

# PHYLOGENETIC RELATIONSHIPS OF EARLY–MIDDLE ORDOVICIAN OSTRACODS OF BALTOSCANDIA

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**ABSTRACT.** Phylogenetic analysis of the Early and early Middle Ordovician (Tremadoc and Arenig) ostracod species of Baltoscandia suggests a polyphyletic origin for the suborder Beyrichiocopa. Binodicopes, leiocopes and eridostracans are excluded from the beyrichiocopide clade. An independent origin from the basal ostracods is suggested for the binodicopes and eridostracans. The palaeocopes form a strongly supported monophyletic clade. Within this suborder, the ctenonotellid and the tetradellid families together form a monophyletic clade. The tetradellids are paraphyletic, being a stem-group for the ctenonotellids. *Nanopsis nanella*, the earliest known ostracod from the Tremadoc, is a basal palaeocope. The early eridostracans *Conchoprimitia* and *Incisua*, with their uncomplicated carapace morphology, might be the most primitive ostracods.

**KEY WORDS:** ostracods, Ordovician, Baltoscandia, phylogeny, taxonomy.

OSTRACODA are a long-standing group of Ordovician to Recent Crustacea. The earliest ostracods with strongly calcified carapaces are abundant in Middle Ordovician strata as, for example, in the shallow-water shelf sedimentary rocks of Baltoscandia. The morphology of their 1–3-mm-long carapaces indicates a mostly benthic (crawling, swimming and perhaps also burrowing) mode of life (Henningsmoen 1965; Siveter 1984). There have been reports of Upper Cambrian and Lower Ordovician leperditiiids from several parts of North America and Greenland (Poulsen 1937; Frederickson 1946; Palmer 1954; Harris 1957) and Siberia (Abushik 1960). However, these records have not yet been confirmed by modern studies (Whatley *et al.* 1993) and the systematic position of the leperditiiids within the class Ostracoda is highly questionable (Vannier *et al.* 2001). Consideration of the Siberian ?Lower Ordovician ostracods (Kanygin 1967, 1971) and the Tremadoc ostracod from China (Huo 1953) is limited by small samples.

In contrast, the early Middle Ordovician ostracod fauna of Baltoscandia is one of the oldest known, and one of the most thoroughly studied ostracod faunas. The early Middle Ordovician ostracods of Scandinavia were described by Hessland (1949), Henningsmoen (1953*a, b*, 1954), Jaanusson (1957) and Tinn and Meidla (1999, 2001). Numerous studies have documented and described other Middle Ordovician ostracods from the Baltic region (Öpik 1935, 1939; Sarv 1959, 1960, 1963; Gailite 1982; Sidaravičienė 1992; Meidla *et al.* 1998; Pöldvere *et al.* 1998), the early ostracod faunas from north-eastern Russia (Ivanova 1979; Melnikova 1999) and these of approximately contemporaneous erratic boulders (Bock 1867; Krause 1889, 1891; Moberg and Segerberg 1906; Bonnema 1909; Kummerow 1924; Schallreuter 1983, 1988*a*, 1989, 1993, 1994). The comprehensive study by Vannier *et al.* (1989) included details of classification, distribution and ecology of the Baltoscandian ostracods. The relationships between Ordovician ostracod taxa have been discussed by several authors (Henningsmoen 1953*a*, 1954; Jaanusson 1957; Schallreuter 1968; Vannier 1986*a, b*). Jaanusson (1957) outlined the principal morphological features of the carapace and Henningsmoen (1965) proposed a morphological series. However, these studies were focused primarily on the higher taxa of the Late Ordovician and the proposed phylogenetic trees are poorly constrained towards their origin. The objective of the present pilot study is to outline phylogenetic relationships between the Early and Middle Ordovician taxa of Baltoscandia.

Cladistic methods have not been extensively applied to determine the phylogenetic relationships of fossil ostracods. The only other attempt to employ cladistics known to us considered both Palaeozoic and Recent myodocope ostracods (Vannier and Abe 1992). Unfortunately, modern analogues of the early

ostracods are rare (Siveter and Curry 1984), and fossilization of ostracod body appendages is exceptional owing to the particular conditions required for preservation (Müller 1979a; Siveter *et al.* 1995; Smith 2000). So far, no fossil ostracods with preserved body appendages have been found in Baltoscandia. Consequently, this study relies on characteristics of the external carapace morphology to determine the phylogenetic relationships of Early Ordovician ostracods of Baltoscandia.

The earliest known ostracod, *Nanopsis nanella* (Moberg and Segerberg 1906), is from the Tremadoc of Norway. This species was described formerly as having an unknown systematic position (Moberg and Segerberg 1906; Henningsmoen 1954). Although the carapace morphology of this ancient species is uncomplicated in comparison with several other ostracods, it does not necessarily follow that all the later ostracods are its descendants. Another objective of this study is to determine the systematic position of *N. nanella* within the early ostracod fauna.

In the course of this study, two species of the eridostracan family were identified as morphologically identical, apart from the retention mark. The origin and characteristics of this disparity between *Incisua ventroincisurata* (Hessland 1949) and *Miniconchoides minutus* (Hessland 1949) are also discussed.

#### GEOLOGICAL SETTING AND STRATIGRAPHY

Throughout the Cambrian and Early Ordovician, the Baltica palaeocontinent, comprising present-day Eastern Europe and Scandinavia, was separated from Laurentia and Siberia by the Iapetus Ocean, and from Gondwana by the Palaeotethys (Scotese and McKerrow 1990; Torsvik *et al.* 1991). It has been suggested that during the Arenig-Llanvirn the faunal provincialism indicated maximum continental dispersal after break-up of the Neo-Proterozoic Rodinia Supercontinent (Dalziel 1992, 1997; Torsvik 1998). The palaeontological evidence (Williams 1973; Jaanusson and Bergström 1980; Cocks and Fortey 1998) shows that during the Early and Middle Ordovician, the fauna of Baltica was distinctive and largely endemic, generally supporting the ideas of separation from Gondwana, Laurentia and Siberia.

The partly buried Ordovician platform cover of Baltoscandia is preserved in a continuous deposit from the Isle of Bornholm in the Baltic Sea through the Eastern Baltic area and into the Moscow Basin. Most of the Ordovician outcrops of the Tremadoc–Llanvirn interval are aligned along the Baltic-Ladoga Klint, a fairly continuous escarpment, extending from Lake Ladoga in Russia to Paldiski in NW Estonia (Text-fig. 1). The isolated outliers of the Ordovician deposits are preserved in the mainland of Sweden, in the Gulf of Bothnia, in southern Norway, and on the Isle of Bornholm.

The stratigraphical context of the Tremadoc and Arenig of the Baltoscandian region is presented in Table 1. Ostracods used for this study were collected from the Varangu Stage of the Upper Tremadoc and Billingen, Volkhov and Kunda stages of the Arenig.

The appearance of ostracods in the Baltoscandian succession coincides with the beginning of the normal marine carbonate sedimentation in the epicontinental sea of Baltoscandia. The base of the Björkåsholmen Formation (formerly also known as Ceratopyge Limestone) is an abrupt change from the shales of the underlying Alum Shale Formation to pale nodular limestone (Owen *et al.* 1990) in the Oslo region, Norway. The sedimentary successions of Varangu and Hunneberg age (Table 1) in the other parts of the palaeobasin are principally composed of terrigenous sedimentary rocks wherein the ostracod data are missing. Although these beds, poorly lithified glauconitic siltstones and sandstones, contain a rich and distinctive assemblage of conodonts, graptolites, trilobites and lingulate brachiopods (Raukas and Teedumäe 1997), in North Estonia no ostracods were recorded. The lack of ostracods in these sections could indicate that they did not inhabit this part of the palaeobasin. It could also result from breakage of the fragile carapaces by quartz grains in a high energy environment or from dolomitization and/or decalcification of the sedimentary rocks. The Hunneberg core sections from Latvia and Lithuania, which come from depths of nearly 1000 m and mostly consist of claystones, have not yielded ostracod carapaces either (Gailīte 1982; Sidaravičienė 1996). However, in the latter case the succession is almost devoid of carbonates and yields only occasional trilobite fragments, suggesting dissolution of most of the carbonate fossils in the course of illitization (Wintsch and Kvale 1994).

Ostracods from strata of Billingen age were previously recorded in several outcrops near St. Petersburg, Russia (Melnikova 1999). The ostracod-bearing beds of the Billingen Stage in the St. Petersburg area are

TABLE 1. Stratigraphical framework for the Tremadoc and Arenig of the Baltoscandian region. Stratigraphy summarized from Löfgren (1995), Nielsen (1995), and Ebbestad (1999). The documented levels of the occurrence of ostracods are marked in grey.

