

Chapter 21

Biogeographical patterns of Ordovician ostracods

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Abstract: The biogeography of marine shelf ostracod genera is analysed for two Ordovician time slabs, the earliest Late Ordovician and the terminal Ordovician, that have been considered to reflect comparatively warmer and cooler global climate states, respectively. The earlier time slab is equivalent to the *Nemagraptus gracilis* graptolite interval (centred about 460 Ma), and defined as the total range of the eponymous species. The Hirnantian time slab comprises the *Normalograptus extraordinarius* and *Normalograptus persculptus* graptolite biozones (445.6–443.7 Ma). The ostracod dataset consists of 160 taxa from 24 early Late Ordovician localities and 86 taxa from 10 Hirnantian localities. Ordination and variation partitioning analyses show that patterns in ostracod distribution in the *gracilis* time slab are largely related to palaeocontinental affinity of the samples and to a lesser degree to palaeolatitude. Some decrease of provincialism can be suggested for the Hirnantian, although the ostracod dataset is limited for this interval.

The Ordovician Period has long been perceived as a time of considerable biogeographical differentiation (e.g. Skevington 1969, 1974; Bergström 1971; Whittington & Hughes 1972; Jaanusson 1979; Zhen & Percival 2003), reflected in the distribution of the majority of fossil groups. This has traditionally been documented from data on trilobites, graptolites, brachiopods and conodonts, and also in more recent studies on other groups such as conulariids (Van Iten & Vyhlásova 2004) and bryozoans (Tuckey 1990). Over the last decade(s), much attention has also been paid to the general pattern of Ordovician biodiversification. Various aspects of the Great Ordovician Biodiversification Event have been summarized in a comprehensive volume (Webby *et al.* 2004) that contains an overview on ostracod biodiversification (Schallreuter in Braddy *et al.* 2004).

Ostracods are small crustaceans that in some species can reach about 3 mm in length as adults. Both today and in the stratigraphical record they are found in virtually all types of aquatic environment. They have a bivalved calcareous shell hinged at the upper (dorsal) margin. The shell accommodates a body and a set of mostly biramous appendages. These anatomical features, however, are unknown in the overwhelming majority of fossil ostracod taxa. Although discoveries of soft tissues preserved in exceptional cases (e.g. Siveter *et al.* 2003, 2010) are important in shedding light on the relationships of fossil and Recent faunas, the taxonomy of fossil Ostracoda is still essentially based on shell morphology.

The first ostracods appeared in the late Tremadocian (Tinn & Meidla 2004) and they were most probably environmental generalists (Williams *et al.* 2008). The latest Early to early Middle Ordovician ostracods were bottom dwellers, crawling on and burrowing in the bottom sediments in shallow marine environments.

Ostracod diversity and assemblage composition vary with environment. The early Middle Ordovician strata of the Baltoscandian area reveal the earliest evidence of distinct ecological zonation (Tinn *et al.* 2006) and of a modern-like diversity pattern, with low-diversity assemblages related to marginal marine or other kinds of stressful environments (Tolmacheva *et al.* 2001,

2003; Tinn & Meidla 2003). Comparison of the faunas from Baltica, Laurentia and Ibero-Armorica allows us to distinguish some fundamental types of ostracod assemblages, binodicope-rich faunas being more common in unstable and clastic environments, and more diversified palaeocope-rich faunas related to more stable conditions, often associated with carbonate environments (Vannier *et al.* 1989). This broad-scale pattern helps facilitate the environmental interpretation of Ordovician ostracod assemblages.

The Ordovician and perhaps also early Silurian ostracods (Siveter 1984) were exclusively marine and benthic or nekto-benthic. The appearance of Myodocopa, the Order which includes the pelagic representatives of Ostracoda in modern environments, is dated back to the late Hirnantian. However, these first myodocopes were probably nektobenthic (Gabbott *et al.* 2003) and the appearance of true pelagic species took place only in the late Silurian (Siveter 1984; Siveter *et al.* 1991, 2010; Perrier *et al.* 2011). Colonization of the freshwater realm took place considerably later, in the early Carboniferous (Bennett 2008).

Our current knowledge of Ordovician ostracod faunas is based on data that are unequally distributed over different palaeocontinents. Most Ordovician ostracod genera have been described from Baltica and Laurentia, and some other areas have revealed a rather continuous record of lower diversity faunas (e.g. Bohemia, Kazakhstan, Siberian Platform and adjacent areas). Many, possibly important regions for ostracod studies are characterized by a sparse and discontinuous record (e.g. China, several terranes from Peri-Gondwana). The total number of known Ordovician ostracod species may exceed 2500 (Braddy *et al.* 2004), but the distribution pattern is strongly biased owing to a very different level of detail and completeness of faunal records in different areas. Another possible source of bias, probably less influential than the quality of the primary taxonomic record, is the different quality of palaeoenvironmental data in many areas.

A global biogeography of Ordovician ostracods has not been reconstructed, although a number of papers have specifically addressed aspects of inter-regional distribution of the ostracod faunas.

Most important in this respect are the comparison of ostracod faunas in southern Britain, Baltoscandia and Ibero-Armorica (Vannier *et al.* 1989) and a summary of ostracod distribution in the Peri-Gondwanan area (Hinz-Schallreuter & Schallreuter 2007). Several inter-regional and comparative aspects are also present in other papers (e.g. Schallreuter & Siveter 1985; Meidla 1996a, 2007; Williams *et al.* 2001a, b, 2003; Salas 2007). None of these contributions includes data from Russian Siberia and Kazakhstan, and there are several other areas that have been insufficiently considered. The approaches used in the papers are very different. For example, Vannier *et al.* (1989) have addressed three important regions, compiling datasets of a reasonably high time resolution (based on the Baltoscandian regional stages). In contrast, Hinz-Schallreuter & Schallreuter (2007) compare data from multiple areas of Ordovician Gondwana and Peri-Gondwana, but lack stratigraphical detail.

An initiative to summarize early Palaeozoic biogeography originated from the IGCP503 project 'Ordovician Palaeogeography and Palaeoclimate'. The present paper represents part of this initiative and is an attempt to establish a preliminary database on the biogeography of Ordovician ostracods. It is potentially a highly complex subject, as the number of relevant papers published over more than a century is huge (see e.g. data in Hinz-Schallreuter & Schallreuter 1999, fig. 130).

Compilation of a full set of palaeobiogeographical maps throughout the Ordovician would require not only a firmly established and stratigraphically complete framework for all fossiliferous locations, but also an up-to-date taxonomy for the many ostracod taxa published over the last century. The scale of that task clearly lies outside the scope of the present study and the results described below should be regarded as preliminary. In this paper, we have focussed our efforts on the analysis of ostracod data from two relatively narrow but easily recognizable time slabs, following the practice used by the PRISM group (Pliocene Research, Interpretation and Synoptic Mapping) of the United States Geological Survey, working on climate reconstructions in the Pliocene, (see Dowsett (2007) for further information).

Selection of time slabs

Palaeobiogeographical reconstruction can differ, firstly, in terms of selected stratigraphy or time resolution. Using a coarse scale of several million years would lose detail of important aspects like the end-Ordovician glacial maximum. Conversely, a fine-resolution palaeobiogeographical study would require near-perfect correlation; moreover, the use of a complete set of Ordovician time slabs (19 units through the Ordovician according to Webby *et al.* 2004) could be complicated as they are not yet widely adopted for several regions. The use of recently published stage 'slices' of a similar time resolution (Bergström *et al.* 2009) has no particular advantage and might even be more problematic as detailed correlation must be specially developed for most areas.

Secondly, the selection of particular study interval(s) would have a strong and direct influence. Our present understanding of Ordovician climates and ocean circulation challenges the original perception of this period as a greenhouse interval of long duration (Saltzman & Young 2005; Trotter *et al.* 2008; Vandenbroucke *et al.* 2010). The end-Ordovician glaciation and its influence on the biota have been discussed over several decades (e.g. Brenchley *et al.* 1994, 2003; Sheehan 2001; Brenchley 2004). In Baltica, the far-field effects of this glaciation apparently caused dramatic changes in the composition of ostracod faunas (Meidla 1996a, b, 2007). There is also increasing evidence of an earlier onset of cooling by at least the early Late Ordovician (for reviews see e.g. Barnes 2004; Page *et al.* 2007; Armstrong 2007; Armstrong *et al.* 2009; Trotter *et al.* 2008). Although this evidence remains controversial, it emphasizes the importance that the selection of

particular time slabs will have relative to the expected results of the analysis.

