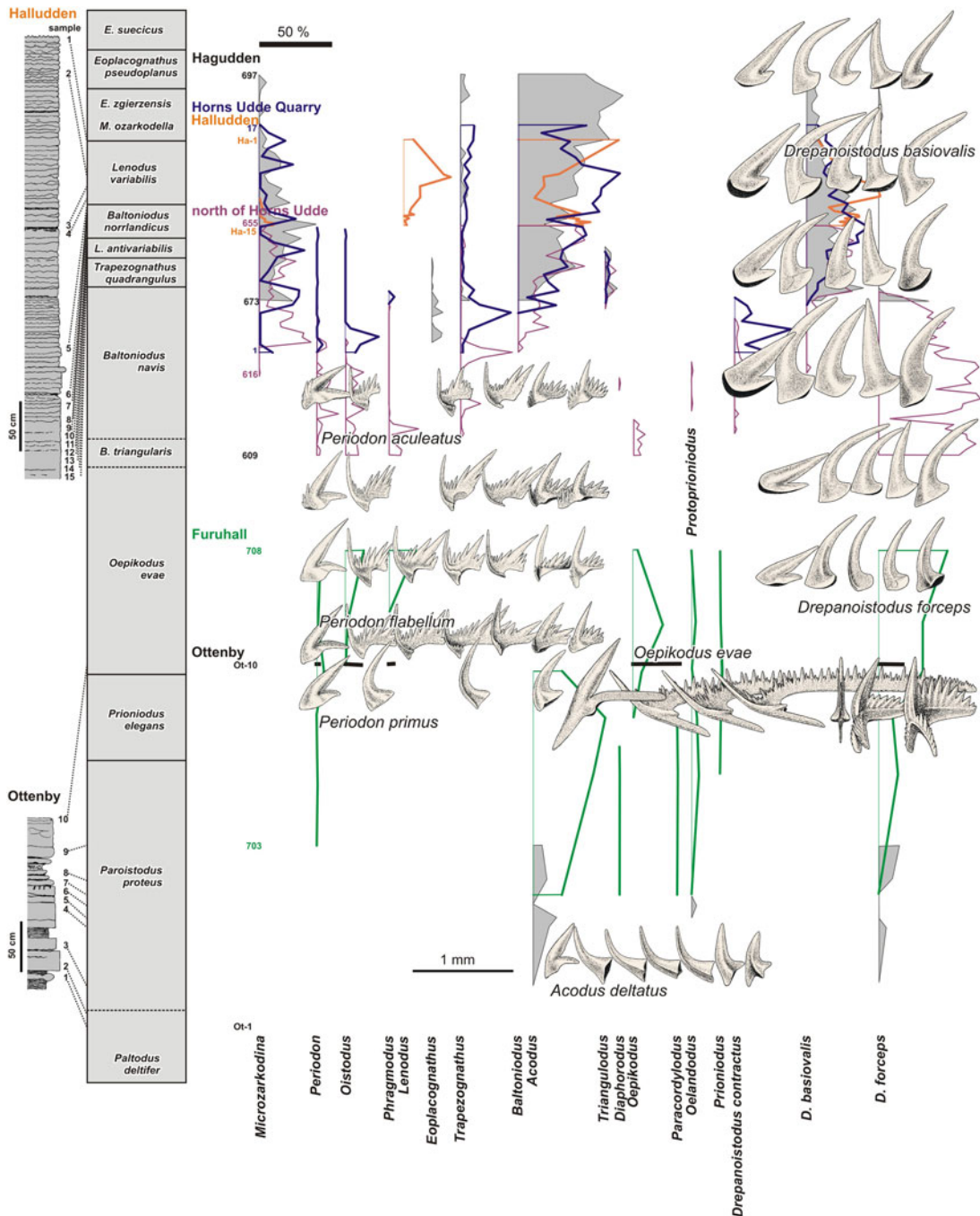
Figure 9 The Ordovician conodonts succession recorded at Hagudden (data from Stouge & Bagnoli 1990; supplementary Table 18), Horns Udde (Bagnoli & Stouge 1997; supplementary Tables 8 and 10), Hälludden (supplementary Table 20), Furuhäll (Bagnoli *et al.* 1988; supplementary Table 27), and Ottenby (supplementary Table 2) in Öland, Sweden.

represents an ontogenetic series of gradual ramification of processes in P_1 elements (Fig. 8). Juvenile specimens (Stouge 1984, pl. 13:10) referred to *P. newfoundlandensis* from older strata (with *H. tableheadensis*) show four processes with bifurcation that develops at some distance from the cusp in the P_1 element. This refers also to the Chinese *Dzikodus hunanensis* Zhang 1998b that seems closely related to *P. clivosus*. However, the pattern of ramification of its ventral(?) process in relatively robust P_1 elements may not be homologous to that in *P. tablepointensis*. Zhang (1998b) noticed that P_2 elements do not form mirror-image pairs in *P. tablepointensis* and *D. hunanensis*. She proposed to use this difference to erect a separate genus.

The brittle thin-walled Baltic specimens of *Polonodus* are never complete enough to exhibit a different ramification from that of the holotype of *P. tablepointensis*. All specimens

illustrated by Viira (1974; also Dzik 1976, fig. 29c, d) represent P_1 elements, but the specimen from sample E-080 photographed in SEM by me (Dzik 1976, pl. 43:1) is a P_2 element. I doubt if more than one species of *Polonodus* occurred in Baltica.

An extrapolation of the trend towards ramification of processes and thinning of the crown in P_1 elements may suggest an alternative for the ancestry for the *Polonodus* lineage. Either this is a balognathid, with the apparatus rooted in that of *Trapezognathus*, as interpreted by Zhang (1998b) or rather a fryxello-dontid rooted in *Kallidontus lofgreni* as proposed by me (Dzik 1983). The nicely documented origin of *Pygodus* from *Polonodus* (Zhang & Sturkell 1998; Zhang 1998a) implies that conodonts of these genera had a similar architecture of their apparatuses. The S elements of Pygodus are of bizarre shapes and denticulation (*inter alia*, McCracken 1991; Zhen *et al.* 2011b). The balognathid
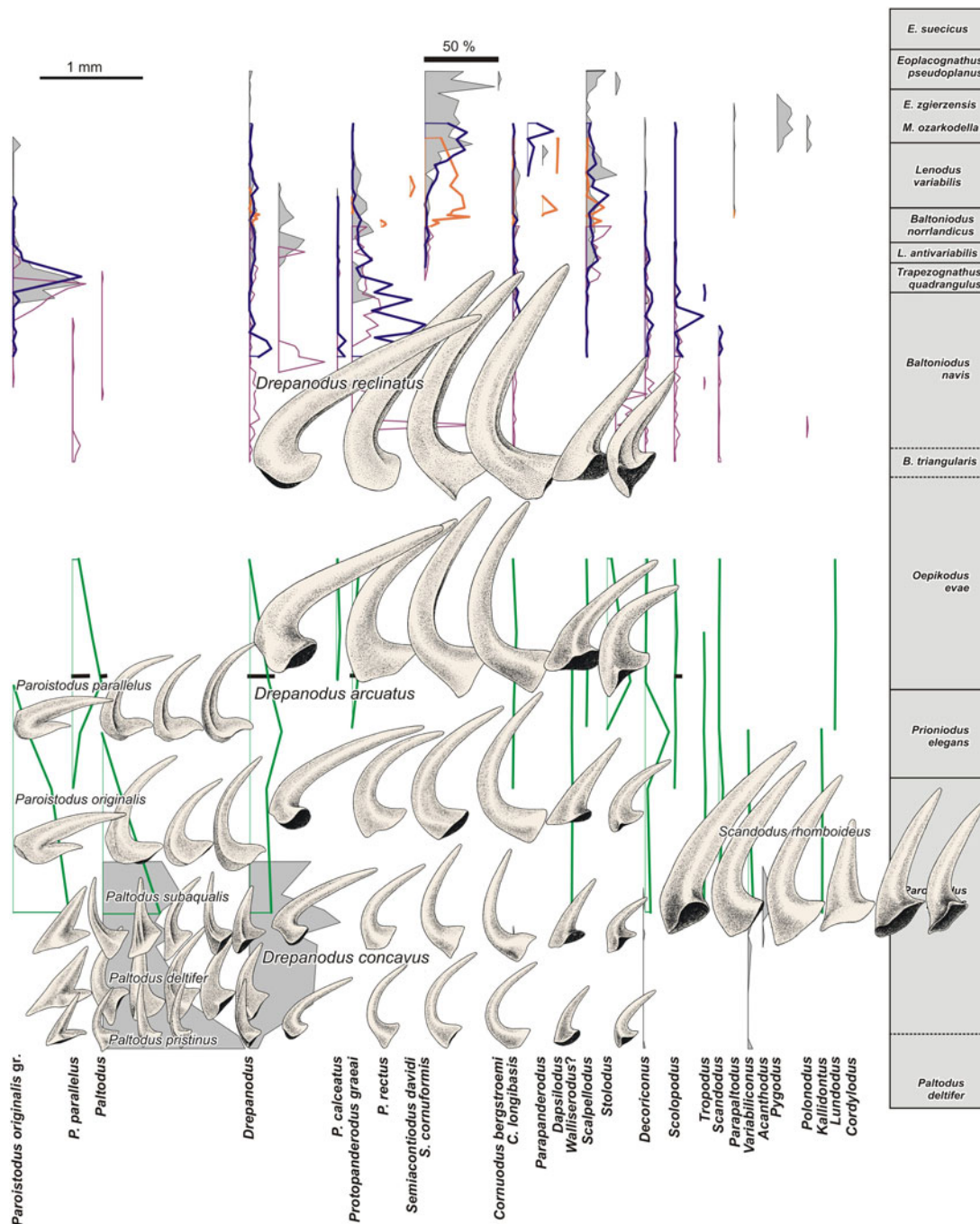
Figure 9 Continued.

elements interpreted by Löfgren (1990) and Zhen *et al.* (2011a) as S and M elements of *Polonodus* may represent an extreme morphotypes of *Baltoniodus*.

3.1.5. *Pygodus trimontis* Hamar 1966. *Pygodus lunnensis* Zhang 1998b and *P. anitae* Bergström 1983 form a connecting link between *Polonodus* and *Pygodus* (Zhang & Sturkell 1998). A complete succession of *Pygodus* species with a set of S elements was assembled by Zhang (1998a).

Specimens of *Pygodus* characterised by the wider space between the ventral denticle rows on the P1 elements do not seem to show extremes of population variability of *P. serra* but rather represent a separate biological species partially coeval with it (Fig. 8). In the borehole Lesieniec IG 1 it is represented by 74 specimens (sample Les-137 1/3; supplementary Table 56). The name proposed by Hamar (1966; and perhaps *P. xinjiangensis* Wang & Qi 2001) is available for it. Its occurrence is inserted

between ranges of *P. serra* and *P. anserinus* both in the Baltic and Małopolska Massif material. In other regions of the world, it continued to occur well within the range of typical *P. anserinus* (Hamar 1966; Zhang 1998a).

3.1.6. *Pygodus serra* (Hadding 1913). The topotype P1 specimen from Fågelsång shows a wide space between the dorsal denticle rows (that houses an additional fourth row in *P. anserinus*), the morphology represented in the *Eoplacognathus lindstroemi* and latest *E. robustus* Zones (Bergström 2007). It is thus conspecific with *P. protoanserinus* Zhang 1998a, which seems to be a part of the continuous transition to *P. anserinus* (Fig. 8; Dzik 1994, fig. 26). In the Lesieniec IG 1borehole (sample Les-137prz), specimens transitional to *P. anserinus* occur; that is, with denticles forming incipient four rows, but the actual transition towards the fourth carina probably took place a little later.

3.1.7. *Pygodus anserinus* Lamont & Lindström 1957. The fourth row of tubercles initially developed at maturity and gradually expanded to earlier and earlier stages in the evolution of this chronospecies. The holotype has this row of tubercles weakly developed, indicating its position in the early stage of evolution, which is well represented in the fossil record (Bergström 1971). A few S elements co-occur with P ones in boulder E-351. Paiste *et al.* (2022) attributed a geniculate M element to *Pygodus anserinus* but its incipient platform and sharp denticulation makes it different from associated unquestionable ramiform elements of *Pygodus*.

3.2. Order *Panderodontida* Sweet 1988, family Strachanognathidae Bergström 1983

3.2.1. *Acanthodus uncinatus* Furnish 1938. Löfgren (1997a) interpreted specimens of this species occurring at the Swedish localities Brattefors and Oreholmen as reworked from older strata. The specimen from Brattefors with dorsally gaping basal cone (Löfgren 1997a, fig. 5b) fits the probably homologous element of *Drepanodus expansus* Chen & Gong, 1986 *sensu* Pyle & Barnes (2002, pl. 6:7). Its affinity to *Drepanoistodus*, proposed by these authors, seems unlikely because geniculate M elements of this genus are missing at Brattefors. Agematsu *et al.* (2008) described specimens from Thailand similar to those from Brattefors.

3.2.2. *Variabiliconus variabilis* (Lindström 1955a). Löfgren *et al.* (1999) presented the apparatus reconstruction and proposed its close relationship to the North American Midcontinent species, *V. bassleri* (Furnish 1938). Rare specimens of the species occur throughout the Ottenby section (supplementary Table 2).

3.2.3. *Strachanognathus parvus* Rhodes 1955. The species is relatively rare in Baltica, but in large samples discrete types of its elements can be arranged into symmetry transition series, including the bilaterally symmetric S_0 element, strongly asymmetric probable M element and relatively robust P elements (Fig. 7; Dzik 1994). The specimen of *Parapaltodus simplicissimus* Stouge 1984 illustrated by Zhen *et al.* (2009a, fig. 2n) differs from *Strachanognathus* only in the lack of ventral denticle and may be related to its ancestor. *P. simplicissimus* preceded *S. parvus* in Baltica but is very rare in samples (Stouge & Bagnoli 1990; Rasmussen 2001; Löfgren 2003; Stouge & Nielsen 2003).

3.3. Order *Panderodontida* Sweet, 1988, family Scolopodontidae Bergström in Clark *et al.* 1981

3.3.1. *Scandodus rhomboideus* (Pander 1856). According to Bergström (1988), *S. furnishi* Lindström, 1955 is its younger synonym. The holotype of *S. furnishi* (Lindström 1955a, pl. 5:3) from the early Latorpian (Hunneberg) Lower Planilimbata Limestone of Skultorp has its dorsal ('anterior') tip of the base broken, but it seems to be gaping there. Lindström (1971), van Wamel (1974; also Johnston & Barnes 2000) included S_0 elements of *Drepanoistodus* morphology in the apparatus and transferred it to this genus under the name *D. conulatus* (Lindström 1955a). In the present samples from Ottenby the set of large hyaline elements, including those similar to the holotype of *S. furnishi*, resembles rather those of *Drepanodus* (Fig. 9). Admittedly, I am not sure of its taxonomic determination.

3.3.2. *Tropodus comptus* (Branson & Mehl 1933). Bagnoli *et al.* (1988) and Tolmacheva *et al.* (2003) identified the main element types of the apparatus. The most characteristic is its S_0 element with five ridges forming incipient processes. *Tropodus sweeti* (Serpagli 1974) as interpreted by Lehnert *et al.* (1998) may be its relative.

3.3.3. *Scolopodus sublaevis* Pander 1856. This is the type species of *Scolopodus* occurring in Baltica from the late *Prioniodus elegans* to *Microzarkodina ozarkodella* Zone (Fåhraeus 1982). Tolmacheva (2006) restored the apparatus (Fig. 7) and proposed to use the name *S. striatus* Pander 1856 for this species because the *S. sublaevis* morphotype had not been identified by herself in the section studied by Pander (1856), but the latter remains the type species of the genus chosen by Lindström (1955a).

3.3.4. *Decoriconus peselephantis* (Lindström 1955a). Löfgren (1998) attributed elements of the apparatus to six ozarkodinid locations. I failed to see them in my material, probably because of not having enough experience with 'simple cones' (Fig. 7). There is apparently an evolutionary continuity of the *Decoriconus* lineage from the Tremadocian to Llandovery. I apply the chronospecies *D. mercurius* and *D. pesequus* introduced by Löfgren (1998) referring to their geological age rather than to morphology (Fig. 2m–t).

A finely striated specimen from the basalmost sample Ot-1 from the Ottenby section may be transitional between *Scolopodus* and *Decoriconus* but the evidence is hardly conclusive. Specimens from Thailand identified by Agematsu *et al.* (2008) as *Parapanderodus striatus* (Graves & Ellison 1941) lack the medial fissure but have a smooth base and the cusp ornamented with numerous riblets resembling in this respect *Decoriconus*.

3.4. Order *Panderodontida* Sweet, 1988, family Belodellidae Khodalevich & Chernikh 1973

3.4.1. *Diaphanodus latus* (van Wamel 1974). *D. latus* is probably conspecific with the Furongian to Tremadocian type species of *Diaphanodus* (Bagnoli *et al.* 1987, 2015; Johnston & Barnes 2000). Its apparatus is known owing to clusters described by Andres (1988). In Baltica it is known from the *Oepikodus evae* Zone at Lava, Russia (Tolmacheva *et al.* 2001b). According to Szaniawski (2015) it is a protoconodont (that is, a chaetognath). The crucial difference between the chaetognath grasping spines and conodont elements is their mode of growth: centripetal versus centrifugal – that is, secreted by the soft tissue located inside the basal cavity or by an epithelium covering the element from outside. In the former the growth increments are visible on the external surface of the grasping spine; in the latter growth lines are within the basal cavity, the element exterior remaining smooth. Some of the *Diaphanodus* elements show transverse striation on their surface (Szaniawski 2015, fig. 2f) but this may be an impression of internal surface of the crown tissue. The evidence for its centripetal growth is rather weak. Moreover, in some conodonts this tissue layer may be very thin and wrinkled (e.g., Dzik 2009; Dzik & Moskalenko 2016, fig. 4).

Rasmussen (2001) suggested the presence of a related species in the *Oepikodus evae* Zone at the Norwegian locality of Herram.