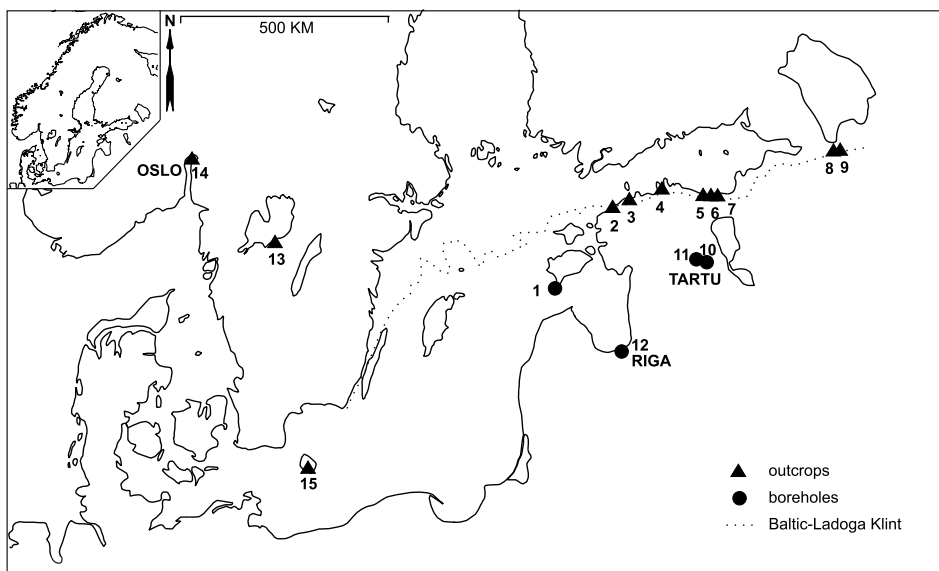
BRITISH SERIES	GRAPTOLITE BIOZONES	CONODONT BIOZONES	TRILOBITE BIOZONES	BALTIC STAGES	OSLO REGION, NORWAY	VÄSTERGÖTLAND, SWEDEN
ARENIG	<i>Didymograptus hirundo</i>	<i>Paroistodus parva</i> <i>P. triangularis</i>	<i>Asaphus expansus</i> <i>Megistaspis limbata</i> <i>M. simon</i> <i>M. polyphemus</i>	KUNDA VOLKHOV	HUK FORMATION	HOLEN LIMESTONE LANNA LIMESTONE
	<i>Pseudophyllogr. elongatus</i> <i>Phyllograptus densus</i>	<i>Oepikodus evae</i>	<i>M. estonica</i> <i>Megistaspides dalecarlicus</i>	BILLINGEN	TØYEN FORMATION	TØYEN SHALE
	<i>D. balticus</i> <i>Tetragr. phyllograptoides</i>	<i>Prioniodus elegans</i>	<i>Megistaspis aff. estonica</i> <i>M. planilimbata</i>	HUNNEBERG		
TREMADOC	<i>Hunnegr. copiosus</i> <i>Araneogr. murrayi</i>	<i>Paroistodus proteus</i>	<i>M. armata</i>	VARANGU	BJØRKÅSHOLMEN FORMATION	ALUM SHALE
	<i>Kiaerograptus supremus</i> <i>Bryograptus</i>	<i>Paltodus deltifer</i> ?	<i>Apatokephalus serratus</i> <i>Shumardia pusilla</i>		ALUM SHALE FORMATION	

composed of quartz glauconitic sand, carbonate sandstone, clays and silty glauconitic limestone with numerous discontinuity surfaces (Melnikova 1999). Occasional ostracods from the Billingen Stage were recorded in the Harku trench section in Estonia (Meidla *et al.* 1998).

Strata of the Volkhov and Kunda stages in the study area indicate shallow, cold-water, carbonate-forming facies (see Meidla *et al.* 1998 and Pöldvere *et al.* 1998). These stages in North Estonia represent shallow near-shore facies, in contrast to the carbonates of the Lanna and Holen limestones in Västergötland, Sweden, which represent a deeper water environment, farther offshore from the Baltoscandian palaeocontinent (Jaanusson 1976, 1982). The ostracod fauna in these stages is abundant, but the relative abundance and species diversity vary considerably between different layers and regions (Meidla *et al.* 1998; Tinn and Meidla 2001).

#### MATERIAL

Ostracod material used for the present study comes from several intensively studied sections in the Baltoscandian area (Text-fig. 1). Bed-by-bed sampling was conducted in seven sections (Väike-Pakri, Harku, Nõmmeveski, Saka, Toila and Päite) in the Baltic-Ladoga Klint. The early Middle Ordovician ostracod fauna was studied in Tartu (Pöldvere *et al.* 1998), Kaugatuma, Laeva-8 and Jurmala (Latvia) core



TEXT-FIG. 1. Location map of sections and boreholes studied. 1, Kaugatuma; 2, Väike-Pakri; 3, Harku; 4, Nõmmeveski; 5, Toila; 6, Saka; 7, Päite; 8, Lava; 9, Putilovo; 10, Tartu; 11, Laeva-8; 12, Jurmala; 13, Hällekis; 14, Slemmestad; 15, Skelbro.

sections. Data presented in a pilot study on the Skelbro section (Bornholm, Denmark) (Tinn and Meidla 1999) were also considered. The Russian material is from Putilovo quarry and the Lava Klint section near St. Petersburg. The Lava section, which probably represents a complete succession of Volkhov age (Dronov *et al.* 2000), also yields ostracods from strata of latest Billingen age. The Lanna and Holen limestones in Hällekis quarry (Västergötland, Sweden) contain an abundant and diverse ostracod fauna (Tinn and Meidla 2001). The specimens of *Nanopsis nanella* studied are from a section at Slemmestad, Oslo-Asker district, Norway.

Thirty five species (see Table 2) were chosen for the phylogenetic analysis. The number of specimens studied from each species varied considerably. The most abundantly represented species were several well-known Volkhov palaeocopes, including *Brezelina palmata*, *Ogmoopsis bocki*, *Protallinnella grewingkii*, *Rigidella mitis*, and the eridostracans *Incisua ventroincisurata* and *Conchoprimitia* spp. This latter group was included at the genus level as it represents at least seven species and subspecies from the Arenig (Hessland 1949; Schallreuter 1993), but requires further revision.

The ostracod material used in this study is calcitic, exhibiting mostly good preservation (Text-figs 4–5; Pls 1–2) with some excellent specimens showing details of ornamentation, like fine punctation or reticulation. The best preserved specimens were yielded from the Volkhov and Kunda stages, whereas the material from the Billingen Stage shows occasional evidence of dolomitization expressed in large dolomite crystals on the valve surface.

For *Nanopsis nanella*, material from Slemmestad in the Oslo-Asker district of Norway was used. In this study, *N. nanella* is represented by 20 specimens of varying quality of preservation. The majority of these are preserved as internal moulds, although some specimens show partly preserved calcitic carapaces.

Most of the carbonate samples were processed by standard methods of physical disintegration (Tinn and Meidla 1999), providing results comparable to that of the natural weathering process. The crushed limestone samples, weighing about 0.5–1.5 kg, were disintegrated by means of sodium hyposulphite as a crystallizing agent. To obtain a satisfactory level of disintegration, heating and cooling cycles were repeated up to ten times for clay-rich marlstones, and more than 50 times in case of well-lithified, thermally altered limestone with CAI 3–5 (Komstad Limestone, Skelbro, Denmark). The washed and dried

TABLE 2. Stratigraphical distribution of the Tremadoc and Arenig ostracods of Baltoscandia.

TREMADOC		ARENIG			SPECIES
VARANGU	HUNNEBERG	BILLINGEN	VOLKHOV	KUNDA	
					<i>Nanopsis nanella</i> (Moberg and Segerberg, 1906)
					<i>Unisulcopleura tolmachovae</i> Melnikova, 1999
					<i>Hithis proximus</i> Melnikova, 1999
					<i>Dronoviella lauta</i> Melnikova, 1999
					<i>Tallinnellina? viridis</i> Schallreuter, 1993
					<i>Brezelina angustolobata</i> Schallreuter, 1993
					<i>Tallinnellina primaria</i> (Öpik, 1935)
					<i>Piretopsis (Protallinnella) growingkii</i> (Bock, 1867)
					<i>Conchoprimitia</i> Öpik, 1935
					<i>Rigidella mitis</i> (Öpik, 1935)
					<i>Unisulcopleura punctosulcata</i> Schallreuter, 1993
					<i>Laterophores ansiensis</i> (Gailite, 1971)
					<i>Brezelina palmata</i> (Krause, 1889)
					<i>Ogmoopsis bocki</i> (Öpik, 1935)
					<i>Incisua ventroincisurata</i> (Hessland, 1949)
					<i>Unisulcopleura irrete</i> Schallreuter, 1993
					<i>Tallinnellina lanceolata</i> (Hessland, 1949)
					<i>Glossomorphites digitatus</i> (Krause, 1889)
					<i>Aulacopsis simplex</i> (Krause, 1889)
					<i>Elliptocyprites? nonumbonatus</i> (Hessland, 1949)
					<i>Laccochilina decumana</i> (Bonnema, 1909)
					<i>Eobromidella (Vendona) cicatriosa</i> Sarv, 1959
					<i>Ctenentoma levis</i> (Sarv, 1959)
					<i>Asteusloffia acuta</i> (Krause, 1891)
					<i>Baltonotella</i> Sarv, 1959
					<i>Pinnatulites procerus</i> (Kummerow, 1924)
					<i>Euprimites reticulogranulatus</i> Hessland, 1949
					<i>Euprimites effusus</i> Jaanusson, 1957
					<i>Euprimites anisus</i> Jaanusson, 1957
					<i>Longiscula curvata</i> (Hessland, 1949)
					<i>Glossomorphites grandispinosus</i> (Hessland, 1949)
					<i>Hesslandella macroreticulata</i> (Hessland, 1949)
					<i>Entomis sigma</i> Krause, 1889
					<i>Ostpreussensia cornuta</i> (Kummerow, 1924)

TABLE 3. Classification of the ostracod species used herein. Primary reference is Schallreuter (1993) with additions from Sarv (1959), Sidaravičienė (1992) and Vannier *et al.* (1989).