This paper will analyse the biogeography of marine shelf ostracod taxa for two time slabs: the earliest Late Ordovician, *Nema-graptus gracilis* graptolite-bearing interval (for definition see Williams *et al.* 2004) equivalent to a c. 2 myr time slab; and the latest Ordovician Hirnantian (encompassing the *extraordinarius* and *persculptus* graptolite zones) equivalent to a c. 1.9 myr interval. For our choice of the *gracilis* time slab, we follow Vandenbroucke *et al.* (2009) for the Sandbian. The early Late Ordovician, like most of the Ordovician, has long been thought to reflect a greenhouse climate state, although recent studies on plankton distribution patterns highlighted discrepancies with this paradigm (Vandenbroucke *et al.* 2009, 2010). The Hirnantian time slab represents the glacial maximum of the Early Palaeozoic Icehouse, together with the following deglaciation. In reality the limits of stratigraphical resolution mean that some ostracod-bearing strata from immediately below and immediately above our chosen time slabs may have been incorporated into the dataset, dependent on the stratigraphical resolution in a particular region. The Hirnantian interval has the advantage that its beginning can also be tracked by its distinctive positive carbon isotope profile. The latter aspect is important, as the time slab includes data from some areas where the exact biostratigraphical age of the ostracod-bearing latest Ordovician strata has still to be resolved (Anticosti Island in particular). Conversely, the Hirnantian provides only a small number of sites where ostracod data are available.

Source data

The use of the whole available record of ostracod taxa in thousands of papers would be impractical. We have included a limited number of publications in this pilot study. For well-studied regions, we have applied data from important monographic papers. This approach still places some limits on the widest possible regional coverage as monographic papers have not been published for some areas. In such cases the dataset has been complemented from a number of more recently published (and occasionally also unpublished) sources. Stratigraphical information available in some ostracod papers was sufficient only for establishing tentative records for the database.



Fig. 21.1. Major Ordovician facies zones of Baltoscandia (after Ainsaar *et al.* 2010). Estonian and Lithuanian shelves comprise limestones formed in shallow and middle shelf or ramp settings; the Scandinavian Basin (including its broad embayment, the 'Livonian Tongue'; see Jaanusson 1976) is characterized by argillaceous carbonates in distal ramp or basinal settings.

Table 21.1. Data points, stratigraphical equivalents to the *N. gracilis* interval and data sources

| Location | Stratigraphical unit(s) | References |
|-----------------------------------|---|---|
| <i>Baltica and adjacent areas</i> | | |
| North Estonia, East Latvia | Kukruse Stage (St) in N. Estonia, Kriaunos Mbr of the Daugavpils Formation (Fm) | Sarv (1959), Meidla (1993), Ulst <i>et al.</i> (1982) |
| Livonian Tongue | Dreimana Fm | Ulst <i>et al.</i> (1982) |
| West Lithuania | Kukruse St | Sidaravičiene (1992, 1996) |
| East Lithuania | Kukruse St | Sidaravičiene (1992, 1996) |
| NE Poland | Kukruse St | Sztejn (1985) |
| East Poland | Kukruse St | Sztejn (1985, 1989) |
| Norway | 4aβ | Henningsmoen (1953) |
| Fjällåsa, central Sweden | Dalby Fm, <i>Nemagraptus gracilis</i> Zone | Jaanusson (1976) |
| Holy Cross Mountains | Kukruse St | Olempska (1994) |
| <i>Gondwana and peri-Gondwana</i> | | |
| Ibero-Armorica | Llandeilo | Vannier (1986a, b) |
| Saudi Arabia | Hanadir Fm | Hinz-Schallreuter & Schallreuter (2007), Vannier & Vaslet (1988) |
| Bohemia | Dobrotiva Fm | Schallreuter & Krüta (1988, 2001) |
| Precordillera | middle and upper Las Aguaditas Fm | Schallreuter (1996, 1999), Salas (2002a, b, 2003, 2007) |
| <i>Laurentia</i> | | |
| Virginia | Linconshire Fm | Schallreuter & Siveter (1982, 1985), Kraft, (1962), Williams (1990) |
| Oklahoma | Tulip Creek Fm | Harris (1931, 1957) Martinsson (1960) Levinson (1961), Guber & Jaanusson (1964), Schallreuter & Siveter (1985), Williams (1990), Lundin <i>et al.</i> (1995), Williams & Siveter (1996) |
| Girvan | Superstes Mudstone | Williams <i>et al.</i> (2001a, b) |
| Yukon | Lower Esbataottine Fm | Copeland (1982), Schallreuter & Siveter (1985) |
| Pennsylvania | Hatter Fm | Swain (1957, 1962) |
| New York/Vermont | Day Point Limestone, Crown Point Limestone, lower Valcour Limestone | Swain (1957, 1962), Copeland (1982), Williams (1990) |
| <i>Siberia and adjacent areas</i> | | |
| Selennyakh Krjazh | Upper Volchin and Kalychan formations | Kanygin (1967) |
| Omulev Mountains | Darpir and lower Kharkindzhan formations | Kanygin (1967) |
| Siberia and adjacent areas | Chertovsk St | Kanygin (1967, 1971) |
| Sette-Daban | Lower sub-formation of the Labystakh Fm | Kanygin (1971) |
| <i>Kazakhstan</i> | | |
| Eastern Kazakhstan | Sarydibaik and Chingiz formations | Melnikova (1986) |

Baltica and adjacent areas

The western part of the Baltica Palaeocontinent has been termed the Baltoscandian Palaeobasin or Baltic basin in many publications (see Meidla *et al.* 2008 and references therein). Detailed sedimentological and palaeontological investigations have revealed a distinct ecological zonation in this area, which apparently mainly reflects a depth zonation of the palaeobasin (Männil 1966; Jaanusson 1976; Männil & Meidla 1994; Ainsaar *et al.* 2010; see also Fig. 21.1). Extensive studies on Ordovician ostracods have been carried out in Estonia, Latvia, Lithuania and northeastern and eastern Poland. Ostracods have been collected from more than 100 core sections. Data from Estonia are also complemented by numerous natural and man-made outcrops. The total number of studied ostracod samples from this area is counted in thousands. Data sources are summarized in Table 21.1 (*gracilis* time slab) and Table 21.2 (Hirnantian time slab).

To summarize information from the two selected stratigraphical intervals and display them in the reconstruction, data were integrated for a number of principal areas representing selected parts of the palaeoecological zones. The near-shore parts of the basin (Estonian and Lithuanian shelves) are represented by data from north Estonia and eastern Latvia, East Lithuania and East Poland. Deeper shelf areas (or the Scandinavian Basin) are represented by the Livonian Tongue (South Estonia and West Latvia; see Jaanusson 1976), West Lithuania and NE Poland.

For the sections from Baltica, the *gracilis* time slab is considered to approximate the Kukruse Stage, although the actual record of *N. gracilis* is unclear in detail (see e.g. Nölvak *et al.* 2006 for

discussion). In east Latvia, the Kukruse Stage of Ulst *et al.* (1982) was reduced to the Kriaunos Member of the Daugavpils Formation (Männil & Meidla 1994). A very large number of taxa are also known from erratic boulders in Germany (see e.g.

Table 21.2. Data points, stratigraphical equivalents to the Hirnantian interval and data sources

| Location | Stratigraphical unit(s) | References |
|-----------------------------------|---|--|
| <i>Baltica and adjacent areas</i> | | |
| North Estonia, East Latvia | Porkuni St, Ārina Fm | Meidla (1996a, b), Meidla & Tinn (2008) |
| Livonian Tongue | Porkuni St, Kuldiga and Saldus formations | Ulst <i>et al.</i> (1982), Meidla (1996a, b, 2001, 2003), Brenchley <i>et al.</i> (2003) |
| West Lithuania | Porkuni St | Sidaravičiene (1992, 1996) |
| NE Poland | Porkuni St | Sztejn (1985) |
| East Poland | Porkuni St | Sztejn (1985, 1989) |
| Norway | Topmost part of 5b | Henningsmoen (1954) |
| Scania, Sweden | Tommarp | Troedsson (1918) |
| <i>Gondwana and peri-Gondwana</i> | | |
| Carnic Alps | Hirnantian | Schallreuter (1990) |
| South Africa | Soom Shale | Gabbott <i>et al.</i> (2003) |
| <i>Laurentia</i> | | |
| Yukon | Uppermost Whittaker Fm | Copeland (1989) |