3.4.2. *Stolodus stola* (Lindström 1955a). Most elements of the apparatus of *S. stola* are similar to those of *Diaphanodus* and *Coelocerodontus* in having a very deep basal cavity and sharp costae (Fig. 6), but distal portions of their cusps are straight, making them similar to S elements of prioniodontids and unlike the chaetognath spines (*inter alia*, Löfgren 1993). In sample E-368 (54 elements, supplementary Table 37) two element types with a short cusp co-occur, one tricostate, the other bicostate. Possibly they correspond to P locations. Already Lindström (1964, fig. 29) noticed that there are two kinds of gracile elements with four costae. Among those with costae developed at two sides there seems to be a bilaterally symmetric one.

3.4.3. *Coelocerodontus trigonius* Ethington 1959. The type horizon of this species is the Late Ordovician Stewartville Member of the Galena Formation in Iowa (Ethington 1959). Nowlan *et al.* (1988), Zhang (1998b) and Zhen *et al.* (2003) presented composition of its apparatus. It includes not only sharply costate S elements but also robust elements with curved tips at least

remotely resembling those in *Diaphanodus* and bicostate elements virtually identical with that illustrated by Rasmussen (2001). Rare specimens in my samples lack ridges on their posterior or anterior sides but share an extremely deep basal cavity with those of *C. trigonius*.

3.5. Order *Panderodontida* Sweet, 1988, family *Panderodontidae* Lindström 1970

3.5.1. *Scalpellodus latus* (van Wamel 1974). M and S_3 elements of this species have a somewhat wider base (Figs 2d–k, 5) than in its successor *S. gracilis*. The holotype of van Wamel's (1974) *Protopanderodus latus* comes from about 1.40 m above the base of the Horns Udde Formation near Horns Udde, Öland and co-occurs with *B. navis* (that is, Volkhov in age).

3.5.2. *Scalpellodus gracilis* (Sergeeva 1974). Löfgren (1978) listed the differences in the M elements (her short-based drepanodiform) that have a sharper ventral keel on the base, more symmetrical in *S. gracilis* than in *S. latus* (Fig. 5). The angular bending was proposed to be higher above the base than is typical for the holotype *S. latus* S element of Kunda age of the Popovka River, Ingria (Sergeeva 1974). Even if these subtle differences between chronospecies are real, they are obliterated by the high population and within-apparatus variation, acknowledged already by Löfgren (1978) and illustrated by Stouge & Bagnoli (1990). The only obvious difference in respect to *S. latus* that I am able to see is the geological age. *Scalpellodus viruensis* Löfgren 1978 may be conspecific with *S. gracilis*.

3.5.3. *Walliserodus costatus* Dzik 1976. The type population of this species comes from the basal, early Kunda age, part of the Mójcza Limestone in the Holy Cross Mountains, Poland. It differs from *W. ethingtoni* in multicostate S_0 and S_1 elements and in their more robust appearance (Fig. 7; Dzik 1994; Albanesi 1998). Löfgren (1978, p. 116) referred early Darriwilian (Kunda age) populations of *Walliserodus* to '*Paltodus*' *iniquus* Viira 1974 but the holotype of the latter species is of late Darriwilian (Lasnamägi) age and morphologically closer to *W. ethingtoni* (Viira 1974, text-fig. 124a, b).

Rasmussen (2001, p. 60) claimed that the Silurian *Acodus curvatus* Branson & Branson 1947 (=*Paltodus debolti* Rexroad 1967), the type species of *Walliserodus* Serpagli 1967, differs from the Ordovician species attributed to this genus in having a less complex apparatus, deeper basal cavities and higher contribution of symmetrical elements. Although there is undoubtedly some difference between them, a continuity of the lineage across the Ordovician–Silurian boundary was traced by Zhang & Barnes (2002). No geniculate M element proposed by Rasmussen (2001) to characterise the genus *Costiconus* is associated with elements of *Walliserodus* morphology in my material.

3.5.4. *Walliserodus ethingtoni* (Fåhraeus 1966). S elements of this species differ from *W. nakholmensis* in bearing only few ribs and having a flat or even concave ventral surface (Fig. 7; Albanesi 1998). The cross-section of the S_0 element is triangular. The holotype of '*P*'. *iniquus* is roughly coeval with the holotype of *W. ethingtoni* and I do not see any significant difference between these forms.

3.5.5. *Walliserodus nakholmensis* (Hamar 1966). The ventral surface of S elements of this species is convex and their cross-section is more oval than in the previous species (Fig. 7). Some samples show transitional morphology, with varying convexity of elements, but to prove the evolutionary transition would require more numerous samples than those available to me at the moment.

3.5.6. *Panderodus sulcatus* Fåhraeus 1966. The contents of the apparatus were illustrated by Viira *et al.* (2006b). This includes a symmetric S_0 element with slits on both sides of the cusp (Fig. 6). It is noteworthy that elements with two slits occur also in some Llandovery species (Zhang & Barnes 2002).

Although the apparatus structure of *Panderodus* points to *Scalpellodus* as the ancestor, no transition has been recognised in the Baltic region, as pointed out by Löfgren (1978). The oldest occurrence of *Panderodus* in the erratic boulders studied here is together with *Baltoniodus norrlandicus*.

Elsewhere, probably the earliest member of this evolutionary lineage is '*Protopanderodus*' *nogamii* (Lee 1975) from the *Oepikodus evae* Zone. Although Zhen *et al.* (2003, p. 207) claim that the slit in its elements 'is not a true panderodontid furrow, and disappears just before reaching the basal margin', I am not able to discern any difference between it and that of *Panderodus*. The main difference between '*P*.' *nogamii* and *P. sulcatus* is the alate appearance of the S_0 element in the former.

3.5.7. *Panderodus gracilis* (Branson & Mehl 1933). The presence of only one slit in all elements of the apparatus (Fig. 6) seems to be the main difference of this species from *P. sulcatus*. This may mean that the medial symmetrical element was lacking in the apparatus. The virtually bilaterally symmetrical elements with prominent costae on both sides (but only one panderodont slit) reported by Trotter & Webby (1994) may represent the S_1 location.

The slit in the panderodontid elements is narrower than the size of secretory cells known from imprints on various conodont elements, and could hardly hide any canal to transfer venom as proposed by Szaniawski (2009); this is further contradicted by the mode of secretion of conodont elements, permanently covered with secretory tissue. Probably a better analogue would be the belemnite alveolar slit; that is, an attachment for a kind of ligament.

3.5.8. *Panderodus panderi* (Stauffer 1935). The specimens of a rather robust appearance that may belong to this species co-occur with *Amorphognathus superbus* in erratic boulder E-305 from Mochty, Poland (Dzik 1983).

3.5.9. '*Belodella*' *serrata* Dzik 1976. This is clearly a close relative of *Panderodus*, as indicated by the presence of the 'panderodont furrow' (Fig. 7) but, unlike the Ordovician and Silurian *Panderodus serratus* Rexroad 1967 (Mellgren 2010), its fine denticles are inclined towards the element base and there is a sharp posterior ridge along the ventral margin of the element (Dzik 1976). Zhang *et al.* (2011, fig. 14.18) identified denticulated specimens also in *P. gracilis*.

3.5.10. *Belodina compressa* (Branson & Mehl 1933). Leslie (1997) proposed a complete reconstruction of the *Belodina* apparatus, composed of 14 asymmetric elements, and thus similar to that of the Silurian *Panderodus* as restored by Dzik & Drygant (1986). This may mean that the lineage of *Belodina* emerged from *Panderodus* after losing the medial S_0 element. Transitional forms are known from Laurentia (e.g., Nowlan *et al.* 1988). The species has been reported from the Åland Islands, Finland by Merrill (1980).

3.5.11. *Belodina confluens* Sweet 1979. The late Ordovician *B. confluens* was a descendant of *B. compressa* (Branson & Mehl 1933), from which it differs in that the external margin of the largest element in the apparatus is regularly curved throughout its length, rather than distinctly flattened for a short distance above its basal corner. Associated elements with oblique orientation of sharp denticles belonged to the same apparatus, as shown by the fused cluster illustrated in Nowlan (1979, fig. 35.2) and reinterpreted by Leslie (1997; also Bergström in Trotter & Webby 1994, p. 485).

3.5.12. *Dapsilodus viruensis* (Fåhraeus 1966). This is the oldest chronospecies of the *Dapsilodus* lineage (Fig. 7). Its apparatus composition was restored already by Löfgren (1978). The element size increased in its evolution and their appearance became more gracile (Dzik 1994).

3.5.13. *Dapsilodus mutatus* (**Branson & Mehl** **1933**). The oblique striae near the external margin of the relatively large elements make the species easy to distinguish (Fig. 7; Dzik 1994).

3.5.14. *Scabbardella altipes* (**Henningsmoen** **1948**). This is a species abundant in subpolar Gondwanan conodont communities, but subordinate in Baltica. Its evolutionary origin remains to be determined. The typical panderodont furrow (Fig. 7) makes it similar to *Dapsilodus*, which frequently co-occurs but apparently had less deep- or cold-water preferences.

3.5.15. *Parapanderodus striatus* (**Graves & Ellison** **1941**). The distinction between the Laurentian populations of this species and its Baltic relative *P. quietus* Bagnoli & Stouge 1997 (Fig. 7) remains unclear. Smith (1991) described fused clusters of *Parapanderodus* composed of nine and five elements, which supports the reconstruction of the apparatus based on isolated elements. They show gradation in their size, although the gradient seems opposite to that in the Silurian *Panderodus* from Podolia (Dzik & Drygant 1986). *Toxotodus*? *gabriellae* Löfgren 1998 from the *O. evae* Zone of Sweden may be related to the *Parapanderodus* lineage.

3.6. Order *Panderodontida* Sweet, 1988, family *Protopanderodontidae* Lindström 1970

3.6.1. *Cornuodus longibasis* (**Lindström** **1955a**). This is an almost cosmopolitan and long-ranging species, easily identified owing to the expanded base of the P_1 element (Fig. 2v–aa; e.g., Zhen *et al.* 2009b, 2015a). It appeared for the first time in Baltica in the *Paroistodus proteus* Zone at Ottenby, found in sample Ot-5 (supplementary Table 2). According to Löfgren (1999b) and Johnston & Barnes (2000) there was only a single lineage of *Cornuodus* in the Baltic realm. This is contradicted by recurrent, although restricted, occurrence of elements with an obliquely cut base.

3.6.2. *Cornuodus bergstroemi* **Serpagli** **1967**. The obliquely cut base of some S elements, identical with those described by Serpagli (1967), as well as twisted cusp of the probable M element (Fig. 7), distinguishes this species from *C. longibasis* (Dzik 1994). Its oldest record in the present material is in the *Eoplacognathus reclinatus* Zone in the borehole Lesieniec IG 1 (sample Les-141/30; supplementary Table 53); as a rare element it occurs up to the *Amorphognathus ordovicicus* Zone. It may also be present elsewhere in older strata but is variously understood by other authorities.

3.6.3. cf. *Teridontus gallicus* **Serpagli** *et al.* **2008**. A single specimen from sample E-389, associated with *B. norrlandicus*, closely resembles P_1 elements of *T. gallicus* from the *P. deltifer* Zone of Montagne Noire, France (Serpagli *et al.* 2008).

3.6.4. *Semiacontiodus cornuformis* (**Sergeeva** **1963a**). The holotype comes from the Kunda age stratum at Popovka (Sergeeva 1963a). According to Löfgren (1999a) this species immigrated to the Baltic region in the *M. parva* Zone together with the evolutionary emergence of *Baltoniodus norrlandicus*. In younger samples (e.g., E-271) the ridge on the cusp of S elements extends almost to the base. Perhaps these late populations deserve a separate chronospecies status. Leslie (2000) proposed to resurrect the name *Scandodus polonicus* Spassov & Teller 1963 and apply it to a species having symmetrical elements with a shallow medial groove, relatively prominent lateral ribs and asymmetrical elements with prominent flange on one side. Such elements characterise the late *S. cornuformis* in my material. It remains unknown which bed in the Mójcza section was sampled by Spassov & Teller (1963), but elements of *Baltoniodus* illustrated by them seem to represent *B. norrlandicus* that at Mójcza is associated with early *S. cornuformis*.

Leslie (2000) suggested that the similarity of this species to the early Tremadocian species of *Semiacontiodus* is convergent and that there is no continuity between them. He included the Darriwilian species in *Staufferella*. I do not share this idea.

3.6.5. *Semiacontiodus longicostatus* (**Drygant** **1974**). Unlike *S. cornuformis*, S_0 elements of this species are roughly rectangular at the cusp base. Other S elements had a flat ridge that extends up to its base, and is not restricted to the distal part of the cusp. The holotype comes from the Uhaku age strata in the borehole Pishcha-16, depth 410 m; that is, from the *Pygodus anserinus* Zone (Drygant 1974). A morphology of S_0 transitional between *S. cornuformis* and *S. longicostatus* is represented in sample Ha-4 at Hälludden, Öland (supplementary Table 19b). A continuous gradation connects also S_0 elements with long cusps and those of *S. bulbosus* (Löfgren 1978) morphology (for instance in sample E-355), which makes their status as separate species uncertain.

3.6.6. *Semiacontiodus davidi* **Löfgren** **1999a**. The S_0 element lacks lateral ribs (Fig. 6) and is medially sharp (Löfgren 1999a). In the latter aspect it resembles the geologically younger, and possibly related, *S. carinatus*.

3.6.7. *Semiacontiodus carinatus* **Dzik** **1976**. The prominent lateral ribs (Fig. 6) may speak in favour of the origin of *S. carinatus* from *S. cornuformis* instead of *S. davidi*. The contents of the apparatus were illustrated by Viira *et al.* (2006b).

3.6.8. *Protopanderodus rectus* (**Lindström** **1955a**). This is the oldest of the Baltic species of its lineage (Mellgren & Eriksson 2006). The most characteristic aspect of most *Protopanderodus* species is the morphology of the M element (Fig. 7). In *P. rectus* its posterior surface is gently convex with a wide furrow along the dorsal margin (Fig. 2ah–am). It is not clear which species was counted by Bagnoli & Stouge (1997) as *Protopanderodus* sp. in sample 652 from Horns Udde, Sweden.

3.6.9. *Protopanderodus cooperi* (**Sweet & Bergström** **1962**). *Protopanderodus cooperi* probably originated from *P. rectus* in the late *Lenodus variabilis* Zone or somewhat later (supplementary Table 15c) and differs from it in the gentle concavity of the external furrow on the posterior surface of the M element, the central convexity being bordered by such furrows on both sides (Fig. 7). This species is frequently referred to as *P. robustus* (Hadding 1913) but the holotype of *Drepanodus robustus* Hadding 1913 seems to me to be truly a *Drepanodus* (Albanesi 1998). Its S element shows 'a marked tendency to develop additional costae' (Lindström 1955b, p. 108), which does not happen in *Protopanderodus*. Therefore, I follow Zhang (1998b) in using the name *P. cooperi* for it. *Protopanderodus formosus* (Fåhraeus 1966) is its junior synonym.

3.6.10. *Protopanderodus parvibasis* (**Löfgren** **1978**). The posterior surface of the M element cusp is acutely convex and bordered by relatively flat surfaces on both sides in specimens from the *Lenodus variabilis* Zone (supplementary Table 44c). In this aspect it is transitional between *P. rectus* and *P. graeai*, being restricted to strata preceding those, in which *P. graeai* appears (its reports from the older strata should be confirmed).

3.6.11. *Protopanderodus graeai* (**Hamar** **1966**). The furrow in M elements along the inner margin is deep and delimits a sharp ridge along the middle of the cusp (Fig. 7). The margin of the base of all elements runs almost transversely, unlike the sinuous one in *P. rectus*.

3.6.12. *Protopanderodus sulcatus* (**Lindström,** **1955**). Together with *P. floridus* and *P. calceatus* this species belongs to the lineage characterised by the presence of a deep furrow along the posterior side of the cusp in some S elements (both sides in S_0 element; Fig. 5). Their M element has a narrow furrow along the posterior surface of the cusp (Fig. 2an–aq). In the boulder E-314a some S elements have the furrow very shallow and are closely similar to those of *P. rectus*. However, there is no discontinuity in the elements' variation, especially in respect of M ones, that would substantiate distinction of two sympatric species.

A single element M shows a sharp ridge resembling that in *P. graeai*, but its large size suggests that this is the end-member of population variability.

3.6.13. *Protopanderodus floridus* Bagnoli & Stouge 1997. According to Bagnoli & Stouge (1997) it differs from *P. sulcatus* in that the central convexity on the posterior surface of the cusp of the M elements is angular and bordered by an external furrow.

3.6.14. *Protopanderodus calceatus* Bagnoli & Stouge 1997. The external narrow furrow in the relatively flat cusp of M element is deeper than in *P. floridus*. The S elements developed a shallow additional furrow near the external margin (Fig. 5).

3.6.15. *Protopanderodus varicostatus* (Sweet & Bergström 1962). Zhen *et al.* (2011a) illustrated the topotype material from the Pratt Ferry Formation of Alabama. The external furrow on S elements is much deeper than in *P. calceatus* (Fig. 5). I referred such specimens to *P. gradatus* (Serpagli 1974) that may be conspecific rather with *P. sulcatus* (Dzik 1994). Armstrong (1997) described under this name a form from Scotland transitional to *P. liripipus*. Bergström (1971, p. 100) dated the transition between these chronospecies as the early *Baltoniodus gerdae* Zone.

3.6.16. *Protopanderodus liripipus* Kennedy Barnes & Uyeno 1979. This is a member of the lineage (Fig. 5) that terminated in *P. insculptus* (Branson & Mehl 1933), all elements of which bear a prominent denticle at the base. Transitional forms are known and both species have a high correlative potential (Nowlan *et al.* 1997, pl. 2:10; Zhen *et al.* 2015a).

3.6.17. *Drepanodus concavus* (Branson & Mehl 1933). Owing to a wide population variability, the early populations of *Drepanodus* are difficult to classify (Fig. 9). The M elements from Ottenby (sample Ot-5) may represent this Midcontinent species as interpreted by Kennedy (1980) but the *Drepanoistodus*-like M element included in the apparatus by Ji & Barnes (1990) may contradict this.