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Order BEYRICHIOCOPA Pokorný, 1954
Suborder PALAEOCOPA Henningsmoen, 1954
Superfamily EURYCHILINACEA Ulrich and Bassler, 1923
<i>L. decumana</i>
Superfamily HOLLINACEA Swartz, 1936
Euprimitidae Hessland, 1949: <i>E. reticulogranulatus</i> , <i>E. effusus</i> , <i>E. anisus</i> , <i>E. cicatriosa</i>
Tvaerenellidae Jaanusson, 1957: <i>H. proximus</i>
Ctenonotellidae Schmidt, 1941: <i>R. mitis</i> , <i>A. acuta</i> , <i>C. levis</i> , <i>P. grewingkii</i> , <i>T. lanceolata</i> , <i>T. primaria</i> , <i>B. palmata</i> , <i>B. angustolobata</i>
Tetradellidae Swartz, 1936: <i>G. digitatus</i> , <i>G. grandispinosus</i> , <i>A. simplex</i> , <i>H. macroreticulata</i> , <i>E. sigma</i> , <i>O. bocki</i>
Suborder BINODICOPA Schallreuter, 1972
Superfamily DREPANELLACEA Ulrich and Bassler, 1923
<i>L. ansiensis</i>
Superfamily SPINIGERITIDAE Schallreuter, 1980
<i>D. lauta</i>
Suborder LEIOCOPA Schallreuter, 1973
Superfamily APARCHITACEA Jones, 1901
<i>Baltonotella</i>
Suborder ERIDOSTRACA Adamczak, 1961
<i>Conchoprimitia</i> , <i>I. ventroincisurata</i>
Order PODOCOPA Sars, 1866
Suborder METACOPA Sylvester-Bradley, 1961b
<i>E. nonumbonatus</i> , <i>L. curvata</i> ,
<i>INCERTAE SEDIS</i>
<i>P. procerus</i> , <i>O. cornuta</i>
Order PLATYCOPA Sars, 1866
Suborder KLOEDENELLOCOPA Scott, 1961b
Superfamily MONOTIOPLEURIDAE Guber and Jaanusson, 1964
<i>U. punctosulcata</i> , <i>U. irrete</i> , <i>U. tolmachovae</i>

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material was sieved into four fractions (>2 mm, 0.5–2 mm, 0.25–0.5 mm, <0.25 mm). Ostracods were picked out from the material under a stereoscopic binocular microscope, with magnifications of ×16–25. Ostracods collected from clay layers in Lava and Putilovo were recovered by washing through 0.25–1 mm sieves. The specimens of *Nanopsis nanella* were selected and prepared by hand from the slabs.

The collections with the original material were supplemented by descriptions and photographs by previous investigators (Henningsmoen 1954; Schallreuter 1983, 1988, 1989, 1993, 1994; Sidaravičienė 1992; Melnikova 1999 and others). The major problem concerning material from the erratic boulders of Baltoscandian origin, described from various places in Central Europe (Schallreuter 1983, 1988a, 1989, 1993, 1994), is the lack of adequate stratigraphic information. However, most of the species that were originally described from the erratics have now been recorded from their original area of distribution and so their detailed stratigraphic distribution has been designated.

*Repositories.* The Estonian and Russian material collected and used in this study is housed at the Museum of Geology, University of Tartu, Estonia (TUG). The material of *N. nanella* is stored in the Palaeontological Museum of Oslo, Norway (PMO).

## PHYLOGENETIC ANALYSIS

### *Character selection*

The morphological characteristics and the character-state matrix used in this analysis are designated in the Appendix. Terminology follows Scott (1961a) and Jaanusson (1957). The classification of Recent

ostracods is based on complex anatomical differences in the appendages, copulatory organs and other soft anatomy (Scott 1961a), whereas the details of carapace morphology are considered to be of lesser significance. The latter is due to high intraspecific variability of carapace morphology, which could have been influenced by a number of environmental factors as well as by genetic polymorphism (Ikeya and Ueda 1988). The present taxonomy of early ostracods, developed by Henningsmoen (1953a), Hessland (1949), Jaanusson (1957) and Schallreuter (1993), probably reflects true biological relationships (Table 3). The problem of homeomorphy of the Palaeozoic ostracods was discussed by Schallreuter (1988b). Most Palaeozoic ostracods are distinguished on the basis of external carapace morphology only: overall lobal, sulcal and dimorphic characteristics of the shell, and the degree of on-valve overlap. In most cases these are the only available characters and may reflect aspects of the soft part anatomy of the ostracods (Vannier *et al.* 1989).

Reconstructing soft part anatomy relying on carapace morphology only is very problematic and most researchers dealing with specific Palaeozoic groups have avoided it. Kesling (1952) proposed a reconstruction of the quadrilobate hollinid species (Palaeocopa) *Ctenoloculina cicatriosa*, assuming that it had the same type of appendages and organs as modern ostracods. Because of specific morphology and the restricted inner space of the carapace, an assumption was made that the larger organs and appendages must have fitted into the lobes. Kesling proposed that the antennulae and antennae occupied Lobe 1, the mandibles probably lay in Lobe 2 and the maxillae with large branchial plates in Lobe 3. The reconstruction showed the thoracic legs functioning in Sulcus 3 and the genital lobes lying in Lobe 4. The position of the genital lobes of *Tetrada krausei* (Steusloff, 1895) was discussed by Schallreuter (1989). The dimorphic Lobe 4 was described as the space for the male genitals in this species.

Vannier and Abe (1992) tested the reliability of the relationships between external carapace morphology and internal characters using fossil and Recent myodocope ostracods, and found comparable patterns of similarities between these distinct character groups. However, as the majority of species included in the present analysis belong to palaeocopes that lack Recent counterparts (Jaanusson 1957), this kind of testing could not be undertaken with the present set of taxa. The relationship of the specific elements of valve morphology to the soft part anatomy can be suggested in certain cases only.

In the present pilot study, 44 external morphological characters were used for phylogenetic analysis (Appendix, section 1). The character set used in our analysis is supposed to be representative of the Tremadoc and Arenig ostracods. However, the character set and character types for analyzing later ostracods would certainly be different. For brevity and convenience in the following discussion, the character numbers are referred to in brackets.

The characters defining the carapace material (1), carapace symmetry (2) and presence of interdorsum (36) are the main aspects distinguishing the ingroup (ostracods) from the outgroup (*Hesslandona*) (see below for discussion of the outgroup). Apart from some lightly mineralized myodocopes that do not occur in the Ordovician, all ostracods possess a calcium carbonate carapace. In the present analysis, all ostracods were defined as showing an asymmetrical carapace, expressed in valve asymmetry. The left-side or reversed valve overlap (8, 9) and the persistence of the width of the overlap (11) define different aspects of the valve relationships. The general outline of the valve is defined as being preplete to postplete (3; see also Jaanusson 1957) and by the features of the hinge-line (4, 5).

The details of the adductor muscle scar are not preserved in the material, but the relative position of the scar is one of the features which may reflect the soft body anatomy of the studied taxa. The related features, together with the length, depth and the main morphology of the second sulcus (S2) (characters 18, 19, 27–29), obviously reflect the character of the adductor muscle. Other elements of the lobal-sulcal structure – the number of lobes and sulci (20, 21) and morphology of the first lobe (L1) (23–25) – were probably related to the anatomy of the soft parts, but their interpretation is speculative. Although the fine valve ornamentation in the present data set does not show much phylogenetic relevance, the corresponding characters (30, 32–35) were included because of their great taxonomic value at discriminating otherwise similar species.

Adventral structures in palaeocopes (37–41) are closely related to sexual dimorphism and possibly brood care (Jaanusson 1957; Vannier *et al.* 1989), while the occurrence (or absence) and the particular type of dimorphism (44) are distinctive for higher taxa. These features should, in principle, be related to soft

anatomy as well, but the function of the external dimorphic structures is still not completely understood. Moulting retention (43), where the earlier growth stages are retained on the ostracod carapace, has been regarded as a peculiar adaptation by Levinson (1951), but probably includes a complex of characters, such as specific hinge structures. Additionally, it must have been related to the ability to assimilate progressive amounts of carbonate for secretion of calcified lamellae (Adamczak 1961).