Table 21.3. *Continued*

| | North Estonia | Livonian Tongue | West Lithuania | East Lithuania | NE Poland | East Poland | Central Sweden | Norway | Holy Cross Mountains | Virginia | Oklahoma |
|---|------------------|--------------------|-------------------|-------------------|--------------|----------------|-------------------|--------|-------------------------|----------|----------|
| <i>Loculocavata</i> , Lundin <i>et al.</i> (1995) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Lodesia</i> , Schallreuter & Lehnert (1993) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Lomatopisthia</i> , Guber & Jaanusson (1964) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Longiscula</i> , Neckaja (1958) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Lubrzankiella</i> , Olempska (1994) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Marquezina</i> , Vannier (1986b) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Martinssonopsis</i> , Ivanova (1962) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Medianella</i> , Neckaja (1966) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Milleratia</i> , Swartz (1936) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Mojczella</i> , Olempska (1988) | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Monoceratella</i> , Teichert (1937) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| <i>Nahanniopsis</i> , Copeland (1982) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Nezamyslia</i> , Přibyl (1955) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Nikitinella</i> , Melnikova (1986) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Ningulella</i> , Warshauer & Berdan (1982) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Oejemyra?</i> , Schallreuter (1968) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Oepikella</i> , Thorslund (1940) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Oepikium</i> , Agnew (1942) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Ogmoopsis?</i> , Vannier (1986b) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Ordoviziona</i> , Schallreuter (1969) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Orechina</i> , Krüta (1968) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Ovornina</i> , Gruendel (1966) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pachydomelloides</i> , Swain (1962) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Parapyxionella</i> , Přibyl (1979) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pedomphalella</i> , Swain & Cornell (1961) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Pentagona</i> , Schallreuter (1964) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Perspicillum</i> , Schallreuter (1964) | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pilla</i> , Schallreuter & Siveter (1988) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pinnatulites</i> , Hessland (1949) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Piretella</i> , Öpik (1937) | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| <i>Piretia</i> , Jaanusson (1957) | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Piretopsis</i> , Henningsmoen (1953) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Platybolbina</i> , Henningsmoen (1953) | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Platyrhomboides</i> , Harris (1957) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| <i>Polyceratella</i> , Öpik (1937) | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Primitia</i> , Jones & Holl (1865) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Primitiella</i> , Ulrich (1897) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| <i>Pseudostrepula</i> , Öpik (1937) | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pseudulrichia</i> , Schmidt (1941) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Quadrirugator</i> , Kesling & Hussey (1953) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Quadritia</i> , Schallreuter (1976) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Raimbautina</i> , Vannier (1984) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Rakverella</i> , Öpik (1937) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Reutenantina</i> , Vannier (1986b) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Revisylthere</i> , Schallreuter (1986) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Rozmaniella</i> , Melnikova (1978) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Sacclatata</i> , Levinson (1961) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Schmidtella</i> , Ulrich (1892) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Septiferina</i> , Melnikova (1986) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Severobolbina</i> , Schallreuter (1974) | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Shenandoia</i> , Kraft (1962) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Sigmobolbina</i> , Henningsmoen (1953) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Sigmoopsis</i> , Henningsmoen (1953) | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Silenis</i> , Neckaja (1958) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Skalka</i> , Schallreuter & Kruta (1996) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Soanella</i> , Kanygin (1967) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Sohniella</i> , Rossi de Garcia & Proserpio (1978) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Spinohippula</i> , Vannier, Krüta & Marek (1987) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Steusloffia</i> , Ulrich & Bassler (1908) | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Steusloffina</i> , Teichert (1937) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Steusloffina?</i> , Teichert (1937) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Swantina</i> , Schallreuter (1986) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Tallinnella</i> , Öpik (1937) | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Tetrada</i> , Neckaja (1958) | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Tetradella</i> , Ulrich (1890) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Tetradellina</i> , Harris (1957) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Trianguloschmidella</i> , Sarv (1963) | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Trispinatia</i> , Schallreuter (1994) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Trubinella</i> , Přibyl (1950) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Tsitrites</i> , Kanygin (1967) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Tvaerenella</i> , Jaanusson (1957) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Uhakiella</i> , Öpik (1937) | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| <i>Ullerella</i> , Henningsmoen (1950) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Ulrichia</i> , Jones (1890) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Valcouropsis</i> , Copeland (1982) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Vannieria</i> , Schallreuter & Krüta (1999) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Velapezoides</i> , McGill (1966) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Vogdesella</i> , Baker (1924) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Winchellatia</i> , Kay (1940) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Total | 33 | 11 | 2 | 21 | 4 | 11 | 13 | 3 | 21 | 22 | 29 |

Data sources: see Table 21.1.

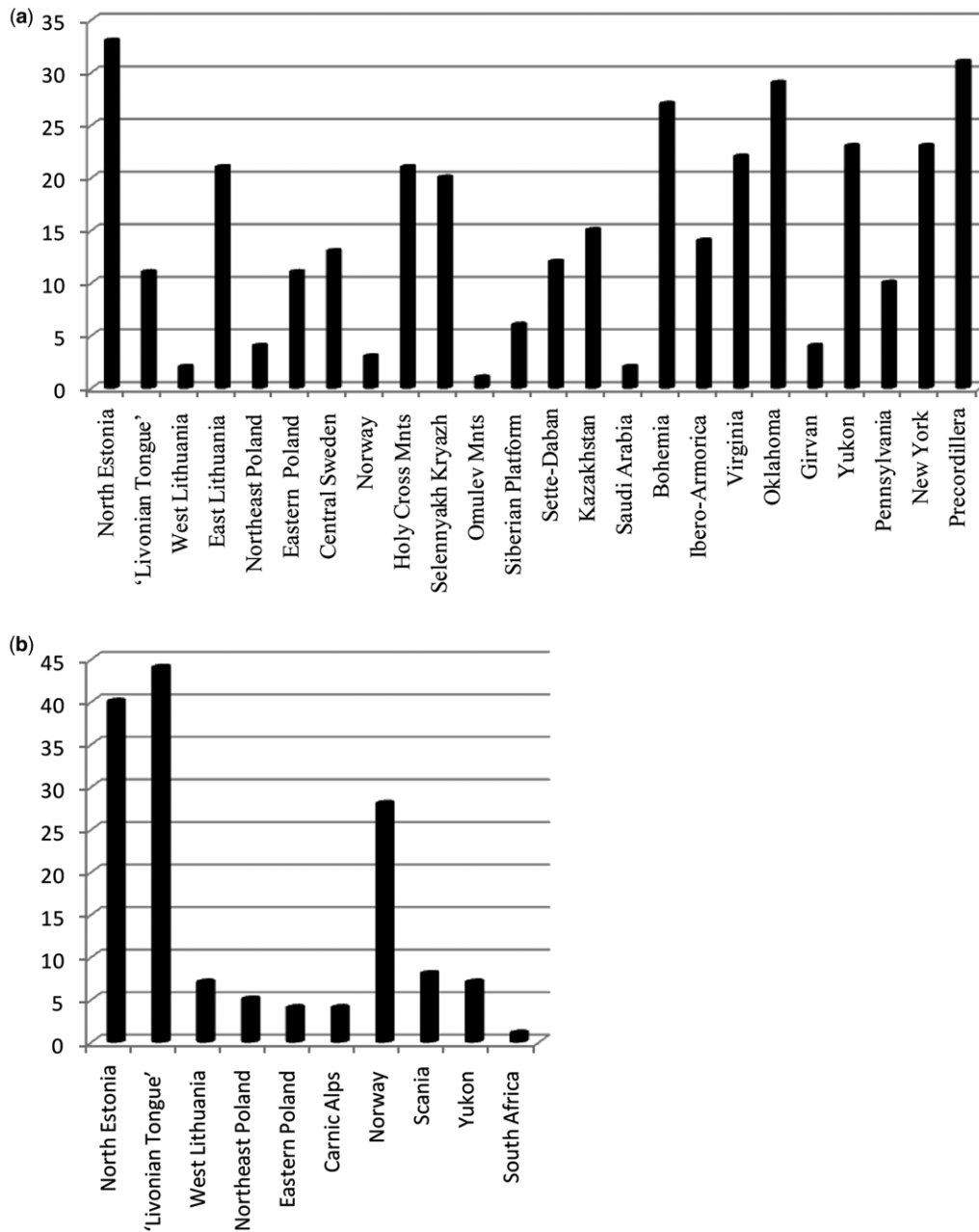


Fig. 21.2. Numbers of recorded ostracod genera in the study areas. (a) *Gracilis* time; (b) Hirnantian.

Schallreuter 1993 and references therein), but uncertainties in the dating of such erratics and on their geographical provenance within the Baltic region (many species and assemblages in erratics are unknown in the bedrock sections of the region) make this material difficult to treat within the present paper.

The Hirnantian interval is represented by the Ärina Formation in north Estonia, and by the Kuldiga and Saldus formations in south Estonia, Latvia and Lithuania (Männil & Meidla 1994). The Ärina Formation is fossiliferous only in its middle to upper parts. The Hirnantian of Poland is considered as being equivalent to the Porkuni Stage as distinguished by Szejn (1985, 1989).

Palaeogeographically, the Holy Cross Mountains, southern Poland, are tentatively regarded as part of a microplate in the vicinity of Baltica (see Servais *et al.* 2008 for a discussion).

Ordovician ostracods from Norway were described by Henningsmoen (1953, 1954). The *gracilis* time slab approximates to unit 4a β of Henningsmoen (1953) and the Hirnantian to unit 5b (calcareous sandstone of the *Dalmanitina* series: Henningsmoen 1954), according to Owen *et al.* (1990).

