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The lowermost Silurian of Jämtland, central Sweden: conodont biostratigraphy, correlation and biofacies

Peter Dahlqvist and Stig M. Bergström

ABSTRACT: The Late Ordovician–Early Silurian succession in Jämtland includes the marine Kogsta Siltstone, which is unconformably overlain by the shallow-water Ede Quartzite that grades into the open-marine Berge Limestone. A *Hirnantia* shelly fauna dates the uppermost Kogsta Siltstone as Hirnantian, and shelly fossils indicate an Aeronian age for the Berge Limestone. Biostratigraphically highly diagnostic conodonts of the early-middle Aeronian *Pranognathus tenuis* Zone provide the first firm date of the Upper Ede Quartzite and the lowermost Berge Limestone. The Lower Ede Quartzite has not yielded fossils, but sedimentological data suggest it to be of Hirnantian age and reflect the glacio-eustatic low-stand. The contact between the Lower and Upper Ede Quartzite, here taken to be the Ordovician–Silurian boundary, appears to be an unconformity associated with a stratigraphic gap that at least includes the Rhuddanian Stage. The biostratigraphically important conodonts *Pranognathus tenuis*, *Kockelella? manitoulinensis*, and *Pranognathus siluricus* are recorded from Sweden for the first time, and these and other conodonts are used for correlations with coeval units in Europe and North America. In a regional review of Aeronian conodont faunas, three intergrading, apparently depth-related, conodont biofacies are recognised, the Jämtland conodonts representing the one characteristic of the shallowest water.

KEY WORDS: Berge Limestone, conodonts, Ede Quartzite, Europe, North America, palaeoecology.

The Ede Quartzite and Berge Limestone are key units for the interpretation of the terminal Ordovician and early Silurian geologic evolution in the Province of Jämtland in central Sweden. These formations are accessible in natural and man-made sections throughout the western Lake Storsjön area (Fig. 1) but both formations are generally not exposed in the same outcrop. The best exposures of both these units are on the shores of the Norderön and Verkön Islands, and on a hill slope at Edefors (Fig. 1c). The Edefors section, the type locality of the Ede Quartzite (Thorslund 1960), is by far the best in terms of stratigraphic control, and it is also important in that this outcrop includes part of the underlying Ashgillian Kogsta Siltstone. For recent studies of the sedimentology and stratigraphy of these formations, see Cherns & Karis (1995), Dahlqvist & Calner (2001, 2004), and Dahlqvist (2003). For information about many aspects of the general geology of the study area, see Thorslund (1943, 1948, 1960, 1968), Cherns & Karis (1995), and Karis (1998).

Until now, biostratigraphic data from the Ede–Berge interval have been very limited, contradictory (Fig. 2), and entirely based on macrofossils. Hence, the Ede Quartzite has been considered to be early Llandoverian (Boucot & Johnson 1964; Thorslund 1960; Grahn 1998; Baarli *et al.* 2003), or Hirnantian–Rhuddanian (Jaanusson *et al.* 1982; Cherns & Karis 1995; Karis 1998), in age. The base of the Berge Limestone has recently been interpreted, in our view incorrectly, to be early–middle Rhuddanian in age (Cherns & Karis 1995; Grahn 1998; Karis 1998; Baarli *et al.* 2003). Based on the presence of an earliest Telychian *turriculatus* Zone graptolite fauna in the basal portion of the overlying Bångåsen Shale, the top of the Berge Limestone has been dated as uppermost Aeronian by recent authors (see e.g. Karis 1998; Baarli *et al.* 2003). As shown by these various interpretations (Fig. 2), there is an urgent need for new biostratigraphic information to clarify the Late Ordovician–Early Silurian geological evolution in this important region.

The purpose of the present paper is to (a) present the first published conodont data from the Ede Quartzite and Berge Limestone; (b) clarify the biostratigraphic age of these formations and establish a conodont biostratigraphy for the lowermost Silurian in Jämtland; and (c) examine the biostratigraphic relations between the Ede Quartzite and the Berge Limestone, and between these units and coeval units in Baltoscandia and elsewhere.

1. Geological setting

During Late Ordovician and Early Silurian times, sediments were deposited in the developing Caledonian foreland basin close to the western margin of the Baltic craton (e.g. Gayer & Greiling 1989), which was situated at tropical palaeolatitudes on the southern hemisphere (Torsvik 1998; Fig. 1b). According to Baarli *et al.* (2003, fig. 1), the sediments in Jämtland accumulated in the northernmost part of this large foreland basin, which extended to the south-southwest, where its southernmost portion included the Oslo Region.

Both the Ede Quartzite, and the broadly equivalent unit in eastern Jämtland, which is known as the Kyrkås Quartzite, overlie the Late Ordovician Kogsta Siltstone (Fig. 3). The former units are characterised by unconformity development and complex lateral facies changes (Dahlqvist 2004; Dahlqvist & Calner 2004). The interval of stratigraphic complexity and terrigenous sediments ends at the top of the Ede Quartzite, which grades into the Berge Limestone, a relatively pure carbonate unit. Graptolitiferous black shales of the Bångåsen Shale overlie the Berge Limestone. This unit contains several K-bentonite beds (volcanic ashes). The most prominent of these is up to 0·5 m thick and occurs at the base of the

