

Neodymium isotopic composition of Cambrian–Ordovician biogenic apatite in the Baltoscandian Basin: implications for palaeogeographical evolution and patterns of biodiversity

ULF STURESSON*, LEONID E. POPOV†, LARS E. HOLMER*, MICHAEL G. BASSETT†‡, SERGEI FELITSYN‡ & BORIS BELYATSKY‡

*Institute of Earth Sciences/Historical Geology and Paleontology, Uppsala University, Norbyvägen 22, 75236 Uppsala, Sweden

†Department of Geology, National Museum of Wales, Cardiff CF10 3NP, Wales, UK

‡Institute of Precambrian Geology and Geochronology, Russian Academy of Science, 199034 St Petersburg, Russia

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Abstract – Biogenic apatite preserved in 148 samples of conodonts and organophosphatic-shelled brachiopods from Cambrian through Ordovician successions of the Baltoscandian Basin (Baltica Plate) preserves a sensitive record of early Palaeozoic sea-water chemistry interpreted via neodymium isotope ratios. Consistent $\epsilon_{\text{Nd}}(t)$ values of -9.6 to -8.3 for Lower to Middle Cambrian samples suggest no significant lateral or temporal variation across the region. Average Upper Cambrian values are -7.2 to -7.7 . Sedimentary analysis suggests that the influence of continental weathering from Baltica as a major source of radiogenic Nd was negligible. Ordovician samples show a rise to -5 to -6 in the early Arenig, early–mid Llanvirn and late Caradoc. Sea-water mixing from the southeast Iapetus Ocean was a constant factor throughout Cambrian–Ordovician times. The rise reflects erosion of obducted volcanic arc complexes along the Caledonian margin, and probably also relates to pollution of the Baltica sector of Iapetus from the approaching Avalonia Plate. Patterns of evolutionary biodiversity and palaeobiogeographical linkages support the geochemical signatures in interpreting the tectonic history of the region. Extinction of lingulate brachiopod faunas in the Tremadoc, followed by subsequent recovery and emergence of benthic assemblages typical of the Ordovician Evolutionary Fauna in the Billingen–early Volkhov regional stages coincide with significant changes in geochemical characteristics of water masses across the Baltoscandian basin. The early and mid Ordovician (Arenig to Llandeilo) brachiopod faunas of the North Estonian Confacies Belt are characterized by high endemism and low turnover rates, whereas increased immigration resulted in the extinction of a number of local lineages in the late Llanvirn. From the mid Caradoc to mid Ashgill, when Baltica was drifting on a course to collide eventually with Avalonia and gradually approach Laurentia, brachiopod assemblages were characterized by higher turnover rates. At the same time they gradually became more cosmopolitan and less influenced by the invasion of new faunas.

Keywords: Cambrian, Ordovician, Baltica, biogenic apatite, neodymium isotopes, palaeogeography, biodiversity, tectonic evolution.

1. Introduction

Lower Palaeozoic sedimentary rocks of Sweden and the East Baltic region preserve an exceptionally detailed and almost continuous stratigraphical record of the environmental and faunal history of the Baltoscandian Basin. Cambrian to Lower Ordovician sands and clays in the East Baltic sequences are commonly unconsolidated and can be studied in the manner of Recent sediments. Ordovician carbonates throughout almost the whole of Baltoscandia are affected only slightly by diagenesis and usually contain skeletal remains with pristinely preserved primary structures (Holmer, 1989; Szaniawski & Bengtson, 1993). The absence

of any significant thermal alteration throughout the sedimentary sequences is indicated by generally low conodont alteration indices (CAI) within the range of 1 to 1.5 (our observations). The basin thus forms an ideal field laboratory for geochemical studies, and in particular for the investigation of various isotopes, including neodymium (Nd), as sensitive indices of geological history (e.g. Felitsyn *et al.* 1998).

Biogenic apatite preserved in a wide range of fossils forms an archive of geochemical/isotopic signatures of contemporaneous sea-waters (see review in Holser, 1997). Incorporation of rare earth elements (REE) into biogenic apatite takes place within 100 to 1000 years of post-mortem and early diagenetic stages of fossil history (Holmden *et al.* 1996). Thus, analyses of the Nd isotopic ratio (expressed as $\epsilon_{\text{Nd}}(t)$, which

§ Author for correspondence: Mike.Bassett@nmgw.ac.uk

represents deviations of the initial $^{143}\text{Nd}/^{144}\text{Nd}$ ratio in parts per 10^4 from the chondritic uniform reservoir) in fossil biogenic apatites can be used for provenance analysis, reflecting the proportion of radiogenic Nd in the sediment source area. Such analyses can then also be applied to the reconstruction of water mass circulation patterns and exchange between discrete oceanic reservoirs, as demonstrated elsewhere in the Phanerozoic, including the earliest Cambrian (Keto & Jacobsen, 1987; Stille, 1992; Stille, Steinmann & Riggs, 1996; Felitsyn & Gubanov, 2002).

Preliminary studies of Nd isotopic ratios from fossil biogenic apatites demonstrate that during the Cambrian and early Ordovician periods, palaeogeography and depositional environments within the Baltoscandian Basin were important factors in controlling $\epsilon_{\text{Nd}}(t)$ variation and REE concentration as preserved mostly in lingulate brachiopod shells and conodont elements (Felitsyn *et al.* 1998). Because there are only a few possible source areas, the Nd isotope compositions of biogenic phosphates also preserve important information relating to the evolution of water masses in the southeastern sector of the Iapetus Ocean during early Palaeozoic times.

The database for this paper incorporates a significantly greater number of Cambrian–Ordovician organophosphatic-shelled brachiopods and conodont elements ($n = 148$) in comparison to a previous initial study (Felitsyn *et al.* 1998). Our intention is to understand in more detail the composition of Iapetus Ocean sea-water through the mid Cambrian to mid Ordovician interval as reflected in geochemical signatures from biogenic apatite in Baltoscandia, and to relate the results to environmental and faunal evolution throughout the region.

2. Geological background

Material for geochemical studies was sampled from Lower Cambrian through Upper Ordovician deposits in central and southern Sweden and in the outcrop area of Lower Palaeozoic deposits south of the Gulf of Finland and of Lake Ladoga in the East Baltic states, the latter area being known as the Baltic–Ladoga Glint (Dronov *et al.* 1995). In Ordovician times the relevant areas of Sweden were within the Central Baltoscandian Confacies Belt, whereas localities in North Estonia and the St Petersburg region (Ingria) were confined within the North Estonian Confacies Belt (Jaanusson, 1976, 1995) (Fig. 1). Both belts existed as distinctive facies realms within the Baltoscandian Basin and differed from one another in characters of sedimentation and in faunal diversity and abundance, which are traceable from the Cambrian onwards.

The mid and late Cambrian were intervals of predominantly clastic deposition in Baltoscandia (Mens, Bergström & Lenzion, 1984; Popov *et al.* 1989).

In North Estonia and the St Petersburg region, sedimentary rocks of these ages comprise mostly well-washed, cross-bedded quartzose sandstones and some sandy siltstones and claystones with significant amounts of bioclastic material comprising almost exclusively the broken phosphatic shells of lingulate brachiopods, which form lenses and coquinoïd beds. Peritidal and shallow shelf depositional environments persisted in this part of the East Baltic for most of mid and late Cambrian times, as indicated by the widespread *Scolithos* ichnofacies and by traces of periodical dehydration of the periostracum in some obolide brachiopods (e.g. '*Obolus eichwaldi*') resulting from intermittent aerial exposure *in vivo* (Artyushkov, Lindström & Popov, 2000).

By the end of the Cambrian Period (*Cordylodus andresi*–*C. proavus* condont biozones), there was extensive accumulation of obolide coquinas in nearshore areas, suggesting substantial increase of biological productivity, while the presence of thin black shale units within shallow water quartzose sands of North Estonia provides evidence of increasing eutrophication of the basin (Popov *et al.* 1989). Such obolide coquinas were later reworked and redeposited in significant part as beach and bar systems of the early Tremadoc (*Cordylodus lindstromi*–*C. angulatus* biozones).

In the mid Cambrian of central and southern Sweden, deposition was mainly of outer shelf siliciclastic deposits, which were then replaced from the beginning of the late Cambrian (*A. pisiformis* Biozone) by finely laminated black Alum Shale facies in basinal environments containing a characteristic faunal assemblage dominated by olenid trilobites (Martinsson, 1974). Rapid regression linked to tectonism occurred in part of southern and central Sweden in the *Acerocare* Biozone (Artyushkov, Lindström & Popov, 1997, 2000). In this time the area now embracing southern and central Öland was raised above sea-level, which led to fresh-water flushing and chemical erosion of Alum Shale facies (Teves & Lindström, 1988).

Rapid sea-level rise on a scale of several tens of metres took place in Baltoscandia in the mid Tremadoc (*C. angulatus* Biozone), when accumulation of black '*Dictyonema*' Shale then became widespread to the east. By that time, the beach and bar systems of the East Baltic were submerged to at least storm wave base and thus saved from complete erosive destruction (Popov *et al.* 1989; Artyushkov, Lindström & Popov, 2000). Concurrently, the shallow-water benthic obolide assemblages disappeared completely, so that hexactinellide sponges remained the only benthic organisms abundant locally in the region.

In the late Tremadoc–early Arenig (*Paltodus deltifer*–*Prioniodus elegans* conodont biozones) the deposition of black shales ceased across the Baltoscandian Basin, and from that time deposition of carbonates (Bjorkasholmen and Latorp limestones) was initiated in the Central Baltoscandian Confacies Belt (Jaanusson,