Ostracod distribution in the *gracilis* time slab of central Sweden was analysed by Jaanusson (1976). Hirnantian data are available

from the Tommarp Stage of Scania (Troedsson 1918). A diverse Hirnantian-like assemblage is described from Östergötland (Meidla 2007), but it is still unclear if the rock material originates from a bedrock section or from erratics (see Bergström & Bergström 1996 for details). The main reason for excluding the latter data from the present analysis is the fact that composition of this ostracod assemblage suggests some mixing of faunas from Hirnantian and pre-Hirnantian strata (Meidla 2007).

Laurentia

Ostracod occurrences in Laurentia are documented from Virginia, Oklahoma, Pennsylvania, New York/Vermont, Yukon and Girvan in Scotland (see Table 21.1 for source papers). Most of the available information comes from the *gracilis* time slab, which has been approximated to the Linconshire Formation in Virginia, Tulip Creek Formation in Oklahoma, Hatter Formation in Pennsylvania, Lower Esbataottine Formation in Yukon and Day Point Limestone, Crown Point Limestone and lower Valcour Limestone in Vermont (Ross *et al.* 1982). The Hirnantian dataset includes

material from the Yukon Territory only (uppermost Whittaker Formation; Copeland 1989). The Hirnantian age of the strata is supported by associated graptolite evidence (Goodfellow *et al.* 1992).

The latest Ordovician ostracod records from the Ellis Bay Formation (Island of Anticosti, Canada) are excluded from the present analysis. The Ellis Bay Formation has been dated as Hirnantian in many papers (see Barnes *et al.* 1981 or Melchin 2008, fig. 1, for a review) but graptolite evidence is controversial (Achab *et al.* 2011). This Hirnantian interpretation also disagrees with the stable carbon isotope curve (Long 1993; Achab *et al.* 2011). Ostracods from the Ellis Bay Formation were documented by Copeland (1973), but unfortunately, the uppermost (Lafromboise) member of this formation has not been studied. The 35–50 feet (c. 12–17 m) unstudied interval between Member 6 of the Ellis Bay Formation and the occurrence level of the Silurian brachiopods in the lower Bescie Formation (Copeland 1973) roughly corresponds to the interval of more positive carbon isotopic values (Long 1993). Thus, the ‘Vauréal–Ellis Bay’ ostracod assemblage is probably immediately pre-Hirnantian.

Siberia and adjacent areas

Ostracod distribution in the Siberian Palaeocontinent is documented by Kanygin (1967, 1971; see Table 21.1). The distribution of ostracods is documented from the *gracilis* time slab only, and this interval is assumed to correspond to the Chertovsk Stage. The youngest part of the Ordovician has not been available for investigation, being eroded or unexposed in most of the marginal areas of the Siberian Platform.

Largely similar faunas of *gracilis* time slab age are recorded from the lower sub-formation of the Labystakh Formation (‘upper assemblage’) in Sette–Daban (Kanygin 1971), from the Darpir and Harkindzhin formations of the Omulev Mountains (Kanygin 1967) and from the Kalychan and Bolchin (upper) formations in Selennyakh Kryazh (Kanygin 1967).

Kazakhstan

Melnikova (1986) documents ostracods from the Middle and Upper Ordovician, from the Karakan Superstage (attributed to the Llanvirn in this paper, or Mid-Dapingian) up to the lower part of the Tolen Superstage, the Chokpar Stage (attributed to the lower part of the upper Ashgill). According to Nikitin *et al.* (1986), equivalents of the *gracilis* zone comprise the upper part of the Tselinograd Stage, whereas the lower part of this stage is referred to the (pre-*gracilis*) *Hustedograptus teretiusculus* graptolite zone. The undivided Tselinograd Stage is thought to correspond to the Sarydibaik and Chingiz formations of Melnikova (1986). As the ostracod record from the *gracilis* time slab could not be distinguished from that of pre-*gracilis* intervals, the entire Tselinograd Stage was included in the dataset.

Peri-Gondwana and Gondwana

Early Late Ordovician ostracods from this region are thoroughly documented from Ibero-Armorica, Bohemia and from the Precordilleran area. For Ibero-Armorica (Vannier 1986a, b), the old chronostratigraphical term ‘Llandeilo’ was taken as the best approximation for the *gracilis* time slab. In accordance with Schallreuter *et al.* (1996), the Dobrotiva Formation was taken as the equivalent of the *gracilis* zone in Bohemia.

The Argentine Precordillera is considered a microplate that accreted to the west margin of Gondwana during the later Ordovician (Benedetto 2004), being an isolated terrane in *gracilis* times. Most of the available ostracod fauna from *N. gracilis* interval comes from the middle and upper parts of the Las Aguaditas Formation (Salas 2007 and references therein). Schallreuter (1999)

described several taxa from the Empozada Formation (middle to upper Ordovician), but uncertainties in age (ostracods are derived from loose blocks) make this material difficult to incorporate.

Another data point in the *gracilis* time slab is marked by Vannier & Vaslet (1988) in central Saudi Arabia, where ostracods are documented from the Hanadir Formation (Hinz-Schallreuter & Schallreuter 2007; but according to some interpretations, it may also be of pre-*gracilis* age).

Hirnantian records from Gondwana are poor. Hirnantian ostracods are documented from the Cellon Profile of the Carnic Alps (Schallreuter 1990), which probably formed a terrane in the vicinity of Gondwana. Only one unique myodocope genus (*Myodoprimgenia*; Gabbott *et al.* 2003) was recorded from the Hirnantian Soom Shale Lagerstätte (c. 200 km north of Cape Town, Hirnantian) from a post-glacial maximum transgressive shale succession.

A possible Hirnantian record of ostracods could also be available from the Farka Muth section of the Himalaya (northern India; Schallreuter *et al.* 2008). Ostracods are found above the level that marks the Boda Event, a warming episode in the late Katian (see Fortey & Cocks 2005). Evidence of this warming is supposedly recorded at Farka Muth in the topmost *Amorphognathus ordovicicus* conodont zone, judging from interpretation of the local carbon isotope record (Suttner *et al.* 2007). However, there is no evidence of the Hirnantian glacial maximum positive carbon isotope excursion in the Ordovician–Silurian boundary beds at Farka Muth.

Taxonomic remarks on source data of ostracods

The number of recorded Ordovician ostracod taxa probably exceeds 2000 species and hundreds of genera. Since the work of Benson *et al.* (1961), many genera have been described and revised from Baltoscandia, North America, southern Europe, Russian Siberia and South America.

The most important ostracod group in the *gracilis* interval is the suborder Palaeocopa, comprising about half of all recorded taxa at generic and species level. Other important groups in this interval are the order Podocopa and suborder Binodicopa. The role of Palaeocopa was substantially reduced in the latest Ordovician, with a slight increase in the diversity of Podocopa and Binodicopa.

Perhaps more than 10% of the records of genera in some areas are tentative. This is mostly due to insufficient descriptions (lack of important diagnostic features) in the older records. Our preliminary analysis confirms that this may have only a minor effect on the resultant overall patterns, as cluster analysis plots produced from the full dataset and those generated by leaving out ‘unrevised records’ are very similar. This comparison indicates that potentially problematic data have little influence on results.

Reliability of the taxonomic record from a particular area may still be of a very different quality. For example, most areas of Baltica are well studied and the size of collections is very large – tens or hundreds of sections, thousands of samples and hundreds of thousands or millions of specimens from an area. In some other cases (e.g. the *gracilis* interval of Norway) the occurrence of a genus may be documented based only on one or a few specimens.