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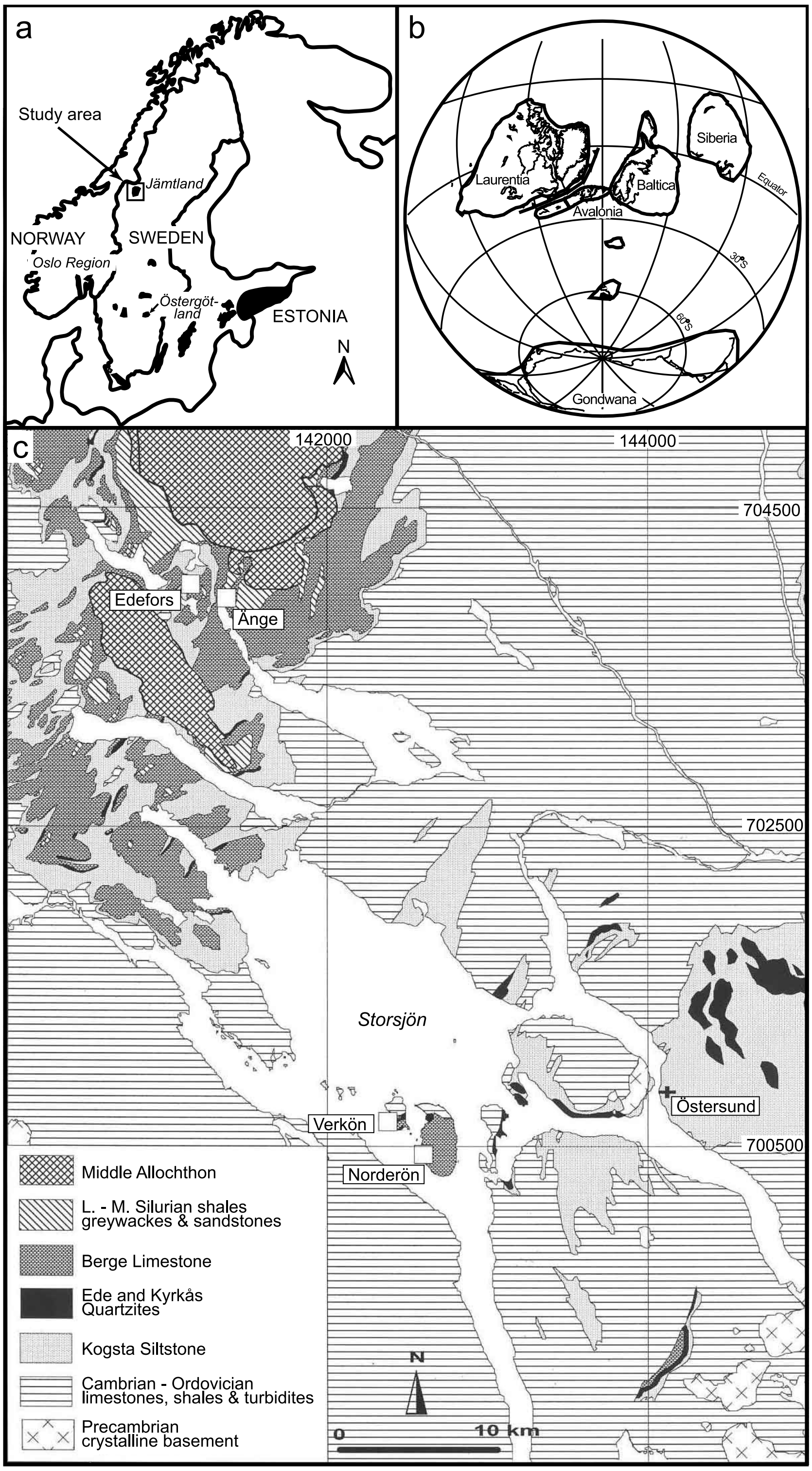

Figure 1 (a) Sketch-map showing location of Lower Palaeozoic outcrop areas (black) in Jämtland and elsewhere in Sweden outside the high Caledonide Mountains as well as in Norway and Estonia. (b) Reconstruction of the Early Silurian palaeogeographic relations between Baltica, Avalonia, Lauentia and Siberia (after Torsvik 1998). Note that all these plates straddle the Equator. (c) Geologic map of the study area in the Lake Storsjön region, Province of Jämtland. Note the main distribution area of the Ede Quartzite northwest of Lake Storsjön and areally more limited occurrences in the Norderön-Verkön area. The key locality of the Ede Quartzite is the type section at Edefors.

shale sequence, where it rests on an uneven surface of the Berge Limestone (Thorslund 1960). It was identified as the Osmundsberg K-bentonite by Bergström *et al.* (1998b).

The deposition of the Upper Ordovician–Lower Silurian succession in Jämtland was influenced by the Late Ordovician (Hirnantian) glacio-eustatic sea level fluctuations. This has been stressed by several recent authors (see e.g. Karis 1998) and is shown by, among others, unconformity development (Dahlqvist & Calner 2004) and the presence of a cold-water macrofossil fauna (the *Hirnantia* fauna) in the Kogsta Siltstone (Bergström 1968; Karis 1998) as well as in the Kyrkås Quartzite (Thorslund 1960; Karis & Larsson 1982; Cherns & Karis 1995). A prominent unconformity within the Ede Quartzite, which is interpreted to reflect the Hirnantian

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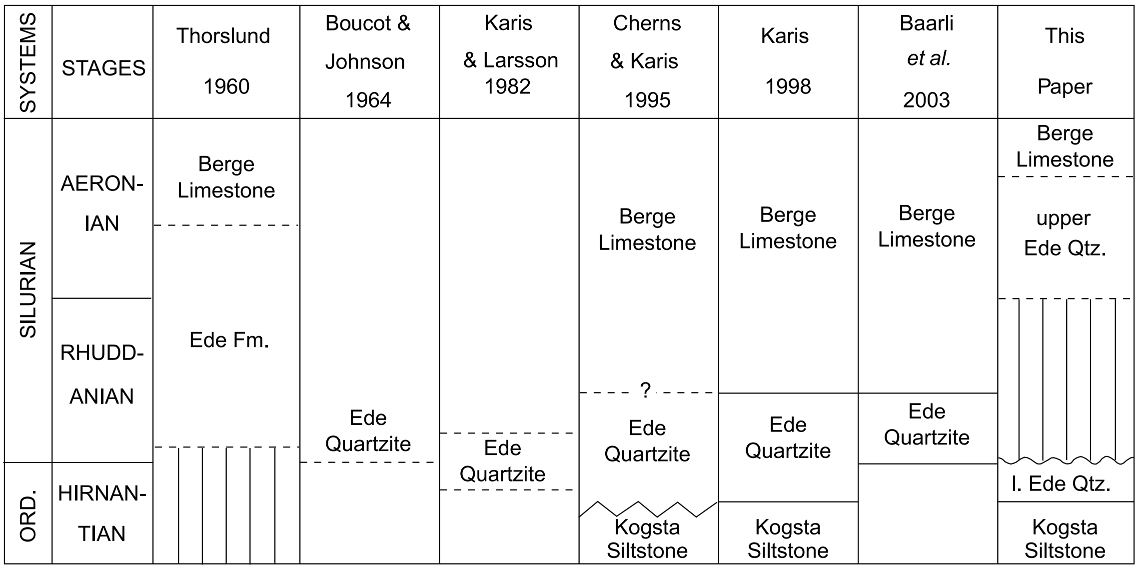

Figure 2 Comparison between different chronostratigraphic classifications of the Ede Quartzite and Berge Limestone since 1960 and that advocated in the present study.

maximum lowstand and a significant stratigraphic gap, separates two major parts of the formation (Fig. 3), which are here referred to as the Lower and Upper Ede Quartzite, respectively.