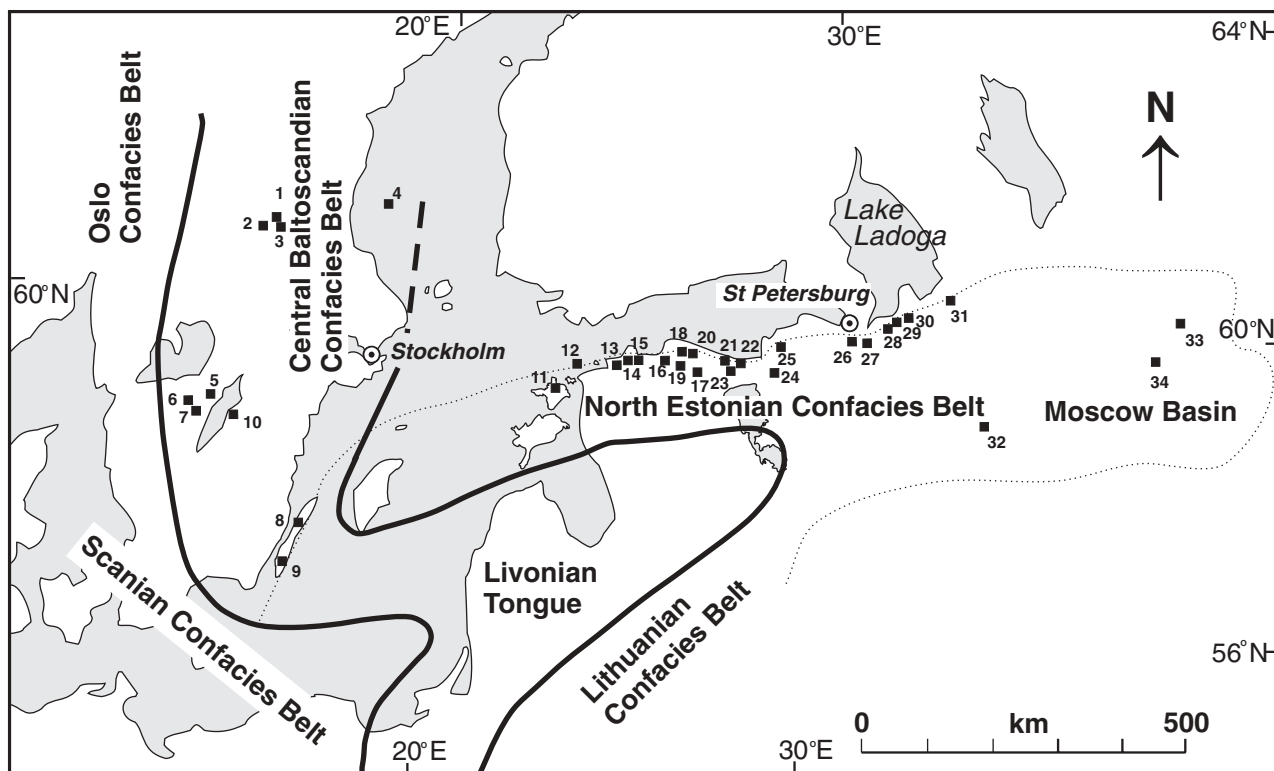


Figure 1. Distribution of Ordovician confacies belts in Baltoscandia, showing location of organophosphatic brachiopod and conodont samples referred to in this paper. Sweden: 1 – Fjäckå; 2 – Kårgårde; 3 – Osmundberg quarry; 4 – Finngrundet core; 5 – Skövde; 6 – Stora Backor; 7 – Älleborg; 8 – Köpingsklint; 9 – Eriksöre; 10 – Bårstad quarry. North Estonia: 11 – Osmussar; 12 – Kõrgessare; 13 – Keila-joa; 14 – Harku and Mäekalda; 15 – Maardu and Ülgase; 16 – Core 77; 17 – Core 1653; 18 – Toolse and core T-3; 19 – Aluvere; 20 – Kunda; 21 – Saka; 22 – Valaste; 23 – Kohtla-Järve. Northwestern Russia: 24 – core 208; 25 – Suma; 26 – Izhora; 27 – Tosna; 28 – Nazya; 29 – Putilovo quarry; 30 – Lava; 31 – Syas; 32 – Seliger core; 33 – Orekhovo core; 34 – Tolbukhino core.

1995). Contemporaneously in the North Estonian Confacies Belt, this was a period of deposition of condensed, laminated glauconitic clays with thin interbeds of fine-grained glauconitic sand and silt representing distal tempestites (Dronov, 1998; Tolmacheva *et al.* 2001). The main source of this clastic material is uncertain, but was not improbably from nearby bar systems built of quartzose glauconitic sand; their remnants are preserved in northwestern Estonia and contain a characteristic *Thysanotus–Leptembolon* linguulate brachiopod assemblage (Popov & Holmer, 1995).

From early Arenig times (*Oepikodus evae* Biozone), carbonate sedimentation became widespread across the whole of Baltoscandia. In the Arenig (Billingen and Volkhov regional stages), storm generated sedimentation was characteristic of the North Estonian Confacies Belt. Background deposits were very slowly accumulating silty clays, whilst beds of bioclastic limestone represent proximal to distal tempestites formed during rare strong storm events (Dronov, 1998; Tolmacheva *et al.* 2001).

In detail the nature of carbonate sedimentation changed gradually through the Ordovician, concomitant with the rapid northerly drift of Baltica (Torsvik, 1998), and up to nine sets of depositional sequences can be recognized. A low average sedimentation rate of only

1 to 3 mm per 1000 years and distinctive characteristics of the carbonate sedimentation (Jaanusson, 1982) suggest that sea-level fluctuation was one of the important factors leading to lithofacies variation and in defining sequence boundaries within the Ordovician (Dronov & Holmer, 1999).

Palaeomagnetic data for the Cambrian Period place Baltica in high southerly latitudes throughout the Cambrian (Torsvik & Rehnström, 2001), in fairly close proximity to the Gondwana margin. This position is also supported by the distribution of olenid trilobite facies in the late Cambrian (Shergold, 1988). Faunal linkage with West Gondwana persisted until the Hunnebergian (latest Tremadoc–early Arenig) when the *Thysanotus–Leptembolon* assemblage was widespread around Baltica (Popov & Holmer, 1994, 1995), but such relationships weakened considerably by mid Arenig times when Baltoscandian benthic faunas became increasingly endemic (Cocks & Fortey, 1998; Cocks, 2000). This interval coincided with rapid northwesterly drift and anticlockwise rotation of Baltica in the Ordovician as recognized from palaeomagnetic data (Torsvik *et al.* 1996). By Caradoc times, Baltica approached low latitudes and collided with Avalonia sometime in the Ashgill (Torsvik, 1998; Torsvik *et al.* 1996).

There is no record of any volcanic activity in the proximity of the Caledonian margin of Baltica in the Cambrian and early Tremadoc. The earliest indirect evidence of input of volcanic ash into sediment is from the isotopic composition of sulphur in the 'Dictyonema' Shale (*Cordylodus angulatus* Biozone) of North Estonia, suggesting a mantle source (Petersell *et al.* 1987). The first beds of tephra are recorded in the Billingen Stage of south-central Sweden (Lindström, 1979), and ash beds then occur sporadically in Baltoscandia within the stratigraphical interval spanning the Kunda–Aseri regional stages (latest Arenig–early Llanvirn); it is likely that the iron forming ferruginous ooids in that interval is from volcanic sources (Sturesson, 1995; Sturesson, Dronov & Saadre, 1999). Numerous K-bentonite beds and interbeds occur in the lower and middle Caradoc. Trace element geochemistry indicates derivation of the pyroclasts from a mature volcanic arc formed on an Andean-type plate margin (Roberts, 1982; Huff, Bergström & Kolata, 1992), probably indicative of the approach of Avalonia prior to collision with Baltica.

Note. For correlation of the long-established Regional Stage divisions in the Ordovician of Baltoscandia with the more widely used Tremadoc to Ashgill Series nomenclature, see Jaanusson (1982), Männil & Meidla (1994) and Raukas & Teedumäe (1997).

3. Geochemistry

Samples used for geochemical analysis mainly comprised late Cambrian and Ordovician organophosphatic-shelled brachiopods and Ordovician conodont elements. Reference data for Vendian to Lower Cambrian sediments were obtained from argillites and phosphorites (Felitsyn & Gubanov, 2002; see Appendix, Table 1). The late Cambrian lingulide and siphonotretide brachiopod genera *Ungula*, *Obolus*, *Schmidtites* and *Helmersenina*, the Ordovician lingulides *Thysanotos*, *Aulonotreta* and *Lingulasma*, and several taxa of micromorphic brachiopods (mostly acrotretides and siphonotretides) provided the main source of data. Conodonts were a mixture of euconodont taxa. Typically, each sample included tens of discrete fossils. Wherever possible, the taxonomic identity was determined (Table 1, Appendix). In some samples with small amounts of fossil apatite (< 0.2–1.5 mg), assemblages of fragments from different taxa or a mixture of brachiopod shell fragments and conodont elements were used. This mixture of sample material has led to a scatter of the data at some levels, with consequences for the statistical evaluation of results.

It is already known (Felitsyn *et al.* 1998) that in the East Baltic there is a significant difference between values of $\epsilon_{\text{Nd}}(t)$ for the Cambrian and those for the Ordovician. The expanded data set employed here for biogenic phosphates shows that the estimated

arithmetic mean value plus or minus one standard deviation of the $\epsilon_{\text{Nd}}(t)$ on the northwestern Baltic Plate is -6.2 ± 1.4 ($n=85$) for Ordovician fossil apatite, and -7.9 ± 1.15 ($n=10$) for the Cambrian. The $\epsilon_{\text{Nd}}(t)$ signatures in fossil apatite and host rock are shown in Figure 2. Only fine-grained shale (Nd content 30–50 ppm) was used for comparison, on the assumption that quartz sand and limestone could not significantly distort the Nd isotope composition of fossil apatite during isotopic exchange in the post-sedimentary stage. A bulk REE content of about 5–10 ppm and Nd content of ~ 2 ppm is characteristic for Ordovician quartz sand and limestone from Baltoscandia. For comparison, the mean value of Nd concentration in fossil apatite is 935 ± 114 ppm ($n=141$).

The absence of correlation between $\epsilon_{\text{Nd}}(t)$ values in Ordovician biogenic phosphates and host rocks (Fig. 2) indicates negligible secondary isotopic exchange in the post-sedimentation stage (see also Felitsyn *et al.* 1998). Fine-grained *Dictyonema* Shale (lowest Tremadoc, St Petersburg region) enriched with organic matter records $\epsilon_{\text{Nd}}(t) = -10.7$, whereas conodont elements of *Cordylodus angulatus* and shells from the same sample have $\epsilon_{\text{Nd}}(t) = -7.0$ and -7.7 , respectively (sample DS-6). Shells of the brachiopod *Broeggeria salteri* from *Dictyonema* Shale on Öland, southern Sweden, on the other hand have $\epsilon_{\text{Nd}}(t) = -9.6$ compared with $\epsilon_{\text{Nd}}(t) = -6.7$ for the host rock (sample 144). The assumption of the original nature of the Nd isotope composition of biogenic apatite is therefore regarded as realistic.

A proportion of radiogenic Nd from source areas bounding a basin reflects the $\epsilon_{\text{Nd}}(t)$ ratio in modern day sea-water, and river input of Nd is the most important mechanism of transport into the basin (Goldstein & Jacobsen, 1987). Thus, Recent water masses have differing Nd isotopic signatures that reflect the chemical input from surrounding land. Values vary from $\epsilon_{\text{Nd}}(0) = -15.1 \pm 3.4$ in the north Atlantic, bordered largely by ancient crystalline basement, through -8.3 ± 1.2 in the Indian Ocean to -3.5 ± 1.7 in the Pacific, which are areas bounded largely by tectonically active margins (Bertram & Elderfield, 1993).