#### *Outgroup selection*

The selection of the outgroup for cladistic analysis of ostracods is a delicate problem. Traditionally, palaeontologists considered that calcitic ostracods might have originated from phosphatic or non-calcified predecessors. Several researchers regarded the Cambrian phosphatocopids as the early ancestors of the later ostracods (Sylvester-Bradley 1961a; Müller 1964; Andres 1969; Jones and McKenzie 1980). Sylvester-Bradley (1961a), Kozur (1974), Müller (1964, 1979b), Andres (1969), and McKenzie and Jones (1979) argued for the classification of Bradoriida as Ostracoda mostly on the basis of shape, hingement, and sexual dimorphism of the carapace. However, Jones and McKenzie (1980) considered bradoriida to be heterogeneous, comprising the ancestral ostracods, other ostracod-like animals and probably phyllocarid-like or branchiopod-like crustaceans. Later work on the Cambrian phosphatocopid fauna (Müller 1982; Müller and Walossek 1991; Walossek and Müller 1992; Siveter *et al.* 2001), which revealed their morphology in full detail, led to the conclusion that the early arthropod radiation involved several different types of convergently bivalved groups and that most of the Cambrian ostracod record is probably spurious (Hou *et al.* 1996). Shu *et al.* (1999) regarded the Archaeocopida with phosphatic carapaces as the stem-group of the eucrustaceans.

The phosphatocopid genus *Hesslandona* Müller, 1964, known from the Lower–Upper Cambrian of Baltoscandia and Britain (Müller 1964, 1979b, 1982; Hinz 1987) was chosen as an outgroup. However, it should be emphasized that in this context the Phosphatocopida are not regarded by us as ostracods, nor the ancestors of Ostracoda, but were chosen only for resolving the polarity of characters.

#### *Analysis*

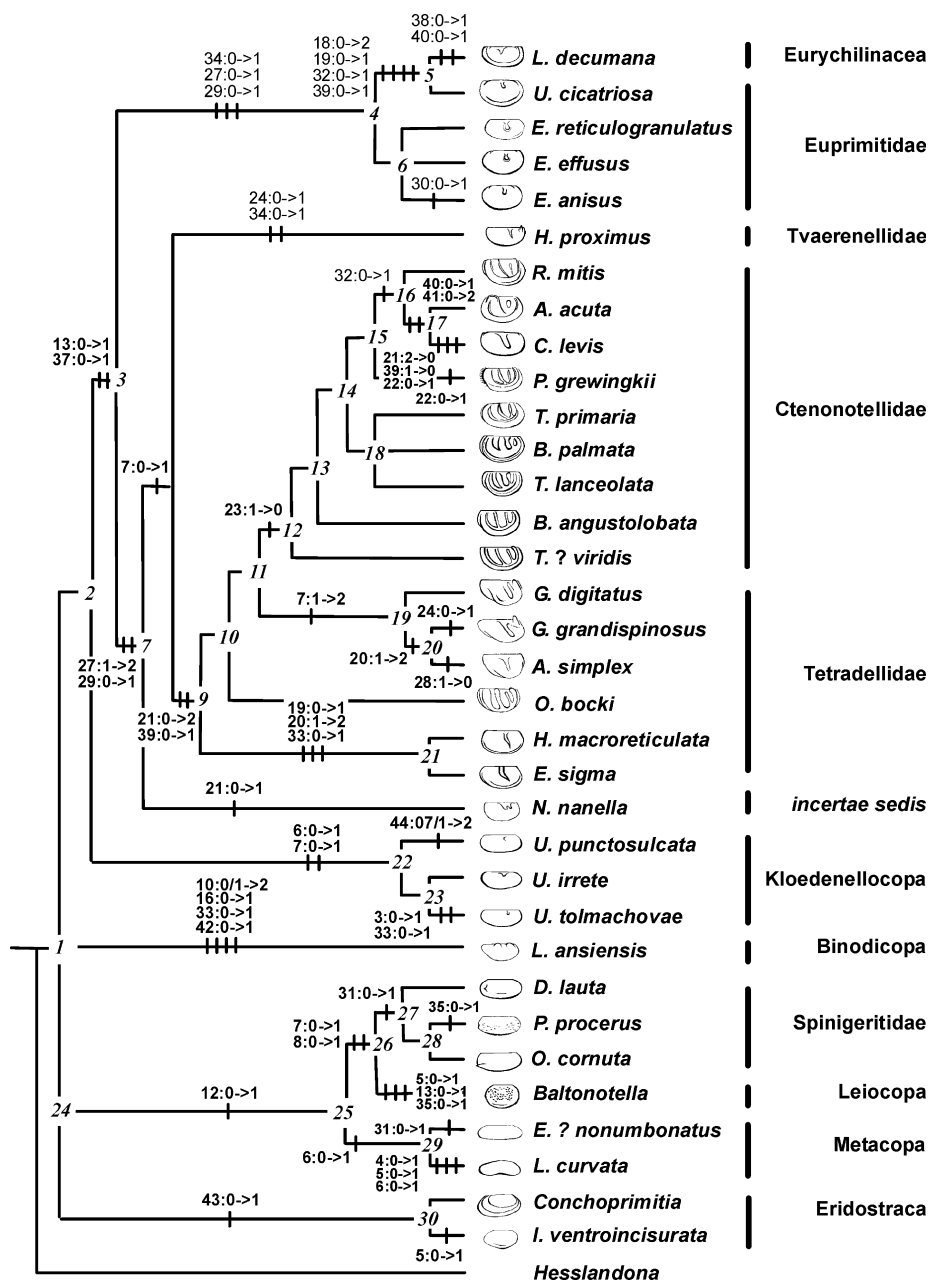
The data matrix of characters was analysed cladistically using the PAUP computer programme (Swofford 2000). The software package MacClade version 3.07 (Maddis and Maddis 1992, 1997) was used to compare tree topologies and to investigate the pattern of character evolution. Tree statistics were then calculated by PAUP. The heuristic search option was selected for a data matrix derived from 44 characteristics. All characters were initially unordered, equally weighted, and none was constrained to be irreversible.

In the strict consensus tree generated by this analysis, two main groups were produced: one containing binodicopes, metacopes, eridostracans and leiocopes, the second containing all palaeocopes and kloedenellocopes. In the first group, all branches collapsed due to polytomy, while in the second group polytomy occurred in the *Euprimites* and tetradellide groups.

In the second analysis, 34 ordered and ten unordered characters were used. The 50 per cent majority rule consensus tree (Text-fig. 2) is presented here as a hypothesis for the phylogenetic relationships of the early Middle Ordovician ostracods. The consistency index (CI) of the tree is 0.524 and the retention index (RI) is 0.781. The phylogenetic tree of the ostracod species studied, showing the phylogenetic relationships and the documented stratigraphic ranges, is presented in Text-figure 3.

Three characters were defined as synapomorphies for ostracods of the present data set (node 1). These were: calcium carbonate carapace, presence of real hinge structure and asymmetrical carapace. The results of the analysis do not support the previous classification of the early calcitic ostracods into three orders: Beyrichiocopa, Podocopa and Platycopa (Vannier *et al.* 1989; Schallreuter 1993). According to present nomenclature, the order Beyrichiocopa Pokorny 1954 (emend. Schallreuter 1980) contains palaeocopes, binodicopes, leiocopes and the eridostracans. The results of the present analysis, however, present the beyrichiocopes as a paraphyletic or even polyphyletic group.

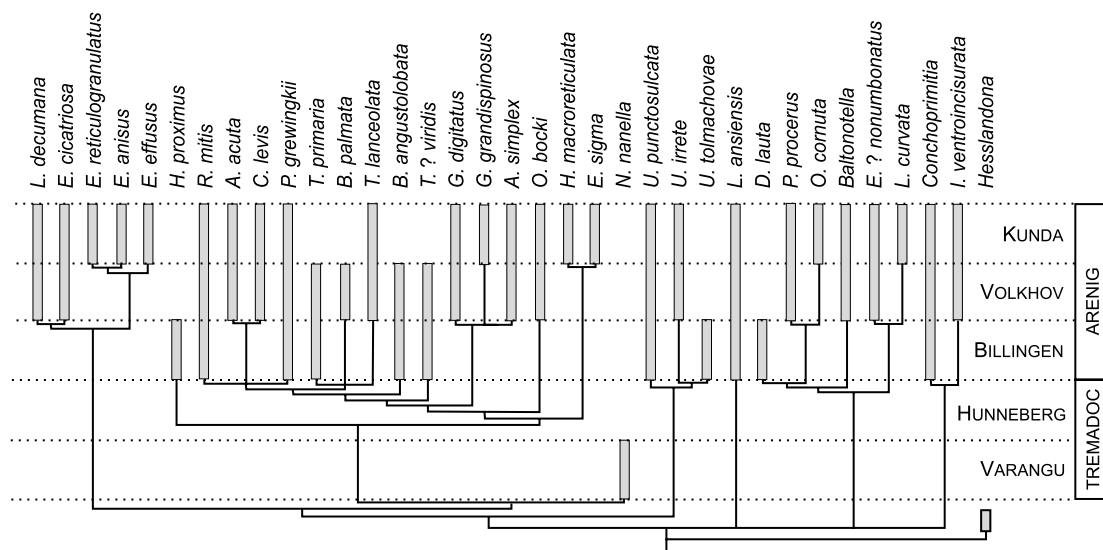




TEXT-FIG. 2. Fifty per cent majority-rule consensus tree of the 35 ostracod species.