Palaeogeography

The palaeogeography was reconstructed from maps generated by means of BugPlates software, provided by T. Torsvik. The data are plotted on the reconstructions for 460 Ma (start of *gracilis* time slab) and 445 Ma (start of Hirnantian); most data points are plotted automatically, based on recent coordinates and palaeo-plate identifications. There are a few exceptions, such as the

Table 21.4. Record (presence 1, absence 0) of ostracod genera from the Hirnantian interval

| | North Estonia | Livonian Tongue | West Lithuania | NE Poland | East Poland | Southern Sweden | Norway | Carnic Alps | Yukon | South Africa | Total |
|---|------------------|--------------------|-------------------|--------------|----------------|--------------------|--------|----------------|-------|-----------------|-------|
| <i>Adamczakia</i> , Schallreuter (1986) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Aechmina</i> , Jones & Holl (1869) | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 5 |
| <i>Ahlintella</i> , Schallreuter (1985) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Airina</i> , Sidaravičiene (1971) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Ampletochilina</i> , Schallreuter (1969) | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| <i>Apatochilina</i> , Ulrich & Bassler (1923) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Ardenita</i> , Sidaravičiene (1992) | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Arpaschmidtella</i> , Meidla (1996a) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Aviacypris</i> , Schallreuter (1977) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Bairdia?</i> , McCoy (1844) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Bairdiocypris</i> , Kegel (1932) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Baltonotella</i> , Sarv (1959) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Bolbihithis</i> , Schallreuter (1967) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Bolbina</i> , Henningsmoen (1953) | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 3 |
| <i>Bollia</i> , Jones & Holl (1886) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| <i>Bulbosclerites</i> , Knüpfer (1968) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Byrsolopsina</i> , Swain & Cornell (1961) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Cadmea</i> , Pranskevičius (1972) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Circulinella</i> , Meidla (1996a) | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 |
| <i>Conchoprimitia</i> , Öpik (1935) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| <i>Conodomyra</i> , Schallreuter (1968) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Cryptophyllus</i> , Levinson (1951) | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| <i>Cystomatochilina</i> , Jaanusson (1957) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Dagoerayella</i> , Meidla (1996a) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Daleiella</i> , Bouček (1937) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Distobolbina</i> , Sarv (1959) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Dornbuschia</i> , Schallreuter (1968) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| <i>Drepanella?</i> , Ulrich (1894) | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Duplexibollia</i> , Schallreuter (1987) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Duplicristatia</i> , Schallreuter (1968) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Easchmidtella</i> , Schallreuter (1967) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Eoaquapulex</i> , Levinson (1968) | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| <i>Eocytherella</i> , Schallreuter (1980) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 2 |
| <i>Estonaceratella</i> , Schallreuter (1984) | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| <i>Estoniosylthere</i> , Meidla (1996a) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Foramenella</i> , Stumbur (1956) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Gryphiswaldensia</i> , Schallreuter (1965) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Harpabollia</i> , Schallreuter (1990) | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 5 |
| <i>Hemeaschmidtella</i> , Schallreuter (1971) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Hemiaechminoides</i> , Morris & Hill (1952) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Hesslandella</i> , Henningsmoen (1953) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Jonesina?</i> , Ulrich & Bassler (1908) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Kiesowia</i> , Ulrich & Bassler (1908) | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| <i>Kinnekullea</i> , Henningsmoen (1948) | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| <i>Klimphores</i> , Schallreuter (1966) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Krausella</i> , Ulrich (1894) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| <i>Krauseloides</i> , Meidla (1996a) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Kroemmelbeinia</i> , Schallreuter (1969) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Leperditella</i> , Ulrich (1897) | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 4 |
| <i>Lilitia</i> , Gailite in Abushik (1990) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Loculibolbina</i> , Schallreuter (1983) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Longidorsa</i> , Schallreuter (1985) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Longiscula</i> , Neckaja (1958) | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 |
| <i>Macronotella</i> , Ulrich (1894) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Medianella</i> , Neckaja (1966) | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 |
| <i>Microcheilinella</i> , Geis (1933) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Moeckowia</i> , Schallreuter (1964) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Myodoprigenia</i> , Gabbott, Siveter, Aldridge & Theron (2003) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| <i>Naevhithis</i> , Schallreuter (1981) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Oepikella</i> , Thorslund (1940) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

(Continued)

Table 21.4. *Continued*

| | North Estonia | Livonian Tongue | West Lithuania | NE Poland | East Poland | Southern Sweden | Norway | Carnic Alps | Yukon | South Africa | Total |
|---|------------------|--------------------|-------------------|--------------|----------------|--------------------|--------|----------------|-------|-----------------|-------|
| <i>Oepikium</i> , Henningsmoen (1954) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Olbianella</i> , Meidla (1996a) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Phelobothocypris</i> , Warshauer & Berdan (1982) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| <i>Platybolbina</i> , Henningsmoen (1953) | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 4 |
| <i>Pseudoancora</i> , Sidaravičienė (1979) | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Pseudorayella</i> , Neckaja (1960) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Pseudulrichia</i> , Schmidt (1941) | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 |
| <i>Pullvillites</i> , Öpik (1937) | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Pyxion</i> , Thorslund (1948) | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Quadritia</i> , Schallreuter (1976) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| <i>Rectella</i> , Neckaja (1958) | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 4 |
| <i>Retiprimites</i> , Meidla (1996a) | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| <i>Reversocypris</i> , Přebyl (1955) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Rimabolbina</i> , Schallreuter (1969) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Satiellina</i> , Vannier (1986a) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| <i>Scanipisthia</i> , Schallreuter & Krūta (1990) | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 4 |
| <i>Sigmobolbina</i> , Henningsmoen (1953) | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| <i>Spinopleura</i> , Schallreuter (1968) | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| <i>Steusloffina</i> , Teichert (1937) | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 4 |
| <i>Tetradella</i> , Ulrich (1890) | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 |
| <i>Trapezisyllthere</i> , Schallreuter (1986) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Tvaerenella</i> , Jaanusson (1957) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>Uhakiella</i> , Öpik (1937) | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 4 |
| <i>Uthoernia</i> , Schallreuter (1986) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Vitteplana</i> , Sidaravičienė (1992) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Vogdesella</i> , Baker (1924) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Total | 40 | 44 | 7 | 5 | 4 | 8 | 28 | 4 | 7 | 1 | |

Data sources: see Table 21.2.

Malopolska Massif (Holy Cross Mountains), which was positioned in the vicinity of Baltica as a microcontinent. The palaeogeographical position of Malopolska is based on palaeomagnetic evidence (Schätz *et al.* 2006) and on the overall composition of the ostracod faunas from the area. Faunal composition does not reflect the substantial increase in Baltoscandian influence in the Middle and Late Ordovician (Olempska 1994).

The ostracod database

The database of the lowermost Upper Ordovician (*gracilis* time slab) ostracods contains information from 24 areas, localities or biofacies. For the majority of locations, data are summarized from a number (up to several tens, for example in the case of north Estonia) of individual sections. The biofacies are distinguished in Baltica only (see Fig. 21.1 and the section 'Source data'). Altogether 160 genera are recorded from this interval (see Table 21.3). Ninety-five of them (60%) are known from one area/locality only. The majority of data points represent Baltica (nine) and Laurentia (six). Numbers of taxa in the areas/localities for both time slabs are shown in Figure 21.2.

Ostracod records from Baltica are the richest, although some of the locations have rather poor documentation (west Lithuania, NE Poland, Norway). Data from the *gracilis* time slab of Norway (Henningsmoen 1953) are probably incomplete and hardly comparable to the faunal lists from other localities because of different collection methods (a very limited collection of hand-prepared material is identified and figured from the surfaces of blocks and slabs). The list of taxa from this particular interval shows only low affinity to other Baltoscandian

localities, but this affinity is remarkably higher for the under- and overlying strata.

The database of the uppermost Upper Ordovician (Hirnantian) ostracods contains information on 10 areas, localities or biofacies. The biofacies are distinguished in the Baltoscandian Palaeobasin only (see Fig. 21.1 and the section 'Source data'). The dataset is strongly dominated by Baltoscandian occurrences (seven data points). Altogether 86 genera are recorded from this interval (see Table 21.3). Forty-eight of them (56%) are known from one area/locality only. Ostracod records from Baltica are the richest in this interval, as for the *gracilis* interval also. Of the few others, the South African record consists of a single myodocoenid genus not recorded elsewhere. Data from Norway (Henningsmoen 1953) are incomplete and may also contain some pre-Hirnantian material (assumption based on a preliminary study of the collections in the Oslo Palaeontological Museum, carried out by T. Meidla in 1991).

Data analysis

We used ordination techniques to investigate the relationships between the different localities on the basis of their ostracod composition for the two datasets (Tables 21.3 & 21.4). Detrended correspondence analysis of all datasets revealed gradient lengths >8 , suggesting considerable species turnover in the dataset. We therefore opted for a unimodal ordination method, namely correspondence analysis (CA), with focus on samples and Hill's scaling (Jongman *et al.* 1987), for both time slabs. For the *gracilis* time slab, we performed analyses on all 24 localities for both the complete ostracod dataset (160 genera) and a reduced dataset without

genera with single occurrences (65 genera). For the Hirnantian time slab, the outlier South Africa, which was characterized by a single genus (*Myodoprimgenia*) that only occurred in this locality, was left out of the analyses. For the remaining nine localities analyses were undertaken for both the complete (86 genera) and reduced (without single occurrences, 38 genera) datasets.

We then used the program Canoco 4.5 for Windows (ter Braak & Šmilauer 2002) to perform a variation partitioning analysis (see e.g. Heikkinen *et al.* 2005) that uses partial regression analyses in order to assess how the variation in a particular dataset (i.e. the ostracod datasets) can be partitioned over different sets of explanatory variables (i.e. palaeolatitude and palaeocontinental affinity). For the *gracilis* time slab dataset, this resulted in three fractions of explained variation, viz. palaeolatitude alone, palaeocontinental affinity alone and the joint effect of both, and a fraction of unexplained variation. Palaeolatitude was read from the BugPlates plots (see Table 21.5) and treated as a quantitative variable, while palaeocontinents (Table 21.1) were coded as dummy variables (see Lepš & Šmilauer 2003). Prior to the variation partitioning analyses, the forward selection procedure was used to select only those dummy variables that significantly contributed to explaining the variation in the ostracod data. Significance testing in both the forward selection and variation partitioning analyses was undertaken using Monte Carlo permutation tests (see ter Braak & Šmilauer 2002). Because of the low number of localities in the Hirnantian time slab, most of which were located in Baltica, no variation partitioning was performed for this dataset.