3.6.18. *Drepanodus arcuatus* Pander 1856. The apparatus (Figs. 2ab–ag, 9) has been restored by Dzik (1994) and Löfgren & Tolmacheva (2003) although with opposite order in elements notation. They interpreted the element proposed by me to be P_2 as the M one, referring to the similarity of the *Drepanodus* apparatus to that of *Cordylodus*. The counterargument can be put forward that there are two kinds of elements of *Drepanodus* with short cusps and a robust appearance, whereas the morphological disparate element with long cusp (pipaform) has a notch that resembles incipient geniculation. Until a complete fused cluster or natural assemblage is found, this problem will remain unsettled. Few large elements in samples from the *O. evae* Zone developed ridges along the dorsal side of the cusp, unlike later populations of *D. reclinatus*, in which most elements are of such morphology. According to Bergström (1988), *D. planus* (Pander 1856), referred to by Bagnoli & Stouge (1997, table 1, text-fig. 5), is synonymous with *D. arcuatus*. Zhen *et al.* (2015a, 2015b) and Agematsu *et al.* (2008) reported this species from as ancient strata as the early Tremadocian *Cordylodus lindstroemi* Zone.

3.6.19. *Drepanodus reclinatus* (Lindström 1955a). Löfgren & Tolmacheva (2003; also Zhen *et al.* 2011a, 2011b) proposed to use this species name instead of *D. robustus* for the costate form of *Drepanodus* (Fig. 9). This is probably a reasonable way to avoid confusion resulting from different interpretation of Hadding's (1913) holotype that 'possesses several small but distinct lateral costae' (Bergström 2007, p. 81) that is typical for *Drepanodus*, not *Protopanderodus*, as pointed out by Dzik (2020).

3.6.20. *Drepanodus parformis* Löfgren & Tolmacheva 2003. This is a species of *Drepanodus* with very wide bases of S elements. Possibly specimens labelled *Drepanoistodus*? sp. in Dzik (2020, fig. 8f–j) belong to it.

3.6.21. *Drepanodus* aff. *santacrucensis* Dzik 1994. The flat M elements associated with rather indifferent *Drepanodus* elements in a sample from the Gałajny IG 2 borehole (Gał-18sp; supplementary Table 59) resemble *D. santacrucensis* and may represent an initial stage towards its development from *D. arcuatus*.

3.7. Order *Panderodontida* Sweet 1988, family *Distacodontidae* Bassler 1925

3.7.1. *Paltodus pristinus* (Viira 1970). The apparatus of this species (Fig. 9) was partially restored by Szaniawski (1980) and completed by Löfgren (1997a). These authors applied subspecies rank to it but this is in conflict with the biological understanding of subspecies as a geographic race. Closely related subspecies should not co-occur in the same locality or its understanding as a segment of evolutionary lineage (chronosubspecies) has to be indicated, as proposed by Dzik & Trammer (1980). *P. pristinus* differs from its successor *P. deltifer* in the lack of geniculation in the M element and lack of angulation at the anterior surface of P elements. It was reported to co-occur with its probable successors in the Uuga section in Estonia (Löfgren *et al.* 2005) but it remains unclear whether this is a result of reworking or application of the vertical concept of chronospecies.

3.7.2. *Paltodus deltifer* (Lindström 1955a). The apparatus (Fig. 9) was adequately illustrated in Bagnoli *et al.* (1988) and Löfgren (1997a). It differs from the preceding stage in evolution in the M element in having geniculate, anteriorly angular P elements, and in the S_0 element having lateral expansions of the base. *Paltodus peracutus* (Lindström 1955a) *sensu* Bagnoli *et al.* (1988) seems to be a morphotype within the population variability of *P. deltifer*.

3.7.3. *Paltodus subaequalis* Pander 1856. The apparatus of this species (Fig. 9) differs from its predecessor, *P. deltifer*, in most of its elements bearing costae along the base of the cusp (Bagnoli *et al.* 1988; Löfgren 1997a).

3.7.4. *Besselodus semisymmetricus* (Hamar 1966). The contents of the apparatus (Fig. 7) were illustrated by Leslie (2000) and Viira *et al.* (2006b).

3.7.5. *Paroistodus numarcuatus* (Lindström 1955a). This is a cosmopolitan species (Agematsu *et al.* 2008). Its M element is of the shape typical for the genus but, unlike its younger species, only rarely do elements of the apparatus show the inversion of basal cavity (Löfgren 1997b).

3.7.6. *Paroistodus proteus* (Lindström 1955a). All elements of the apparatus developed an inverted basal cavity in their external parts that is not as much expanded as is in *P. originalis* (Löfgren 1997b).

3.7.7. *Paroistodus parallelus* (Pander 1856). P and S elements of this species bear sharp ridges on both sides of the cusp (Fig. 9). According to Johnston & Barnes (2000), both costate and acostate elements co-occur in the lower part of the stratigraphic range of this species, suggesting ancestry in *P. proteus* (Löfgren 1997b). However, there is no such transition between *P. parallelus* and *P. originalis* and their co-occurrence as separate species is accepted (Fig. 3h).

3.7.8. *Paroistodus originalis* (Sergeeva 1963a). This species is similar to *P. proteus* (Figs 3i–m, 9), from which it apparently derived allopatrically, reappearing in the Baltic region after some time of almost exclusive occurrence of *P. parallelus* (Löfgren 1997b).

3.7.9. *Paroistodus horridus* Barnes & Poplawski 1973. Löfgren (1997b) pointed out that denticulation of P and S elements developed in *Paroistodus* several times. Albanesi & Barnes (2000) applied vertical concept of chronospecies to the apparently anagenetic evolution from *P. originalis* to *P. horridus*, which resulted in artificial overlap ranges of allegedly sympatric species.

3.7.10. *Drepanoistodus basiovalis* **(Sergeeva 1963a).** This seems to be a cosmopolitan species (e.g., Albanesi 1998; Agematsu *et al.* 2008). The holotype comes from the Volkhov age strata at Volkhov (Sergeeva 1963a). Among a total of 1,029 elements of *Drepanoistodus* in the erratic boulder E-368, 13 M elements represent *D. basiovalis*, 266 of *D. forceps*, and there are 19 intermediate forms (Figs. 3q–v, 9).

D. stougei Rasmussen 1991, characterised by a rounded ventral part of the M element, may be within the population variability range of *D. basiovalis*. It was referred to as *D. basiovalis* by Stouge & Bagnoli (1990), *D.* aff. *D. contractus* by Bagnoli & Stouge (1997) and *D. contractus* by Dzik (2020). The inverted basal cavity characterises some specimens but I am not convinced that this is not a trait of advanced ontogenetic age of the individuals.

3.7.11. *Drepanoistodus contractus* **(Lindström 1955).** '*Oistodus*' *contractus* is characterised, according to Lindström (1955a, 1955b), by a very short base (and extremely long cusp). M elements of such morphology in the present sample are not sufficient to decide whether they truly represent a separate species or are rather extremes of the population variability of *D. basiovalis*.

3.7.12. *Drepanoistodus forceps* **(Lindström 1955a).** Apparatus elements of the distacodontid conodonts are of a rather simple morphology and very variable (Figs. 3n–p, 9), providing little information of taxonomic value. This especially refers to sympatrically co-occurring Dapingian and Darriwilian species of *Drepanoistodus*, population variability of which may exceed the difference between species. Dzik (1983) performed a biometric study to delimit the most commonly occurring Baltic species. The length of the base, length of the cusp and height of the external margin of M elements were measured in 101 specimens from boulder E-116 of the *Baltoniodus navis* Zone and from boulder E-314 of the *Oepikodus evae* Zone (supplementary Tables 5, 37). As expected, the ranges of their variation strongly overlap, but at least in the case of the combined height of the external margin and the ratio of basis to cusp length, the standard deviations from the mean values do not overlap (Dzik 1983, fig. 8b). This indicates that they significantly differ from each other, which may be interpreted as an evolutionary change towards a longer and longer cusp and higher external margin of the M elements between the time horizons represented by the boulders.

Alternatively, there are at least two separate biological species (*D. basiovalis* and *D. forceps*) represented in the younger sample E-116, but only one of them (*D. forceps*) is present in the older sample E-314B. M elements in this sample bear a longitudinal ridge on the cusp, but all associated S and P elements have both sides smooth. The latter lineage, characterised by almost equal length of the base and cusp, probably evolved towards an acute external end and a prominent costa along the cusp, typical for even younger species of *Venoistodus*. It is noteworthy that the M specimens with acute ventral end are not the most common in samples with *D. forceps*.

The same goal to delimit *Drepanoistodus* species was undertaken by Rasmussen *et al.* (2021) with application of basically different methodology. They applied principal component analysis for 58 specimens selected from more than 20 samples of different age and geographic origin. I find such an approach hardly meaningful in terms of evolutionary population biology.

An enigmatic aspect of early populations of probable *D. forceps* is the co-occurrence of rare S elements with prominent anterior costa (Fig. 3n, o). Even the very large number of elements in sample E-360 (supplementary Table 41) has not helped in solving the taxonomic status of these elements. They are tentatively interpreted as a plesiomorphic trait consistent with the stratigraphic position of the sample.

3.7.13. *Venoistodus balticus* **Löfgren 2006.** The holotype of this species comes from the *Eoplacognathus pseudoplanus* Zone (Fig. 7); the type population is thus very close to its probable ancestor, *D. forceps*. The S elements identified by Löfgren (2006) have their sides almost smooth, with only indistinct ridge on the cusp.

3.7.14. *Venoistodus venustus* **(Stauffer 1935).** The holotype of *V. venustus* comes from the Sandbian Glenwood Formation of Minnesota (Stauffer 1935) and the apparatus was described by Nowlan *et al.* (1988). M elements of this morphology are associated with prominently costate S elements in the Holy Cross Mountains, Poland and Baltic strata of similar age (Dzik 1994). The oldest *Venoistodus* occurs in the erratic boulder E-334 of *Eoplacognathus robustus* Zone age (supplementary Table 58).

3.8. Order *Prioniodontida* Dzik 1976, family *Prioniodontidae* Bassler 1925

3.8.1. *Prioniodus robustus* **Lindström 1955a.** The species preceded *P. elegans* and may be the oldest denticulated member of the lineage in the Baltic region (Löfgren 1985, 1994; Rasmussen 2001; Tolmacheva *et al.* 2001b, 2003). Perhaps undenticulated '*Prioniodus* cf. *gilberti*' of Löfgren *et al.* (2005) belongs to it, but an alternative relationship to *Diaphorodus* is likely as well. Zhen *et al.* (2023) proposed its Chinese ancestry.

3.8.2. *Prioniodus elegans* **Pander 1856.** This is a species that was cosmopolitan for a brief environmental change event in the earliest Floian (e.g., Löfgren 1978; Bergström 1988; Stouge & Bagnoli 1988; Bagnoli & Stouge 1997; Zhen *et al.* 2015b).

3.8.3. *Stiptognathus microdentatus* **(van Wamel 1974).** This species preceded not only *O. evae* but also *P. elegans* (van Wamel 1974, fig. 15) and probably has its relatives in the Canning Basin Emanuel Formation, Australia (Zhen & Nicoll 2009).

3.8.4. *Oelandodus elongatus* **(Lindström 1955a).** Johnston & Barnes (2000) reported a cluster of at least four pairs of S elements, similar to each other, and a pair of M elements. The apparatus reconstruction by van Wamel (1974) of *O. elongates* erroneously includes *Protoprioniodus* elements. A poorly preserved juvenile M element from Ottenby (sample Ot-6) may represent this species.

3.8.5. *Oelandodus costatus* **van Wamel 1974.** Elements of this species have an incipient platform at the base (e.g., Bergström 1988). Bagnoli & Stouge (1997) mentioned the occurrence at Horns Udde of '*Cooperognathus aranda*', a highly derived representative of this Australian lineage (Zhen *et al.* 2003), but did not illustrate or describe the specimens.

3.8.6. *Protoprioniodus papiliosus* **(van Wamel 1974).** This is another derived species of Australian affinity (Zhen 2023), reported also from Argentina by Lehnert (1993) and from Newfoundland by Johnston & Barnes (2000).

3.8.7. *Paracordylodus gracilis* **Lindström, 1955.** Tolmacheva & Löfgren (2000; also Tolmacheva & Purnell 2002 and Tolmacheva 2014) presented the apparatus structure of this deep-water species and identified biometric distinctions between populations from different regions of the world.

3.8.8. *Oepikodus evae* **(Lindström 1955a).** *Oepikodus communis* (Ethington & Clark 1964), having a tetraramous S_0 element diagnostic for the genus, preceded *O. evae* (*inter alia*, Lehnert 1995; Zhen *et al.* 2007). According to Pyle & Barnes (2002) it is a descendant of *Acodus neodeltatus* Pyle & Barnes 2002, adenticulate but with M elements bearing an elongated dorsal process. This is unlikely and roots of the lineage are rather in Australia, where another adenticulate forms with tetraramous S_0 elements have been found (Nicoll & Ethington 2004; Zhen & Nicoll 2009). Smith (1991) described a cluster of elements of *O. communis*, lacking M elements and with two sinistral P elements displaced to the centre of the cluster, which suggests its coprolithic

(or regurgitated) origin. This suggests that early prioniodontids had apparatuses of composition similar to that of the ozarkodinids.

The S elements of *O. evae* bear a very long dorsal process (Fig. 9) that rarely is preserved in loose material (Landing 1976, pl. 4:1). In the Argentinian San Juan Formation, *O. evae* is succeeded by *O. intermedius* Serpagli 1974 that differs from its predecessor in lacking denticulation on the anterior process of P elements and apparently being the next step in the evolution (Serpagli 1974). In a sense, this is a case of evolutionary reversal to the morphology of *O. communis* that differs from *O. intermedius* only in being of a more gracile appearance (Lehnert 1995).

3.9. Order *Prioniodontida* Dzik, 1956, family *Balognathidae* Hass 1959

3.9.1. *Diaphorodus delicatus* (Branson & Mehl 1933). Kennedy (1980), while proposing the genus *Diaphorodus* with *D. delicatus* as its type species, pointed out that the apparatus of the type species of *Acodus*, *A. erectus* Pander 1856, remains unknown but *A. deltatus* is generally assumed to be representative for its genus (Zhen & Nicoll 2009). *Diaphorodus delicatus* differs from *Acodus* in having a more prominent cusp and longer processes. Perhaps together with *Triangulodus amabilis* Rasmussen 2001 from the *O. evae* Zone, it is an early chronospecies of the *Triangulodus* lineage.

3.9.2. *Triangulodus brevibasis* (Sergeeva 1963a).. The holotype comes from Volkhov strata at Popovka, Ingria (Sergeeva 1963a). The apparatus (Figs. 3a–g, 6) was restored by Lindström (1971). Tolmacheva (2001, pl. 3:1–9 and 4:1–10) reported in open nomenclature two species of *Tripodus* from the Lava section in Ingria. The one from the upper part of the *Oepikodus evae* Zone differs from that occurring in the lower part in having longer and more widely disposed processes of S_0 elements. Perhaps they both represent parts of the *Triangulodus* lineage.

3.9.3. *Triangulodus alatus* Dzik 1976. The fossil record of this species is not in a continuity with *T. brevibasis* but, being different only in more prominent processes (Fig. 6), such a relationship seems likely.

3.9.4. *Acodus deltatus* Lindström 1955a. The apparatus of this species (Fig. 9) is well known (*inter alia*, Bagnoli *et al.* 1988; Viira *et al.* 2006b). As indicated above, it is closely related to *D. delicatus* and probably gave ancestry to *Baltoniodus* by developing denticulation on processes, but the transition remains untraced (Stouge & Bagnoli 1990).

3.9.5. *Baltoniodus triangularis* (Lindström 1955a). Stouge & Bagnoli (1990; Bagnoli & Stouge 1997) considered this species as representing the *Trapezognathus* lineage. It was suggested by the morphology of its tetraramous S_1 element but is contradicted by the M elements shape (Fig. 7). As identified by Lindström (1971), its dorsal process is not perpendicular to the cusp (Wu *et al.* 2017). However, Bergström & Löfgren (2009) allowed a very wide range of variability of M elements included in this species, ranging from the morphology typical of *Baltoniodus* (Bergström & Löfgren 2009, fig. 4t), through those with the undenticulated dorsal process perpendicular to the cusp, typical of early *Trapezognathus* (Bergström & Löfgren 2009, fig. 4c, r, z, ac), up to prominently denticulated specimens of *Trapezognathus pectinatus* morphology (Bergström & Löfgren 2009, fig. 4d, s). The same refers to S elements that probably represent co-occurring species of *Baltoniodus* and *Trapezognathus*.

3.9.6. *Baltoniodus navis* (Lindström 1955a). According to Stouge & Bagnoli (1990, p. 10) this is the oldest recognised species of its lineage, but *B. triangularis* as understood by Lindström (1971) and partially by Bergström & Löfgren (2009, also Wang *et al.* 2009) better fits such place in the evolutionary sequence. *Baltoniodus navis* (Fig. 7) differs from its successor, *B.*

norrlandicus, in a more robust appearance of all elements, as well as in shorter processes of P_1 and M elements (Fig. 4a–h). Large samples are necessary to trace the transition. Unfortunately, this is not offered by the Les-154ko to Les-148prz series of samples from the Lesieniec IG 1 core (supplementary Tables 39, 41). Attribution of *Baltoniodus* elements sets from the middle of the sequence to either chronospecies has to remain arbitrary.

3.9.7. *Baltoniodus norrlandicus* (Löfgren 1978). Stouge & Bagnoli (1990) understood this species in terms of the vertical chronospecies concept and they even introduced *B. clavatus,* corresponding to morphotype 8 on fig. 13 in Dzik (1994). Potentially, it would be possible to interpret it in population concept terms and apply to the segment of the lineage with such modal value for S_3 elements, but this does not seem practical. *Baltoniodus norrlandicus* (Fig. 7) may be conspecific with *Falodus parvidentatus* Sergeeva, 1963.

3.9.8. *Baltoniodus medius* (Dzik 1976). The species (Fig. 7) is characterised by a short but still distinct anterior process in S_2 (S_3 according to Dzik's 2015 interpretation).

3.9.9. *Baltoniodus prevariabilis* (Fåhraeus 1966). In this species the anterior process in S_2 is completely reduced (Fig. 7) and almost undistinguishable from that in S_3 elements.

3.9.10. *Baltoniodus variabilis* (Bergström 1962). The contents of the apparatus (Fig. 7) were illustrated by Viira *et al.* (2006b). The posterior part of the basal cone in the P_1 element developed a platform with triangular outline.