*Palaeocopa*

The largest clade (22 species) is formed by the palaeocopes (node 3; Pl. 1, figs 1–18; Pl. 2, figs 1–8). The palaeocope clade is characterized by the presence of marginal and velar structures, accompanied by a long straight hinge-line, smooth to lobate surface and variable ornamentation. At present, the palaeocopes are normally regarded as a suborder-level group (Schallreuter 1993).

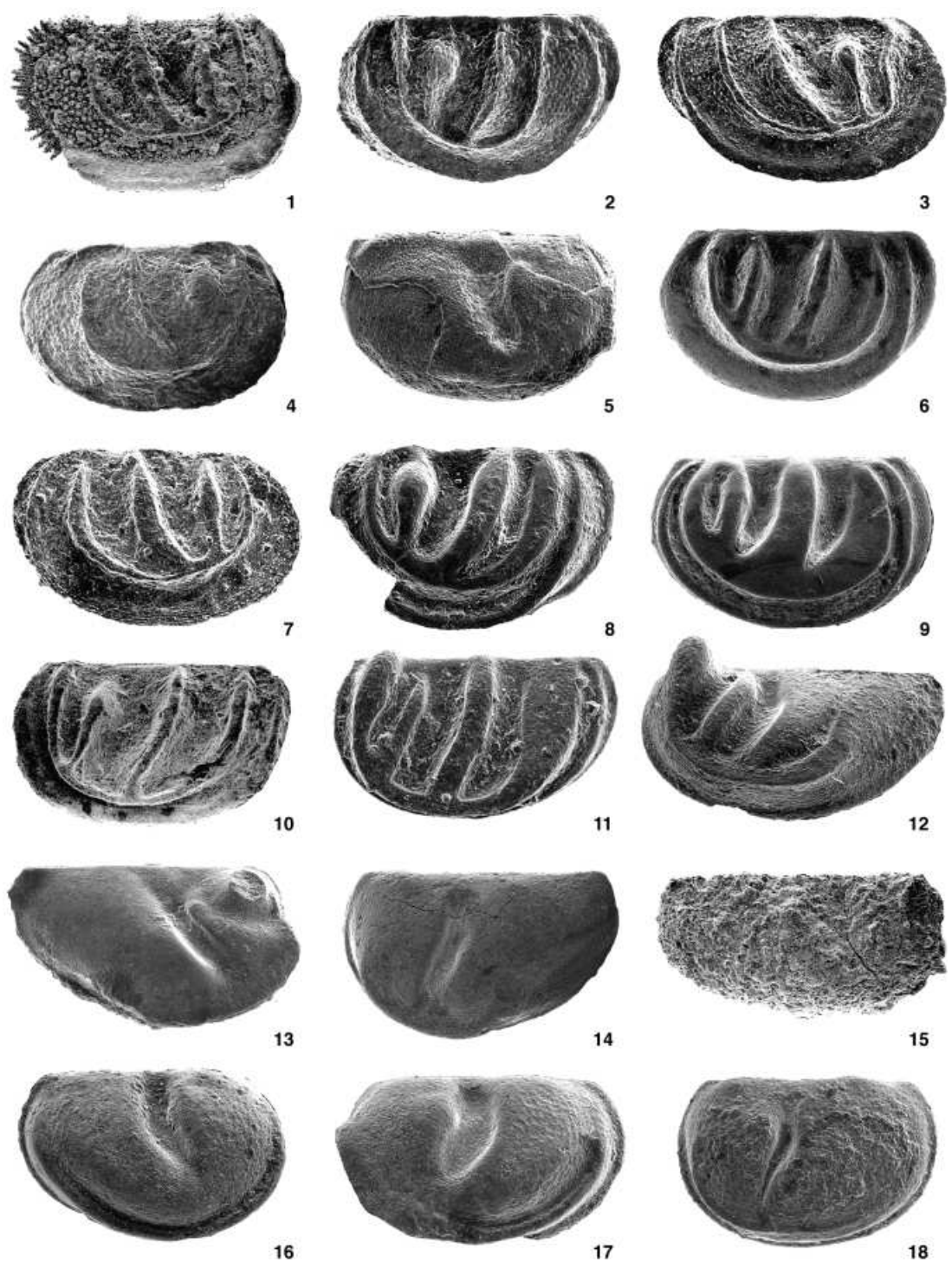


TEXT-FIG. 3. Phylogenetic tree of the early Middle Ordovician ostracod species showing their phylogenetic relationships and the documented stratigraphic ranges.

The palaeocopes are represented in this analysis by two superfamily-level groups, the eurychilinaceans and the hollinaceans. The results show the eurychilinaceans to be most closely related to the representatives of the hollinacean euprimitid family and their independent origin from the basal palaeocopes (node 4). The synapomorphy shared by eurychilinaceans and euprimitids is the short and nearly straight sulcus 2 that reaches up to one-third of the lateral area. This type of sulcus 2 does not occur in any other analyzed ostracod species. Jaanusson (1957) regarded these taxa as members of one superfamily on the basis of the presence of the velar structure, the velar dimorphism and the absence of histial structure. However, all these are symplesiomorphic characteristics, shared by several palaeocope lineages, and they may also

#### EXPLANATION OF PLATE I

- Fig. 1. *Protallinnella grewingkii*, heteromorphic right valve, TUG 9/1109,  $\times 30$ , Volkhov Stage, Putilovo.  
 Figs 2–3. *Rigidella mitis*. 2, tecomorphic left valve TUG 2/1045, Lanna Limestone, Hällekis;  $\times 40$ . 3, heteromorphic right valve 10/1109, Volkhov Stage, Lava;  $\times 40$ .  
 Fig. 4. *Asteusloffia acuta*, right valve TUG 11/1109, Volkhov Stage, Lava;  $\times 40$ .  
 Fig. 5. *Ctenentoma levis*, right valve TUG 11/1045, Holen Limestone, Hällekis;  $\times 35$ .  
 Fig. 6. *Brezelina angustolobata*, left heteromorphic valve TUG 12/1109, Volkhov Stage, Väike-Pakri;  $\times 40$ .  
 Fig. 7. *Tallinnellina primaria*, right heteromorphic valve TUG 13/1109, Volkhov Stage, Lava;  $\times 35$ .  
 Fig. 8. *Tallinnellina lanceolata*, left tecomorphic valve TUG 9/1045, Lanna Limestone, Hällekis;  $\times 35$ .  
 Fig. 9. *Brezelina palmata*, left tecomorphic valve TUG 11/1065, Volkhov Stage, Päite;  $\times 35$ .  
 Fig. 10. *Tallinnellina? viridis*, left heteromorphic valve TUG 14/1109, Billingen Stage, Lava;  $\times 40$ .  
 Fig. 11. *Ogmoopsis bocki*, left tecomorphic valve TUG 15/1109, Volkhov Stage, Harku;  $\times 40$ .  
 Fig. 12. *Glossomorphites digitatus*, left tecomorphic valve TUG 8/1045, Holen Limestone, Hällekis;  $\times 40$ .  
 Fig. 13. *Glossomorphites grandispinosus*, right valve TUG 6/1045, Lanna Limestone, Hällekis;  $\times 30$ .  
 Fig. 14. *Aulacopsis simplex*, left valve TUG 16/1109, Holen Limestone, Hällekis;  $\times 35$ .  
 Fig. 15. *Hithis proximus*, right valve TUG 17/1109, Billingen Stage, Lava;  $\times 40$ .  
 Figs 16–17. *Entomis sigma*, Holen Limestone, Hällekis. 16, tecomorphic carapace TUG 19/1045, right view;  $\times 50$ .  
 17, heteromorphic left valve TUG 20/1045;  $\times 45$ .  
 Fig. 18. *Hesslandella macroreticulata*, left valve TUG 18/1109, Holen Limestone, Hällekis;  $\times 50$ .



TINN and MEIDLA, Ordovician ostracods

depend on how precisely these features are defined by a particular author. The euprimitids have also been regarded as the members of the hollinacean superfamily (Vannier *et al.* 1989; Schallreuter 1993) mainly on the basis of construction of the velar structure.

*Laccochilina decumana* (Pl. 2, figs 2, 8) and *Eobromidella (Vendona) cicatriosa* (Pl. 2, fig. 6) share three synapomorphic characters (node 5): the depressed adductorial pit, preadductorial node and convex heteromorphic velum, developed along the entire free margin. The euprimitide clade [node 6; *Euprimites anisus* (Pl. 2, fig. 3), *E. effusus* (Pl. 2, fig. 4) and *E. reticulogranulatus* (Pl. 2, fig. 1)] collapsed due to polytomy.