Leaving out the single occurrences focusses the analysis on the shared genera (and hence the similarities between localities), rather than on the unique taxa. This approach would give better results if data quality in different localities was expected to be similar. However, judging from published data and unpublished information, a remarkable collection bias very probably exists in

the ostracod dataset. Many researchers systematically ignored a remarkable part of the material (podocope ostracods), and mostly did not even collect them. Another source of bias is very different collection sizes. A reliable estimate on faunal composition of an assemblage should be based on a reasonable number of specimens. The influence of limited collecting on the assemblage structure is discussed in several papers (e.g. Watkins 1979; Tolmacheva *et al.* 2001). In the case of the ostracod data discussed here, the number of recorded genera and collection size are mostly in good correlation for the localities with very low diversity (fewer than five genera), and this suggests that sampling bias must be considered. Assuming that low numbers of taxa means a bias (most probably only dominant taxa recorded), we need an approach that reduces the influence of the size differences of datasets from the particular areas. We therefore also used cluster analysis with the Simpson similarity coefficient (program PAST; Hammer *et al.* 2001), which assumes that differences in total species number are due to sampling differences. For the *gracilis* time slab, this resulted in a self-explanatory dendrogram that is largely in agreement with the results of the correspondence analysis, but the scarce data from the Hirnantian time slab are still more difficult to interpret.

The *gracilis* time slab

Correspondence analysis of the complete dataset (all localities, all genera) reveals three distinct clusters of localities, Siberia, Laurentia and Baltica + Gondwana, and a few more-or-less isolated ones (Norway, Argentine Precordillera and Kazakhstan; Fig. 21.3). Leaving out all genera with single occurrences in the dataset preserves the three main clusters, but re-unites Norway with the other Baltica samples and places the Argentine Precordillera closer to Kazakhstan in between the Laurentia and Baltica + Gondwana clusters (Fig. 21.4). The variable positioning of Norway and the Precordillera is due to the large proportions of unique genera (two out of three in the former, 22 out of 31 in the latter).

The dendrogram of cluster analysis is largely self-explanatory. Clusters of Siberia and Laurentia can be recognized both in the dendrogram of cluster analysis (Fig. 21.5) and in the plot of correspondence analysis (Fig. 21.3). Baltica and Gondwana are still rather distinct in the dendrogram of cluster analysis (Fig. 21.5), and Kazakhstan and the Argentine Precordillera stand separately.

For each of the localities, large-scale palaeoenvironmental metadata are available. This comprises their palaeolatitude (which could be read from the BugPlates plots; see Table 21.5) and palaeocontinental affinity (Table 21.1). Variation partitioning analysis of the early Late Ordovician interval which was based on this metadata revealed that palaeocontinental affinity alone significantly explained more than one-third of the total variation in the ostracod datasets (44% for the complete dataset, 34.6% for the reduced dataset). After partialling out the effect of the palaeocontinental dummy variables, the contribution of palaeolatitude alone in explaining the variation in the data was very small and not significant (3.7% for the complete dataset; 2.6% for the reduced dataset). Palaeocontinent and palaeolatitude jointly explained 5 and 9.8% in the complete and reduced datasets, respectively. The latter is due to the fact that the position of a locality on a palaeocontinent is to a certain degree also related to its palaeolatitude position (see Fig. 21.6).

The Hirnantian time slab

Correspondence analyses on the complete (Fig. 21.7) and reduced (not shown) datasets of the Hirnantian interval yielded different results. There is no clear distinction between the Laurentian (Yukon), Gondwanan (Carnic Alps) and Baltica localities.

Table 21.5. Palaeolatitudes of the localities according to the palaeogeographical reconstructions of 460 Ma (early Late Ordovician) and 445 Ma (Hirnantian)

| Location | Early Late Ordovician (<i>gracilis</i>) | Hirnantian |
|----------------------|---|------------|
| North Estonia | 37°S | 27°S |
| Livonian Tongue | 39°S | 30°S |
| West Lithuania | 41°S | 33°S |
| East Lithuania | 40°S | |
| NE Poland | 41°S | 33°S |
| East Poland | 43°S | 35°S |
| Central Sweden | 33°S | |
| Southern Sweden | | 32°S |
| Norway | 33°S | 27°S |
| Holy Cross Mountains | 51°S | |
| Virginia | 21°S | |
| Oklahoma | 8°S | |
| Girvan | 20°S | |
| Yukon | 12°N | 15°N |
| Pennsylvania | 20°S | |
| New York/Vermont | 20°S | |
| Selennyakh Krjazh | 3°S | |
| Omulev Mountains | 7°N | |
| Siberian Platform | 6°S | |
| Sette-Daban | 10°N | |
| Kazakhstan | 11°S | |
| Saudi Arabia | 48°S | |
| Bohemia | 59°S | |
| Carnic Alps | | 60°S |
| Ibero-Armorica | 78°S | |
| South Africa | | 34°S |
| Precordillera | 30°S | |

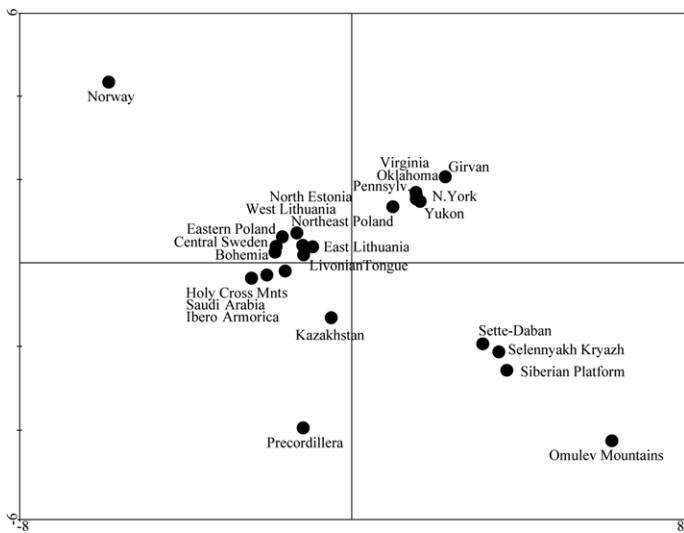


Fig. 21.3. Plot of correspondence analysis of full dataset of the early Late Ordovician ostracod faunas. Three major clusters comprise Laurentia, Baltica + Gondwana and Siberia (together with adjacent areas).

Figure 21.7 does not show much variation and suffers from scarce data. The fact that remote localities (Carnic Alps of Gondwana, Yukon from Laurentia) plot together with Baltica is the only remarkable feature. North Estonia, east Poland, Norway and Livonian Tongue, most of which are located on the Estonian and Lithuanian shelves of Baltica, and Yukon are located on the left side of the first CA axis, while on the right side the localities of the Scandinavian Basin (southern Sweden, NE Poland, western Lithuania) and Carnic Alps are situated. Note that the

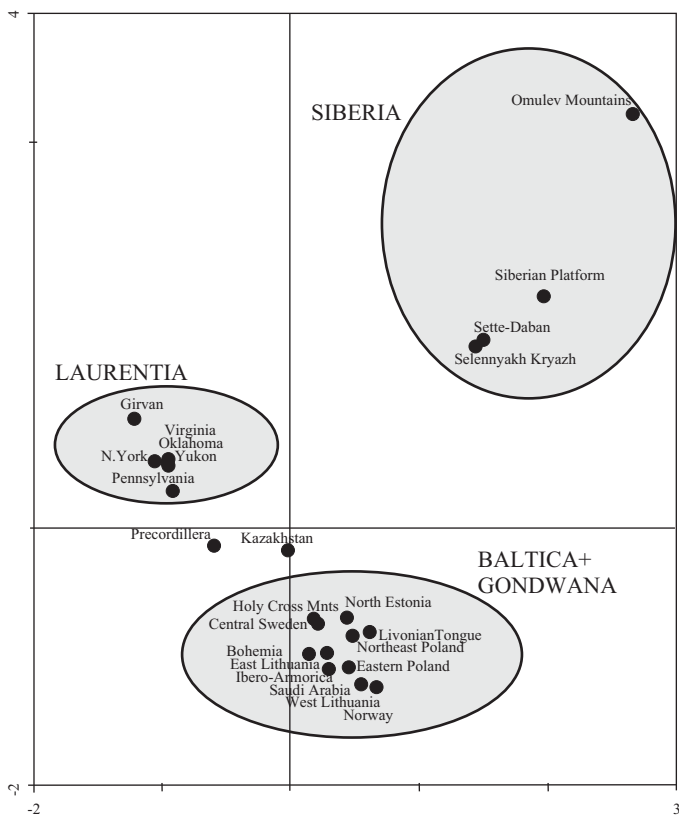


Fig. 21.4. Plot of correspondence analysis of a reduced dataset (59 genera) of the early Late Ordovician ostracod faunas. Genera occurring in only one dataset are excluded.