The recent study by Holmden *et al.* (1998) reveals significant lateral variation in Nd and C isotope composition across the mid Caradoc epeiric seas covering eastern Laurentia, which suggests restricted circulation between epicontinental and oceanic water masses and allows the identification of three different aquafacies. No similar lateral variation has been recognized from our samples across the Baltoscandian Basin during the mid Cambrian to mid Ordovician. Lower to Middle Cambrian apatite from the region south of Lake Ladoga, Estonia and from various parts of Scandinavia shows an average $\epsilon_{\text{Nd}}(t)$ value of -8.9 . The similarity of Upper Cambrian $\epsilon_{\text{Nd}}(t)$ values (average -7.3) in lingulate brachiopod shells

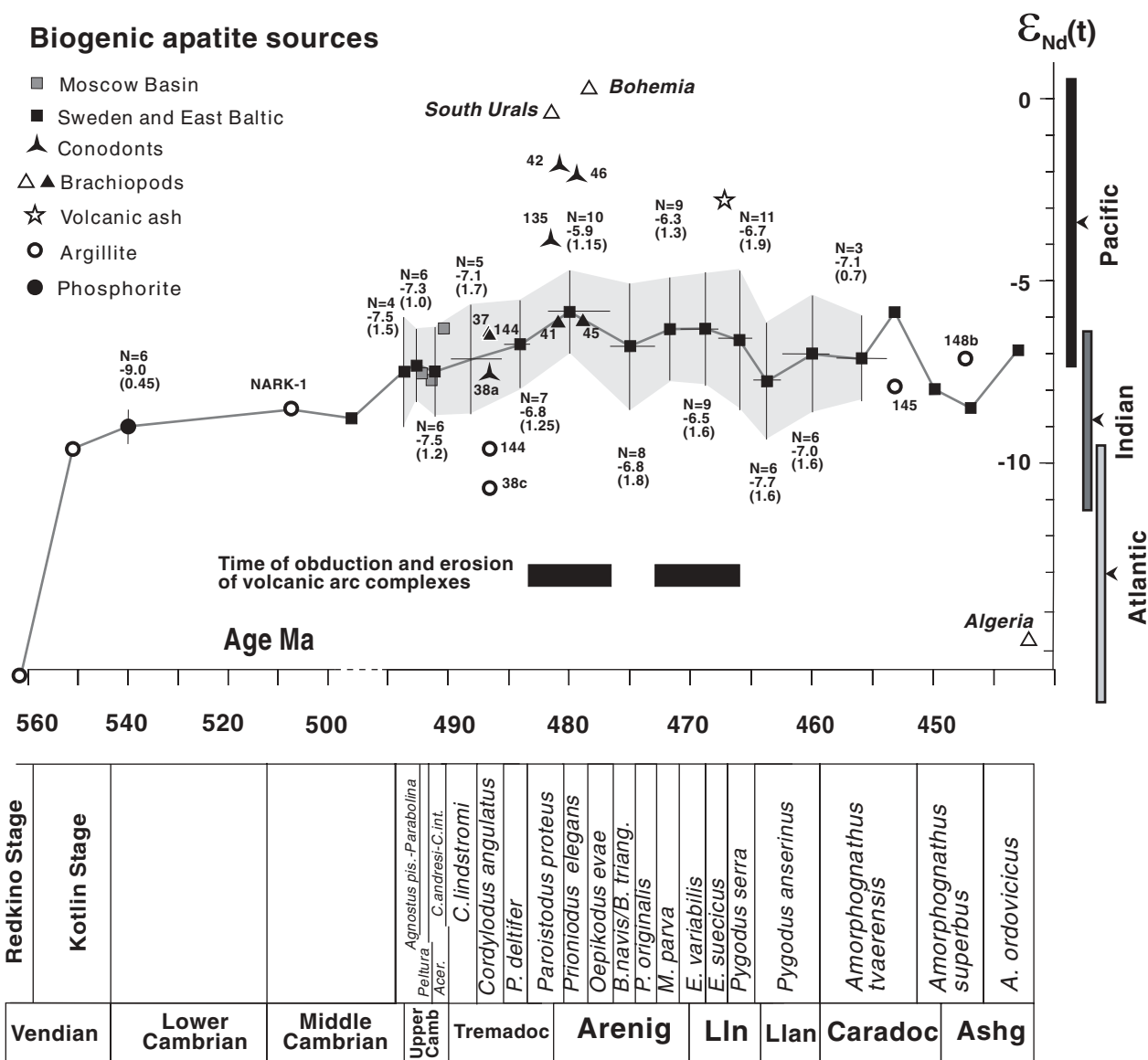


Figure 2. Variation of average ϵ_{Nd} values (black squares) and their standard deviations in Vendian to Middle Cambrian sediments (argillite and phosphorite) and Middle Cambrian to Ordovician biogenic apatite, plotted at the mid-point in each time interval. Reference data for ϵ_{Nd} values of biogenic apatite from the Upper Cambrian of the Moscow Basin are shown as grey squares and for regions outside Baltoscandia as white triangles. The black squares and circles denote average values from a number of samples in the same time slice; individually numbered samples are based on a single analysis from one locality. Nd isotopic composition of Recent oceans is shown on the right side of the diagram as ϵ_{Nd} mean values indicated with arrows plotted against bars at 95 % confidence interval (modified from Bertram & Elderfield, 1993). Original geochemical data used are set out in Table 1. Lln – Llanvirn; Llan – Llandeilo; Ashg – Ashgill.

from a number of localities within Baltica, including the Moscow Basin ($\epsilon_{Nd}(t) -7.2 \pm 0.8, N=3$), St Petersburg region ($\epsilon_{Nd}(t) -7.7 \pm 1.0, N=6$), Estonia ($\epsilon_{Nd}(t) -7.2 \pm 1.4, N=9$), and Sweden ($\epsilon_{Nd}(t) -7.2$) is evident. These data, as well as the unimodal distribution of the $\epsilon_{Nd}(t)$, indicate median values of about -7.0 to -8.0 as original signatures of water masses for the whole Baltoscandian Basin during late Cambrian times (Fig. 2; Appendix, Table 1).

The most important difference between the pattern described by Holmden *et al.* (1998) for the mid

Caradoc Mohawkian sea of Laurentia and that of the Baltoscandian Basin is the absence of low negative values characteristic of Midcontinent aquafacies ($\epsilon_{Nd}(t) -15.4 \pm 2.6$). A similar value was also obtained from a reference sample from the late Ashgill of the West Gondwana margin affected by glaciation ($\epsilon_{Nd}(t) -14.9$) (Hamoumi, 1999). The Cambrian values for Baltoscandia are comparable with those reported by Holmden *et al.* (1998) for the Taconic aquafacies ($\epsilon_{Nd}(t) -7.5 \pm 2.3$), which characterize a foreland basin and probably resulted from mixing of Midcontinent and

Iapetus ocean waters. This may suggest that input of 'old' Nd by freshwater runoff from the Precambrian shield into the Baltoscandian Basin was negligible, and that a significant part of the East European Platform was either covered by a shallow sea or was a lowland not affected significantly by erosion. Very low, distinctive negative $\epsilon_{\text{Nd}}(t)$ values (-13 to -32) are also reported for the Laurentian Midcontinent and Newfoundland in the early and mid Ordovician by Wright, Barnes & Jacobsen (2002; see also Shields & Veizer, 2004, p. 69), but the data set summarized in these papers is insufficient for recognition of $\epsilon_{\text{Nd}}(t)$ variations in sea-water around the Laurentian margin through this interval. As there is no evidence of volcanic island arcs in the proximity of the Caledonian margin of Baltica in the Cambrian, and because of the passive margin development during that period along the southeastern sector of the Iapetus Ocean, it is most probable that mid and late Cambrian $\epsilon_{\text{Nd}}(t)$ values for Iapetus oceanic waters were more negative by comparison with the Ordovician and are comparable with mean values recorded in the Recent Atlantic and Indian oceans (Fig. 2). Thus the Baltoscandian water masses probably exchanged freely with those of the adjacent sector of Iapetus, and their Nd isotopic composition represents an original or only slightly modified signature of the relatively adjacent contemporaneous oceanic water masses.

With a transgressive sea-level rise in the mid Tremadoc and a eustatic high sea-level stand during most of early and mid Ordovician times (Barnes, Fortey & Williams, 1995; Artyushkov, Lindström & Popov, 2000), the influence on Nd isotopic composition of freshwater runoff into the Baltoscandian Basin should have been lower than in the Cambrian. However, from late Cambrian–early Ordovician times, the introduction of a new source of radiogenic Nd into the basin resulted instead in a rise of $\epsilon_{\text{Nd}}(t)$ values in Sweden and the East Baltic through the late Arenig–Llanvirn (Hunneberg–Lasnamägi regional stages).

The most positive values are in the upper Hunneberg and Billingen regional stages ($\epsilon_{\text{Nd}}(t) -5.9 \pm 1.15$, $N=10$), which approach the lower limit estimated for unmodified waters of the Iapetus Ocean in the Ordovician (Samson *et al.* 1989; Holmden *et al.* 1998). This change is approximately coeval with the deposition of the earliest recorded tephra beds in south-central Sweden (Lindström, 1979), marking a significant tectonic event in the southeast sector of Iapetus involving the generation of a volcanic island arc outboard of the Caledonian margin to Baltica.

There is then an assumed drop in values to $\epsilon_{\text{Nd}}(t) -6.8 \pm 1.8$ ($N=8$) in the mid Arenig (*navis* and *originalis* biozones), and from the late Volkhov to Aseri interval (late Arenig to mid Llanvirn), the values seem to remain high but do not reach the average values of the early Arenig (Fig. 2). In the mid Llanvirn,

which was possibly the time of docking of the volcanic arc with the Caledonian margin of Baltica (Sturt & Roberts, 1991), $\epsilon_{\text{Nd}}(t)$ values again begin to drop, reaching -7.5 ± 1.8 ($N=6$) in the Uhaku Regional Stage (early Llandeilo), which is close to the Cambrian figures, and they remain low until the early Caradoc. From this pattern it is reasonable to interpret the higher values of $\epsilon_{\text{Nd}}(t)$ in the earlier Arenig and in the late Arenig–mid Llanvirn as reflecting an initial phase of obduction and erosion, followed by tectonic quiescence. It should be emphasized, however, that only the Arenig values are significantly higher than the early to mid Cambrian values, and minor deviations from the major trend are not statistically significant within the sampling density, and the interpretations are tentative.

From our data (Table 1), we note that in two conodont samples from early Arenig (Hunneberg) deposits of the St Petersburg region, $\epsilon_{\text{Nd}}(t)$ values increase up to -1.94 , with standard deviation well above the mean values characteristic of the Baltoscandian Basin, whereas $\epsilon_{\text{Nd}}(t)$ values from organophosphatic brachiopods obtained from the same localities or in the same lithostratigraphical unit are usually close to or somewhat below the average values (Fig. 2). Otherwise there are no significant differences in neodymium isotope composition of various types of biogenic phosphates in our samples (Fig. 2), and the one observed anomaly could represent an artefact related to the small sample size used in the analysis. These values are not used in the statistical evaluation of results.

A second rise of $\epsilon_{\text{Nd}}(t)$ during mid and late Caradoc times, with a maximum in the Oandu Regional Stage ($\epsilon_{\text{Nd}}(t) -5.8$), is apparent in our data; although weak, this can be linked probably with extensive volcanism in approaching Avalonia. When island arc volcanism ceased in Avalonia at the end of the Caradoc, the input of radiogenic neodymium into the Baltoscandian Basin then decreased rapidly; three Ashgill samples show low values varying from -6.5 to -8.9 .