3.9.11. *Baltoniodus alobatus* (Bergström 1971). The platform in the P_1 element is robust but relatively narrow, of irregular outline (Fig. 7). A gradual transition connects *B. variabilis* with *B. alobatus* in the Holy Cross Mountains (Dzik 1994). This may mean that the latter species is an immigrant to Baltica that replaced *B. gerdae*.

3.9.12. *Baltoniodus gerdae* (Bergström 1971). The range of this species, which is characterised by the denticulated process (Fig. 7) that replaced the platform in P_1, was traced within a 0.25 m thick interval in the Dalby Limestone in Sweden. It persisted longer in the Appalachians than in the Baltic region (Bergström 1971). In Estonia it is missing in some localities as a result of sedimentary hiatus (Paiste *et al.* 2020). A shallowing and erosional event is evidenced also by the co-occurrence of reworked Kunda age conodonts with *B. gerdae* in the boulder E-358. This presumably warm-water species is not present in the Holy Cross Mountains. (Dzik 1994).

3.9.13. *Barrandegnathus bohemicus* (Dzik 1983). Stouge (2005) reported this species, originally known only from the locality Mýto near Prague, from the late Volkhov *B. norrlandicus* to *L. antivariabilis* Zones at localities Skelbro in Bornholm, Denmark, as well as Limensgade, Fågelsång and Albjära in Skania, Sweden. According to Stouge & Nielsen (2003), the Volkhov conodont communities at Fågelsång show a Gondwanan coldwater affinity whereas those of the Kunda age contain Laurentian elements.

3.9.14. *Trapezognathus pectinatus* (Dzik 2020). The diagnostic aspect of the species is the prominently denticulated dorsal process of the M elements (Fig. 5). *Zentagnathus gertrudisae* Albanesi, 2023 from the early Darriwilian of Argentina (Albanesi *et al.* 2023) seems conspecific. I suggest that some specimens attributed to *B. triangularis* by Bergström & Löfgren (2009) belong to *Z. pectinatus*. Its presence in Morocco suggests the Gondwanan source area for its immigration to the Holy Cross Mountains and marginal areas of Baltica.

3.9.15. *Trapezognathus diprion* (Lindström 1955a). P and S elements in this species are adenticulated (Fig. 8) or weakly denticulated (Bagnoli & Stouge 1997). As pointed out above, the M elements differ from those of *Baltoniodus* in orientation of the dorsal process that is perpendicular to the cusp (Fig. 4i–h).

3.9.16. *Trapezognathus quadrangulum* Lindström 1955a.
The P elements are weakly denticulated (Fig. 8; Stouge & Bagnoli 1990) and with a sharp almost transversely oriented posterior lobe on the dorsal process (Viira *et al.* 2001). Perhaps elements determined as *Baltoniodus triangularis* Carlorosi *et al.* (2013) belong here. Specimens from the Lesieniec IG 1 borehole (samples Les-154ko, 154tyl and 154śr) have incipiently denticulated posterior lobes and may represent advanced *T. quadrangulum* or *T. falodiformis* Sergeeva 1963b.

The holotype of *Lenodus falodiformis* is an M element of Volkhov age from the Popovka River, Ingria (Sergeeva 1963b). Its dorsal and ventral processes are finely denticulated but no ridge, diagnostic for *Lenodus*, is developed on the basal cone of the holotype. This makes it rather a member of the *Trapezognathus* grade, although not necessarily synonymous with *T. quadrangulum* as proposed by Stouge & Bagnoli (1990).

Lindström (1977) applied the name *Amorphognathus falodiformis* for the transitional form between *Baltoniodus* and *Amorphognathus* but Bergström (1983) pointed out that its apparatus was too poorly known to be of use. A few specimens from Hälludden, Öland were attributed to this species and have been illustrated by me (Dzik 1983, fig. 7a–e), but Rasmusssen (1991) suggested that this is a morphotype within the range of variability of *L. variabilis*. The nomenclatorial problem remains to be settled (Stouge 1989).

3.9.17. *Lenodus antivariabilis* (An 1981). The species as understood by Bagnoli & Stouge (1997), with undivided posterior process of its P$_1$ (Pb in Bagnoli & Stouge 1997) element and the posterior lobe of the dorsal process almost parallel to it (Fig. 8), is the first member of the *Lenodus* lineage, possibly next to *T. falodiformis*. Its Baltic successor, *L. variabilis* (but also *L. antivariabilis* as understood by Wu *et al.* 2018), has this process bifurcated. Zhang (1998b) included in the Chinese *L. antivariabilis* forms even more advanced, having the ventral branch of the process longer that the dorsal one. This is a morphology close to that of *Eoplacognathus zgierzensis*.

The oldest occurrence of *Lenodus* M elements is in an erratic boulder from Mokrzeszów in the Sudetes, Poland, transported there in the most extensive Pleistocene glaciation (E-374; supplementary Table 17d). Their ventral margin is virtually smooth in juveniles but developed distinct denticulation in adults. The ridge on its basal cone extends into a weakly denticulated process of at least double the length of the cusp. The posterior process of the P$_1$ elements is variable, in juveniles lacking bifurcation that apparently developed later in the ontogeny. The holotype of the type species of *Lenodus*, *L. clarus* is an M element from the Kunda age strata at the Popovka River, Ingria (Sergeeva 1963b). Its ventral process is prominently denticulated; the posterior process is also finely denticulated. This makes its synonymy with *L. antivariabilis* likely.

3.9.18. *Lenodus variabilis* (Sergeeva 1963a). The diagnostic trait of this species is a P$_1$ element with bifurcated posterior process (Fig. 8), its rami being of not more than equal length (Dzik 1994; Löfgren 2003). Such an element has been found in sample Ha-4 at Hälludden, Öland (supplementary Table 19b).

3.9.19. *Lenodus crassus* (Chen & Zhang in Wang 1993). Dzik (1976) suggested that the beginning of the *Eoplacognathus* lineage is marked by elongation of the dorsal branch of the posterior process in the P$_1$ element. In this respect *L. crassus* is at the *Lenodus* grade. Bifurcation of the posterior process with its branches of similar length points to early *Lenodus variabilis* as its probable ancestor (Zhang 1997). Although typical for the Yangtse Platform (Zhang 1998b), it had its Baltic acme of early Kunda age (Männik & Viira 2012; S. Stouge, pers. comm. 2023).

3.9.20. *Amorphognathus tvaerensis* (Bergström 1962). The contents of the apparatus (Fig. 6) were illustrated by Viira *et al.* (2006b). Dextral P$_1$ elements with relatively straight dorsal

process have been found in the boulder E-173 and in the Lesieniec IG 1 borehole sample Les-134śr (supplementary Tables 60, 62).

3.9.21. *Amorphognathus viirae* Paiste *et al.* 2023. Populations of *Amorphognathus* from the *Baltoniodus alobatus* Zone differ from those preceding in a sinuous dorsal process of the dextral P$_1$ element (Fig. 6; Paiste *et al.* 2023).

3.9.22. *Amorphognathus ventilatus* Ferretti & Barnes 1997. This species precedes *A. superbus* Rhodes 1955 in the Holy Cross Mountains, Poland (Dzik 1999) and Estonia, being a member of the Oandu age fauna (Nõlvak *et al.* 2006; Männik & Viira 2012). Its origin from the advanced *A. tvaerensis* seems well substantiated by the M element morphology, with a fan-like arrangement of denticles (Fig. 6). Its type horizon, the Kalkbank horizon in Thuringia (Ferretti & Barnes 1997), seems to mark a global expansion of warm-water conodonts preceding the Late Ordovician cooling (Dzik 1999).

3.9.23. *Amorphognathus superbus* (Rhodes 1953). The diagnostic character of this species, distinguishing it from the ancestral *A. tvaerensis*, is the absence of postero-dorsal lobe in the dextral P$_1$ element (Fig. 6). M elements are very variable in populations of the late *Amorphognathus* and usually rare in conodont samples because of their small size (*inter alia*, Dzik 1994, 1999; Männik 2017). This is the main cause of controversies in determining particular species. Ferretti *et al.* (2014a), in their taxonomically important study on the Late Ordovician conodonts from Wales, proposed co-occurrence of at least four species of *Amorphognathus* in the same sample and allowed up to nine sympatric species of this genus in their material. I find this biologically unrealistic. The within-sample variation of the diagnostic character for the species is unimodal throughout the Mójcza Limestone in the Holy Cross Mountains (Dzik 1990, fig. 17; 1999). Without considering frequencies of particular morphotypes within their Gaussian distribution, it is hardly possible to determine position of particular chronospecies in an evolutionary continuum.

3.9.24. *Amorphognathus* sp. n. Dzik 1999. Merrill (1980) illustrated the M element from the Åland Islands, Finland, associated with other element types he attributed to *A. complicatus* Rhodes 1955 and *A. superbus* (Bergström 1971), but it seems to represent rather this unnamed species.

3.9.25. *Amorphognathus ordovicicus* Branson & Mehl 1933. The only M element of the Katian *Amorphognathus*, with a dominant cusp diagnostic for this species (Fig. 6; Bergström & Leslie 2010), has been found in erratic boulder E-207 (supplementary Table 69). Zhang *et al.* (2016) illustrated its almost intact specimen. Other element types are undistinguishable from those of related species but presumably erratics of the Ostseekalk lithology are of similar age and *Amorphognathus* specimens from them represent *A. ordovicicus*.

3.9.26. *Amorphognathus duftonus* Rhodes 1955. A characteristic dorsal spur on the M elements (Fig. 6) is the diagnostic trait of this species (e.g., Ferretti *et al.* 2014a, 2014b), well known from Podolia (Dzik 1999). Despite the relatively sparse Late Ordovician conodont fossil record in Estonia (Männik & Viira 2012), Kaljo *et al.* (2008, fig. 8f, g) collected the diagnostic element of *A. duftonus* from the earliest Porkuni age bed immediately preceding the immigration of *Noixodontus girardeauensis* (Satterfield 1971). They identified the species as *A. ordovicicus* and it is unclear if such determined conodont from the Hirnantian of Latvia (Hints *et al.* 2010) is conspecific.

3.9.27. *Rhodesognathus elegans* (Rhodes 1953). Specimens from the borehole Lesieniec IG 1 (Les 124 1/3; supplementary Table 67), although rather poorly preserved, provide a complete set of element types of this species (Bergström & Sweet 1966). Possibly conspecific elements of somewhat larger size have

been found in the erratic boulder E-213 (supplementary Table 67).

The *Rhodesognathus* lineage is closely related to *Amorphognathus* (Fig. 5) but its exact ancestry remains unknown. I suggested (Dzik 1994) that the main trend in its evolution is the reduction of ramification in the platform of P_1 elements. If true, *R. elegans* would be the end-member of the lineage.

3.9.28. Sagittodontina sp.. The mid Darriwilian (Kunda age) early populations of the lineage, co-occurring with *Eoplacognathus zgierzensis*, differ from those of the late Darriwilian type species in a relatively wide angle between dorsal and ventral processes of P_2 elements. Also, the M element, probably erroneously referred to *Eoplacognathus* by Dzik (1994, pl. 20:15) differs from that of the type species population in having a less posteriorward-oriented prominently denticulated postero-dorsal process (Fig. 8). M elements are invariably broken in the Baltic material but two relatively complete elements from the borehole Lesieniec IG 1 (sample Les-145) bear an extremely long transversely oriented posterior process, more than two times longer than the cusp and with 13 rather prominent denticles.

3.9.29. Sagittodontina kielcensis (Dzik 1976). The species (Fig. 8) appears in Estonia in the *P. anserinus* Zone (Hints *et al.* 2012). After a long gap in occurrence, the last member of this lineage, *Noixodontus girardeauensis*, enters the Baltic region again close to the end of the Ordovician (Männik & Viira 2012). It marks the global Hirnantian cooling (McCracken & Barnes 1982; Bergström *et al.* 2006). Its co-occurrence with *Kockelella* and *Ozarkodina* (Männik & Viira 2012) indicates surprisingly early immigration of the Silurian fauna from an unknown refuge (unless the *Noixodontus* specimens are reworked).

3.9.30. Eoplacognathus zgierzensis Dzik 1976. Erratic boulders E-211 and E-266 (supplementary Table 47) yielded P_1 elements with branches of the bifurcated posterior process of proportions diagnostic for *E. zgierzensis*. This is the most ancient member of the Baltic *Eoplacognathus* lineage (Fig. 5), characterised by the elongated ventral branch of posterior process in the P_1 element (the homologous bifurcated process was originally short in *Lenodus* and remained such in *Sagittodontina*, *Amorphognathus* and *Rhodesognathus*). The Chinese *L. antivariabilis sensu* Zhang (1998b) had the ventral branch of the process slightly longer than the dorsal one, which may mean that the *E. zgierzensis* lineage is rooted there. Saadre *et al.* (2004) preferred to classify *E. zgierzensis* (as well as *E. pseudoplanus*) in *Lenodus*, although both lineages seem to co-occurred in the mid Kunda.

The M element with prominently denticulated postero-dorsal process, referred to *E. zgierzensis* by Dzik (1994, pl. 20:15), belonged to a co-occurring unnamed early species of *Sagittodontina*. However, there is a gradation within the same sample ranging to morphologies typical of *Lenodus*, presumably characterising also *E. zgierzensis*.

3.9.31. Eoplacognathus pseudoplanus (Viira 1974). The holotype of *Ambalodus pseudoplanus* Viira 1974 is a P_2 element that comes from the Kunda age strata in the borehole Ohesaare (depth 508.87 m; Viira 1974, p. 54, fig. 43). It does not differ from the homologous element of *E. zgierzensis* found at 510.44 m. The distinguishing and diagnostic aspect of these species is the length of the dorsal branch of the anterior process of the P_1 element (Dzik 1976). Also, the posterior process in the P_1 element of this species was much more elongated that in the preceding *E. zgierzensis* (Fig. 5).

Stouge & Bagnoli (1990) described non-P elements in *E. pseudoplanus*, contradicting Dzik (1976) in that non-P elements were lost in the course of evolution from *Lenodus* to *Eoplacognathus*. Dzik (1994) already corrected this in respect to *E. zgierzensis*.

3.9.32. Eoplacognathus suecicus Bergström 1971. The holotype chosen by Bergström (1971, pl. 1:6) is a juvenile dextral P_2 element. Specimens of such ontogenetic age do not differ much

from those of stratigraphically preceding species and this has resulted in their different interpretation by some authors. The associated sinistral element, as well as sinistral elements from the type locality (Zhang 1999), shows the ventral process (Zhang & Sturkell 1998) significantly longer than that of *E. pseudoplanus*, from which *E. suecicus* evolved (Fig. 5). Diagnostic for the species is also the short and bifurcated posterior process of the P_1 element (Zhang 1999, fig. 1), in Estonia characterising the late Aseri age. Juveniles recapitulate the morphology of ancestral *E. pseudoplanus* (Zhang 1999, fig. 3). Specimens attributed to these species described by Mestre & Heredia (2019) from Argentina under the generic name of *Lenodus* truly represent species of this genus.

3.9.33. Eoplacognathus reclinatus (Fåhraeus 1966). The diagnostic P_2 elements of this species changed during their ontogeny, with the ventral process becoming longer. Mature specimens are closely similar to those of *E. robustus* and some of the differences between these chronospecies may be due to a change in population dynamics (distribution of mortality) rather than evolution, which was traced in Sweden by Bergström (1971). There is an evolutionary continuity from this chronospecies (the type for *Baltoplacognathus* Zhang, 1998b) to *E. lindstroemi* (the type for *Eoplacognathus* Hamar 1966) eventually resulting in a decrease of asymmetry of P_2 elements, and their separation into different genera seems redundant (Fig. 5).

3.9.34. Eoplacognathus robustus Bergström 1971. The ontogenetic change of P_2 elements is expressed in the length of the dorsal process also in this species. It deserves its name owing to a generally large size of elements. Still, even juveniles are clearly different from the preceding and apparently ancestral *E. reclinatus* in respect to the dorsal process length (Fig. 5).

The erratic boulder E-294 yielded two S_3 elements of *E. robustus*. Heredia & Mestre (2019) identified some S and M elements of this apparatus, although their elements are much more gracile than elements under study here, and puzzlingly similar to those of *Baltoniodus*.

3.9.35. Eoplacognathus lindstroemi (Hamar, 1964). Heredia & Mestre (2019), Paiste *et al.* (2022) and Ferretti & Bergström (2022) proposed a controversial partial reconstruction of the apparatus including *Baltoniodus*-like ramiform elements (Fig. 5).

3.9.36. Eoplacognathus elongatus (Bergström 1962). The characteristic star-like P_1 elements of this species (Fig. 5) occur from the latest *Pygodus anserinus* to early *Baltoniodus gerdae* Zones (Bergström 1971, p. 100).

3.9.37. Yangtzeplacognathus foliaceus (Fåhraeus 1966). According to Zhang (1999), the first populations of *Y. foliaceus* co-occur with *E. suecicus*, which is probably their ancestor, but the transition has not been traced in the Baltic region (Fig. 5). In the Goldwyer Formation, Canning Basin, Australia, *Y. foliaceus* co-occurs with *Lenodus*, as shown by a short bifurcation of the anterior process in P_1 element, identified as *E. suecicus* by Watson (1988, pl. 6:33), that seems to agree with reinterpretation of its age by Zhen (2020).

3.9.38. Yangtzeplacognathus protoramosus Chen et al. 1983. The Yangtse lineage of *Yangtzeplacognathus* reappeared in Estonia (Männik & Viira 2012), the Holy Cross Mountains (Dzik 1994) and the Lesieniec IG 1 borehole (sample Les-138) in the late *E. robustus* Zone.

3.9.39. Cahabagnathus sweeti (Bergström 1971). The holotype of *C. sweeti* comes from the base of the Effna Formation in Virginia and this chronospecies is a continuation of the North American Midcontinent lineage initiated by *C. friendsvillensis* (Bergström 1971; Leslie & Lehnert 2005). Drygant (1974) based his *Petalognathus bergstroemi* on two P_2 specimens from the depth of 405 m in the Pishcha-16 borehole in Volhynia, Ukraine, of morphology virtually identical with the Appalachian type specimen. Its age is roughly determined by the occurrence of

Eoplacognathus elongatus at the depth of 407 m. Another species exotic to Baltica but of the Yangtse affinity, *Complexodus pugionifer*, co-occurs in the same interval of the core (405–407 m) as well as in the Fågelsång section in Sweden, where *B. variabilis* has also been found (Bergström 2007), but in Estonia it ranges only up to the *Pygodus anserinus* Zone (Männik & Viira 2012).