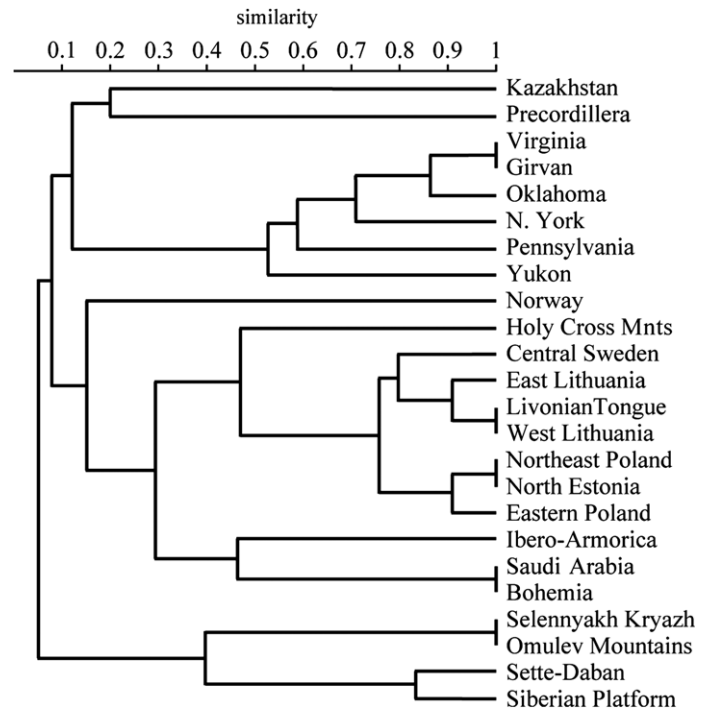


Fig. 21.5. Results of cluster analysis on early Late Ordovician ostracod faunas (paired groups, Simpson's similarity).

localities of the latter group are more different from one another, witnessing the larger spread along the second CA axis. Essentially the same groups occur in the dendrogram of cluster analysis (Fig. 21.8). Paired groups clustering does not resolve the position of the South African Soom Shale, but other localities form two distinct clusters, which are not related to the palaeocontinental attribution of the particular localities.

Ordovician ostracod biogeography

Ostracods first appear conclusively in rocks of Tremadocian age (Salas *et al.* 2007; Tinn & Meidla 2004; Williams *et al.* 2008) and formed a diverse component of marine benthic assemblages by the early Middle Ordovician (Tinn *et al.* 2006). Ostracod biodiversity reached a peak in the Late Ordovician (Schallreuter, in Braddy *et al.* 2004). This general pattern especially reflects ostracod dynamics in Baltica from which, compared with other regions, the diversity is documented in greatest detail and is by far the highest. The data from Baltica also suggest a marked decrease in

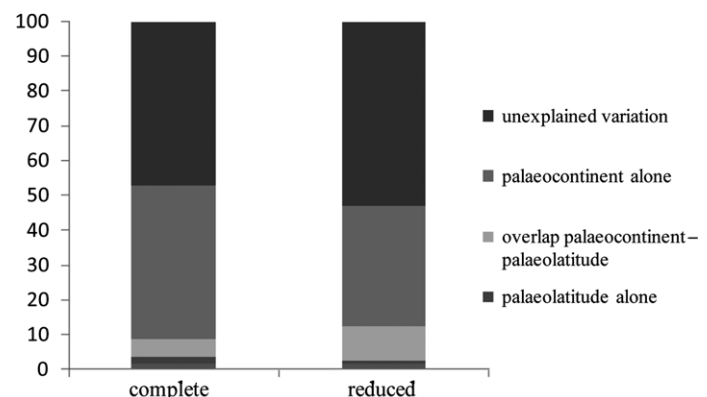


Fig. 21.6. Influence of palaeolatitude and palaeocontinental affinity on the distribution of ostracod genera.

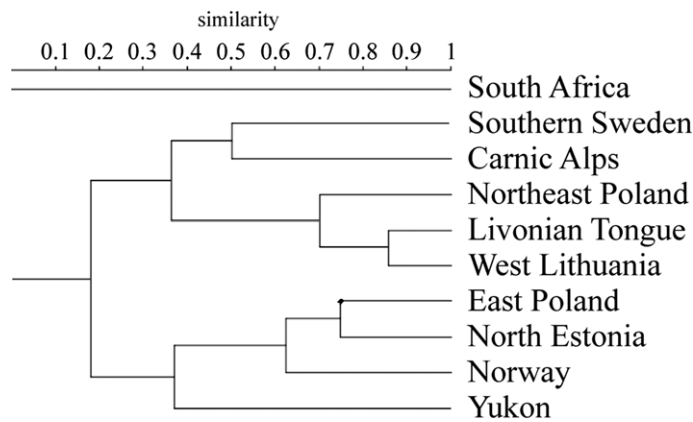


Fig. 21.7. Plot of correspondence analysis of the latest Ordovician ostracod faunas. Note proximity of southern Sweden and the Carnic Alps.

ostracod diversity and an associated turnover, owing to global climate cooling and associated oceanographic effects during the latest Ordovician (Meidla 1996a, 2007; Meidla *et al.* 2009a, b). Against this background, the lowermost Upper Ordovician, represented by the *gracilis* time slab, is close to the peak diversity of Ordovician ostracods. The Hirnantian time slab coincides with climate-forced re-arrangement of patterns of ostracod biodiversity.

Analysis of the distribution of the ostracods from the *gracilis* time slab clearly resolves three to four major ostracod biogeographical provinces, that is, Laurentian, Siberian and Baltic, which may or may not include Gondwana (Fig. 21.9). The biogeographical affinity of the Argentine Precordillera ostracod faunas is intermediate between the Laurentian and Gondwana/Baltic faunas. This may be due to the complex tectonic history of the area (Benedetto 2004), considered an allochthonous terrane in the western margin of Gondwana, which may have resulted in affinities with other provinces and a significant endemic signature at generic level (36%). The Kazakhstan faunas seem to be distinct as well.

Of the major ostracod provinces, only the Siberian Province may be regarded as reflecting endemism, having several endemic egorovellid and cherskiellid genera common to all or

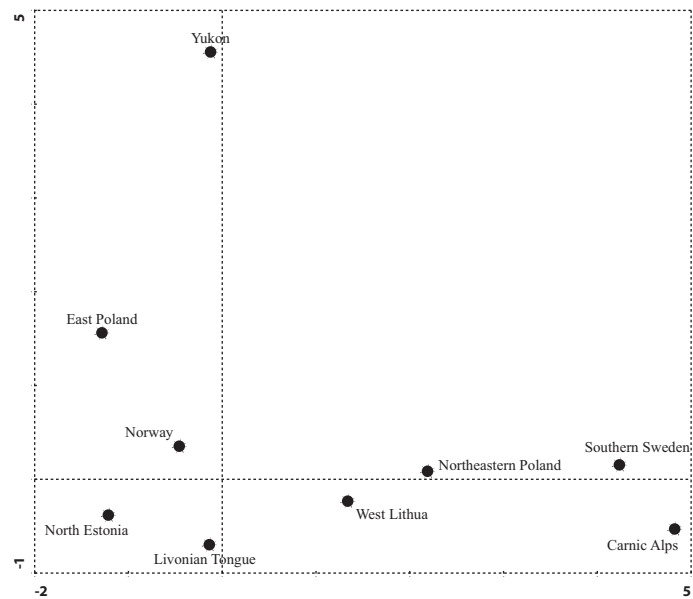


Fig. 21.8. Results of cluster analysis on the latest Ordovician ostracod faunas (paired groups, Simpson's coefficient). Two major clusters are obviously not related to palaeocontinents, but comprise binodicope-poor (tropical?) and binodicope-rich (cool-water?) faunas.