In summary, it thus appears that the main source of radiogenic neodymium in the mid Cambrian through Ordovician interval in the Baltoscandian basin was from oceanic water masses of the southeastern sector of Iapetus. This interpretation is supported by the data produced by Andersen & Sundvoll (1995), which indicate clearly that neodymium values in the Precambrian basement of the adjacent Baltica shield were consistently depleted (that is, elevated). All sedimentological and palaeogeographical reconstructions are consistent in indicating that the greater part of the Baltica platform was not covered by Lower Palaeozoic sediments but that the Precambrian basement rocks were exposed consistently throughout this interval; the implications are that the shield was essentially planated with very little surface relief and thus with negligible riverine run-off to provide a

Baltoscandian Basin (Popov, 1993). The diversity of lingulate taxa dropped to three to four genera by the end of that interval, and low diversity assemblages of the shallow clastic shelf and nearshore dominated by endemic lingulides (e.g. *Obolus*, *Schmidtites*, *Ungula*) became extinct (Popov *et al.* 1989). This was also a time of marked environmental changes in Baltoscandia, including substantial sea-level rise and the spread of extensive black shale accumulation towards the East Baltic (Artyushkov, Lindström & Popov, 2000). The latter event signified an increase of primary bioproductivity and possible stagnation of the basin.

Recovery in lingulate brachiopod diversity then took place during the *Paltodus deltifer* and *Paroistodus proteus* biozonal interval, when a distinctive micromorphic assemblage emerged together with the *Ceratopyge* trilobite fauna in the Central Baltoscandian and Scania confacies belts, and the *Thysanotos–Leptembolon* assemblage spread across the shallow shelf. These two assemblages had little in common with lingulate faunas evolved within the Baltoscandian Basin during the Cambrian, and their appearance is a clear indicator of major immigration by new faunas (Popov & Holmer, 1994, 1995). The short-lived *Thysanotos–Leptembolon* fauna has a circum-Baltica distribution (it is known also from the Holy Cross mountains in Poland and from the South Urals: Popov & Holmer, 1994, 1995) and occurs too in high-latitude faunas from northern peri-Gondwana, being known from Bohemia (Mergl, 1997) and Iran (Basset, Dastanpour & Popov, 1999). By contrast, associated assemblages of micromorphic lingulates had distinct affinities with faunas representative of some island arcs located eastwards of Baltica and which are now incorporated within a collage of orogenic belts in Kazakhstan and Central Asia (Holmer *et al.* 2000). Some of these arcs could represent remnants of an active eastern margin of Baltica during Cambrian–earliest Ordovician times (Popov & Holmer, 1994). It is likely that the dispersion of these faunas took place at temperate latitudes.

Micromorphic brachiopod assemblages (dominated by acrotretides) form a diverse and distinctive component of the Ordovician lingulate fauna (Fig. 3). After rapid diversification during the late Tremadoc–early Arenig, they remained fairly stable until the mid Caradoc, and declined slowly towards the end of the Ashgill. In terms of rates of faunal turnover, origination and extinction rates show negative correlation (correlation coefficient -0.69) in the Arenig–early Llanvirn (Billingen–early Kunda in Baltoscandian regional stratigraphy), but were then more or less equal and closely correlated from Aseri time (correlation coefficient $+0.80$ through the Aseri to Nabala interval; Fig. 3), with values that generally do not exceed 0.2 Lma. There are only two exceptions in the early Kunda, when origination rates (0.35 Lma) and extinction rates dropped to zero. This was then followed

by a marked increase in the extinction rate (0.21 Lma) near the Kunda–Aseri boundary, in a pattern closely comparable with that of rhynchonelliform brachiopods (Figs 4, 5). This latter group comprises the main stocks of organocarbonatic-shelled brachiopods, which we do not use in our isotopic analyses; nevertheless, it is instructive to plot diversity patterns for the rhynchonelliforms as an independent measure of biotic and environmental changes against which to interpret the factors leading to biochemical changes in the linguliform shells.

Figures 4 and 5 are diversity plots for 144 rhynchonelliform and craniiform genera across 21 stratigraphical intervals; the basis for plotting these data is the same as employed for Figure 3. Rhynchonelliforms comprise a minor and insignificant part of benthic assemblages in the Baltoscandian Basin until the Arenig, and they are completely absent in the East Baltic until the late Hunneberg–early Billingen interval (*Prioniodus elegans* Biozone; Fig. 4). The earliest Ordovician rhynchonelliform brachiopod-dominated benthic assemblages became established in the North Estonian Confacies Belt only from the early Arenig (Billingen), when a new medium-diversity benthic fauna of brachiopods, trepostomate bryozoans, ostracodes and echinoderms together with a new trilobite fauna dominated by asaphides immigrated into the region (Popov, 1993).

The generic diversity of rhynchonelliform assemblages increased gradually towards the mid Llanvirn (Aseri Regional Stage), followed by a considerable drop (Fig. 5). In the Llandeilo to mid Ashgill interval the number of genera oscillated between 24 and 33 for each time unit, and then rose in the mid Ashgill (Pirgu Regional Stage) to 42, followed again by a drop in the late Ashgill (Porkuni Regional Stage), marking the well-documented terminal Ordovician extinction (Barnes, Fortey & Williams, 1995).

Two different patterns emerge in the general character of turnover rates of rhynchonelliforms in the East Baltic Ordovician. After a relatively short interval of turnover in Billingen and early Volkhov times (*Prioniodus elegans–Baltoniodus navis* condont biozones), extinction rates achieved a relatively even background level, oscillating slightly between 0.06 and 0.09 Lma until the early Caradoc, apart from a single strong pulse in the mid Llanvirn (*Eoplacognatus suecicus*–lowermost *Pygodus serra* biozones) when it rose to 0.46 Lma. This is comparable only with the terminal Ordovician extinction rate (0.48 Lma). Background extinction rates for early to mid Ordovician brachiopods of Baltoscandia are twice as low as background levels for late Ordovician brachiopods of eastern North America (Patzkowsky & Holland, 1997).

Origination rates demonstrate a more dynamic pattern, with the highest values at about 0.30–0.40 Lma in the early Arenig, then with a gradual decline towards low values oscillating between 0 to 0.13 Lma during

Llandeilo–early Caradoc times (*Pygodus anserinus*–lower *Amorphognatus tvaerensis* biozones). This general trend was interrupted by two strong pulses in the latest Arenig (basal Kunda, *Eoplacognatus?variabilis* Biozone) and late Llanvirn (uppermost Kunda to Lasnamägi, *Eoplacognatus suecicus*–*Pygodus serra* biozones), each accentuated by a significant drop in origination rates just before each pulse.

The appearance of the new brachiopod fauna (Fig. 5) in the late Hunneberg–early Billingen of the East Baltic clearly reflects a major immigration. Because this fauna remains unknown in contemporaneous or slightly older deposits elsewhere around Baltica, with the exception of *Tetralobula* and *Angusticardinia* in the South Urals (Popov, unpub. data), it is natural to conclude that this early Ordovician fauna evolved originally outside Baltica, but it is difficult to define its source with certainty. It is remarkable that the assemblage already contains a significant number of Baltic endemics such as clitambonitides (*Neumania*) and gonambonitides (*Oslogonites*), *Lycophoria*, *Porambonites*, the earliest strophomenides (*Plectella*) and endopunctate orthides (*Paurorthis*). Some other genera occur in approximately contemporaneous deposits of South America (*Orthidium*) (Herrera & Benedetto, 1989), North Africa and Bohemia (*Apheoorthina*, *Ranorthis*, *Prantlina* and *Angusticardinia*) (Havlíček, 1971, 1977), which could be indicative of some West Gondwanan connections for the immigrating benthic fauna. The high origination rates at the beginning of the Ordovician thus result in significant part from the immigration of new taxa. Other terranes involved as likely migratory routes across Iapetus became significant only from Llandeilo times onward (Harper, Mac Niocaill & Williams, 1996; Harper & Mac Niocaill, 2002).

Significant generic originations within endemic lineages increased towards the end of the Arenig (Popov, 1993), but two strong pulses in late Arenig and late Llanvirn times probably reflect increasing immigration, although the source of these new faunal elements remains enigmatic. In particular, orthides such as *Orthis* and *Orthambonites* were newcomers and it would be difficult to determine an ancestral stock within the older Baltic brachiopod faunas, but at the same time they then formed distinctive Baltic endemics during the early Llanvirn, as demonstrated convincingly by Jaanusson & Bassett (1993). *Inversella* and *Athiella* may have a Baltic connection, but their characteristic strongly resupinate shells are unknown among older Baltic plectambonitids. These genera are reported from the Llanvirn (San Juan Formation) of the Argentinian Precordillera (Benedetto & Herrera, 1986; Herrera & Benedetto, 1989) and they are known also from eastern North American and Caledonian terranes that presumably represent the remnants of intra-oceanic volcanic arcs (Neuman, 1972). Other exotic elements were also present in oceanic terranes outboard of Baltica (Bruton & Harper, 1981, 1985, 1988).

New genera from the Aseri and Lasnamägi regional stages also only partly represent descendants of local lineages (e.g. *Orthisocrania*, *Plectambonites*, *Equirostra*, *Noetlingia*, total 29%), but in significant part have an obscure origin (most of the strophomenoideans and plectambonitoideans, total 66%). Among newcomers, the earliest *Christiania* is also reported from island arc terranes located some where in Iapetus (Neuman, 1968), whereas the oldest *Sowerbyella* is from Avalonia (Williams, 1974).

The mid Llanvirn extinction strongly affected long-lived Baltic genera that appeared originally in the Volkhov or Billingen intervals (e.g. *Lycophoria*, *Paurorthis*, *Productorthis*, *Gonambonites*, *Oslogonites*, *Lacunarites*, *Psudocrania*) and which comprise 40% of the number of genera that became extinct between the end of Kunda and the beginning of the Uhaku times. At the same time, some genera possibly immigrated to Baltica at the beginning of the Kunda (20%).

General characteristics of accelerated faunal turnover and increased extinction of local lineages may have been products of mixing resulting from new faunas introduced into the Baltoscandian Basin during the approach of an intra-oceanic island arc to the Caledonian margin of Baltica and its subsequent collision in the mid Llanvirn (Sturt & Roberts, 1991). Indications of the proximity of the volcanic arc to the Caledonian margin during the early Llanvirn is evident also from increased input of volcanic material into the Basin and, in particular, from the presence of tuff beds in Sweden (Sturesson, 1992a,b). Two episodes of maximum formation of ferruginous ooids, in the early Kunda and Aseri, most probably indicate the presence of reworked pyroclastic material, with less negative $\epsilon_{\text{Nd}}(t)$ values in the Aseri Stage.

The late Ordovician interval between the Keila and Pirgu regional stages (mid Caradoc to mid Ashgill) was a time of high faunal turnover rates, characterized by a significant increase of extinction rates (up to 0.25 Lma) and also of origination rates (up to 0.30 Lma), culminating in the Oandu Regional Stage when 12 brachiopod genera became extinct and 15 new genera appeared. The number of genera was relatively stable, oscillating between 24 and 33 for each particular stage, with an increase only up to 42 in the Pirgu Stage just before the terminal Ordovician extinction. Within this interval the immigration of new taxa represented a significant contribution to the diversity of the brachiopod fauna, and the source of these new components now becomes clearer. Endopunctate orthides (e.g. *Onniella*, *Horderleyella*) were derived most probably from the approaching Avalonia. There was also a gradually increasing number of genera common with Laurentia, including the orthides *Plaesiomys* and *Hebertella*, the strophomenide *Holtedahlinea*, the rhynchonellides *Hypsiptycha* and *Rhynchotrema*, and the atrypides *Anazyga* and *Catazyga*. The third significant source of new taxa

was in assemblages characteristic of carbonate mud-mounds and which originated in Central Asian terranes from the Llandeilo–early Caradoc (so-called Hiberno-Salairian faunal assemblages *sensu* Jaanusson, 1979), appearing in Baltoscandia in the late Caradoc–early Ashgill, together with the somewhat younger fauna of early pentameridines such as *Holorhynchus*, which spread across Baltoscandia in the mid Ashgill (Pirgu Regional Stage). However, such faunas are very poorly studied in Baltoscandia and are characteristic mostly of the Central Scandinavian Confacies Belt. In the North Estonian Confacies Belt they are represented only by the rare trimerellide *Eodinobolus* and the atrypide *Eospirigerina*.