2. Sedimentology

Relatively little information has been published on the sedimentology of the Ede Quartzite and Berge Limestone and the role played by their deposition in the evolution of the Jämtland basin. Hence, it is appropriate to present a brief review of these matters, which is based mostly on recent studies. For more detailed information, see Dahlqvist & Calner (2004).

2.1. Ede Quartzite

The Ede Quartzite is about 6 m thick in its main outcrop area (Figs 3, 4, 5). Toward the northwest, it is thicker and sandier, and it is more calcareous to the south on Norderön and Verkön (Karis 1998). It rests on the Kogsta Siltstone whose top is an erosion surface showing 0·5–1·0 m relief. The lower part of the formation, here referred to as the Lower Ede Quartzite, consists of medium- to thick-bedded quartzite, which was deposited in a shoreface environment. The top of this interval is marked by an unconformity exhibiting only minor local relief. This unconformity is overlain by a 0·1–0·5 m thick favositid biostrome, which forms the lowermost portion of the Upper Ede Quartzite. The Upper Ede Quartzite consists of thin-bedded calcareous sandstone, limestone, and intensely bioturbated shale, which were apparently deposited in a wave-dominated proximal shelf environment. Analysis of stratigraphic boundaries and lithofacies succession suggests that the Kogsta Siltstone–Lower Ede Quartzite contact interval represents a downward shift in coastal onlap, which led to the

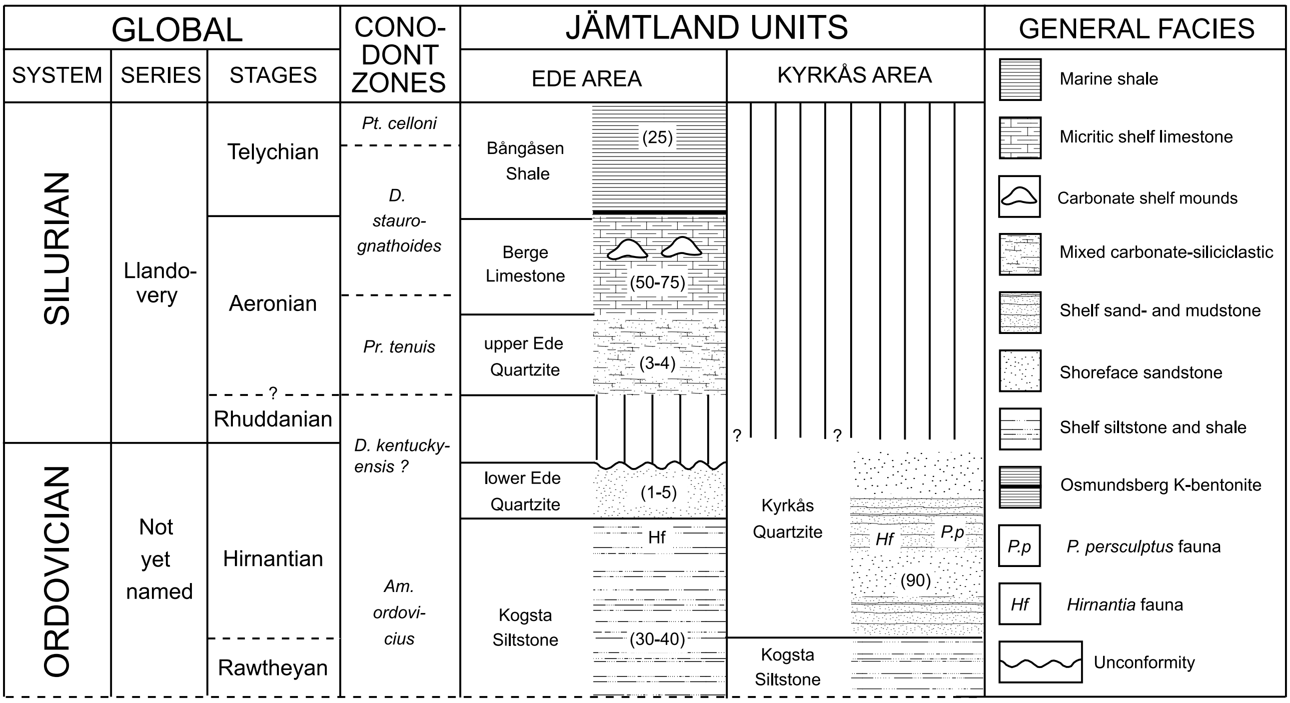

Figure 3 Stratigraphic classification and lithology of latest Ordovician to early Telychian units in the study area. Figures in the lithologic column for the Ede and Kyrkås areas indicate approximate thickness in metres.

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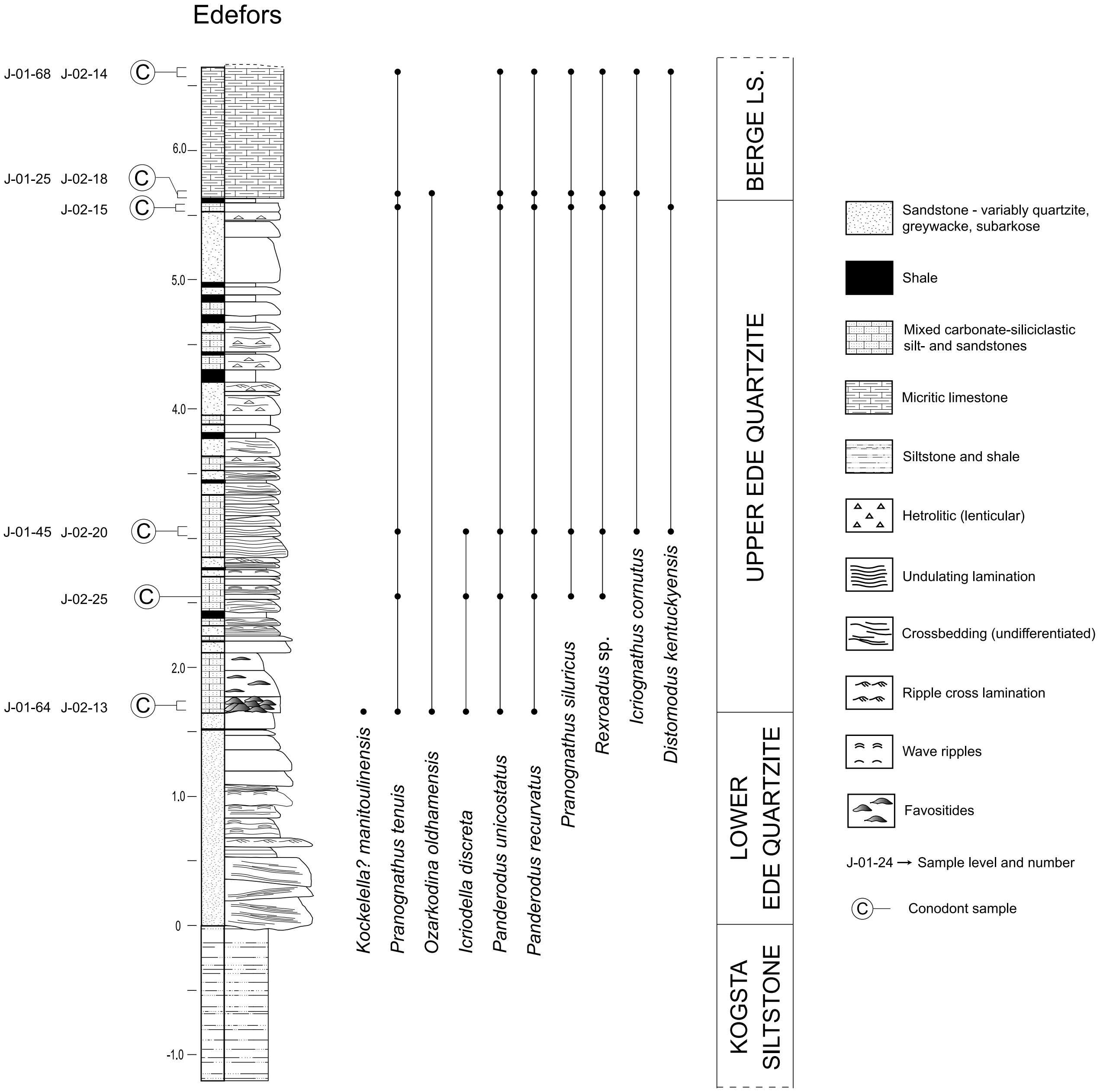