3.10. Order *Prioniodontida* Dzik, 1956, family *Cyrtoniodontidae* Sweet 1988

3.10.1. *Phragmodus costulatus* (Lindström 1955a). The apparatus (Fig. 7) was restored by Bagnoli & Stouge (1997). This is probably the ancestral chronospecies of the *Phragmodus* lineage, an early offshoot of the balognathids that appeared in the Baltic region in the *Oepikodus evae* Zone (Dzik 1994, 2015; Bagnoli & Stouge 1997). Gutiérrez-Marco *et al.* (2008) claimed that it had its ancestry in the Andean part of Gondwana.

3.10.2. *Phragmodus polonicus* Dzik 1978. This chronospecies differs from *P. costulatus* in the sinuosity of the dorsal process of S_{0-2} elements (Fig. 7; Dzik 1994). It occurs in the Holy Cross Mountains, Poland in the *Lenodus variabilis* Zone, and appeared somewhat later in Norway (as *Nordiora torpensis* Rasmussen 2001) and the Canning Basin, Australia (as *Phragmodus polystrophos* Watson 1988; Zhen 2019). In Estonia, it occurs in the *E. robustus* to *B. variabilis* Zones (Viira *et al.* 2006a; Hints *et al.* 2012). Probably the Late Ordovician *P. undatus* Branson & Mehl 1933 is the last member of the lineage. It was typical for Laurentia but appeared also in the Baltic Oandu age together with *Belodina confluens* (Paiste *et al.* 2022).

3.10.3. *Complexodus originalis* Chen & Zhang 1984. This species is of Yangtse origin but known also from Turkey (Kozlu *et al.* 2002). Biometrical data from the Mójcza Limestone in the Holy Cross Mountains, Poland show that soon after its immigration to the region, *C. originalis* gradually developed sinuosity of the ventral branch of the anterior process in the course of evolution towards *C. pugionifer* (Dzik 1994). Thereafter a return to the original morphology is observed, with some gap in the record. An even more complex succession of immigration events was reported in Estonia by Männik & Viira (2012). A species of *Complexodus* is recorded there already in the *E. suecicus* and *Y. foliaceus* Zones, while *C. pugionifer* appeared after a gap in the *E. lindstroemi* Zone to continue its presence until the *B. variabilis* Zone, replaced by *C. originalis* in the middle of its range.

3.10.4. *Complexodus pugionifer* (Drygant 1974). The species was originally identified in the Pishcha-16 borehole in Volhynia, Ukraine (Drygant 1974) and its complete apparatus has been restored by me (Dzik 2015), based on materials from the Mójcza Limestone.

3.11. Order *Prioniodontida* Dzik, 1956, family *Icriodontidae* Müller & Müller 1957

3.11.1. *Icriodella superba* Rhodes 1953. The *Icriodella* lineage had its root in Avalonia (Dzik 1990). The species co-occurs with *A. superbus* in the erratic boulder E-305 from Mochty, Poland (supplementary Table 67; Dzik 1983). Two kinds of M elements can be distinguished in a loose material (Fig. 6). A complete apparatus structure of a Late Ordovician close relative is known, owing to natural assemblages from the Soom Shale, South Africa (Aldridge *et al.* 2013).

3.12. Order *Prioniodontida* Dzik, 1956, family *Ansellidae* Fåhraeus & Hunter 1985

3.12.1. *Ansella jemtlandica* (Löfgren 1978). The apparatus of this species was illustrated and described in detail by Stouge (1984), Zhang (1998b), and Zhen *et al.* (2011a, 2011b). Zhang (1998b) determined its position in a Chinese lineage showing a gradual increase in the basal cavity depth. Fåhraeus & Hunter (1985) identified an *Ansella* species with denticulation extended to the P elements, which is apparently a derived trait. This may mean that the ancestral apparatus for the lineage was undenticulated, with relatively shallow basal cavity. This places *Ansella* in proximity to *Walliserodus*, having a similar ground-plan of S_0 elements. It is preceded in the Table Head Formation of Newfoundland by *A. sinuosa* (Stouge 1984), characterised by a rather generalised appearance of M elements (Stouge 1984), and may be ancestral to it.

3.12.2. *Ansella* sp.. Hints *et al.* (2012) determined *Ansella* species with obliquely oriented denticles as *A. serrata* (Dzik 1976) but '*Belodella*' *serrata* Dzik 1976 has fine denticles inclined towards the element base, opposite to the *Ansella* pattern. Moreover, '*B.*' *serrata* bears the panderodont furrow, which means that a separate panderodontid genus should be erected for it.

3.12.3. *Hamarodus brevirameus* (Walliser 1964). Together with *Dapsilodus* and *Scabbardella*, all characterised by thin element walls (Fig. 7), this is a member of the cold- or deep-water Late Ordovician fauna (e.g., Stouge & Rasmussen 1996; Ferretti & Barnes 1997; Ferretti 1998) but is known also from the Appalachians (Nowlan *et al.* 1997). In the Nanjing region of China this species seems to have a longer range than elsewhere (Chen & Zhang 1984). Only a single element possibly belonging to *Hamarodus* has been found in the *Baltoniodus alobatus* Zone in the borehole Niwa (sample 1093sp; supplementary Table 66), which would be one of the earliest known occurrences of this lineage.

3.13. Order *Ozarkodinida* Dzik 1976, family *Oistodontidae* Lindström 1970

3.13.1. *Oistodus lanceolatus* Pander 1856. Element S_0 of this species (Fig. 6) is much smaller than other parts of the apparatus (e.g., Löfgren 1994, fig. 6:39). The Laurentian species '*Acodus*' *bransoni* (Ethington & Clark 1981) from the *Paroistodus proteus* to *Prioniodus elegans* Zones (Ji & Barnes 1990, 1994) may be ancestral to it.

3.13.2. *Jumudontus gananda* Cooper 1981. Nicoll (1992) restored its apparatus with an alate S_0 element suggesting affinity to *Histiodella*, but the geniculate M element he attributed to this species does not fit the rest of the apparatus.

3.13.3. *Histiodella holodentata* Ethington & Clark 1982. The composition of the apparatus of *Histiodella* and its early evolution was traced by McHargue (1982) and Zhen *et al.* (2022) based on the Oklahoma material. The lineage is probably of Laurentian ancestry and only sporadically immigrated to Baltica.

3.13.4. *Histiodella kristinae* Stouge 1984. The denticles of the ventral process are of the same height as the cusp (Fig. 7). It is a successor, of high correlative value, of *H. tableheadensis* Stouge 1984, characterised by the cusp in P_1 element being higher than the denticles of the ventral process (Stouge 1984; Zhang 1998b).

3.14. Order *Ozarkodinida* Dzik 1976, family *Chirognathidae* Branson & Mehl 1944

3.14.1. *Erraticodon alternans* (Hadding 1913). *Polygnathus alternans* (Hadding 1913) from the *E. robustus* Zone at Fågelsång, Sweden is a senior synonym of *E. balticus* Dzik 1978 (Bergström 2007). This cosmopolitan warm-water species (Fig. 8) appeared in Baltica as early as the *M. parva* Zone (Löfgren 1985) and continued to reappear sparsely until the *E. lindstroemi* Zone (Männik & Viira 2012).

3.14.2. *Spinodus spinatus* (Hadding 1913). This is a lineage of extremely long duration extending from the *O. evae* to *A. superbus* Zone but still poorly known because of rarity (Zhen

et al. 2011a; Stouge 2012). The apparatus of an early species of *Spinodus* from the Floian Lower Head Formation of Newfoundland was reconstructed by Johnston & Barnes (2000) who pointed out its similarity to *Periodon*. It differs from *S. spinatus* (Fig. 7; Albanesi 1998) in closely spaced denticles of S elements. The M element bears two denticles on its ventral process, which makes it different from *Erraticodon*.

3.15. Order Ozarkodinida Dzik, 1956, family *Periodontidae* Lindström 1970

3.15.1. *Periodon primus* Stouge & Bagnoli 1988. *Periodon selenopsis* Serpagli 1974 was listed in Bagnoli & Stouge (1997) as co-occurring with *P. primus* in samples from north of Horns Udde but not commented on in the text. Presumably, these are undenticulated and denticulated specimens within population variability of a single biological species (Fig. 9).

3.15.2. *Periodon flabellum* (Lindström 1955a). The P and S elements of *Periodon* are rather variable (Figs. 4aa–af, 9) and *P. macrodentatus* (Graves & Ellison 1941) as understood by Rasmussen (2001; also Stouge *et al.* 2016 and Zhen *et al.* 2009a) seems to represent the transitional stage of evolutionary transformation to *P. aculeatus* in respect to the diagnostic incipient denticulation of M elements.

3.15.3. *Periodon aculeatus* Hadding 1913. Johnston & Barnes (2000, text-fig. 4) and Stouge (2012) observed gradual development of denticulation of M elements in the *Periodon* lineage in the Floian Lower Cow Head Formation. *Periodon* species (Fig. 9) were typical for deeper-water environments than their relative *Microzarkodina* (Löfgren & Tolmacheva 2008, p. 44).

3.15.4. *Microzarkodina russica* Löfgren & Tolmacheva 2008. This is the oldest Baltic species of *Microzarkodina* from the latest *Oepikodus evae* Zone (Fig. 5). Its P elements have a few small denticles on the ventral process and the S_1 (Sb2 in Löfgren & Tolmacheva 2008) elements have a long denticulated medial process. In these aspects it is somewhat closer to *Periodon* than the majority of *Microzarkodina* species. Somewhat surprisingly, a similar denticulation on the medial process developed late in the evolution of the lineage in *M. hagetiana* and, even more prominent, in its successor *M. ozarkodella*, but in S_2 elements. This means that a rather profound reorganisation of the S series took place.

Microzarkodina buggischi Lehnert 1995 that occurs in the San Juan Formation in Argentina below *M. flabellum*, has the S_0 element with prominently denticulated medial process (Lehnert 1995), which makes it similar to early *Periodon* (elements S_1 and S_2 remain unknown). However, in contrast to *M. buggischi*, lacking ventral denticulation, the P elements of *M. russica* may develop more than one ventral denticle. Albanesi *et al.* (2006) and Löfgren & Tolmacheva (2008) proposed to transfer *M. buggischi* to *Texania* and would therefore be related to *T. heligma* Pohler, 1994 that co-occurs with *Oepikodus evae* and above the first occurrence of *Periodon primus* and *P. selenopsis* in the San Juan Formation (Albanesi 1998; Mango & Albanesi 2020). Anyway, the apparatus structure of both *M. russica* and *M. buggischi* points to at least distant relationship between *Microzarkodina* and *Periodon*.

3.15.5. *Microzarkodina flabellum* (Lindström 1955a). Löfgren & Tolmacheva (2008) identified a population transitional in morphology and age (early *B. triangularis* Zone) between *M. russica* and *M. flabellum* in Kinnekulle, Sweden. This is the next in order chronospecies of the *Microzarkodina* lineage that continued to have the S_1 elements bearing only a single denticle or lacking denticulation of the medial process (Figs 4t–z, 5). The P elements only rarely bear more than one ventral denticle. All the *Microzarkodina* species presented by Löfgren & Tolmacheva (2008, fig. 1) in their meticulous study have partially overlapping

stratigraphic ranges. This means that they were defined in vertical (typologic) terms, the approach followed by most authors dealing with this genus. This unavoidably implies presence of pairs of artificially sympatric species at each evolutionary transition.

3.15.6. *Microzarkodina parva* Lindström 1971. The S_0 elements that developed rudimentary fourth process and adenticulate S_1 elements make this species different from the segments of the lineage preceding and following it (Fig. 5; Löfgren & Tolmacheva 2008, fig. 14).

3.15.7. *Microzarkodina hagetiana* Stouge & Bagnoli 1990. This species is characterised by the medial process in S_2 elements (Sb1 in Löfgren & Tolmacheva 2008) with a few denticles, the S_1 elements remaining adenticulate, which points to *M. ozarkodella* as its phylogenetic successor (Fig. 5). The stratigraphic range of *M. hagetiana* strongly overlaps with *M. bella* Löfgren 2000, restricted in its occurrence to Öland and Finngrundet in Sweden, where it is represented by small, possibly juvenile specimens (Löfgren & Tolmacheva 2008, fig. 1). It is not clear to me whether these are series of sympatric populations of distinct biological species or results of differences in population dynamics (distribution of mortality). Conodont elements grew by adding denticles (Dzik & Trammer 1980, fig. 3) and the appearance of elements classified as *M. hagetiana* and *M. bella* (to me difficult to discern and separate from population variability so nicely presented by Löfgren & Tolmacheva 2008) may be due to their ontogenetic age at the moment of death.

According to Löfgren & Tolmacheva (2008, p. 36, fig. 9x–z) 'some levels of the upper stratigraphical range [of *M. hagetiana*] yield elements with up to three' ventral denticles. This suggests a gradual transition to *M. ozarkodella*, as this is the most characteristic diagnostic character of the species. A sample (Les-151śr) taken from the core of the borehole Lesieniec IG 1 somewhat below the first occurrence of *M. ozarkodella* (Les-149tył; supplementary Table 40), yielded P elements with only one ventral denticle. Co-occuring elements of *Baltoniodus* show a morphology transitional between *B. navis* and *B. norrlandicus*.

3.15.8. *Microzarkodina ozarkodella* Lindström 1971. Löfgren & Tolmacheva (2008, fig. 12) quantitatively documented the gradual increase of the number of ventral denticles in the P elements from numerical domination of specimens with two denticles to those with domination of three denticles and rare specimens with five denticles (Fig. 5). In the large sample from the erratic E-348 (supplementary Table 46) specimens of *M. ozarkodella* are not especially variable and bear three to four denticles, but in samples from the borehole Lesieniec IG 1 of comparable size (Les-145) from one to four.

Elements of this species occur sporadically in as young strata as the *B. gerdae* Zone, but this is probably due to reworking.

3.16. Order *Ozarkodinida* Dzik 1976, family *Spathognathodontidae* Hass 1959

3.16.1. *Yaoxianognathus rhodesi* (Lindström 1970). Leslie's (2000) restoration of the apparatus of *Ozarkodina*? *abrupta* Branson & Mehl 1933 shows a close similarity to this species. He proposed to classify it in *Yaoxianognathus* and I adhere to such a taxonomic decision (Fig. 5) despite derived morphology of the type species of this genus. An almost complete set of elements co-occurring with those of *Amorphognathus superbus* was found in erratic boulder E-305 from Mochty, Poland (supplementary Table 67; Dzik 1983). In Estonia it occurs in the early Katian *Amorphognathus ventilatus* Zone (Oandu age) but also in the late Katian early *A. ordovicicus* Zone (Vormsi age) (Viira 1974). In Podolia, it co-occurs with *A. duftonus*, which in England characterises the latest Katian (Orchard 1980).

Zhen *et al.* (2010) proposed that *Tasmanognathus careyi* Burrett 1979 from the latest Sandbian or earliest Katian of Tasmania

is ancestral to the Laurentian *Y. abruptus* (Branson & Mehl 1933) as interpreted by Leslie (2000). A problematic aspect of such interpretation is that, in the apparatus of *Y. abruptus*, the symmetrical element bears a strong medial process and very short lateral processes, unlike *T. careyi* that lacks any medial denticulated process in these elements, of a unique morphology as for ozarkodinid conodonts. Its morphology in the type species of *Yaoxianognathus* remains unknown.

In *Y. rhodesi* the S_0 element is of morphology typical for the post-Ordovician ozarkodinids (Orchard 1980) and it may be near their roots. If the non-M (that is, the non-holotype) elements of *Gallinatodus elegantissimus* Albanesi in Albanesi *et al.* (2023) from Argentina (Albanesi *et al.* 2023) are joined with the M element attributed to *Pyramidens cactus* Albanesi in Albanesi *et al.* (2023) (unfortunately a prioniodontid P_1 element was chosen as its holotype), this may be an early Darriwilian species ancestral for the *Yaoxianognathus* lineage.

4. Faunal dynamics of Ordovician Baltic conodonts

Baltic conodont assemblages are highly speciose from the late Tremadocian to the late Katian (Viira *et al.* 2001; Hints *et al.* 2012; Männik & Viira 2012). Their diversity to a great degree was controlled by global environmental changes (Bergström *et al.* 2009; Popov *et al.* 2019), but the succession of faunas is only superficially known. The problem is in the disproportion between the complex dynamics of appearances and disappearances of particular conodont lineages and the achieved resolution of sampling. This is especially troublesome in respect of the stratigraphically condensed Dapingian and Floian parts of the succession. They are represented mostly by brief sedimentation events separated by long non-deposition periods. Furthermore, available literature data on the post-Darriwilian conodont faunal dynamics are biased by being mostly quantitative, which does not allow one to recognise the real changes in importance of particular species. In this respect, evidence offered by boreholes drilled in the Polish margin of Baltica and by erratic boulders may fill some gaps in knowledge of the conodont faunal dynamics in the region.

4.1. Boreholes in the Warmia–Masuria region

The Ordovician succession starts in Lesieniec IG 1 core from a calcareous glauconitic sandstone (Fig. 5) covering the Cambrian quartz sandstone. The number of conodont elements in the basalmost sample (Les-glauk; supplementary Table 28) is too small to determine its geological age. It yielded *Drepanoistodus forceps*, a few elements of *Oistodus*, fragmentary elements possibly representing *Oepikodus*, a single M element of *Paroistodus* and other coniform conodont elements of little biostratigraphic importance. The presence of *Cordylodus* suggests that the assemblage is partially reworked. A relatively high contribution of *Paroistodus originalis* in another sample from the same glauconitic unit (Les-155?; supplementary Table 28) suggests that the transgression reached this region near the beginning of the *Baltoniodus navis* Zone. Most of the zone is probably not represented by the rock.

The marl and marly claystone overlying a glauconitic limestone bed (samples Les-154ko–153prz; supplementary Table 39) initiated more or less continuous sedimentation. The two basal samples yielded numerous *Trapezognathus quadrangulum* elements associated with *B. navis*, but *Microzarkodina* P elements from the middle sample have a rather short cusp, suggesting the *M. parva* chronospecies.