In general summary, the early and mid Ordovician (Arenig to Llandeilo) brachiopod faunas of the North Estonian Confacies Belt are characterized by high endemism and low turnover rates, whereas increased immigration resulted in the extinction of a number of local lineages in the late Llanvirn. From the mid Caradoc to mid Ashgill, when Baltica was drifting on a course to collide eventually with Avalonia and to gradually approach Laurentia, brachiopod assemblages were characterized by higher turnover rates. At the same time they gradually became more cosmopolitan and less influenced by the invasion of new faunas.

5. Palaeogeographical evolution

The combined geochemical and biodiversity data analysed above demonstrate that the early Palaeozoic history of the Baltoscandian Basin can be divided into two distinct phases, separated by a short transitional interval corresponding essentially with the Tremadoc. The turnover coincides closely with marked changes in the tectonic development of Baltica and the adjacent southeastern segment of the Iapetus Ocean. Palaeogeographical reconstructions of Baltica suggest that it was at high southern latitudes during most of Cambrian–Tremadoc times (Torsvik *et al.* 1996; Hartz & Torsvik, 2002), possibly in proximity to West Gondwana. However, Fortey & Cocks (1992) postulated a tripartite geographical pattern of mid Cambrian trilobite faunas, with Baltica assemblages placed somewhat distantly from those characteristic of Gondwana and Laurentia.

Shergold (1988) included the late Cambrian trilobite fauna inhabiting the outer shelf environments of Baltoscandia within a Baltic Trilobite Province, confined mainly to high or temperate latitudes, but the olenid trilobite biofacies characteristic of that province, together with the somewhat younger latest Cambrian to Tremadoc *Broeggeri*–*Hysterolenus* fauna, was present mainly in the widespread disaerobic outer shelf and basinal environments of that time, and their biogeographical signature is not very clear (Fortey & Cocks, 1992; Popov & Holmer, 1994). The only known

tenuous biogeographical link is the presence in Spain (Armorica) of an obolide biofacies associated with *Skolithos* trace fossils across the Cambrian–Ordovician transition (e.g. Hamman, Robardet & Romano, 1982), but this relationship requires further study. Low diversity benthic faunas characteristic of the shallow shelf, combined with mainly siliciclastic sedimentation across the Baltoscandian Basin, are indirect indications of a temperate to high-latitude position of Baltica during most of the Cambrian.

Low faunal turnover rates, low taxonomic diversity, and the stability of mid Cambrian–mid Tremadoc shallow marine, obolide-dominated benthic assemblages were also typical of Baltoscandia (Popov *et al.* 1989). These characteristics contrast markedly with the changing trilobite-dominated faunas of the epeiric seas of Laurentia, where there was predominantly low-latitude carbonate deposition. In Baltica there is no indication of significant regional extinctions in Cambrian faunas, and the occurrence of ‘biomeres’ is not evident. With only a few insignificant fluctuations, peri-tidal depositional environments persisted in the East Baltic region throughout almost all this time and contain a continuous record of conodont biozones from *Proconodontus* to *Cordylodus angulatus* across the Cambrian–Ordovician boundary (Popov *et al.* 1989; Kaljo *et al.* 1986). These features are indicative of prolonged remarkable tectonic stability in the Baltoscandian sector of the craton and of insignificant eustatic sea-level fluctuations until the mid Tremadoc (Artyushkov, Lindström & Popov, 1997, 2000). The pattern of stability also suggests that geographical displacement of Baltica during this time was insignificant. Palaeogeographical reconstructions for Gondwana suggest migration of the southern Pole from the Andean coast of South America in the late Vendian to the North African coast in the Ordovician (Torsvik *et al.* 1996). There is no indication that the southern margin of Baltica was active in the Cambrian, nor of its attachment to Gondwana as proposed by Pickering & Smith (1995), but instead it is most likely that there was a transform boundary between Gondwana and the Baltica Plate (Fig. 6) as proposed by Torsvik (1998; see also Torsvik & Rehnström, 2001; Hartz & Torsvik, 2002). Furthermore, by contrast with the interpretation by Torsvik *et al.* (1996, p. 252) of an active Caledonian margin of Baltica in the late Cambrian, the low $\epsilon_{\text{Nd}}(t)$ of about -7.0 to -8.0 , which we regard as a signature of Iapetus oceanic water, suggests a passive margin development and continuous expansion of Iapetus until the mid Tremadoc.

The environmental and biodiversity stasis characteristic of the mid and late Cambrian was transformed distinctly by the beginning of the Arenig to a very different pattern. The Tremadoc transitional interval introduced the main Ordovician trends of environmental and biotic evolution in the Baltoscandian Basin. The almost continuous existence of peri-tidal environments across

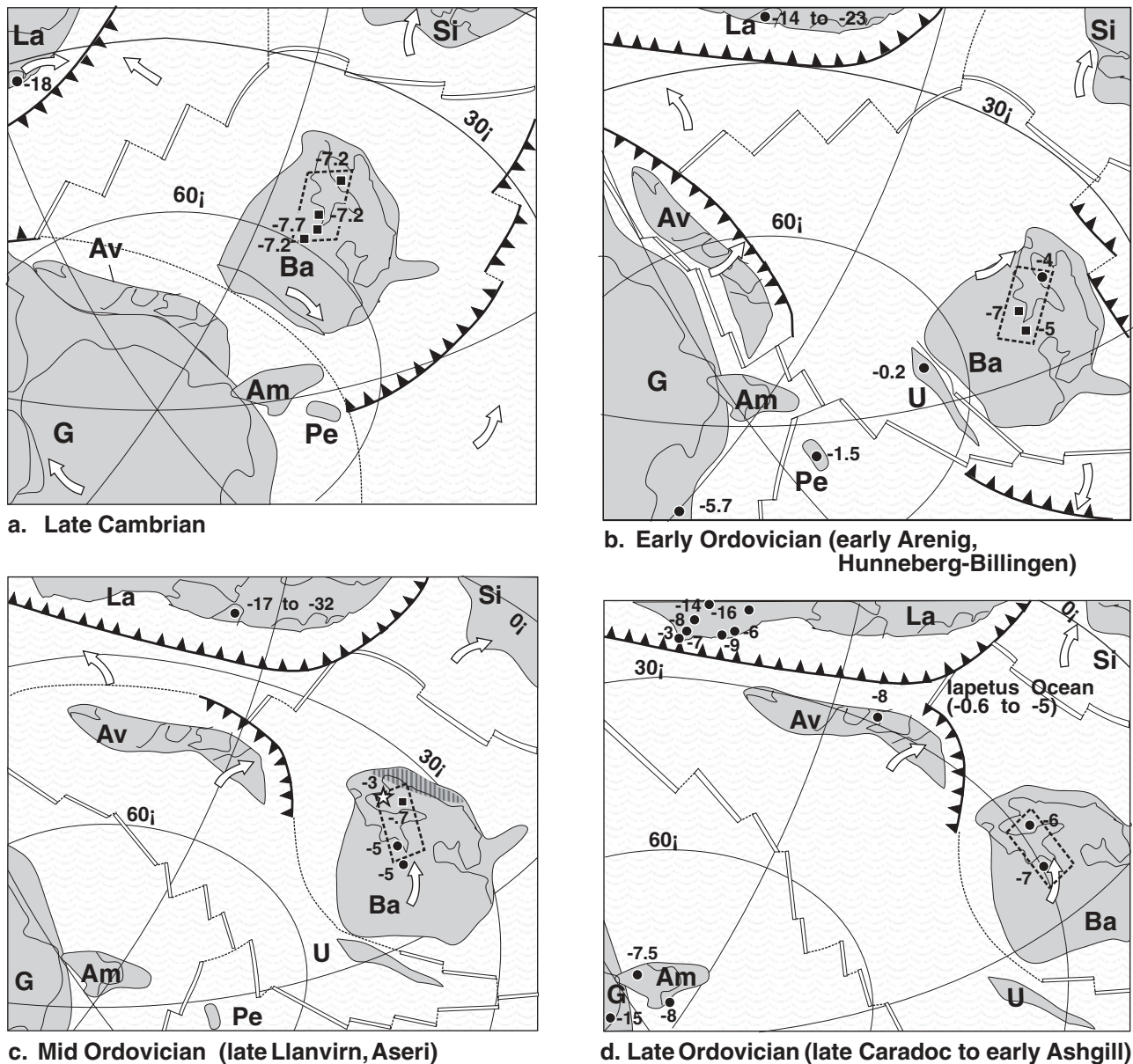


Figure 6. Continental distribution around the northern sector of the Iapetus Ocean in the late Cambrian to late Ordovician (modified after Torsvik, 1998; Torsvik *et al.* 1996; Hartz & Torsvik, 2002). Abbreviations: La – Laurentia, Si – Siberia; Av – Avalonia, G – Gondwana, Am – Armorica, Pe – Perunica, Ba – Baltica, U – Uralian microcontinent. The area of this study on Baltica is outlined. Reference data for ϵ_{Nd} values of biogenic apatite shown as black dots, squares (average based on several measurements), and asterisks (for volcanic ash). Reference data for ϵ_{Nd} values for the Laurentian margin and Iapetus Ocean are after Holmden *et al.* (1998, fig. 1). Arrows show the assumed direction of relative rotation of the plates. (a) Late Cambrian represents the time of expansion of Iapetus; Baltica underwent clockwise rotation, while maintaining its position in temperate latitudes in relative proximity to Gondwana, but separated by a transform fault zone and with an active eastern margin. (b) By the early Ordovician (early Arenig) the development of a new spreading zone resulted in the detachment of volcanic arcs, which formed along the active eastern margin of Baltica. At the same time the Uralian microcontinent rifted, and Baltica changed its direction of rotation to counter-clockwise. The island arcs that appeared in the proximity of the Caledonian margin of Baltica could have been derived from its active Cambrian margin. Rifting of Avalonia from the Gondwana margin could have been caused by the development of the same spreading system. (c) Mid Ordovician (late Llanvirn) was the time of maximum biogeographical isolation of Baltica and Avalonia from the surrounding continents; by this time volcanic activity along the Caledonian margin ceased and the obducted island arc complexes were eroded. (d) Late Ordovician (late Caradoc); by this time the approach of Avalonia towards Baltica was reflected by extensive development of bentonite beds through the early to mid Caradoc and the mixture of benthic faunas; Iapetus was reduced substantially and spreading zones separating Laurentia from Avalonia and Baltica mainly disappeared. Faunal exchange between Laurentia and Baltica became increasingly evident.

the Cambrian–Ordovician boundary counters earlier proposed significant eustatic sea-level fluctuations (Artyushkov, Lindström & Popov, 1997, 2000), but then the mid Tremadoc (*Cordylodus angulatus* Biozone) was a time of conspicuous sea-level rise in the order of several tens of metres. Early Tremadoc beach and bar systems in the East Baltic were flooded to below storm wave base depths and were protected from erosion, and deposition of the black ‘*Dictyonema*’ Shale facies was widespread across the region. This transgression correlates with the Black Mountain eustatic event proposed by Miller (1984) and recognized globally. The beginning of this biozone also coincides with the regional elimination of almost all brachiopod taxa that had evolved in the Basin through the mid and late Cambrian.