Figure 4 Lithologic sequence of the Ede Quartzite and lowermost Berge Limestone in the Ede type section at Edefors (after Dahlqvist & Calner 2004) and the vertical distribution of conodont taxa through this interval. No conodonts are known from the Lower Ede Quartzite and the uppermost Kogsta Siltstone but the latter unit in the Edefors section contains shelly fossils of the *Hirnantia* fauna (*Hf*). The Edefors section is located on the slope of a small hill about 1 km southeast of Offerdal church (Swedish coordinates E1411158/N7040198).

formation of the erosional surface at the top of the Kogsta Siltstone. The unconformity that separates the Upper and Lower Ede Quartzite probably reflects the maximum lowstand of the sea. Along with the overlying biostrome, it was formed during a period of reduced clastic influx, and the stratigraphic gap associated with the unconformity reflects a significant period of local non-deposition and at least minor erosion. The mixed siliciclastic–carbonate succession in the Upper Ede Quartzite grades into the overlying Berge Limestone without any apparent interruption in the deposition although the siliciclastic component in the deposited material became greatly reduced.

2.2. Berge Limestone

The Berge Limestone is a dark coloured, micritic, rather pure limestone that is relatively homogenous in composition throughout the region. It is highly fossiliferous locally and contains a diverse normal-marine shelly fauna. Its lowermost part, which is approximately 1 m thick at Edefors, consists of thin- to medium-bedded skeletal micritic limestone. Skeletal grains are mainly from crinoids, trilobites, brachiopods, bryozoans, and gastropods. The limestone generally varies from lime mudstone to wackestone but there are also thin beds of grainstone. The siliciclastic content is low and decreases upwards in the succession where the carbonate becomes more pure. Sedimentary structures are very rare. The high content of carbonate mud may indicate deposition below the effective wave base. Some parts of the Berge Limestone contain accumulations of pentamerids with shells piled valve-in-valve, sorted by size, and with their concave side facing upward. According to Johnson (1989), who recorded similar beds in Norway, these represent assemblages of shells *in situ* and as well as shells transported by storm events. In the upper part of the formation on Norderön, small mounds have been recorded

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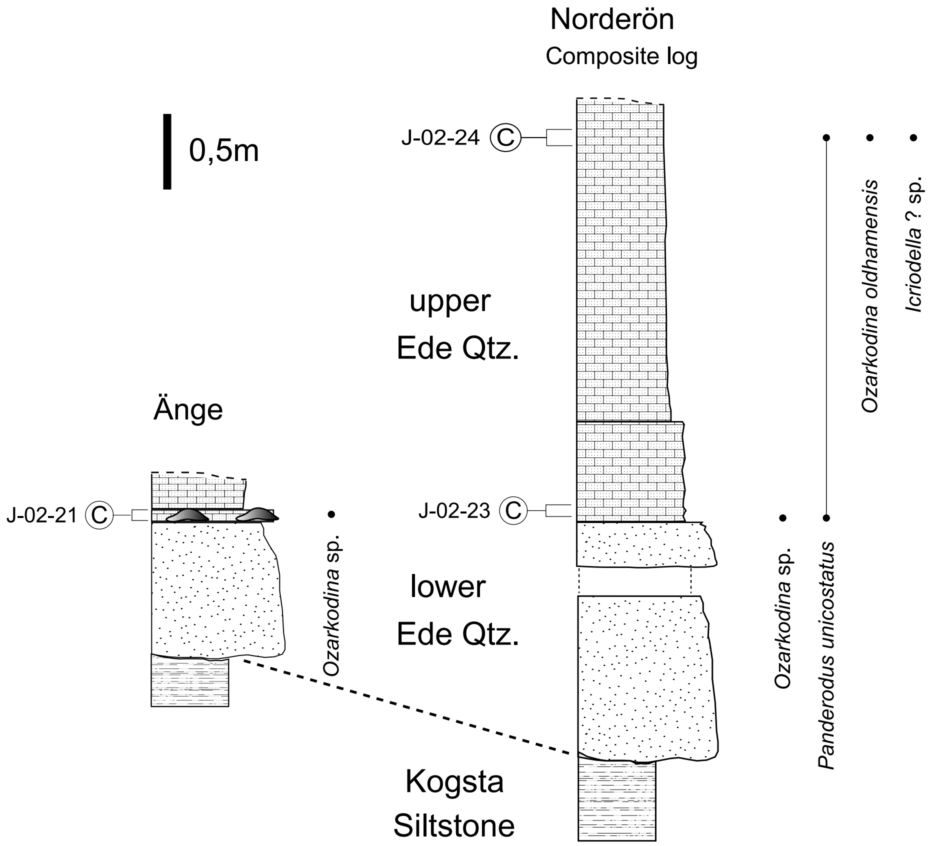

Figure 5 Lithology of the Ede Quartzite in sections at Änge and on Norderön and the vertical ranges of conodont taxa in the Upper Ede Quartzite. Note that the conodonts are much more sparse and show far less diversity than in the Edefors section. The Änge section is a road cut along the east side of an unpaved road about 100 south of intersection with the main road to Änge (Swedish coordinates E1413913/N7039384). The Norderön outcrop is on the western shore of the island about 200 m south of the ferry landing place (Swedish coordinates E1426253/N7004542).

that mostly consist of halysitids (Dahlqvist 1999). The depositional environment of the Berge Limestone seems to have been between fair-weather wave base and storm wave base, and within the photic zone. Fauna and lithology indicate an offshore muddy/silty environment, with normal sedimentation from suspension alternating with storm deposition events.