The sample mistakenly labelled Les-141 yielded fragmentary *Pygodus*-like elements and a few other lightly coloured elements. Virtually all of its contents are identical to the correctly labelled sample Les-151 that yielded a single S element of *Trapezognathus*.

Possible *Baltoniodus norrlandicus* with still relatively robust elements is present in sample Les-150. The M element from sample Les-148śr may represent *Trapezognathus pectinatus* (supplementary Table 40), previously unknown from Baltica. This is a surprising finding, but more complete specimens from the nearby borehole Gałajny IG 2 give credence to it (Gał-24; supplementary Table 36). In another sample from the Lesieniec IG 1 borehole (Les-148prz), an M element with a ridge on the swollen basal cone occurs, which means that it probably belongs to a *Lenodus* species. *Baltoniodus* S_1 elements have adenticulated anterior processes being close to those of *B. norrlandicus*. Undoubted *B. norrlandicus* associated with *Lenodus* P_2 elements appears in sample Les-147tył. The next segment of the lineage, *B. medius*, appears in sample Les-146ś/t associated with *Microzarkodina parva*. The latter species changes, after a series of low occurrence of the lineage in samples Les-146śr and Les-145tył, into *M. ozarkodella* in sample Les-145śr. The associated robust balognathid elements may represent *Eoplacognathus zgierzensis* or *E. pseudoplanus*. Relatively elongated processes of incomplete P_2 elements from sample Les-144tył suggest *E. suecicus*.

At the transition from red to grey limestone (sample 144c/s), *E. suecicus* is replaced with *E. reclinatus* with relatively elongated ventral processes (thus perhaps even *E. robustus*). This means that a sedimentary gap covers the *Yangtzeplacognathus foliaceus* Zone and probably the basal part of *E. reclinatus* Zone. The *Yangtzeplacognathus* lineage reappears with *Y. protoramosus* in sample Les-138.

There are distinct sedimentary discontinuity surfaces in the early Darriwilian of the Baltic region (Holmer 1983). Such discontinuity marking change from pink organodetrital and grey marly limestone is represented also in the Gałajny IG 2 core within the *E. reclinatus* Zone (samples Gał-20A–D; supplementary Fig. 1). Surprisingly, there is no change in composition of the conodont assemblages immediately below and above the discontinuity (supplementary Table 55). Such continuity in the composition of conodont assemblages despite numerous pronounced sedimentary discontinuities was shown by Bergström & Carnes (1976) for the *E. suecicus*–*Y. foliaceus* interval.

Above the hiatus there is a period of more or less stable domination of the main *Baltoniodus* lineage until the replacement of *Baltoniodus gerdae* (sample Les-128śr) with *B. alobatus* about 1 m higher (sample Les-128śr). According to Bergström (1971, p. 146) 'the evolution of *P. gerdae* from *P. variabilis* was quite rapid and is marked by a series of transitional forms occurring in a less than 0.5-m-thick stratigraphic interval at the localities investigated in the Balto-Scandic area'.

The associated distacodontid and protopanderodontid conodont species, including the large size *Protopanderodus liripipus*, show relatively high diversity in the borehole Lesieniec IG 1 (supplementary Table 64). They are associated with *Amorphognathus viirae* and *B. alobatus*. Their contribution to the assemblages gradually decreases with increase of contribution from *Baltoniodus*. This changes with the end of the *B. alobatus* Zone, when *Baltoniodus* disappears. Eventually, a low-diversity fauna dominated by *Panderodus* emerges. It is unclear whether the topmost sample from the borehole Jezioro Okrągłe IG 1, with *Yaoxianognathus rhodesi*, is of *Amorphognathus superbus* or rather *A. ordovicicus* Zone age, as no M element has been encountered.

The presence of *Hamarodus brevirameus* in the borehole Lesieniec IG 1 (samples Les-124śr to Les-122prz; supplementary Table 67) agrees with its occurrence in coeval strata at Risebæk, Bornholm (Stouge & Rasmussen 1996). In this sample *Scabbardella altipes*, indicative for the Late Ordovician faunas of Gondwana (e.g., Bergström & Massa 1991; Ferretti & Barnes 1997; Ferretti 1998; Dzik 1999), is represented by an unusually high, as for Baltica, number of elements. This suggests a climate cooling episode (Edward *et al.* 2022).

The most surprising aspect of the Warmia–Masuria region fauna is the presence of the Gondwanan element *Trapezognathus pectinatus*, previously known only from Morocco, Argentina and the Holy Cross Mountains. This suggests exposure of the region to the Tornquist Sea and makes it similar to the conodont fauna of the Skania region. Stouge & Nielsen (2003) reported the Gondwanan species *Barrandegnathus bohemicus*, previously known from Bohemia from Bornholm and Skania (locality Fågelsång; supplementary Table 19a).

4.2. Boreholes in the Podlasie region
The conodont assemblages from the Niwa and Widowo boreholes differ from those in the Warmia–Masuria region in a much higher contribution from *Baltoniodus*, but the most informative difference is in contribution of coniform conodont species (Fig. 6). The Warmia–Masuria sections show much higher contribution from the *Protopanderodus rectus* lineage in the early Darriwilian than the Podlasie sections. The opposite relationship is shown by contribution of *Panderodus* in the late

Darriwilian. This seems to be an expression of a more inland location of the latter. In this respect, the Podlasie region is similar to Estonia and Podolia.

Although only a few samples have been taken from the Widowo core, covering a rather brief time segment, it closely resembles the coeval Kohtla section in Estonia in a high contribution from *Baltoniodus* and *Panderodus* (Viira *et al.* 2006a). The Kohtla succession shows a relative stability in composition of the conodont fauna and its surprisingly low taxonomic diversity (Fig. 6; supplementary Table 63). The conodonts from the Estonian exposures of younger age and boreholes were intensely sampled but only qualitative data on ranges of particular species are available. The closest geographic area with exposures of Ordovician rocks south of Podlasie is Podolia in Ukraine. The already mentioned Kytaihorod section has yielded a low-diversity shallow-water Katian assemblage dominated by *Panderodus* and *Amorphognathus*, with contribution from *Icriodella* and *Yaoxianognathus* (Fig. 6; Dzik 2020).

Generally, the sampling of the boreholes in the Podlasie region is too sparse to exhibit short-term changes in biodiversity.
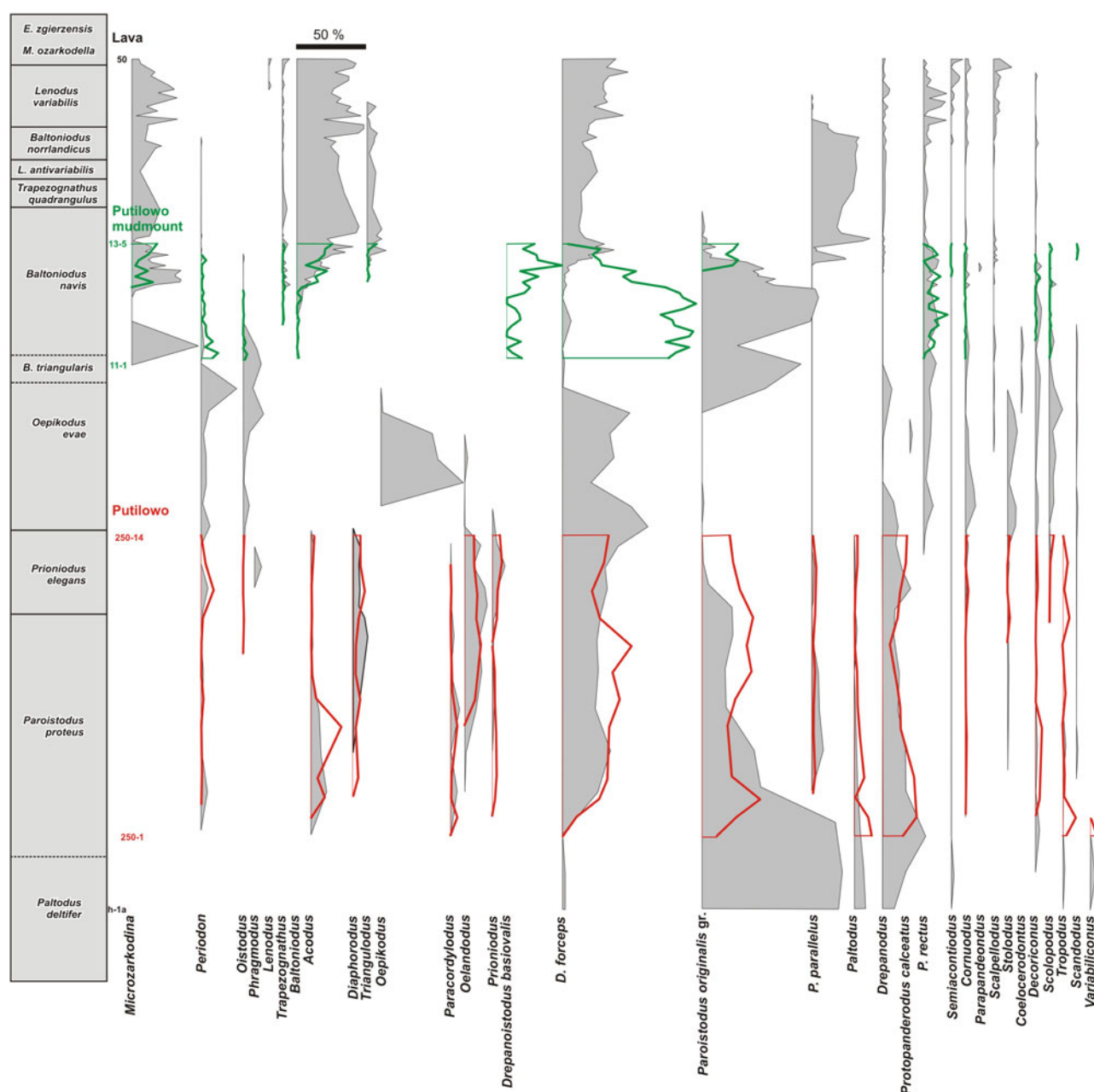

Figure 10   The Ordovician conodonts succession recorded at Lava (data from Tolmacheva *et al.* 2001b; supplementary Table 4), the Putilovo Quarry (Tolmacheva *et al.* 2003; supplementary Table 6), and the Putilovo mud mound (Tolmacheva *et al.* 2003; supplementary Table 11) in Ingria, Russia.
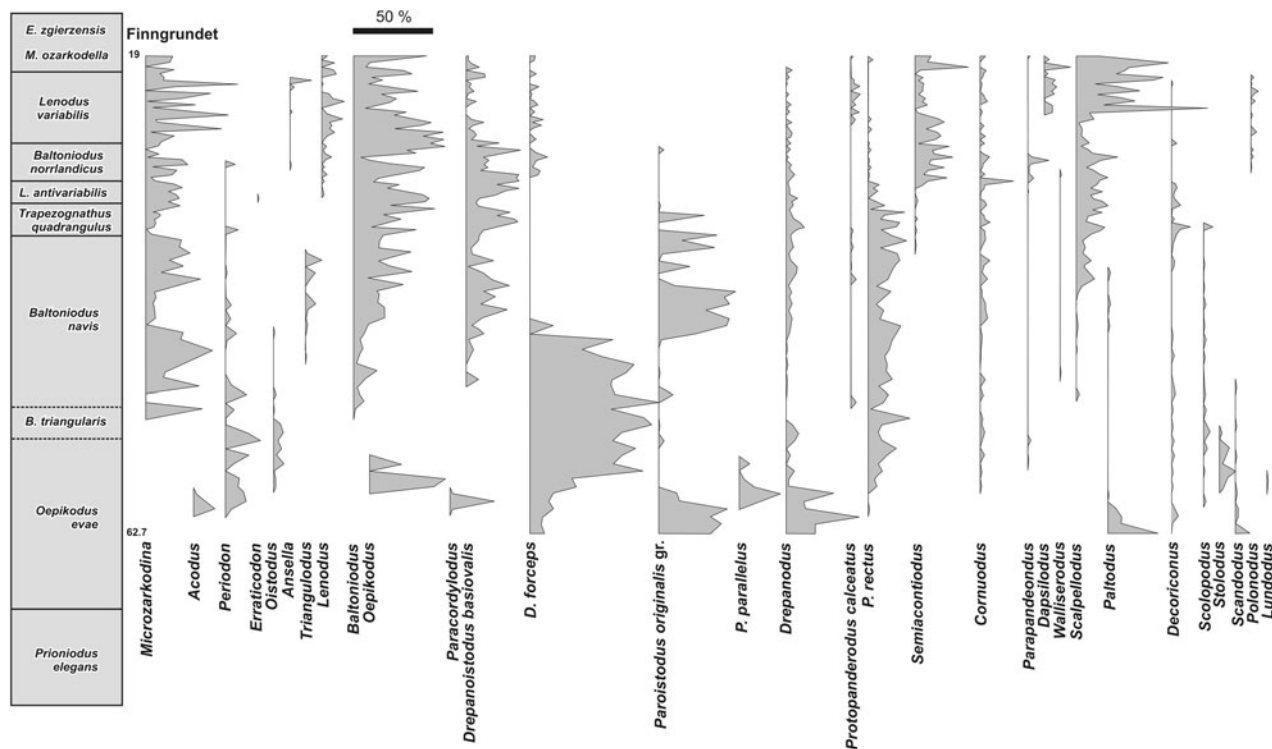
Figure 11 The Ordovician conodonts succession recorded in the Finngrundet borehole drilled in the Bothnian Bay, Sweden (data from Löfgren 1985; supplementary Table 31).

Unfortunately, the literature data on the post-Darriwilian record of conodont faunas succession in Scandinavia is also limited. This is understandable, as most of the sedimentary rock cover was removed and transported to central Europe by movements of continental glacier in at least eight glaciation epochs (Ber 2005). The original picture can be to some degree restored, owing to glacial erratic boulders from regions south of the Baltic Sea.

4.3. Glacial erratic boulders
There is some difference between succession of the Ordovician strata inferred from erratic boulders from eastern (Fig. 7) and western (Fig. 8) Poland. In the west, the Dapingian to early Darriwilian red cephalopod limestone is common and the succession starts at least from the *Oepikodus evae* Zone. In the east, green glauconitic sandy limestone corresponds in age to this time interval. The abundance of the *Baltoniodus* lineage is slightly higher in the western erratics than in those from the eastern part, but otherwise the picture of diversity is surprisingly uniform. Some difference, although not apparent, continues up to the Katian. *Yaoxianognathus*, but also *Hamarodus*, are present in boulders from western Poland but not in eastern ones, possibly due to a difference in exposure to external faunal influences. It has to be noted that the generally higher contribution of *Microzarkodina* and *Periodon* to the eastern record makes it similar to successions at Finngrundet and Ingria. Probably local environmental differences controlled the distribution of these conodont lineages and especially the distacodontids. The latter is well exemplified by the replacement of *Paroistodus* by *Drepanoistodus* in the microbial mud mound at Putilovo in Ingria (Fig. 10; Tolmacheva *et al.* 2003).

It was rather surprising to find a red limestone boulder E-314 with numerous distinct discontinuity surfaces at Jóźwin in central Poland. Conodont assemblages in particular layers of the boulder are virtually identical, dominated by *Oepikodus evae* (Fig. 7; samples E-314A–D; supplementary Fig. 2; supplementary Table 6). Its probable source region was Sweden, but rocks of such lithology are exposed far to the east, in Ingria.

4.4. The quaternary glacial drift source region
Most of the Scandinavian Ordovician rocks are now present in the glacial drift and only a small part of the original record is available in Sweden. The routes of transport were complex and material from the same source may be scattered over a large area (Overweel 1977; Hall & van Boeckel 2020).

4.4.1 Bothnian Bay. The most detailed quantitative sampling of the Ordovician at the main route of the glacier along the Bothnian Bay is the Finngrundet borehole studied by Löfgren (1985). The core covers the late Floian, Dapingian and earliest Darriwilian conodont succession (Fig. 11). The late Floian is marked by the sudden alternation of *Paltodus*, *Acodus*, *Paracordylodus* and *Oepikodus*. Apparently, this is an expression of a global environment instability that resulted in short migration events (or rather changes in areas inhabited by these species). An intriguing aspect of the late Floian to early Dapingian transition is the gradual increase and then decrease in contribution of the *Drepanoistodus forceps* lineage and corresponding decrease and then recovery of the *Paroistodus* lineage. Perhaps this is a case of replacement by competing species, mentioned above in respect to the Putilovo mud mound (Tolmacheva *et al.* 2003). Like all other Baltic sections, *Baltoniodus* gradually and slowly increased its contribution during the Dapingian until it became the dominant element of the assemblage. It was followed, in a more chaotic pattern, by *Microzarkodina*. A gradual increase from the latest Floian to a decrease in the Darriwilian is also shown by *Protopanderodus rectus*, which was replaced by *Semiacontiodus cornuformis*. The Finngrunded record of the conodont succession is especially instructive because it shows the actual changes in frequencies of conodont species almost not distorted by uneven sampling.