Biogeographical links with Gondwana during late Tremadoc–early Arenig times (*Drepanoistodus proteus* Biozone) are noted above. These connections are also supported by the distribution of rhynchonelliformean brachiopod assemblages. In particular, *Apheoorthina*, *Angusticardinia*, *Prantlina* and *Ranorthis* occur at approximately the same level not only in Baltica but also in Bohemia and Morocco (Rubel, 1961; Havlíček, 1971, 1977). *Protambonites* occurs in Bohemia, North Africa, Spain (Havlíček, 1977) and Iran (Bassett, Dastanpour & Popov, 1999) and is also reported from the Uralian margin of Baltica (Popov, Vinn & Nikitina, 2001).

The faunal similarity between Baltica and West Gondwana decreased rapidly by the mid Arenig, when the onset of carbonate deposition commenced across the whole of the Baltoscandian Basin. During late Arenig–Llanvirn times, the benthic faunas were strongly endemic (Williams, 1973; Cocks & Fortey, 1998), indicating distinct geographical isolation and rapid drift away from West Gondwana towards temperate latitudes by the mid Ordovician, and to low latitudes by the Silurian (Torsvik, 1998).

The rise of $\epsilon_{Nd}(t)$ values in biogenic apatite from the Baltoscandian Basin during the Tremadoc suggests that there was considerable tectonic reorganization of the southwestern sector of the Iapetus Ocean and the margins of the Baltica Plate. There is no evidence of island-arc-type volcanism in the west and northwest proximity of Baltica during the Cambrian (e.g. Hartz & Torsvik, 2002). Water masses of the Baltoscandian Basin in that period were homogenized and show $\epsilon_{Nd}(t)$ values characteristic of Atlantic type oceans (Felitsyn *et al.* 1998) with a possible spreading zone situated to the west or northwest. At the same time, the existence of island arc volcanism and subduction along the eastern margin of Baltica can be predicted during the mid Cambrian–early Ordovician. Such remnants of early Palaeozoic arcs are probably preserved within the northeastern part of the Chingiz–Tarbagatay region of Kazakhstan (Popov & Holmer, 1994). The early Arenig lingulate microbrachiopod and rhynchonellate

assemblages from the Koagash Formation of the South Urals and the Olenty Formation of north Central Kazakhstan are closely similar (Nikitin, 1956; Popov & Holmer, 1994) and most likely belong to the same biogeographical province. This configuration of plate margins suggests that the eastern drift may have been caused by clockwise rotation in relation to the northern margin of West Gondwana.

The Tremadoc–early Arenig marked a period of break-up of the Uralian margin of Baltica, which faced southward at the beginning of the Ordovician (Torsvik & Rehnström, 2001), involving the origin of a new spreading zone southeast of Baltica. Cambrian margins are not now preserved along the Uralian side of the East European Platform, but its passive margin development in the latest Cambrian–early Ordovician is documented from geophysical studies (Berzin *et al.* 1996) showing relationship to rifting of the East Uralian (or Mugodzary) microcontinent (Zonenshain, Kuzmin & Natapov, 1990). It is also likely that island arc systems rooted to the east margin of Baltica were separated from that plate by back-arc spreading in late Tremadoc–early Arenig times.

Anticlockwise rotation and northwestern drift of Baltica probably began in response to the generation of the newly formed spreading zone (Torsvik, 1998, fig. 1). Two samples of biogenic apatite from the late Tremadoc to early Arenig of the South Urals and Bohemia show high $\epsilon_{Nd}(t)$ values (Fig. 2). These changes in direction of plate movements also led to the origin of an intraoceanic island arc and subduction somewhere northwest of the Caledonian margin of Baltica. Some influence of island arc volcanism is recorded as early as the mid Tremadoc (*Cordylodus angulatus* Biozone), from where fine grains of mica and a mantle-like isotopic composition of sulphur in the ‘*Dictyonema*’ Shale of Estonia were reported by Loog & Petersell (1987). Increased $\epsilon_{Nd}(t)$ values (Fig. 2) in Sweden and in the East Baltic during the Hunneberg and Billingen stages suggest a significant new source of radiogenic neodymium, possibly from erosion of island arc complexes obducted on to the Caledonian margin in the early Arenig and from ash falls from the approaching island arc. The latter source appears to constitute a significant component of background deposition in the East Baltic from the late Tremadoc to the Billingen Regional Stage (Arenig).

Later, in Llanvirn time (*c.* 460 Ma), the obduction zone along the Caledonian margin of Baltica (Torsvik, 1998) became a source of young Nd input into the basin, as shown by preserved visible relics of volcanic ash in the upper Llanvirn of south-central Sweden (Sturesson, 1992a) and by the coeval appearance of a distinct island arc tholeiitic geochemical signature in sediments within the Oslo region and Scania (Schovsbo, 2003). The increased faunal turnover and appearance of some new benthic taxa (e.g. *Christiania*, *Sowerbyella*, *Echinospaerites*) near the Kunda–Aseri

boundary suggests that collision took place during mid Llanvirn time.

The influence of Avalonian volcanism became evident in Baltoscandia from the beginning of the Caradoc, when the Idavere complex of bentonites appeared in the East Baltic. Faunal exchange between these two plates also increased by that time (Williams, 1973; Cocks & Fortey, 1998). The appearance in Avalonia in the mid Caradoc of the craniide brachiopod *Orthisocrania*, which had very low potential for dispersal (Lockley, 1980), suggests that Baltica and Avalonia approached very close together by that time. However, it is important to note that increased pyroclastic input into sediments of the North Estonian Confacies Belt cannot be related to $\epsilon_{\text{Nd}}(t)$ values for the Idavere and Jõhvi regional stages, where numerous K-bentonite beds are preserved. This factor may be related to the different character of volcanism by comparison with that of the early Ordovician, and supports similar observations made by Holmden *et al.* (1998) on the negligible contamination of biogenic apatite via bentonite-derived neodymium in carbonate sequences of eastern Laurentia.

Three characteristic faunal assemblages can be recognized as forming the basis for the Baltica Ordovician fauna, which evolved and diversified in Baltoscandia during this period. These are: (1) a medium diversity benthic fauna of orthide and strophomenide brachiopods, ostracodes, asaphide trilobites, bryozoans and echinoderms, which appeared suddenly in Billingen age rocks (early Arenig) of the East Baltic; (2) the *Ceratopyge* trilobite fauna, which appeared in Baltoscandia and along the Uralian margin of Baltica sometime in the late Tremadoc; and (3) a linguulate microbrachiopod assemblage with characteristic Ordovician acrotretides of the families Biernatidae, Ehippelasmatidae, Torynelasmatidae and Eoconulidae, the lingulides *Diencobolus* and *Paterula*, and siphonotretides, which appeared in Baltoscandia, the Holy Cross Mountains (Poland) and the South Urals sometime in the late Tremadoc–early Arenig and is traceable also in the terranes of eastern Central Kazakhstan (Popov & Holmer, 1994, 1995).

The first of these assemblages represents possibly the earliest known Ordovician fauna with a community structure typical of the Palaeozoic Evolutionary Fauna (Sepkoski, 1991). It is characterized by a predominance of filter feeders (rhynchonelliformean brachiopods, bryozoans and pelmatozoan echinoderms: Rubel, 1961; Popov, 1993; Pushkin & Popov, 1999). There is some similarity with western peri-Gondwanan faunas, as discussed above, but the core of the assemblage is of unknown origin. There is no record of similarly structured benthic assemblages from contemporaneous or somewhat earlier faunas of Siberia and Laurentia, so that some unknown mid-latitude island arc or eastern peri-Gondwanan benthic faunas could have been a potential source of origin. The early occurrence of

bryozoans in South China (Hu & Spjeldnaes, 1991), where they are known already from the Tremadoc, and relatively abundant archaic rhynchonelliformean brachiopod faunas known from the early Middle Cambrian of Australia (Roberts & Jell, 1990), suggest that temperate to low-latitude shelves of East Gondwana and its associated terranes were possible *loci* for the origin of the earliest benthic assemblages characteristic of the Palaeozoic Evolutionary Faunas.

The *Ceratopyge* trilobite fauna is regarded as typically Baltic (Cocks & Fortey, 1998), but with few exceptions it includes genera lacking Baltic roots and its appearance in the Baltoscandian Basin was apparently by immigration. Most taxa characteristic of the *Ceratopyge* fauna are related to assemblages of the late Cambrian South China Province of Shergold (1988), and especially those from Australia, South China and the Malyi Karatau Range, and thus signal distinct eastern peri-Gondwanan connections. However, as noted by Cocks & Fortey (1998), the Tremadoc trilobite faunas of West Gondwana, typified by assemblages from Armorica and the Lake District in England, are completely different. A degree of climatic control can be interpreted, with the migration paths of the *Ceratopyge* fauna confined most probably within temperate latitudes. The late Tremadoc to early Arenig trilobite fauna described partly by Lissagor (1961) from the Kendyktas Range of North Tien-Shan has mixed Gondwana and Baltica features, but otherwise trilobite faunas of that age remain very poorly known.

The linguulate microbrachiopod assemblage appearing in Baltoscandia in the late Tremadoc–early Arenig apparently also had its roots in the late Cambrian faunas of Central Asian and Kazakhstani terranes, where the families Scaphelasmataidae and Ehippelasmatidae and genera such as *Diencobolus* and *Pomeraniotreta* were present already in late Cambrian time. Early Eoconulidae and distinctive acrotretides such as *Acrotreta* and *Ombergia* are also reported from the late Tremadoc–early Arenig of these regions (Popov & Holmer, 1994; Holmer, Popov & Bassett, 2000; Holmer *et al.* 2001).