The formation of the erosional surface at the base of the Ede Quartzite, as well as the unconformity separating the Lower and Upper Ede Quartzite, and the subsequent regional change from a high-supply high-energy siliciclastic shelf setting to a low-energy carbonate-dominated shelf environment, are interpreted to reflect the Hirnantian glacio-eustatic event, related climatic changes and the subsequent eustatic transgression (Dahlqvist & Calner 2004).

3. Previous conodont work

The data presented in the present paper are the first record of conodonts from the Ede Quartzite and Berge Limestone, and hence this investigation has the character of a pioneer study. This is also shown by the fact that whereas late Llandoverian and later Silurian conodonts have been the subject of very extensive studies in Sweden (see, e.g., Jeppsson 1983, 1997; Jeppsson *et al.* 1994), early and middle Llandoverian conodont faunas have remained very poorly known, the only previous publication being Bergström & Bergström (1996). On the other hand, a considerable amount of work has been carried out on conodont faunas of early Silurian age in Norway (Aldridge & Mohamed 1982; Idris 1984; Nakrem 1986) and Estonia (e.g. Männik 1992a, b; Viira & Männik 1997). These studies, and those on conodonts from coeval strata in other parts of the world, have been essential for the interpretation of the Ede–Berge conodont biostratigraphy presented herein.

4. Preparation methods

The present study is mainly based on 12 conodont samples varying in weight from 0·7–12·9 kg. Eight of the 12 samples are from the Upper Ede Quartzite and four from the lowermost Berge Limestone. These samples were collected at Edefors (9 samples, Fig. 4), Änge (1 sample, Fig. 5) and Norderön (2 samples, Fig. 5). After processing using the acetic acid method described by Jeppsson *et al.* (1985), the samples produced about 650 elements representing nine species, amongst which five have not been recovered previously in Sweden. The number of specimens in each of the 12 processed samples ranges greatly from 0 to more than 200. The state of preservation varies from mediocre to good. All specimens show thermal alteration and their CAI (Colour Alteration Index; see Epstein *et al.* 1977) is 4·5–5, indicating a heating of about 300 degrees C.

5. Conodont fauna

A summary of the conodont taxa present in each sample is given in Table 1, and the ranges of species in the studied sections are shown in Figures 4 and 5. Important species are illustrated in Figure 12. As shown in Figures 4 and 5, the species associations in the samples do not change greatly through the studied stratigraphic interval and the present

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Table 1 List of number of identified specimens of multi-element conodont taxa recorded in the studied samples. Note that there is some uncertainty regarding the proper species reference of morphologically similar S elements in the case of some species, especially in *Pranognathus*. However, this is unlikely to markedly affect the relatively frequency of the various taxa.

	J-01-64	J-02-13	J-02-25	J-02-20	92B26-1	J-02-15	J-02-18	J-01-68	J-02-14	J-02-23	J-02-24	J-02-21	Total	%
Distomodus kentuckyensis	—	—	—	3	—	2	—	—	2	—	—	—	7	0·8
Icriodella discreta	—	11	—	—	—	—	—	—	—	—	1	—	12	1·4
Icriognathus cornutus	—	—	—	2	—	2	1	1	3	—	—	—	9	1·1
Kockelella? manitoulinensis	2	—	—	—	—	—	—	—	—	—	—	—	2	0·2
Ozarkodina oldhamensis	1	—	5	—	6	—	1	—	—	—	1	—	14	1·7
Ozarkodina sp.	—	2	—	—	1	—	2	—	2	1	—	1	9	1·1
Panderodus recurvatus	1	1	—	—	2	1	—	—	4	—	—	—	9	1·1
Panderodus unicostatus	—	13	20	16	86	103	21	8	76	—	2	2	347	41·1
Pranognathus siluricus	—	—	1	1	18	16	1	1	71	—	—	—	109	12·9
Pranognathus tenuis	—	2	33	37	78	69	13	18	72	—	—	—	322	38·1
Rexroadus sp.	—	—	—	1	—	2	1	1	—	—	—	—	5	0·6
Total	4	29	59	60	191	195	40	29	230	1	4	3	845	

authors consider their collection to represent the same conodont fauna. The composition of this fauna is unusual compared to most previously described faunas of this age in that *Pranognathus tenuis* (Aldridge, 1972; Fig. 12p-aa) is the dominating compound species and represents as much as 37% of the total number of specimens (Table 1). It is associated with less common species of *Icriodella* (Fig. 12a–b), *Icriognathus* (Fig. 12g–h), *Kockelella?* (Fig. 12i–j), and *Pranognathus* (Fig. 12c–e) along with abundant specimens (about 41%) of the ubiquitous and probably pelagic *Panderodus* (Fig. 12m–o). Common taxa in coeval faunas elsewhere, such as *Dapsilodus*, *Decoriconus*, and *Walliserodus*, appear to absent, and the very widespread genera *Distomodus*, *Ozarkodina*, and *Rexroadus* are represented by only small numbers of specimens. As discussed below, the unusual composition of the fauna is attributed to ecologic control, the Ede–lowermost Berge faunas being interpreted to represent a special conodont biofacies characteristic of a very shallow-water, at least at times high-energy, environment. This special habitat is not well represented amongst previously described Lower Silurian conodont faunas, most of which are from lower-energy, subtidal, open shelf to slope, depositional settings.