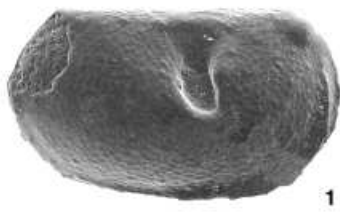
Node 8 defines a clade with complex topology and connects representatives of the rest of the hollinacean superfamily. The ctenonotellids form a well-defined clade (node 12) within the hollinacean superfamily, whereas the origin of the tetradellids remains unclear. The ctenonotellids share one synapomorphic character, Lobe 1 (L1), which reaches the dorsal end of the domicilium. The ctenonotellids *Rigidella mitis* (Pl. 1, fig. 2), *Asteusloffia acuta* (Pl. 1, fig. 4) and *Protallinnella grewingkii* (Pl. 1, fig. 1) are common Volkhovian species with complex carapace morphology. According to the present analysis they form the crown group of the ctenonotellid clade. The tetradellid family is represented in the analysis by six species: *Ogmoopsis bocki* (Pl. 1, fig. 11), *Glossomorphites digitatus* (Pl. 1, fig. 12), *Glossomorphites grandispinosus* (Pl. 1, fig. 13), *Aulacopsis simplex* (Pl. 1, fig. 14), *Hesslandella macroreticulata* (Pl. 1, fig. 18) and *Entomis sigma* (Pl. 1, figs 16–17). The analysis shows the tetradellids as the stem-group for the ctenonotellids and does not support monophyly of the whole group. The diagnosis (Swartz 1936; Henningsmoen 1953a; emend. Jaanusson 1957) characterizes this group as non-sulcate to quadrilobate, mostly with preplete outline. Early genera show either velar and histial structure in both dimorphs or only velar structure in tecnomorphs (Jaanusson 1957, p.377). The present analysis shows the six species evolving in three monophyletic lineages from basal node 3. These are a *H. macroreticulata* – *E. sigma* clade (node 21), *O. bocki* (node 10) and a *G. digitatus* – *G. grandispinosus* – *A. simplex* (node 20) clade.

The rare Billingen Stage species *Hithis proximus* (Pl. 1, fig. 15), defined as a tvaerenellid (Melnikova 1999), shows its origin near the base of the palaeocope clade (node 18). According to our analysis, *Nanopsis nanella*, by far the earliest known ostracod species, belongs to the basal palaeocopes (node 7). The detailed morphology of *N. nanella* is discussed in the systematic palaeontology section below.

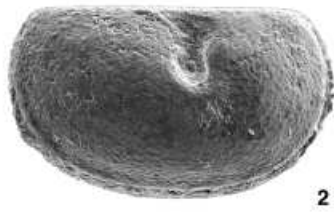
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#### EXPLANATION OF PLATE 2

- Figs 1–2. *Euprimites reticulogranulatus*, Holen Limestone, Hällekis;  $\times 45$ . 1, heteromorphic right valve TUG 26/1045. 2, carapace TUG 25/1045, right view.
- Fig. 3. *Euprimites anisus*, tecnomorphic carapace TUG 21/1045, right view, Holen Limestone, Hällekis;  $\times 30$ .
- Figs 4–5. *Euprimites effusus*, Holen Limestone, Hällekis. 4, tecnomorphic carapace TUG 23/1045, right view;  $\times 35$ . 5, heteromorphic right valve TUG 19/1109;  $\times 30$ .
- Fig. 6. *Eobromidella cicatriosa*, right valve TUG 13/1045, Holen Limestone, Hällekis;  $\times 40$ .
- Figs 7–8. *Laccochilina decumana*;  $\times 40$ . 7, tecnomorphic left valve TUG 20/1109, Volkhov Stage, Lava. 8, heteromorphic left valve TUG 12/1045, Lanna Limestone, Hällekis.
- Fig. 9. *Laterophores ansiensis*, left valve TUG 14/1045, Lanna Limestone, Hällekis;  $\times 70$ .
- Fig. 10. *Unisulcopleura tolmachovae*, left valve TUG 21/1109, Billingen Stage, Lava;  $\times 70$ .
- Fig. 11. *Unisulcopleura punctosulcata*, carapace TUG 16/1045, right view, Holen Limestone, Hällekis;  $\times 60$ .
- Fig. 12. *Unisulcopleura irrete*, carapace TUG 22/1109, left view, Volkhov Stage, Väike-Pakri;  $\times 40$ .
- Fig. 13. *Elliptocyprites? nonumbonatus*, carapace TUG 23/1109, Holen Limestone, Hällekis;  $\times 50$ .
- Fig. 14. *Longiscula curvata*, carapace TUG 24/1109, Holen Limestone, Hällekis;  $\times 50$ .
- Fig. 15. *Dronoviella lauta*, left valve TUG 24/1109, Billingen Stage, Lava;  $\times 45$ .
- Fig. 16. *Pinnatulites procerus*, left valve TUG 30/1045, Lanna Limestone, Hällekis;  $\times 30$ .
- Fig. 17. *Ostpreussensia cornuta*, left valve TUG 25/1109, Holen Limestone, Hällekis;  $\times 30$ .
- Fig. 18. *Baltonotella* sp., carapace TUG 32/1045, right view, Lanna Limestone, Hällekis;  $\times 30$ .



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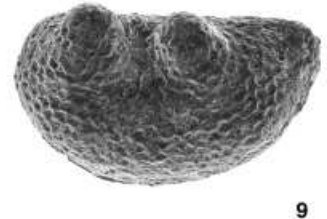
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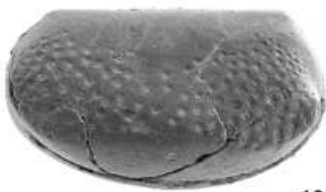
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18

*Kloedenellocoptes*

Three species of the genus *Unisulcopleura* represent the kloedenellocoptes (node 22, Pl. 2, figs 10–12) in the analysis. Of these, *Unisulcopleura tolmachovae* is one of the early species documented from the ostracod fauna of Billingen age (Melnikova 1999). These small species have a simple morphology with a straight ventral margin. The presence of domiciliar dimorphism has been discussed in *U. punctosulcata* (Hessland 1949).

*Binodicopes*

Binodicopes form one of the major Ordovician ostracod suborders. While occurring abundantly in the Ordovician of Ibero-Armorica (Vannier *et al.* 1989) and being represented in many Ordovician faunas elsewhere, this group is represented by a single species in a separate node 1 (*Laterophores ansiensis*, node 1; Pl. 2, fig. 9) in the Arenig of Baltoscandia. The synapomorphies shared by the binodicopes are two dorso-lateral nodes and the occurrence of a pseudovelum, a rounded non-dimorphic velum-like ventral bend. A characteristic of the group is also the intraspecific reversal of valve overlap (Schallreuter 1980). Although possible domiciliar dimorphism has been discussed in some binodicope species (Schallreuter 1980; Vannier 1986b), this character has not been observed in *L. ansiensis*.

*Metacopes*

This distinct suborder-level group (node 29) is represented in the analysis by two species [*Elliptocyprites? nonumbonatus* (Pl. 2, fig. 13) and *Longiscula curvata* (Pl. 2, fig. 14)] that occur abundantly in the Volkhov and Kunda stages (Middle Ordovician). The species are strongly inequivalved, exhibiting a distinct type of ventral valve overlap in which the centro-ventral marginal part of the larger valve covers the opposite valve more widely than it does posteriorly and anteriorly. Typical diagnostic structures are the internal contact grooves or stop-pegs, recorded in both genera. Uniquely among early ostracods, *L. curvata* exhibits a concave ventral margin.

The systematic positions of *Pinnatulites procerus* (node 28; Pl. 2, fig. 16) and *Ostpreussensia cornuta* (Pl. 2, fig. 17) were unclear. Vannier *et al.* (1989) regarded *P. procerus* as a metacope. However, Schallreuter (1993) described both species as having uncertain family affinities within the suborder Binodicopa. The present analysis shows these species to be closely related to the early spinigeritid *Dronoviella lauta* (node 27). The synapomorphy shared by these three species is the posterior spine. Although this character is common in several later ostracod groups, it is rare among members of the early fauna and is certainly characteristic of the Spinigeritidae, thus suggesting a close relationship to metacopes for all three species.

*Leiocopes*

Leiocopes are represented in the Arenigian by *Baltonotella* sp. (Pl. 2, fig. 18), with the only recorded specimens from the Kunda Stage. The present analysis shows its close relationship with the *P. procerus* – *O. cornuta* – *D. lauta* clade. The short hinge-line and the presence of marginal structures serve as autapomorphies for this group.

*Eridostracans*

The eridostracans *Conchoprimitia* and *Incisua ventroincisurata* (node 30; Text-fig. 5) represent the simplest type of ostracods, which could be closely related to the early ancestor of the whole group. However, this assumption cannot be approved without knowing soft part anatomy. The characters that distinguish eridostracans from most of the taxa studied include lack of distinct lobation and dimorphic structures, simple overlapping pattern, and undifferentiated ventral and dorsal surfaces. The characters shared by *Conchoprimitia* and *I. ventroincisurata* are moult retention and postplete carapace. As the majority of the later Ordovician eridostracans are characterized by simple valve contact without ventral

overlap (Adamczak 1961; Schallreuter 1977), the left valve overlap in the Arenig taxa should be regarded as the plesiomorphic state.

Jaanusson (1957) proposed the early splitting of eridostracans from the other ostracods in the context of discussing the phylogeny of the major ostracod groups. The hypothesis is probably supported by the stratigraphical data, as *Conchoprimitia* is abundant and represented by several species in the Billingen Stage (Melnikova 1999).