This review suggests that substantially increased immigration was the most important factor in the clear definition and recognition of the Baltica Ordovician fauna. Because of the position of Baltica close to the Gondwanan margin during the Tremadoc, oceanic space between its eastern margin and East Gondwana was relatively narrow. In late Cambrian–early Ordovician times, this narrow ocean was occupied by island arcs and microplates incorporated later into the orogenic collage of Central Asia and Kazakhstan. Some of these tectonic units were possibly part of the active eastern margin of Baltica, whereas others originated in the mid Cambrian–early Ordovician as a result of the breakup of Gondwana and its associated terranes (Holmer *et al.* 2001) and served as faunal bridges which allowed increasing migration in temperate and low latitudes. Substantial sea-level rise in the middle–late

Tremadoc created new, widespread ecospace on the Early Palaeozoic continental shelves where the faunas could then mix and diversify. Later in the Ordovician, rapid northwesterly drift of Baltica and the break-up of Avalonia related to newly developed spreading zones led to isolation and increasing endemism of the newly diversified faunas. It is notable that such evolution in biodiversity patterns and the geochemical changes of oceanic waters in the southeastern sector of Iapetus are not a matter of coincidence, but go hand in hand in reflecting significant changes in the tectonic evolution of the region separating Baltica and Gondwana. The low $\epsilon_{Nd}(t)$ values correspond approximately with periods of evolutionary stasis and low faunal turnover. The rise of $\epsilon_{Nd}(t)$ in late Tremadoc–early Arenig times was followed by regional extinction and immigration of new faunas, and then the two subsequent rises in the early–mid Llanvirn and late Caradoc correspond with periods of increased faunal turnover and partial extinction of local taxa, possibly linked with the immigration of new faunas from approaching volcanic arcs.

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Appendix. Materials and methods

De-ionized water was used to separate brachiopod shells and conodonts from unconsolidated host rock formed of silty clay and sand, whilst carbonate rocks yielded material following dissolution in weak acetic acid. Each sample was examined microscopically to remove bioclasts contaminated with pyrite and clay minerals etc. Scanning electron microscopy with energy dispersive spectrometry (EDS), instrumental neutron activation analysis (INAA), and X-ray diffraction analysis (XRD) were used to reveal any degree of calcification or silicification. Late Cambrian and early Ordovician lingulate brachiopods usually contain internal secondary apatite formed via *post-mortem* recrystallization and bacterial degradation of organic components within the shells (Nemliher & Puura, 1997).

Carefully purified bioclasts were powdered with an agate mortar and pestle. The phosphate powder was spiked with ^{146}Nd – ^{149}Sm and decomposed for 48 to 144 hours in an oven at 120 °C. Samarium and neodymium separation was carried out by standard methods of two-stage ion-exchange and extraction chromatography. Measurements were undertaken on a Finnegan Mat-261 mass spectrometer equipped with 8-collectors under static mode at the Institute of Precambrian Geology and Geochronology, St Petersburg, Russia. The $^{143}\text{Nd}/^{144}\text{Sm}$ ratio was corrected within run to $^{148}\text{Nd}/^{144}\text{Nd} = 0.241570$ and then adjusted to a $^{143}\text{Nd}/^{144}\text{Nd}$ value of 0.511860 for La Jolla standard. Forty to sixty ratios for Nd were obtained to achieve a final ratio value with adequate precision. Assigned errors (2σ) for $^{147}\text{Sm}/^{144}\text{Nd}$ and $^{143}\text{Nd}/^{144}\text{Nd}$ were +0.3% and +0.000014 of the standard (external reproducibility). The 2σ errors cited for $^{143}\text{Nd}/^{144}\text{Nd}$ in Table 1 reflect in-run precision. The blank level for Sm was 0.01 ng and 0.05 ng for Nd. The data obtained for BCR-1 USGS standard sample during the run of this analytical work are Sm = 6.487 ppm, Nd 28.45 ppm, $^{143}\text{Nd}/^{144}\text{Nd} = 0.512663 \pm 9$, $^{147}\text{Sm}/^{144}\text{Nd} = 0.13829$, $n = 24$. Original Nd isotopic compositions are reported in the standard epsilon notation $\epsilon_{\text{Nd}}(t) = [(^{143}\text{Nd}/^{144}\text{Nd})_{\text{sample}}(t)/^{143}\text{Nd}/^{144}\text{Nd}_{\text{CHUR}}(t) - 1] \times 10^4$ where CHUR is the Chondritic uniform reservoir with a present-day $^{143}\text{Nd}/^{144}\text{Nd} = 0.512638$ and $^{147}\text{Sm}/^{144}\text{Nd} = 0.19670$.

Absolute ages for calculation of $\epsilon_{\text{Nd}}(t)$ are 545 Ma for the base of the Cambrian according to Bowring & Erwin (1998), 545–c. 443 Ma for the Cambrian–Ordovician time-span (Shergold, 1995), and 550 Ma for late Vendian phosphate-bearing layers on the Russian platform (Compston *et al.* 1995).

Table 1. Summary of sample data, analysed material (fossil taxa/lithology), stratigraphical ages and geochemical data

No.	Sample	Taxa/Lithology	Age	Sm (ppm)	Nd (ppm)	$\frac{^{147}\text{Sm}}{^{143}\text{Nd}}$	$\frac{^{144}\text{Nd}}{^{144}\text{Nd}}$	ϵ_{Nd}
Vendian								
<i>Moscow Basin</i>								
	23 2 BS	argillite	Redkino Fm.	6.3	36.1	0.10562	0.51105 ± 13	-15.7
	24 8 BS	argillite	Kotlin Fm.	6.84	39.11	0.10612	0.51836 ± 13	-9.6
Cambrian								
<i>Moscow Basin</i>								
	VF5-Ph	phosphorite	Lower Cambrian, Rovno Fm.	95.4	542	0.12308	0.51915 ± 9	-9.0
	VTyR	phosphorite	Lower Cambrian, Rovno Fm.	108.4	606	0.13377	0.51985 ± 4	-8.6
	37 BS	phosphorite	Lower Cambrian, Rovno Fm.	61.23	21.77	0.11786	0.518990 ± 8	-9.3
		phosphorite	Lower Cambrian, Lezha Fm.	95.4	542	0.12308	0.511915 ± 9	-9.1
		phosphorite	Lower Cambrian, Lezha Fm.	108.4	602	0.13377	0.51985 ± 4	-9.6
29		obolides	Upper Cambrian	485.9	1689	0.17445	0.512167 ± 13	-7.9
31		<i>Westonia pinegensis</i>	Upper Cambrian	312.8	1330	0.13367	0.512122 ± 15	-6.3
32		obolides	Upper Cambrian	139.8	648.1	0.12728	0.512045 ± 17	-7.4
<i>St Petersburg–Lake Ladoga region</i>								
26	L1/5	<i>Ungula convexa</i>	Upper Cambrian (Ladoga)	115.9	617.4	0.12318	0.512068 ± 15	-6.7
27	L19/5b	<i>Oepikites</i> sp.	Upper Cambrian (Ulgase)	134.1	650.1	0.12501	0.512021 ± 18	-7.7
	Syas-1	<i>Helmersenia ladogensis</i>	Upper Cambrian (<i>proavus</i>)	68.51	297.9	0.13947	0.512124 ± 9	-6.4
	Lava-1	obolides	Upper Cambrian (<i>proavus</i>)	54.96	239.1	0.13937	0.512112 ± 27	-8.6
33	L47/6	<i>Ungula</i> sp.	Upper Cambrian (Ladoga)	145.6	603.4	0.14224	0.512198 ± 20	-8.3
48	Core 208	<i>Oepikites koltchanovi</i>	Middle Cambrian (Sablinka)	44.06	206.1	0.12965	0.512139 ± 16	-8.7
<i>Estonia</i>								
34	E6/4	<i>Schmidites celatus</i>	Upper Cambrian. (<i>proavus</i>)	48.39	219	0.13399	0.512148 ± 18	-5.8
20	Core 1653	<i>Ceratreta tanneri</i>	Upper Cambrian (Ulgase)	153.9	752.8	0.12405	0.512155 ± 21	-5.1
21	E54/1	obolides	Upper Cambrian (Tsitre)	176.6	661.9	0.16182	0.512244 ± 16	-5.6
22	E54/2	obolides	Upper Cambrian (Maardu)	134.6	654.7	0.12467	0.511975 ± 18	-8.6
	Ma-U1	<i>Ungula</i> sp.	Upper Cambrian (Ulgase)	27.39	126.4	0.13149	0.511926 ± 13	-8.5
	U83-8/9	<i>Ungula</i> sp., <i>Schmidites</i> sp.	Upper Cambrian (Maardu)	48.92	223.96	0.13246	0.512036 ± 6	-7.65
24	U-83-6	<i>Ungula</i> sp.	Upper Cambrian (Maardu)	34.55	155.3	0.13494	0.512033 ± 46	-7.9
	M-77/9	<i>Schmidites celatus</i>	Upper Cambrian (Tsitre)	71.84	290.2	0.15013	0.512062 ± 9	-8.3
	T-3/28	obolides	Upper Cambrian (Tsitre)	59.88	275.6	0.13178	0.512051 ± 7	-7.3
	L1/13	obolides	Upper Cambrian	195.6	738.2	0.16071	0.512149 ± 14	-7.4
<i>Sweden</i>								
	NARK-1	<i>Mickwitzia monilifera</i>	Lower Cambrian	327.2	1367	0.15388	0.512081 ± 16	-8.3
		fossil apatite	Middle Cambrian	54.14	210.3	0.15613	0.512084 ± 16	-8.5
141	Ög-9	<i>Ceratreta tanneri</i>	Upper Cambrian	135.7	673.9	0.12207	0.512038 ± 19	-7.2
<i>Poland</i>								
		phosphorite	Lower Cambrian, Mazowsze Fm.	169.8	450.2	0.28329	0.512410 ± 14	-7.6
Ordovician								
<i>St Petersburg–Lake Ladoga region</i>								
37	6817/5-1	<i>Helmersenia ladogensis</i>	Tremadoc (<i>angulatus</i>)	156.5	663.0	0.14315	0.512147 ± 17	-6.4
38a	Cyf-6	<i>Cordylodus angulatus</i>	Tremadoc (<i>angulatus</i>)	90.57	417.2	0.13167	0.512042 ± 16	-7.7
38b	Cyf-6	conodont elements	Tremadoc (<i>angulatus</i>)	119.3	492.9	0.14675	0.512121 ± 21	-7.0
51	L10/2	<i>Obolus apollinis</i>	Tremadoc (<i>lindstromi</i>)	120.3	516.4	0.14124	0.512215 ± 17	-4.9
38c	DS-6	bulk host shale	Tremadoc (<i>angulatus</i>)	4.516	20.64	0.13266	0.511904 ± 21	-10.65
39	250-1	conodont elements	Tremadoc (<i>Ceratopyge</i>)	58.05	237.6	0.14818	0.512183 ± 12	-5.8
40	250-4	brachiopods	Arenig (Hunneberg, <i>proteus</i>)	330.4	1376	0.13164	0.512130 ± 24	-6.0
41	250-10	brachiopods	Arenig (Hunneberg, <i>proteus</i>)	357.2	1422	0.13056	0.512122 ± 14	-6.1
42	250-10	conodont elements	Arenig (Hunneberg, <i>proteus</i>)	67.74	288.7	0.14230	0.512371 ± 23	-1.9
43	250-13	brachiopods	Arenig (Hunneberg, <i>proteus</i>)	658.3	3087	0.13218	0.512122 ± 24	-6.2
44	250-13	conodonts	Arenig (Hunneberg, <i>proteus</i>)	39.85	157.0	0.15392	0.512168 ± 14	-6.5
45	250-16	brachiopods	Arenig (Hunneberg, <i>elegans</i>)	258.6	1228	0.13461	0.512134 ± 21	-6.1
46	250-16	conodont elements	Arenig (Hunneberg, <i>elegans</i>)	58.32	254.6	0.14164	0.512365 ± 22	-2.0
	6817-8C	<i>Acrotreta</i> sp., siphonotretides	Arenig (Billingen)	355.1	1375	0.15665	0.512295 ± 5	-4.1
47	106-1	conodont elements	Llanvirn (Kunda)	595.5	2427	0.14882	0.512237 ± 16	-4.95
<i>Estonia</i>								
8	MB alpha	conodont elements	Arenig (Hunneberg)	97.78	425.6	0.13933	0.512149 ± 13	-5.9
9	Kj BI beta	<i>Acrotreta</i> sp., siphonotretides	Arenig (Billingen)	199.3	881.0	0.13718	0.512036 ± 7	-7.95
10	MB Ib	conodont elements	Arenig (Billingen)	14.99	56.11	0.13668	0.512122 ± 16	-6.2
12	EP-15	conodont elements	Arenig (<i>B. navis</i>)	169.9	695.1	0.14833	0.512121 ± 5	-6.0
13	Tonu-5	obolides	Arenig (<i>B. navis</i>)	250.0	1079	0.14045	0.512165 ± 8	-5.6
14	Tonu-24	<i>Aulonotreta</i> sp.	Arenig (<i>flabellum parva</i>)	189.7	857.2	0.13420	0.512129 ± 12	-5.9
15	Tonu-30	brachiopods, conodont elements	Arenig (<i>originalis</i>)	207.9	899.1	0.14024	0.512219 ± 6	-4.6
	U29-2	conodont elements	Llanvirn (Aseri)	125.9	484.4	0.15771	0.512282 ± 16	-4.7
	EO	biogenic apatite	Llanvirn (Kunda)	107.6	461	0.14155	0.512225 ± 5	-4.5
	E22-2	biogenic apatite	Llanvirn (Kunda)	218.1	842.1	0.15703	0.512281 ± 11	-4.4
	E11-5	biogenic apatite	Llanvirn (Kunda)	390.8	1475	0.16230	0.512106 ± 5	-8.2
	E21-4	biogenic apatite	Llanvirn (Kunda)	118.3	470.3	0.15269	0.512109 ± 11	-7.5
52		<i>Siphonotreta intermedia</i>	Llandeilo (Kukruse)	39.83	207.2	0.12761	0.512141 ± 16	-5.55
53	Br 125721	<i>Alichovia ramispinosa</i>	Caradoc	79.81	378.2	0.15192	0.512167 ± 17	-6.5
54		<i>Pseudolingula quadrata</i>	Ashgill (Vormsi)	133.6	650.8	0.12450	0.512058 ± 18	-7.0
<i>Sweden</i>								
144a	Eriksöre	<i>Broeggeria salteri</i>	Tremadoc (<i>Dictyonema</i>)	358.6	1411	0.15406	0.512013 ± 11	-9.6
144	Eriksöre	bulk host shale	Tremadoc (<i>Dictyonema</i>)	10.17	73.20	0.08457	0.511063 ± 18	-6.7
139a	Ö192	obolides	Tremadoc (<i>Ceratopyge</i>)	266.7	1233	0.13116	0.512126 ± 13	-6.1
139b	Ö192	conodont elements	Tremadoc (<i>Ceratopyge</i>)	33.39	141.8	0.14272	0.512028 ± 12	-6.9