6. Conodont biostratigraphy

6.1. Age of formations

Although the conodonts obtained are of low taxonomic diversity, the conodont fauna, which exhibits an overall typical Silurian aspect (Barnes & Bergström 1988) with no distinctive Ordovician taxa, includes some biostratigraphically restricted taxa that permit a rather precise age-dating of the studied succession. These taxa include *Icriodella discreta* Pollock, Rexroad & Nicoll, 1970, *Icriognathus cornutus* Männik, 1992a, *Kockelella? manitoulinensis* (Pollock, Rexroad & Nicoll, 1970), *Ozarkodina oldhamensis* (Rexroad, 1967), *Pranognathus tenuis* (Aldridge, 1972), and *P. siluricus* (Pollock, Rexroad, and Nicoll, 1970). The fact that the Ede conodont fauna is closely similar to that of the lowermost Berge Limestone indicates that there is no marked age difference between these formations, as is also suggested by their gradational contact.

Four calcareous intervals in the Upper Ede Quartzite in its type section at Edefors have produced conodonts (Fig. 4). Conodont taxa from the lowermost productive level include, amongst others, *Icriodella discreta*, *Kockelella? manitoulinensis*, *Ozarkodina oldhamensis* and *Pranognathus tenuis*. *Kockelella? manitoulinensis* and *P. tenuis* have not previously been recorded from Sweden but *I. discreta* occurs in the Motala Formation (Bergström & Bergström 1996) and *O. oldhamensis* has been found in strata as old as the Hirnantian Loka Formation (formerly *Dalmanitina* Beds) in central Sweden (Bergström 1971). *Icriodella discreta*, *K.? manitoulinensis*, and *Pranognathus siluricus*, which are present in the next younger sample, were first described (Pollock *et al*. 1970) from strata dated as early (but probably not very earliest) to middle Llandovery of Ontario and Michigan (Berry & Boucot 1970). The highly distinctive species *Pranognathus tenuis* was first described from an interval in the Pentamerus Limestone of the Welsh Borderland containing early late Aeronian (C1–C2) brachiopods (Aldridge 1972). From the upper part of the Skomer Volcanic Group of southwestern Wales, Aldridge (2002) recently described a conodont fauna that included, amongst others, *Pranognathus tenuis*, *Icriodella deflecta*, *Ozarkodina hassi*, and *O. oldhamensis*. His collections came from a stratigraphic interval containing the brachiopod *Eocoelia hemisphaerica* which indicates a mid-Aeronian age. A species association of *Icriognathus cornutus*, *K.? manitoulinensis*, O. ex gr. *oldhamensis*, and *P. tenuis* is characteristic of a portion of the Raikkülan Stage in Estonia (Männik & Viira 1990; Viira & Männik 1997) that is interpreted to be of early to middle Aeronian age. Likewise, in Norway *I. discreta, O. oldhamensis*, and *P. tenuis* occur in the upper portion (formerly referred to as Etage 6c, now the Leangen Member; cf. Baarli 1985) of the Solvik Formation and the uppermost Sælabonn Formation (Aldridge & Mohamed 1982). This interval was interpreted by Worsley (1982) to be early Aeronian, but Baarli & Johnson (1988) considered it middle Aeronian, in age. Because the top samples in the Ede Quartzite have essentially the same conodont species association as the older samples, including *P. tenuis*, which has a very short range, it is concluded that the sampled interval of the Ede Quartzite and lowermost Berge Limestone is of Aeronian, and probably early (but probably not earliest) to middle Aeronian, age. For a summary of the stratigraphic ranges of key conodonts in the Aeronian of Sweden, Norway, Estonia, and United Kingdom, see Figure 6.

As noted above, the Ede Quartzite grades into the Berge Limestone in the Ede type section. That there is no marked age difference between the former formation and the lowermost Berge Limestone is also indicated by the fact that the conodont species associations of these units are virtually identical. Hence, it is concluded that the studied part of the lower-

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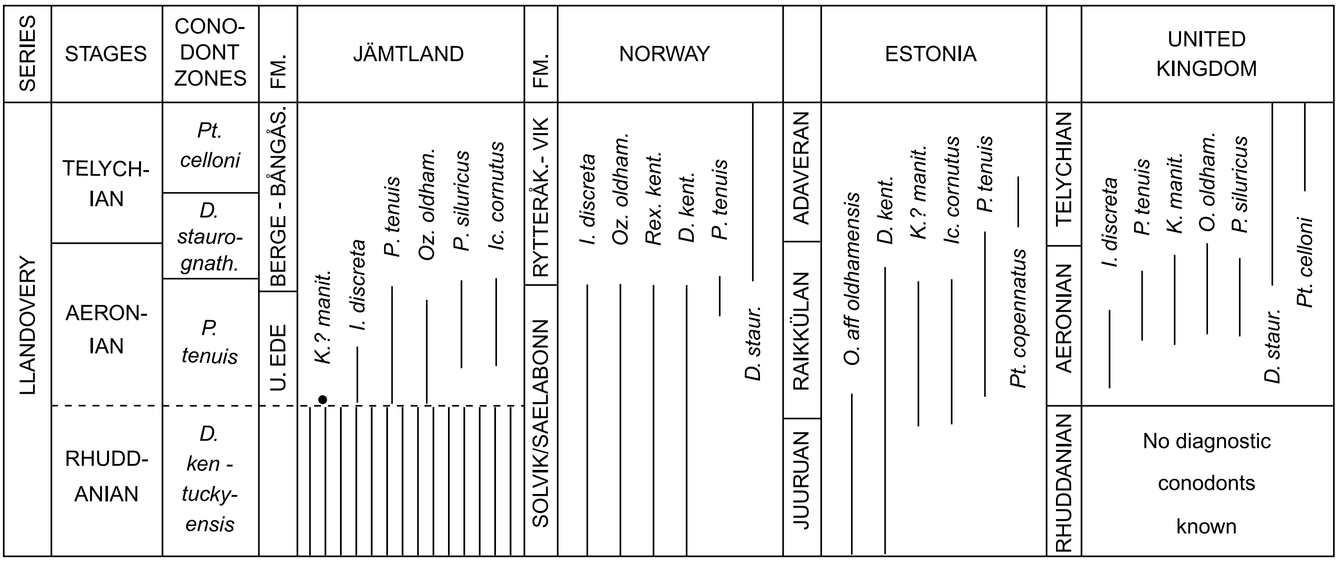

Figure 6 Comparison of ranges of biostratigraphically important conodont species in the *Distomodus kentuckyensis* through *Pterospathodus celloni* Zones in Norway (after Aldridge & Mohamed 1982), Estonia (after Viira & Männik 1997), United Kingdom (after Aldridge 1972, 1975, 2002) and the Upper Ede Quartzite–lowermost Berge Limestone in Jämtland. Note the very close similarities that indicate that the Jämtland fauna represents the early–middle Aeronian *Pranognathus tenuis* Zone.

most Berge Limestone is no younger than the early–middle Aeronian. This is also consistent with the fact that there are no taxa in our collections from the lowermost Berge Limestone that are diagnostic of the next younger conodont zone, the *Distomodus staurognathoides* Zone, the base of which is considered to be of late Aeronian age in United Kingdom (Aldridge 1975) as well as in Estonia (Viira & Männik 1997).