4.4.2. Ingria. Almost equally detailed is the succession in Ingria, ranging from the latest Tremadocian to early Darriwilian (Fig 10; Tolmacheva *et al.* 2001b, 2003; supplementary Tables 4, 6, 11). The exclusive relationship between *Paroistodus* and *Drepanoistodus forceps* is recorded there in the *Oepikodus evae* Zone and near the Tremadocian–Floian boundary, but not
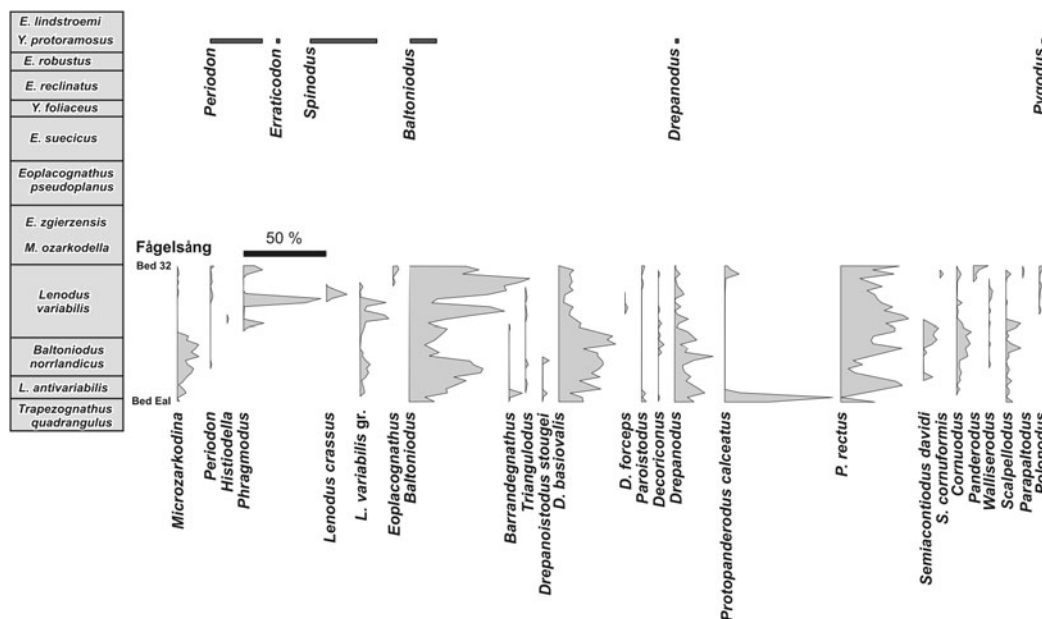
Figure 12 The Ordovician conodonts succession recorded at Fågelsång in Scania, Sweden (data from Stouge & Nielsen 2003 and Bergström 2007; supplementary Table 19).

later. The discrepancy between the record of these species' succession at the Putilovo mud mound and the coeval Lava section is intriguing. In more general terms, the Ingria succession shows a relative stability of conodont faunas until the *Oepikodus evae* immigration. Actually, the appearance of this exotic elements did not cause any profound reorganisation of the conodont community.

4.4.3. Bornholm and Scania. Faunal influences from opposite directions in the late Dapingian and early Darriwilian are recorded in Bornholm and Scania (Fig. 12; supplementary Table 19; Stouge & Rasmussen 1996). The source of *Barrandegnathus*, identified by Stouge (2005) in the Komstad Limestone, is the Czech part of Gondwana, whereas *Histiodella* (Stouge & Nielsen 2003) is of Laurentian origin. Warm climate elements include *Erraticodon*, *Spinodus* and *Cahabagnathus* in the Almelund Shale at the classic locality Fågelsång in Scania (Hadding 1913; Lindström 1955b; Bergström 2007). *Spinodus spinatus* was a species preferring deeper-water environments. It is extremely rare in other Baltic localities. *Complexodus* is probably of the South Chinese Yangtse continent affinity. Such disparity in
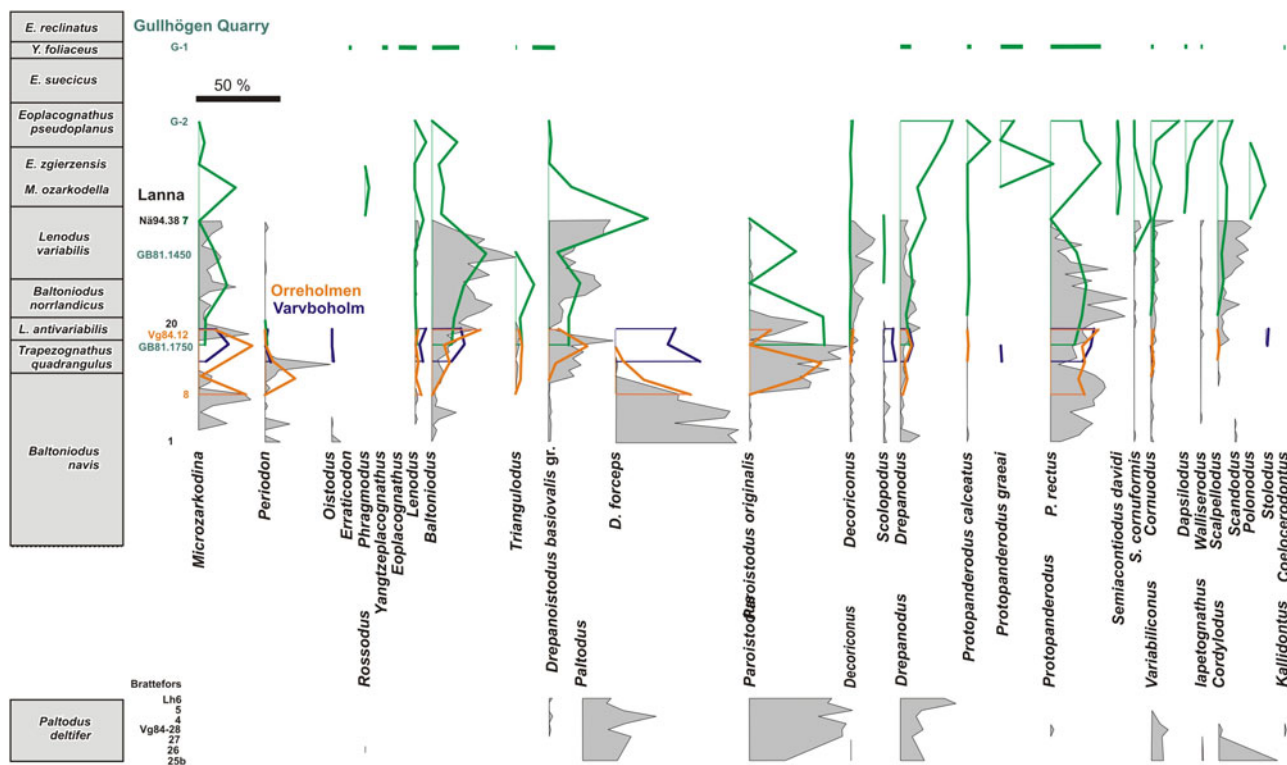

Figure 13 The Ordovician conodonts succession recorded at the Gullhögen Quarry (data from Löfgren 1995, 2003; supplementary Tables 35, 45, 49, 50), Lanna and Orreholmen (Löfgren 1995; supplementary Tables 32, 34), and Brattefors, (Löfgren 1997a; supplementary Table 1) in Västergötland, Sweden.
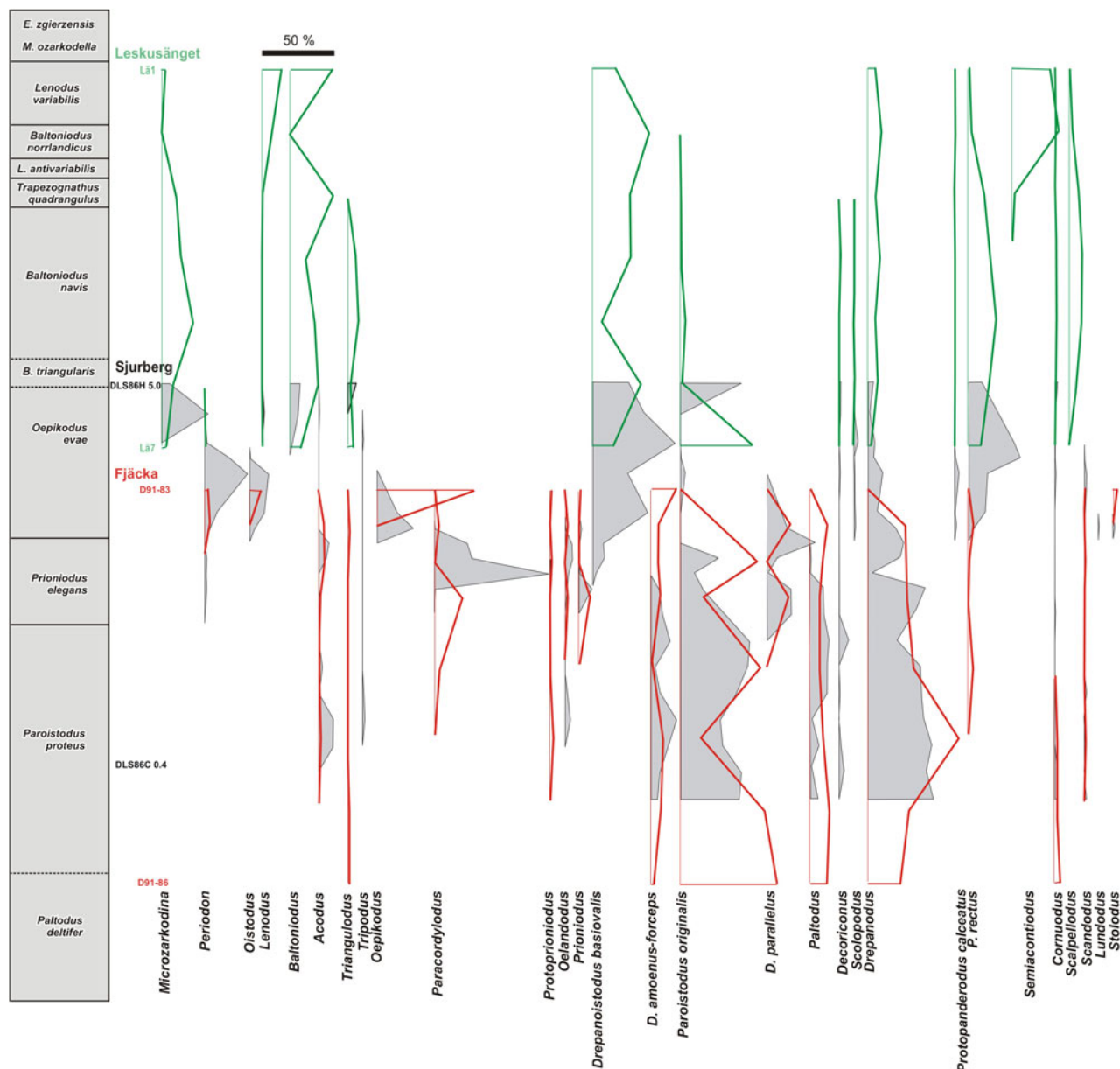
Figure 14 The Ordovician conodonts succession recorded at Leskusänget (data from Löfgren 1995; supplementary Table 33), Sjurberg (Löfgren 1985; supplementary Table 28), and Fjäcka (Löfgren 1994; supplementary Table 4) in Dalarna, Sweden.

source areas for immigrants may have resulted from the location of Scania exposed on the margin of Baltica.

4.4.4. Island Öland. A closer approximation to the beginning of colonisation by conodonts is offered by exposures in the Swedish island Öland (Fig. 9; Stouge & Bagnoli 1990; Bagnoli & Stouge 1997; Bagnoli *et al.* 1988; supplementary Tables 2, 8, 10, 18, 20, 27). The quantitatively described succession starts there from the latest *Paltodus deltifer* Zone and ends with *Eoplacognathus pseudoplanus* Zone. Unlike for Ingria, the oldest conodont assemblage sampled at Ottenby is dominated by *Paltodus*, not *Paroistodus*. *Drepanodus* is second in importance; other species are rare, except for *Acodus*. Assemblages from younger strata are similar to those in eastern Baltica.

4.4.5. Västergötland. One would expect that the Ordovician conodonts from Swedish localities located westward of Scania, thus exposed to the Laurentian influences, would contain Midcontinent faunal elements. This is not necessarily the case and may be restricted to the initial stage in the formation of the Baltic conodont faunal realm. Probably the most complete record of the latest Tremadocian succession is that from Brattefors

(Fig. 13; Löfgren 1997a; supplementary Table 1). It starts from the Laurentian lineage of *Variabiliconus* (Löfgren *et al.* 1999; supplementary Table 1). Darriwilian assemblages recorded in a few other localities are clearly Baltic (Löfgren 1995, 2003; supplementary Tables 32, 34, 35, 45, 49, 50). *Paroistodus* and *Paltodus* are dominant there, followed by *Drepanodus*. Some reworked material is also present.

4.4.6. Dalarna. A different pattern to that in Västergötland can be observed in central Sweden (Fig. 14; Löfgren 1985, 1994, 1995; supplementary Tables 4, 28, 33). The Floian conodont community is virtually the same as at Brattefors (Fig. 13). However, as long as the limited data allow one to infer, the Darriwilian is characterised by a relatively low contribution from *Baltoniodus* (Löfgren 1995). This places it relatively close to the Caledonides.

4.4.7. Jämtland. Northward of Dalarna, the faunal succession shows gradual increase in contribution from the *Baltoniodus* lineage typical for the Baltic region (Fig. 15; supplementary Tables 14, 22, 24–26, 30). It slowly became more and more important after its appearance as *B. triangularis* and, after a
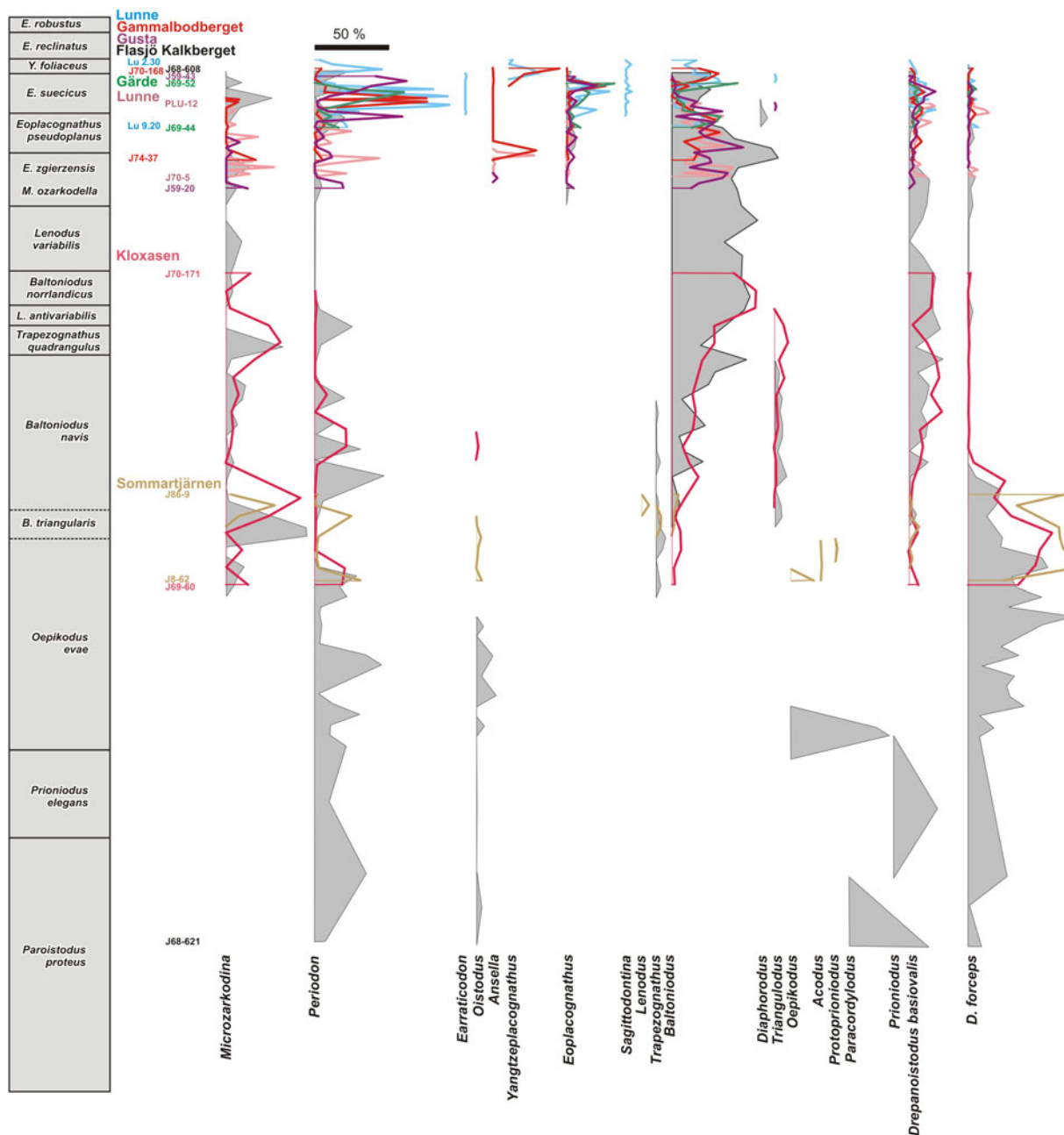
Figure 15 The Ordovician conodonts succession recorded at Gammalbodberget, Gusta, Gärde, Kloxåsen, Sommartjärnen and Lunne (data from Löfgren 1978; Zhang & Sturkell 1998; supplementary Tables 14, 22, 24–26, 30) in Jämtland, Sweden.

period of domination, retreats near the end of the local conodont record in the *Eoplacognathus robustus* Zone (Löfgren 1978; Zhang & Sturkell 1998; Zhang 1999).

4.5. Exposures of the Ordovician rocks within the Caledonides

The true Caledonian conodont communities, as represented in Swedish (Fig. 16; supplementary Tables 14–16; Rasmussen 2001) and Norwegian (Fig. 17; supplementary Table 17; Rasmussen 2001) localities, show a relatively low contribution from *Baltoniodus* but high contribution from *Protopanderodus rectus*. This was proposed to be an expression of the marginal position in respect to oceanic cold waters (Rasmussen & Stouge 2018). Equally high frequency of *P. rectus* in Scania supports this idea. The relatively high frequency of *Polonodus* is an expression of proximity to Newfoundland.

The faunal disparity between Baltic and North American Midcontinent conodont faunas is well recognised (e.g., Sweet & Bergström 1974). Conodonts of clearly Laurentian affinities occur in the Trondheim region, Norway and in western Sweden, well within the Caledonian orogenic belt (Bergström 1979, 1997; Tolmacheva & Roberts 2007). Perhaps of some significance is also the co-occurrence of *Oepikodus evae* with *Trapezognathus* in Herram and Steinsodden, located relatively westward (Rasmussen 2001). Unless a result of reworking, this would indicate significantly longer persistence of *Oepikodus* there than in other parts of Baltica.