Table 1. Continued

No.	Sample	Taxa/Lithology	Age	Sm (ppm)	Nd (ppm)	$\frac{^{147}\text{Sm}}{^{143}\text{Nd}}$	$\frac{^{144}\text{Nd}}{^{143}\text{Nd}}$	ϵ_{Nd}
142	Br 16931	obolides	Tremadoc (<i>Ceratopyge</i>)	164.9	704.9	0.14201	0.512134 ± 22	6.55
137a	St Backor	obolides, acrotretoids	Tremadoc (<i>Ceratopyge</i>)	369.7	1399	0.16019	0.512040 ± 10	-9.5
137b		conodont elements	Tremadoc (<i>Ceratopyge</i>)	145.6	536.7	0.16154	0.512087 ± 13	-6.6
135	GB-81	conodont elements	Arenig (<i>Hunneberg, proteus</i>)	31.39	140.1	0.13585	0.512249 ± 11	-3.9
101	SK 16	conodont elements, <i>Phosphannulus</i> sp.	Arenig (<i>B. navis</i>)	137.9	522.5	0.16011	0.512065 ± 18	-9.0
102	SK 22.5	conodont elements	Arenig (<i>B. navis</i>)	302.4	1029	0.17813	0.512121 ± 16	-9.0
103	SK29.5	conodont elements	Arenig (<i>originalis</i>)	377.5	1041	0.17643	0.512156 ± 17	-8.2
104	SK44	acrotretoids	Arenig (<i>originalis</i>)	241.8	964.4	0.15358	0.512289 ± 14	-4.65
105	SK49	acrotretoids, conodont elements	Arenig (<i>originalis</i>)	244.1	703.4	0.16721	0.512166 ± 14	-7.45
106	SK54	conodont elements	Arenig (<i>flabellum parva</i>)	175.7	671.7	0.15862	0.512207 ± 12	-6.1
107	SK55	<i>Schaphelasma</i> sp.	Arenig (<i>flabellum parva</i>)	217.5	886.1	0.14219	0.512290 ± 21	4.0
108	SK57	acrotretoids	Arenig (<i>flabellum parva</i>)	989.1	3035	0.19762	0.512242 ± 19	-7.8
109	SK59	acrotretoids	Arenig (<i>flabellum parva</i>)	516.2	1839	0.14892	0.512206 ± 17	-5.1
110	SK61	conodont elements	Arenig (<i>flabellum parva</i>)	320.5	1216	0.15983	0.512100 ± 21	-8.3
111	SK62	conodont elements	Arenig (<i>flabellum parva</i>)	218.9	837.2	0.15859	0.512239 ± 17	-6.0
138a	St Backor	obolides	Arenig (Volkhov)	669.6	2387	0.17012	0.512180 ± 16	-7.35
138b		conodont elements	Arenig (Volkhov)	130.6	490.2	0.16153	0.512200 ± 16	-6.4
140	GB-80	acrotretoids	Llanvirn (Aseri)	305.4	1359	0.13626	0.512007 ± 19	-8.7
143	Bothnia-3	conodont elements	Llanvirn (Aseri)	41.6	186.6	0.13522	0.512213 ± 21	-4.8
123	segk-6	acrotretoids	Llanvirn (Aseri)	356.8	1233	0.17547	0.512131 ± 23	-8.6
124	segk-8	acrotretoids	Llanvirn (Aseri)	169.3	682.2	0.14299	0.512199 ± 11	-5.2
125	segv-3	acrotretoids	Llanvirn (Aseri)	241.9	954.2	0.15378	0.512026 ± 17	-9.4
126	sä-1	obolides, acrotretoids	Llanvirn (Aseri)	365.2	1374	0.15916	0.512120 ± 14	-7.8
127	sä-5	acrotretoids	Llanvirn (Aseri)	284.4	1066	0.15388	0.512279 ± 18	-4.9
128	sä-7	acrotretoids	Llanvirn (Aseri)	383.2	1439	0.16141	0.512169 ± 11	-7.0
129	se-1	obolides, acrotretoids	Llanvirn (Lasnamägi)	321.8	1215	0.16063	0.512113 ± 16	-8.1
130	fa-1	acrotretoids	Llanvirn (Lasnamägi)	262.1	1037	0.15322	0.512276 ± 11	-4.5
	HK-2	fossil apatite	Llanvirn (upper Kunda–Aseri?)	122.6	512.4	0.14515	0.512209 ± 22	-5.4
	HK-4	fossil apatite	Llanvirn (upper Kunda–Aseri?)	166.8	696.2	0.14530	0.512115 ± 13	-7.3
	HK-5	conodonts	Llanvirn (upper Kunda–Aseri?)	36.87	96.29	0.09765	0.511905 ± 25	-8.6
	HK-6	brachiopods	Llanvirn (Kunda)	248.6	897.7	0.16796	0.512171 ± 18	-7.5
131	fur-2	obolides, acrotretoids	Llandeilo (Uhaku)	329.5	1182	0.16911	0.512164 ± 18	-7.6
132		acrotretoids	Llandeilo (Uhaku)	400.8	1398	0.19218	0.512349 ± 17	-5.2
113	D60-221	<i>Schizotreta</i> sp., obolides, acrotretoids	Llandeilo (Uhaku)	365.9	1155	0.19215	0.512333 ± 12	-5.7
114	D60-215	acrotretoids	Llandeilo (Uhaku)	389.6	1492	0.15841	0.512074 ± 14	-8.7
	GB2-9	<i>Conotreta</i> sp.	Llandeilo (Uhaku)	817.3	2735	0.14761	0.512065 ± 18	-8.2
119	GB1-3	<i>Conotreta</i> sp., <i>Cyrtonotreta</i> sp.	Llandeilo (Uhaku)	154.5	683.2	0.13715	0.511951 ± 11	-9.8
134	dalby-7	<i>Eoconulus</i> sp.	Llandeilo (Kukruse)	153.1	617.6	0.15013	0.512306 ± 26	-5.1
115	D60-211	<i>Eoconulus</i> sp.	Llandeilo (Kukruse)	336.0	1489	0.13680	0.511976 ± 13	-8.3
116	D60-205	acrotretoids	Llandeilo (Kukruse)	478.9	1676	0.15721	0.512075 ± 16	-8.6
133	dalby-4	obolides, acrotretoids	Llandeilo (Kukruse)	319.3	1272	0.14287	0.512177 ± 18	-6.1
121	GB80+50	<i>Conotreta</i> sp., <i>Cyrtonotreta</i> sp.	Llandeilo (Kukruse)	294.4	1341	0.13316	0.512021 ± 17	-8.2
117	D60-160	obolides	Caradoc (<i>multidens</i>)	449.6	2027	0.13453	0.512043 ± 17	-7.8
118	D60-157	obolides, acrotretoids	Caradoc (<i>multidens</i>)	857.5	3834	0.13563	0.512091 ± 16	-7.0
136	D85	obolides, <i>Schizotreta</i> sp., <i>Eoconulus</i> sp.	Caradoc (Fjäckå)	217.3	948.1	0.13900	0.512162 ± 18	-5.85
147	Br10145	<i>Orbiculoidea concentrica</i>	Ashgill	372.3	1472	0.15644	0.512057 ± 15	-6.9
148a		<i>Orbiculoidea</i> sp.	Ashgill	735.5	2342	0.19040	0.512183 ± 15	-8.5
		bulk host shale	Ashgill	10.52	47.12	0.13539	0.512094 ± 14	-7.1
<i>South Urals</i>								
443		<i>Eurytreta chabakovi</i>	Upper Tremadoc–Lower Arenig	508.6	1746	0.17603	0.512563 ± 13	-0.2
<i>Bohemia</i>								
444		<i>Leptembolon</i> sp.	Lower Arenig	617.4	1760	0.21193	0.512608 ± 9	-1.5
<i>Algeria</i>								
445		<i>Schizocrania</i> sp.	Upper Ashgill	88.73	144.93	0.36999	0.512388 ± 8	-14.9