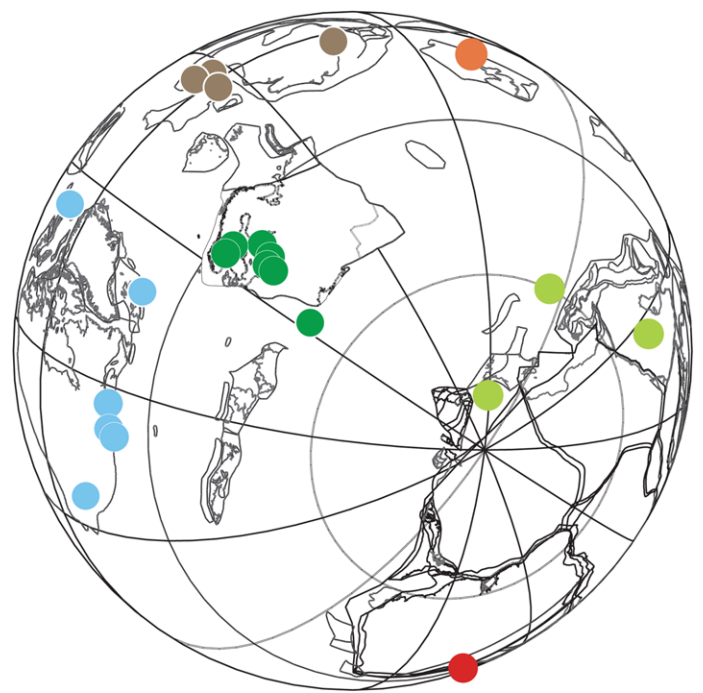


Fig. 21.9. Early Late Ordovician (*gracilis* time slab) ostracod biogeography. Provinces: green, Baltic (dark green) + Gondwanan (light green) Province; blue, Laurentian Province; brown, Siberian Province; orange, Kazakhstan; red, Argentine Precordillera.

most of the localities but lacking in all other areas. Other ostracod families are more widely distributed and the various provinces (including Siberia) share several genera in the early Late Ordovician. Although the Ordovician ostracods were most probably benthic (cf. Siveter 1984 for Silurian ostracods) and possible mechanisms for their dispersal are unclear (see Schallreuter & Siveter 1985; Williams *et al.* 2003), some communication between the provinces was seemingly possible.

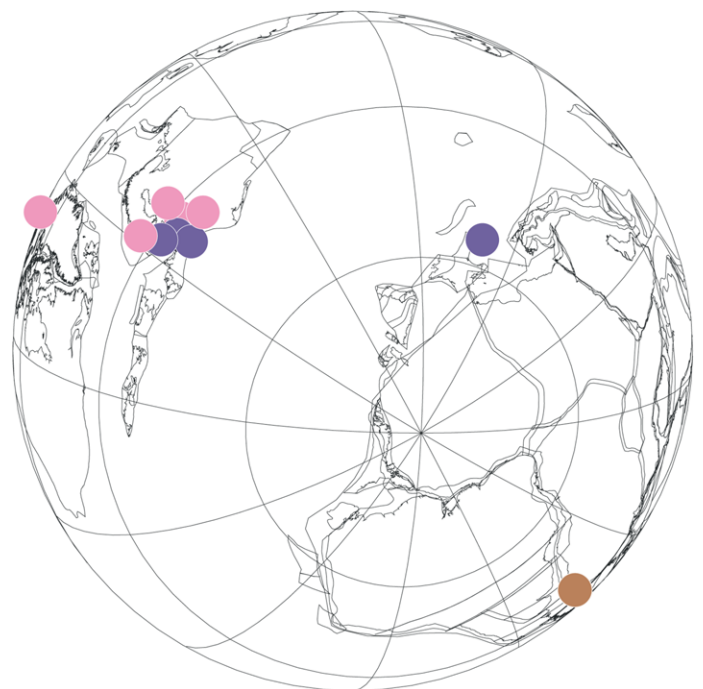


Fig. 21.10. Summary of latest Ordovician (Hirnantian time slab) ostracod biogeography. Legend: pink, tropical faunas; violet, cool-water faunas; light brown, South Africa.

As demonstrated by the correspondence analysis, biogeographical variation in the ostracod fauna in the early Late Ordovician is mainly related to palaeocontinental affinity and appears to be little influenced by the latitudinal sea-surface temperature gradient. In this respect, the patterns observed for the benthic ostracod faunas of the *gracilis* time slab contrast with the patterns determined for Ordovician planktonic 'mixed-layer' organisms such as chitinozoans and graptolites, where palaeolatitude appears to have been a more significant control (Vandenbroucke *et al.* 2009, 2010). However, the latter studies did not include Siberian data.

The data available in the literature (the monographs cited above) suggest that at generic level ostracod provincialism was probably present already in the Middle Ordovician. This distribution pattern is generally similar to that of many other marine invertebrate groups (see above). Major changes in this pattern could tentatively be ascribed to Late Ordovician cooling, which resulted in a major faunal turnover and diversity decrease.

By comparison with the dataset on ostracods from the *gracilis* time slab, that for the Hirnantian is considerably smaller and is strongly dominated by occurrences in Baltica (Table 21.4). The 'nearshore cluster', which included North Estonia together with eastern Latvia, East Poland and Norway, is seemingly metacope-rich in all locations (notwithstanding the fact that systematic documentation of non-palaeocopes is lacking in Norway; see Henningsmoen 1954, p. 71). Surprisingly, the Yukon shows faunal links to the shallow-water ostracod assemblage of Baltica, in particular with respect to latest pre-Hirnantian assemblages (cf. generic lists of Meidla 1996a), suggesting that it, too, may represent a tropical shallow-marine assemblage.

The Hirnantian ostracod assemblages of the two principal palaeoecological zones of Baltica are quite distinct (Meidla 1996b, 2007; Fig. 21.1). A high-diversity, metacope-dominated nearshore assemblage characterizing the shelf areas in Estonia and Lithuania, is succeeded more offshore within the Scandinavian Basin by a low-diversity binodicope-dominated assemblage, namely the *Harpabollia harparum* Association (Meidla 2007). Based on evidence from chitinozoans (graptolites are not recorded in these strata), the nearshore assemblage is of early Hirnantian age (Kaljo *et al.* 2004 and references therein). In the Scandinavian Basin the *Harpabollia harparum* Association ranged into the Late Hirnantian: in Sweden the eponymous species co-occurs with *Normalograptus persculptus* (Meidla 2007). In the *Harpabollia harparum* Association binodicoopes prevail, metacopes are of low diversity and hollinoideans are almost lacking. However, the differences in composition of the associations may also partly reflect ecological differentiation.

Hirnantian links between the ostracod faunas of the Scandinavian Basin of Baltica and those of the Carnic Alps (Peri-Gondwana) are well documented (Meidla 1996b, 2007; Meidla *et al.* 2009a, b). Appearance of 'new' genera, which are unknown from the well-studied pre-Hirnantian of Baltica, are interpreted as representing migration from higher latitudes, as several of these genera are documented from pre-Hirnantian peri-Gondwanan localities. Records of conspecific material (e.g. *Harpabollia harparum*, *Scanipisthia rectangularis*) from both sides of the Rheic Ocean (Schallreuter 1990; Meidla 1996b) are unique for the Ordovician.

In summary, the analysis of the Hirnantian ostracod distributions reveals a pattern that can be interpreted as reflecting tropical ('warm-water') and temperate ('cooler-water') faunas (Fig. 21.10). This interpretation is in good agreement with the observations by Vannier *et al.* (1989) who document the relationships between the assemblage composition, diversity and related environmental conditions in Ordovician ostracods: binodicope-rich faunas of lower diversity and persistent community structure are typically associated with unstable environments, and more diversified, palaeocope-rich faunas of high spatial heterogeneity tend to be related to more stable conditions. This partitioning is

in good agreement with data from the Baltoscandian area (Meidla 1996b). Other areas could be assigned to the two principal Baltoscandian clusters based on taxonomic similarity to the high-diversity assemblage (Yukon) or to the binodicope-rich assemblage (Carnic Alps). More specific or detailed interpretations are not possible, as there is not enough ostracod-based data to test for possible shifts of climatic/temperature zones in the Hirnantian.

Concluding remarks

Analysis of the biogeography of Ordovician (benthic shelf) ostracod genera from the early late Ordovician *gracilis* time slab and late Ordovician Hirnantian time slab can be used to test for possible palaeogeographical, palaeoecological and/or palaeoclimatic controls influencing the ostracod distribution pattern. Notwithstanding the limitations of the dataset available, for the *gracilis* time slab three to four major biogeographical regions are identified: Laurentia, Siberia and Baltica, which may include Gondwana. Laurentia and Siberia lie at low-latitude; their proximity might in principle facilitate intercontinental migration and formation of a more uniform low-latitude fauna. The distribution pattern contains no evidence of such faunal mixing, suggesting that the shelf faunas in palaeocontinents of the low-latitude zone were not capable of crossing the intercontinental oceanic barrier. This evidence suggests that climate was not the primary control on ostracod distribution in the earliest Later Ordovician. The relatively poor ostracod dataset for the Hirnantian time slab precludes detailed assessment of geographical v. palaeoclimatic effects, but the faunas are of a much lower diversity, perhaps reflecting the major environmental perturbation of this interval.

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