A discussion of the age of the Ede Quartzite should also include its presumed equivalent, known as the Kyrkås Quartzite (Karis 1998), which is distributed in the Östersund–Häggenås region east of the distribution area of the Ede Quartzite. A detailed sedimentological study of the Kyrkås Quartzite and correlation with the Ede Quartzite was made by Dahlqvist (2004). The Kyrkås Quartzite is an approximately 90 m-thick succession which is built up by two depositional sequences, each indicating shallowing from offshore mudstones to mid-upper shoreface sandstones, probably reflecting Late Ordovician glacioeustatic changes (Dahlqvist 2004). These deposits differ lithologically from the Ede Quartzite in having, along with thick quartzite beds, substantial intervals of mud and siltstones and no calcareous interbeds. This absence of carbonate beds precludes conodont work. Other differences include the fact that it rests on the Kogsta Siltstone with gradational, rather than unconformable, contact and no intraformational unconformity corresponding to that between the Lower and Upper Ede Quartzite has been recognised. Karis (1998, fig. 4) suggested that the Kyrkås Quartzite is overlain by the Berge Limestone in the Norderön–Verkön area, but no unfaulted, continuously exposed, boundary section has been described and the contact relations at the top of the quartzite remain speculative. Other authors (Cherns & Karis 1995; Dahlqvist 2004) have assumed that post-Kyrkås Silurian sediments have been removed by erosion (Fig. 2), at least in the Östersund region. Shelly fossils of the *Hirnantia* fauna are present in a siltstone interval in the middle part of the Kyrkås Quartzite and a slightly higher interval in the siltstone contains graptolites of the *Persculptograptus persculptus* Zone (Cherns & Karis 1995; Karis 1998). Although no diagnostic Silurian fossils have been found, it is assumed, perhaps incorrectly, that the upper part of the quartzite is of Silurian age and similar in age to the Upper Ede Quartzite (Cherns & Karis 1995). In contrast, according to Dahlqvist (2004), all strata of the Kyrkås Quartzite are most probably Ordovician and represent almost the entire Hirnantian Stage. Unfortunately, available outcrops are insufficient to assess the regional facies relations between the Kyrkås and Ede quartzites.

6.2. Conodont zones

For the establishment of precise regional chronostratigraphic relationships of stratigraphic units it is convenient to use fossil-based zones, and this applies also to the studied Jämtland succession. However, a zone classification of the latter succession is complicated by the fact that in the past 40 years, several, partly quite different, conodont zone schemes have been proposed for the Llandovery in different parts of the world (Fig. 7). The most detailed and most recent such scheme (Zhang & Barnes 2002a) is based on the Anticosti Island succession (Fig. 7). Unfortunately, some of Anticosti Island zone and subzone indices for the Rhuddanian–Aeronian interval have not yet been found in Sweden or elsewhere in Baltoscandia and accordingly, their zone succession is not applicable to the Jämtland succession. Aldridge & Mohamed (1982) did not recognise formal conodont zones in their study of Norwegian Silurian sections. Männik & Viira (1990) distinguished only the *Distomodus kentuckyensis* Zone in the Rhuddanian–Aeronian interval in Estonia but noted the range of *Pranognathus tenuis* as a tentative subunit. In this respect, they followed Aldridge & Schönlaub (1989) who recognised a *P. tenuis* Subzone in the uppermost *D. kentuckyensis* Zone in their global conodont biozonation of the Silurian. More recently, Viira & Männik (1997) distinguished a separate *P. tenuis* Zone in the Raikkülan Stage underlain by a restricted *D. kentuckyensis* Zone and overlain by the *D. staurognathoides* Zone (Fig. 7). In view of its wide geographic distribution, short stratigraphic range, and distinctive appearance, *P. tenuis* has good potential to be a useful zone index, and the present authors refer the Upper Ede–lowermost Berge succession to the *P. tenuis* Zone. The base of this zone is taken to be the level of the first appearance of *P. tenuis*, which appears to be at, or slightly above, the base of the Aeronian Stage. To clarify the chronostratigraphic position of the study interval in terms of

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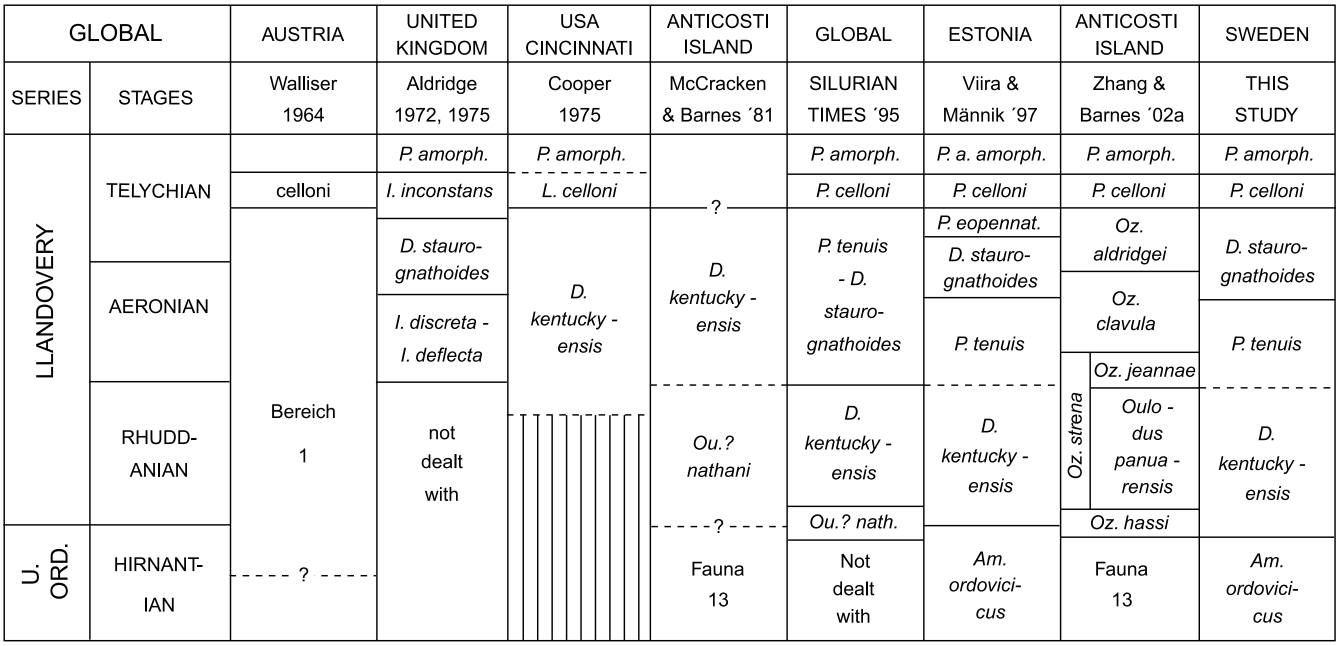