5. Origins and decline of the Baltic conodont fauna

The only euconodont lineage that undoubtedly passed the Cambrian–Ordovician boundary in the Baltic region is that of the cordylodontids. Its oldest member is *Cordylodus andresi* Viira & Sergeeva in Kaljo *et al.* 1986 in the Maardu Member of the Kallavere Formation (early Pakerort age; Viira *et al.* 1987).
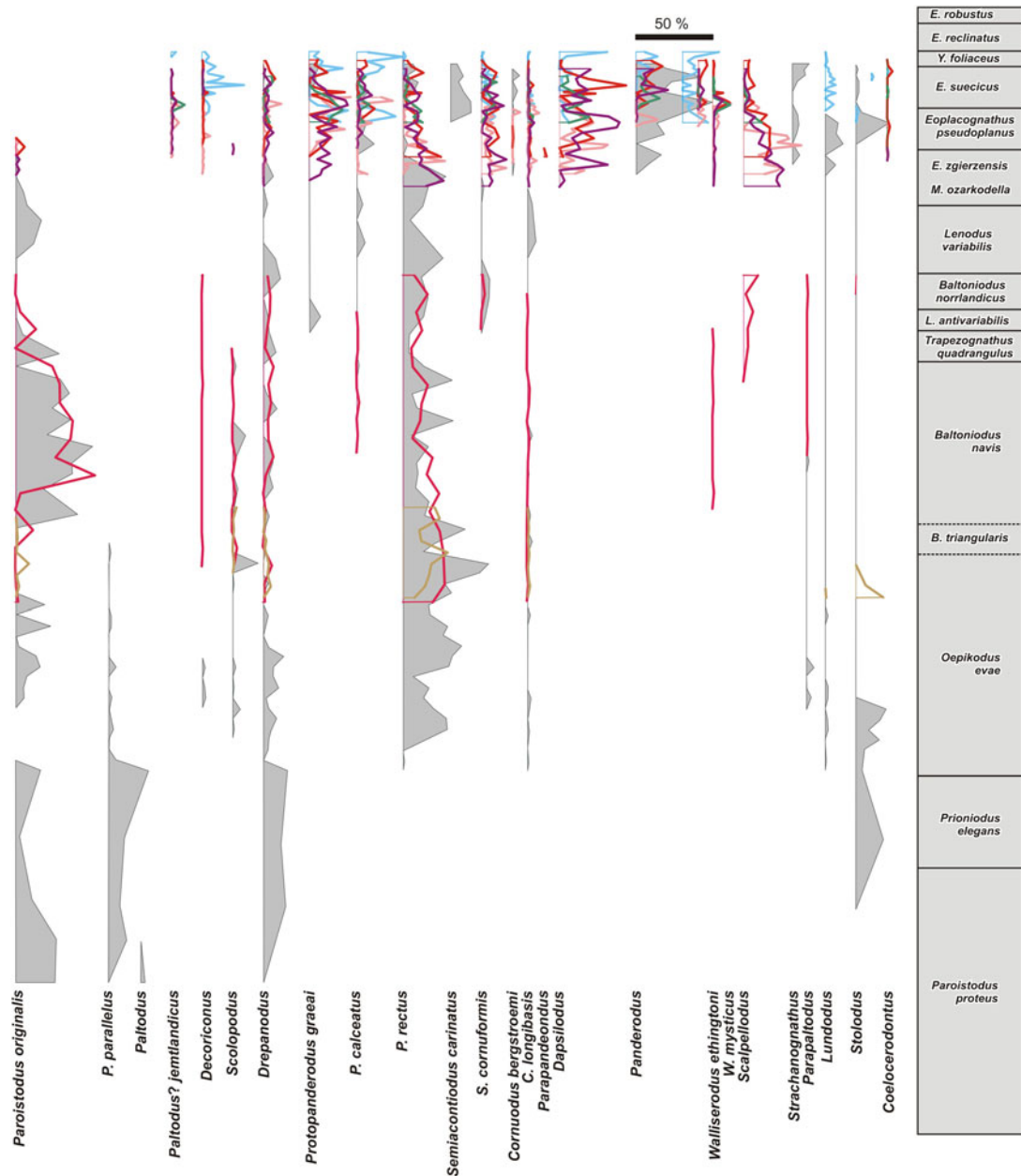
Figure 15 Continued.

Conodonts of this age are known also from Öland (Bagnoli & Stouge 2014) and erratic boulders in mainland Sweden (Löfgren & Viira 2007). All elements of the *C. andresi* apparatus are prominently denticulated, which probably originated from the serration in *Proconodontus serratus* Miller 1969. *Cordylodus proavus* Müller 1959, the next in the lineage, characterises the latest Cambrian (Mens *et al.* 1993, 1996), being known in Estonia but not in Sweden, where this time span probably corresponds to a stratigraphic hiatus (Szaniawski & Bengtson 1998). The earliest Tremadocian in both areas is represented by the *Dictyonema* Shale. The presence of ikaite crystals pseudomorphs in the *Dictyonema* Shale and in preceding late Cambrian black shales indicates sedimentation in low temperatures (Popov *et al.* 2019). This may mean that the dramatic transformation of the conodont faunas that follows was a result of an environmental change, possibly the northward drift of the Baltic continent and change of the climate from subpolar to temperate in the late Tremadocian to Dapingian.

The earliest euconodonts, as well as their probable relic late Palaeozoic successors (Dzik 2009), had a thin-walled crown (Szaniawski & Bengtson 1998), a feature of conodonts living in cold-water environments (Dzik 1997, p. 114). This makes isolated organic-rich basal bodies difficult to distinguish from complete earliest conodonts with an extremely thin (and perhaps weakly mineralised in some Cambrian 'paraconodonts') crown tissue cover. The extent of the crown may occasionally be visible on the surface of elements that otherwise look like 'paraconodonts' (Dzik & Moskalenko 2016, fig. 4). The latest Cambrian form attributed to the relatively advanced euconodont *Acodus* by Müller & Hinz (1991) is related rather to the westergaardodinid (paraconodont) *Furnishina*.

The finding of *Iapetognathus* in the sandy Rannu Member of the Kallavere Formation marks the beginning of the Ordovician in Estonia (Heinsalu *et al.* 2003; Nõlvak *et al.* 2006). The conodont assemblage there is dominated by species of *Cordylodus*. A transgressive black shale follows upward. Above its bioeroded surface, another set of sandy sediment, well represented in boreholes, yielded the first member of the *Paltodus* lineage, *P. pristinus* Viira, in Viira *et al.* (1970). In the most complete Swedish late Tremadocian section at Brattefors in Västergötland, this
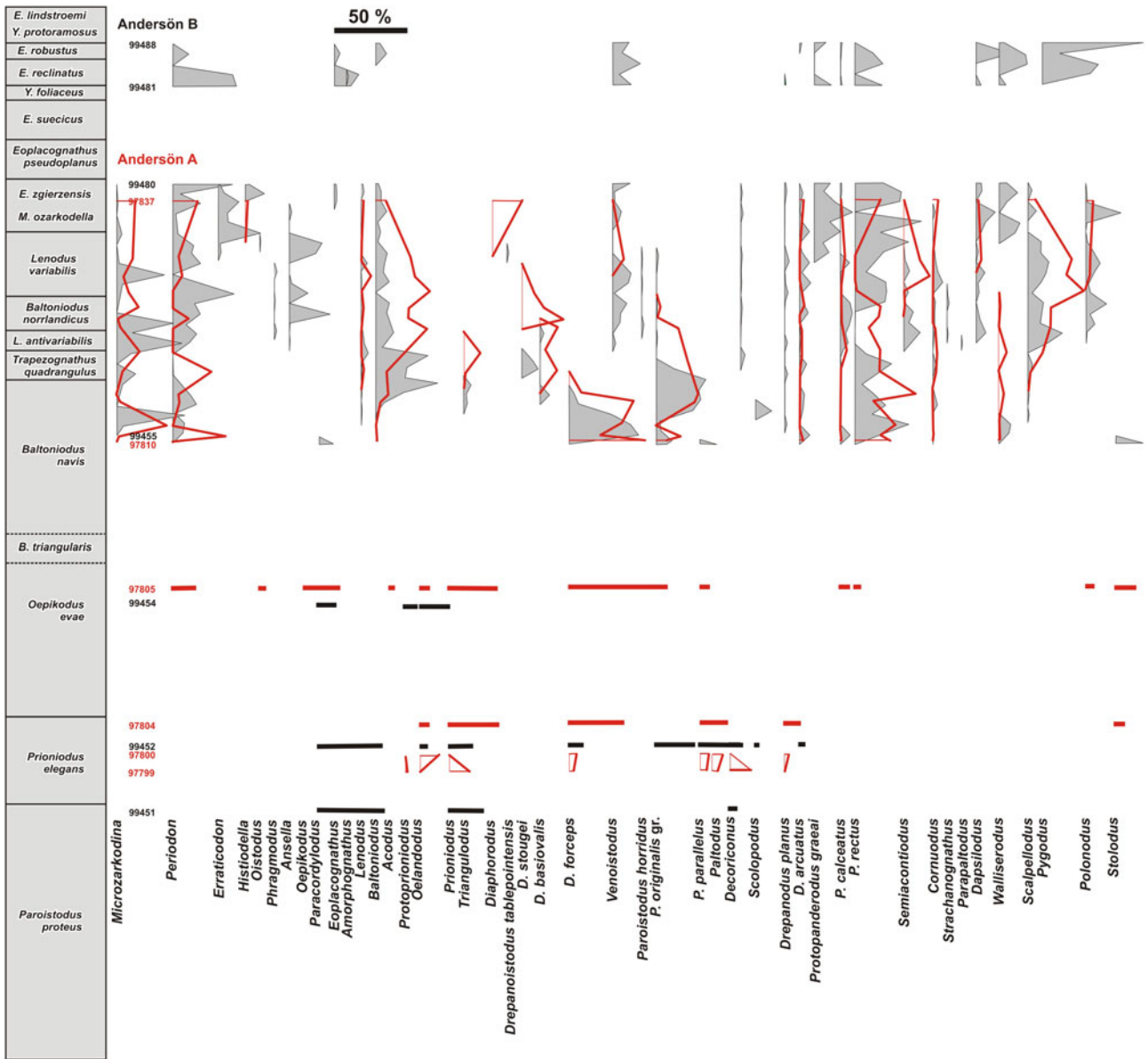
Figure 16 The Ordovician conodonts succession recorded at Andersön (data from Rasmussen 2001; supplementary Table 15) in the Swedish Caledonides.
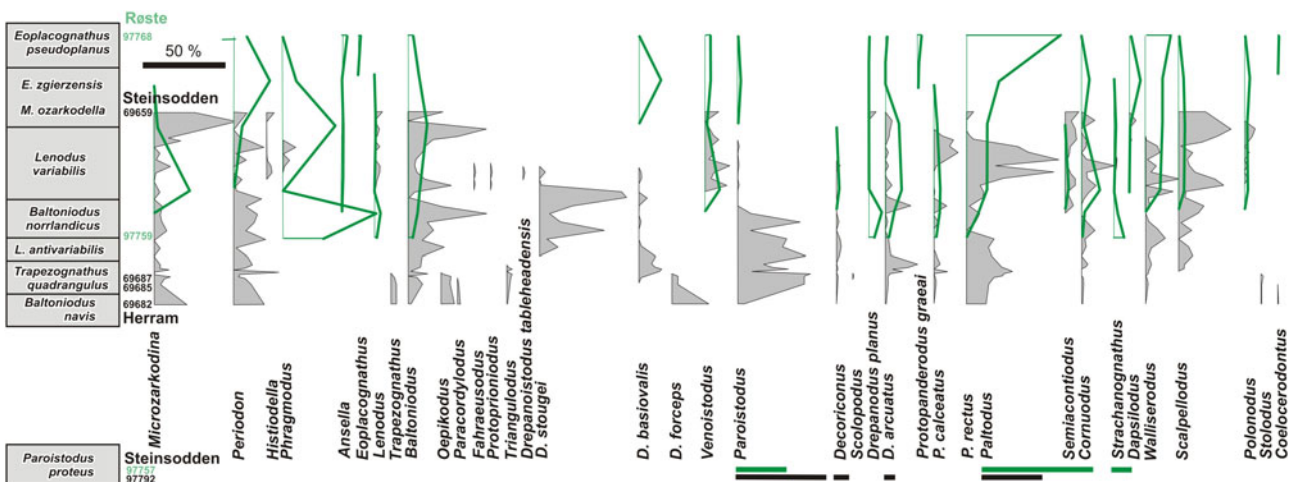

Figure 17 The Ordovician conodonts succession recorded at Herram, Steinsodden, and Røste (data from Rasmussen 2001; supplementary Tables 3, 17) in the Norwegian Caledonides.

species occurs as reworked with *Cordylodus*, *Iapetognathus* and several other species of Laurentian affinity (Löfgren 1997a). The origin of *P. pristinus* remains unknown but its presence in transgressive chalcedonites (Szaniawski 1980) in the Holy Cross Mountains, representing the Małopolska microcontinent of Gondwanan affinity (Dzik 2020), suggests its immigration as a part of a whole fauna with an eustatic sea-level rise possibly connected with a global climate warming.

The *Paltodus* lineage continued its occurrence in Baltica long enough to record its morphological transformation. It occurs in Estonia usually redeposited in a sandstone succession, mixed with specimens of *P. deltifer* morphology (Löfgren *et al.* 2005), which may result from reworking or from application of the vertical concept of chronospecies. In northern Estonia the late Tremadocian strata with *Paltodus deltifer* are mostly represented by argillaceous clay that changed to glauconitic sandstone in the *Paroistodus proteus* and *Prioniodus elegans* Zones and to the glauconitic limestone near the *P. elegans*–*Oepikodus evae* Zones transition (Viira *et al.* 2006b). Members of the *Paltodus* lineage dominated many Baltic fossil assemblages and this can be seen also at Ottenby in Öland. Soon it was supplemented with *Drepanodus*. The distacodontids invaded later and gradually increased their contribution, but generally the Tremadocian conodont faunas in Baltica are of low taxonomic diversity.

Jumudontus, the conodont of Australian origin (Nicoll 1992), occurred sporadically in the *P. elegans* Zone (e.g., Bergström 1988; Tolmacheva *et al.* 2001b; Viira *et al.* 2006b). Bagnoli & Stouge (1997) found it at Horns Udde, Öland, well above the *O. evae* Zone.

Based on data from the Horns Udde locality in Öland, Bagnoli & Stouge (1997) concluded that the conodont communities changed from cosmopolitan to provincial Baltic during the time span from the late Tremadocian (Hunneberg age) to early Darriwilian (Kunda age). The beginning of this transition has its best record in limestone concretions within black shale at Brattefors in Västergötland (Löfgren *et al.* 1999), limestone at Ottenby in Öland and sandstone at Uuga, Estonia (Löfgren *et al.* 2005). In the last locality, reworking significantly obliterated the record and makes it difficult to interpret. The Ingria region near St Petersburg, where the Christian Pander's Ordovician samples came from, provided a good record of conodont species succession in the Volkhov and Kunda ages owing to detailed works by Tolmacheva *et al.* (2001a, 2001b, 2003) but younger strata there are poor in conodonts.

After the global scale episode of *Oepikodus evae* expansion, the standard Baltic conodont community, dominated by *Baltoniodus*, *Eoplacognathus*, *Microzarkodina*, *Protopanderodus* and *Scalpellodus*, emerged. More lineages enriched the fauna, probably an effect of immigration from environmentally similar regions, where they allopatrically had speciated. Most of these changes can be explained as a result of continental drift of Baltica from its originally subpolar to equatorial position (Rasmussen & Stouge 2018). A significant enrichment of the fauna occurred in the Sandbian, with immigration of *Amorphognathus*, *Panderodus* and other less significant lineages. They all evolved anagenetically in place. The prolonged faunal stability in the Darriwilian to Sandbian was probably a result of temperate climatic conditions. Apparently the climate was the main factor controlling the transformation of Baltic conodont fauna. Brief global warmings were probably responsible for the short time immigrations of lineages of low biological productivity, which do not significantly contribute to fossil assemblages (*Erraticodon*, *Spinodus*, *Cahabagnathus*, and *Complexodus*).

There were apparent changes in the degree of provincialism of Baltic conodonts (Bergström 1990). The Katian Oandu age experienced immigration of Laurentian species to Baltica, probably as the result of global warming (Männik 2017). The Late Ordovician sediments were generally shallow-water in the East Baltic and conodont assemblages preserved in them are usually of low diversity (Kaljo *et al.* 2008; Hints *et al.* 2010; Männik & Viira 2012; Kröger *et al.* 2014) as are those from the Baltic limestone (Ostseekalk) erratics (Kröger *et al.* 2020). The late Katian experienced a rather profound rebuilding of the fauna. It was supplemented by a mix of subtropical forms (such as *Yaoxianognathus* and *Rhodesognathus*). The immigration of the *Yaoxianognathus* lineage, ancestral to post-Ordovician ozarkodinids, is the most significant. Its close relative is known from the North American Midcontinent (Leslie 2000), but the evolutionary roots were probably in the Darriwilian of the Argentinian part of Gondwana (Albanesi *et al.* 2023). The Oandu warming was terminated with the immigration of conodonts with thin basal cone walls typical of subpolar environments (such as *Icriodella*, *Hamarodus*, *Scabbardella*, *Pseudooneotodus* and *Sagittodontina*). This was connected with a reduction of species richness and with generally lower secondary biological productivity of the ecosystem (if the generally low contribution of conodont elements to the rock is meaningful).

The Hirnantian global cooling marks completion of the Ordovician epoch in the evolution of conodonts. The glaciation had its expression in immigration of the cold-water *Noixodontus* fauna at the beginning of the Porkuni age (Nõlvak *et al.* 2006; Kaljo *et al.* 2008). The latest Ordovician sees a decrease in conodont diversity and their abundance in the rocks has been recognised in Sweden (Bergström *et al.* 2011).

Admitting all methodological limitations of the inference on biology of conodonts, one may conclude that their fossil record offers probably the richest and most complete information about ecology and evolution among the fossil taxa. In terms of the volume, but not number of individuals, the Baltic Ordovician conodont species *Scandodus rhomboideus* in the Floian, *Trapezognathus pectinatus* and *Eoplacognathus robustus* in the Darriwilian, and *Protopanderodus liripipus* and *Yaoxianognathus rhodesi* in the Katian ruled in their communities. The opposite end of the spectrum was occupied by species of the longranging *Decoriconus*. Its elements are of minute size, but their contribution in number of elements is equally insignificant.

6. Competing interests

The author declares none.

7. Supplementary material

Supplementary material is available online at https://doi.org/10.1017/S1755691024000070.

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