### CONCLUSIONS

Cladistic analysis of the Early and early Middle Ordovician ostracod species of Baltoscandia suggest a polyphyletic origin for the suborder Beyrichiocopa. The cladistic analysis excludes binodicopes, leiocopes and eridostracans from the beyrichiocope clade. Independent origin from basal ostracods is suggested for the binodicopes and eridostracans. Metacopes were found to be closely related to the spinigeritid species *Dronoviella lauta*, *Pinnatulites procerus* and *Ostpreussensia cornuta*.

The palaeocopes form a strongly supported monophyletic clade. Within this suborder, the ctenonotellide and tetradellide families form a monophyletic clade. The tetradellides are paraphyletic, being a stem-group for the ctenonotellide family. The earliest known true ostracod, *Nanopsis nanella* from the Tremadoc, was found to be a basal palaeocope.

The early eridostracans, *Conchoprimitia* and *Incisua ventroincisurata*, which exhibit simple carapace morphology with the greatest number of plesiomorphic characters, are likely to be the most primitive ostracods. *Incisua ventroincisurata* is an eridostracan species that exhibits molt retention like *Conchoprimitia*.

### SYSTEMATIC PALAEOONTOLOGY

Suborder PALAEOCOPA Henningsmoen, 1953a

Superfamily HOLLINACEA Swartz, 1936

Family *Insertae sedis*

Genus NANOPSIS Henningsmoen, 1954

*Nanopsis nanella* (Moberg and Segerberg, 1906)

Text-figure 4A–B

1906 *Beyrichia nanella* Moberg and Segerberg, p. 76, pl. 3, figs 27–28.

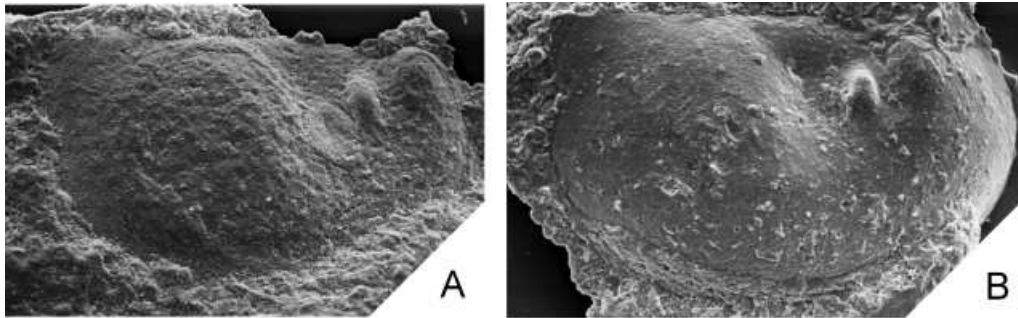
1934 *Beyrichia? nanella* Moberg and Segerberg; Bassler and Kellett, p. 201.

1954 *Nanopsis nanella* (Moberg and Segerberg, 1906); Henningsmoen, pp. 54–55, pl. 1, fig. 1.

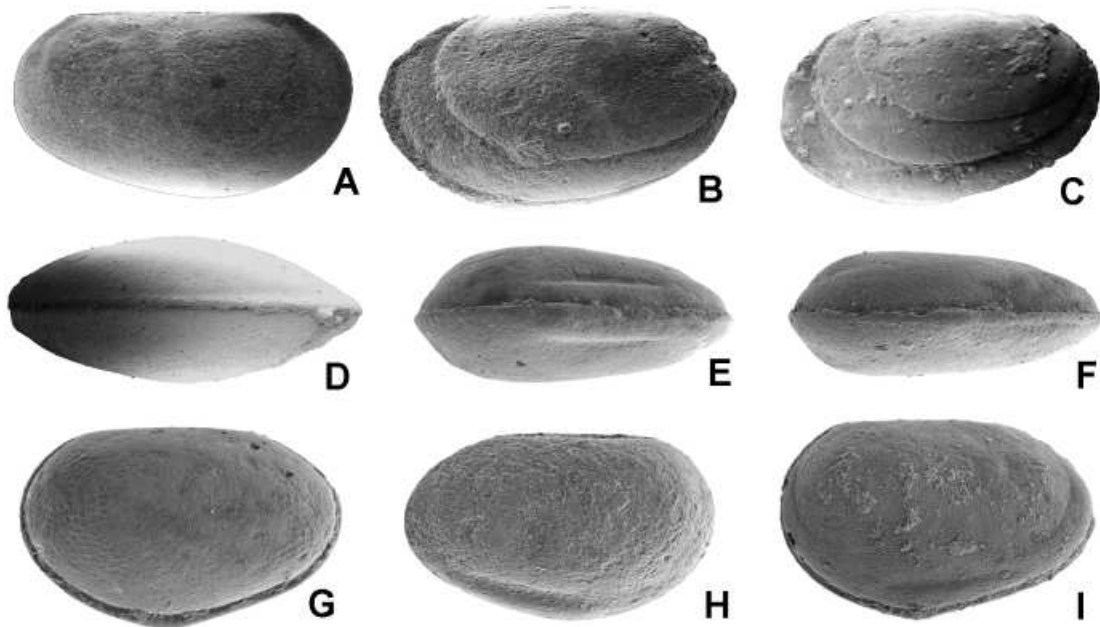
*Lectotype*. Left valve, Ceratopyge Shale, Ventlinge, Öland, Sweden; figured by Moberg and Segerberg (1906, pl. 3, fig. 28); selected by Henningsmoen (1954).

*Diagnosis*. Small trilobate (bisulcate) species. Valves convex, with convex ventral margin and convex ventral area. Lobe 1 wide and bulbous, reaches dorsal hinge-line or extends beyond it. Lobe 2 short. Adductorial sulcus wide, extends over nearly half of the lateral area. Surface almost smooth or slightly nodose. Admarginal structures unknown. Sexual dimorphism unknown.

*Remarks*. The results of the present phylogenetic analysis permit *N. nanella* to be assigned to the suborder Palaeocopa. The position of *N. nanella* in the consensus tree (Text-fig. 2) shows the species to be a sister-group to the families Tvaerenellidae Jaanusson, 1957, Ctenonotellidae Schmidt, 1941, and Tetradellidae Swartz, 1936. This result is supported by the presence of the distinct lobal-sulcal morphology, which distinguishes this suborder from other ostracod taxa. However, admarginal structures are unknown in *N. nanella*. In palaeocopids, the admarginal structures are often dimorphic, but at present dimorphism is unknown in *N. nanella*. It cannot be ruled out completely that it is just owing to the absence of



TEXT-FIG. 4. *Nanopsis nanella* (Moberg and Segerberg, 1906), Bjørkåsholmen Formation, Slemmestad, Oslo-Asker Region, Norway. A, PMO 1174a, right valve with partly preserved carapace;  $\times 120$ . B, PMO 1174a, right valve, internal mould;  $\times 145$ .



TEXT-FIG. 5. Eridostracans *Conchoprimitia* Öpik, 1935 and *Incisia ventroincisurata* (Hessland, 1949) from the Arenig of Baltoscandia. A–D, *Conchoprimitia* sp., Volhov Stage, Lava. A, carapace TUG 1/1109, left view;  $\times 38$ . B, carapace TUG 2/1109, right view;  $\times 35$ . C, carapace TUG 3/1109, right view;  $\times 20$ . D, carapace TUG 4/1109, ventral view;  $\times 20$ . E–I, *Incisia ventroincisurata* (Hessland, 1949), Volkhov Stage, Nömmeveski. E, carapace TUG 5/1109, ventral view;  $\times 50$ ; F, carapace TUG 6/1109, ventral view;  $\times 43$ . G, carapace TUG 7/1109, right view;  $\times 50$ . H, carapace TUG 8/1109, left view;  $\times 50$ . I, carapace TUG 9/1109, right view;  $\times 48$ .

heteromorphic specimens in the collection. The trilobate morphology of *N. nanella* is unique among the early palaeocopes of Baltoscandia, although this condition occurs in several later ostracod taxa. The study of ontogeny of two Arenigian ostracod species *Ogmoopsis bocki* and *Brezelina palmata* reveals a similar trilobate condition in the juvenile instars of these species (Tinn and Meidla 2003).

Regardless of the early occurrence in the Tremadoc, *N. nanella* shows distinct and specific palaeocope morphology and thus it cannot be regarded as a primitive ostracod species.



*Occurrence.* Bjørkåsholmen Formation, Oslo–Asker Region, Norway; Alum Shale (Ceratomyge Shale), Öland; Shumardia Zone, Scania, Sweden.

Suborder ERIDOSTRACA Adamczak, 1961  
Family CONCHOPRIMITIIDAE Henningsmoen, 1953a  
Genus INCISUA Schallreuter, 1993

*Incisua ventroincisurata* (Hessland, 1949)

Text-figure 5F-I

- 1949 *Conchooides ventroincisurata* Hessland, pp. 172–174, pl. 2, figs 8–9.  
1949 *Conchooides minuta* Hessland, pp. 175–177, pl. 3, figs 2–3, 5–6.  
1949 *Conchooides minuta* ab. *posteroreticulata* Hessland, p. 178, pl. 2, fig. 11.  
1993 *Miniconchooides minutus* (Hessland, 1949); Schallreuter, p. 125, pl. 22A, fig. 3; pl. 24B, fig. 4; pls 26B–27; pl. 28A, fig. 2; pl. 62B, fig. 4.  
1993 *Incisua ventroincisurata* (Hessland, 1949) Schallreuter, p. 126, pl. 20B, fig. 1; pl. 21; pl. 25A, fig. 2; pl. 25B.

*Holotype.* Complete carapace, PIU ar. os. 173, Röjeråsvägen, Dalecarlia, Sweden; figured by Hessland (1949, pl. 2, fig. 8).

*Diagnosis.* Small postplete species. Valve surface smooth, rarely showing slight reticulation. Ventral margin of left valve often bulged near the mid-length. Hinge-line straight, short.

*Remarks.* Two species and one subspecies of *Conchooides* originally described by Hessland (1949) are considered to be conspecific. The main distinction between the species was the ventral ‘score’, a longitudinal ventral furrow. This is always distinct in *Incisua ventroincisurata*, but absent in *Miniconchooides minutus*, which otherwise exhibits very similar carapace morphology (Hessland 1949). Our observations show that this peculiar feature is a retention mark that cannot be used for distinguishing the species.

The species is common in the Volkhov Stage of Estonia and the St. Petersburg region, Russia. Certain strata may yield up to several hundred *I. ventroincisurata* specimens per sample and comprise up to half of the ostracod assemblage found. The study of the *I. ventroincisurata* populations shows that normally about one-third of the specimens, both adult and young instars, bear the characteristic ventral furrow. It may be accompanied by slight depressions in the anterior and posterior regions of the carapace, thus representing a characteristic retention mark, typical of the eridostracans (Adamczak 1961). However, the retention mark in *I. ventroincisurata* differs from those of other eridostracans from the same level (*Conchoprimitia* Öpik, 1935). The conchoprimitids typically show retention marks on the anterior and posterior parts of the carapace, but shells of younger moults (Text-fig. 4) are rarely found. However, the *Incisua*-type deeper ventral furrow has not been documented in *Conchoprimitia*. The difference between these types of retention marks is probably due to the distinct ventral morphologies of these two species. Unlike *Conchoprimitia*, *I. ventroincisurata* has a slightly bulbous mid-ventral area in the left valve which is most likely responsible for the particularly deeper retention furrow centro-ventrally.

*Occurrence.* ‘Lower Grey Limestone’, Siljan District, Sweden; Volkhov Stage, Estonia; St. Petersburg region, Russia.

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## APPENDIX

### *Characters used in the phylogenetic analyses*

1. carapace material: phosphatic (0); calcitic (1)
2. carapace symmetry: present (0); absent (1)
3. anterior/posterior ends: equal (amplete) (0); posterior end wider/higher than anterior (postplete) (1); anterior end wider/higher than posterior (preplete) (2)
4. hinge line: straight (0); convex (1)
5. length of hinge-line vs. total length:  $>L/2$  (0);  $<L/2$  (1)
6. ventral margin: convex (0); straight (1); concave (2)
7. ventral area: convex (0); flat (1); concave (2)
8. laterovelar bend: absent (0); present (1)
9. left-side overlap: absent (0); present (1)
10. reversed overlap: absent (0); present (1)
11. ventral valve overlap: of uniform width (0); of variable width (1)
12. internal contact groove: absent (0); present (1)
13. marginal structure (tubercles): absent (0); present (1)
14. lamellar ultrastructure: present (0); absent (1)
15. duplicature: present (0); absent (1)
16. lateral nodes: absent (0); present (1)
17. lobal/sulcal structures: absent (0); present (1)
18. adductor pit: absent (0); distinct (1); depressed (2)
19. preadductor node: absent (0); present (1)
20. lobation: trilobate (0); quadrilobate (1)
21. sulcation: unisulcate (0); bisulcate (1); trisulcate (2)
22. lobes: smooth (0); cristate (1)
23. L1: reaching dorsal end of domicilium (0); reaching over dorsal end of domicilium (1)
24. spinose L1: absent (0); present (1)
25. L1: reaching dorsal end of domicilium (0); reaching over dorsal end of domicilium (1)
26. ridge on L2: absent (0); present (1)

27. S2: not developed (0); reaching 1/3 of the domicilium (1); reaching ventral area (2)  
 28. S2: shallow (0); deep (1)  
 29. S2: nearly straight (0); transversely curved (1)  
 30. zygalcrista (elevation around S2): absent (0); present (1)  
 31. posterior spine: absent (0); present (1)  
 32. plica (dorsal crest): absent (0); present posterodorsally(1), present dorsally (2)  
 33. reticulate ornamentation: absent (0); present (1)  
 34. nodose oranamentation: absent (0); present (1)  
 35. punctate ornamentation: absent (0); present (1)  
 36. interdorsum: present (0); absent (1)  
 37. velum: absent (0); present (1)  
 38. velum: solid (0); tubulose (1)  
 39. velum: developed anteriorly (0); developed on 3/4 of free margin (1); developed over whole free margin (2); absent ventrally (3)  
 40. heteromorphic velum: flat (0); convex (1)  
 41. heteromorphic velum wider: anteriorly (0); ventrally (1); over the whole length (2)  
 42. pseudovelum: absent (0); present (1)  
 43. molt retention: absent (0); present (1)  
 44. dimorphism: absent (0); velar (1); domiciliar (2)

*Data matrix used for the phylogenetic analyses*

Characters for *Hesslandona* specified after Müller (1982) and Hinz (1993)

	5	10	15	20	25	30	35	40	44
<i>L. decumana</i>	11000	00010	00111	0121-	0--0-	-1100	01010	11121	0001
<i>E. reticulogranulatus</i>	11000	00010	00111	0101-	0--0-	-1101	00110	11000	1001
<i>E. effusus</i>	11100	00010	00111	0101-	0--0-	-1101	00000	11000	1001
<i>E. anisus</i>	11000	00010	00111	0100-	0--0-	-1101	00010	11000	1001
<i>U. cicatrisosa</i>	11000	00010	00111	0121-	0--0-	-1100	01010	11020	1001
<i>H. proximus</i>	11000	01010	00?11	0100?	0-11-	-2110	00010	1100-	-001
<i>R. mitis</i>	11000	01010	00111	01001	21000	12110	01010	11010	0001
<i>A. acuta</i>	11000	01010	00111	01001	21000	12110	01010	11011	2001
<i>C. levis</i>	11000	01010	00111	0101-	0--0-	-2110	01010	11001	2001
<i>P. grewingkii</i>	11000	01010	00111	01001	21001	12110	00010	11010	0001
<i>T. lanceolata</i>	11200	01010	00111	01001	20001	02110	00000	11011	2001
<i>B. angustolobata</i>	11000	01010	00111	01001	20000	02110	00000	11010	2001
<i>T. primaria</i>	11100	01010	00111	01001	20001	02110	00000	11010	2001
<i>T. viridis</i>	11000	01010	00111	01001	20001	02110	00000	11010	2001
<i>B. palmata</i>	11000	01010	00111	01001	20001	02110	00000	11010	2001
<i>G. digitatus</i>	11200	02010	00111	01001	20101	02110	00000	110-0	2001
<i>G. grandispinosus</i>	11200	02010	00111	01002	2011-	-2110	00000	110-0	1001
<i>A. simplex</i>	11200	02010	00111	01002	20-0-	-2010	00000	110-0	1001
<i>H. macroreticulata</i>	11200	01010	00111	01012	00-0-	-2110	00100	11000	1001
<i>E. sigma</i>	11200	01010	00111	01012	00-0-	-2110	00100	11000	0001
<i>O. bocki</i>	11200	01010	00111	01001	20101	02110	00000	11010	0001
<i>L. ansiensis</i>	11200	00010	00011	1000-	--0-	-0--	00100	10--0	0100
<i>D. lauta</i>	11000	011??	??011	0000-	--0-	-0--	10000	10-0-	-000
<i>Baltonotella</i>	11001	01101	01111	0000-	--0-	-0--	00001	10--	-000
<i>Conchoprimitia</i>	11100	00000	00011	0000-	--0-	-0--	00000	10--	-010
<i>I. ventroincisurata</i>	11101	00000	00011	0000-	--0-	-0--	00000	10--	-010
<i>E. nonumbonatus</i>	11100	10001	11011	0000-	--0-	-0--	10000	10-0-	-000
<i>L. curvata</i>	11111	20001	11011	0000-	--0-	-0--	00000	10--	-000
<i>P. procerus</i>	11100	011?1	11011	0000-	--0-	-0--	10001	10--	-000
<i>O. cornuta</i>	11100	01111	11011	0000-	--0-	-0--	10000	10--	-000
<i>U. punctosulcata</i>	11000	11010	00011	0101-	--0-	-1000	00000	10--	-002
<i>U. irre</i>	11100	11010	00011	0101-	--0-	-1100	00100	10--	-000
<i>U. tolmachovae</i>	11100	110?0	00011	0100-	--0-	-1000	00100	10--	-000
<i>N. nanella</i>	1?000	000??	???11	01000	10101	02110	00000	1????	?00?
<i>Hesslandona</i>	00000	000--	00000	0000-	---0-	-----	00000	00---	-000