Figure 7 Comparison of different conodont zone schemes proposed in Europe and North America. At the present time, there is no universally accepted standard zonation of the Lower Silurian, and the zone scheme used in the present study is somewhat tentative, especially in the uppermost Hirnantian–lower Rhuddanian interval, from which few diagnostic conodonts are known (Barnes & Bergström 1988). The Silurian Times column refers to a correlation chart proposed by The Subcommission on Silurian Stratigraphy and published without specific author in *Silurian Times, A Newsletter of the Silurian Subcommission*, No. 3, May 1995, p. 8.

conodont biostratigraphy outside Jämtland, it is useful to compare it with successions elsewhere in northern Europe and in North America.

7. Regional comparison of conodont faunas

7.1. Sweden

The only previously described Rhuddanian–early Aeronian conodonts in Sweden are from the Upper Ordovician–Lower Silurian succession at Råssnäsudden in Östergötland (Bergström & Bergström 1996). Still undescribed extensive late Aeronian–early Telychian conodont collections carefully assembled by Eva-Marie Widmark from the Kallholn Formation of Dalarna appear to represent the late Aeronian *D. staurognathoides* Zone and they differ substantially from the Jämtland ones discussed herein.

Bergström & Bergström (1996) recorded more than a dozen conodont species from the Motala Formation at Råssnäsudden, including *Distomodus kentuckyensis* Branson & Branson, 1947, *Icriodella discreta*, and *Ozarkodina oldhamensis*, along with relatively abundant elements of *Panderodus* and *Dapsilodus obliquicostatus* (Branson & Mehl, 1933). The Motala Formation is overlain, possibly disconformably, by black shale of the Kallholn Formation that has graptolites of the middle Aeronian *leptotheca* Zone. Bergström & Bergström (1996) interpreted the Motala Formation species association as representing a part of the middle–late Rhuddanian–early Aeronian *D. kentuckyensis* Zone of Cooper (1975).

Although the Motala conodont fauna shares *O. oldhamensis* and species of *Panderodus* and *Distomodus* with that of the Ede and lowermost Berge, the general aspect of the two faunas is quite different. That is, the former fauna is dominated by *Dapsilodus obliquicostatus*, which apparently is missing in the Jämtland fauna, and it lacks the common representation of *Pranognathus tenuis* and *Pranognathus siluricus* that is characteristic of the Jämtland fauna. These differences are interpreted as probably related to both age and biofacies. The Motala fauna is older than the Jämtland fauna, most, if not all, of it being Rhuddanian rather than Aeronian, as is suggested by its close similarity to the Rhuddanian faunas from the lower Solvik and lower Sælabonn Formations in Norway (Aldridge & Mohamed 1982).

Further, it appears quite probable that the Motala Formation was deposited in deeper water than the shallow-water Ede Quartzite and lowermost Berge Limestone. This difference in depositional environment and its associated biofacies may also explain why *Kockelella? manitoulinensis* is missing in the Motala Formation as well as in moderately deep-water deposits in Norway (Aldridge & Mohamed 1982) but is present in very shallow-water strata in Jämtland, Estonia (Viira & Männik 1997), Greenland (Armstrong 1990), and central North America (Pollock *et al.* 1970).

7.2. Norway

The broad similarity in sediments and faunas between the studied succession in Jämtland and that in the Oslo region, Norway suggests that sediments in the two areas were deposited in the same trough that was located parallel to the developing Caledonides (Howe 1982). Possibly coeval lower allochthonous sequences to the north and south of Jämtland have not yielded fossils due to metamorphism, but it cannot be ruled out that the same Silurian facies were distributed along much of the Caledonian frontal zone (Basset 1985). Johnson *et al.* (1991), among others, described the Solvik–Rytteråker–Vik succession in the Oslo region as exhibiting a shallowing-upward trend that was followed by a deepening-upward sequence. If these rocks were deposited in the same trough as those in Jämtland, and also in view of the fact that eustatic patterns mostly override the effects of tectonic movements (cf. Johnson *et al.* 1991), one would expect finding the same depositional pattern in the Oslo region as in Jämtland. However, one has also to take into account that differences in palaeotopography of the two regions could result in differences in depositional patterns.

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Early Silurian strata in Norway have been extensively investigated (see, e.g., Worsley, 1982; Baarli *et al.* 2003). In the Oslo region, *Pranognathus tenuis* has been found (Fig. 6) in the upper part, now referred to as the Leangen Member, of the Solvik Formation and in equivalent strata in the uppermost Sælabonn Formation. It has also been recorded from the very lowermost part of the overlying Rytteråker Formation (Aldridge & Mohamed 1982). This narrow stratigraphic interval was formerly referred to Etage $6c_{\beta}$ (top part of Solvik and Sælabonn Formations) and 7a (lower Rytteråker Formation) and was regarded as Idwian to earliest Fronian (=early to middle Aeronian) in age by Worsley (1982, fig. 3) but mid-Aeronian by Baarli & Johnson (1988).

The occurrence of *Pranognathus tenuis* in Jämtland is in good agreement with a correlation proposed long ago (Nestor 1972), namely that the lower boundary of the Berge Limestone correlates with the base of the Rytteråker Formation. However, this correlation is substantially different from that recently advocated by Baarli *et al.* (2003), who by referring the base of the Berge Limestone to the early–middle Rhuddanian (Fig. 3), showed the bases of the Berge Limestone and the Rytteråker Formation as representing quite different stratigraphic levels. In clarifying the relations between these units, it is also of interest to note that Bergström *et al.* (1998b) identified a prominent ash bed in the lower part of the Eke Formation, which overlies the Rytteråker Formation, as the widespread Telychian Osmundsberg K-bentonite, which is located just above the top of the Berge Limestone in Jämtland. This evidence, combined with the conodont and graptolite biostratigraphy, suggests that the Berge Limestone and the Rytteråker Formation have a closely similar stratigraphic range. Both these units were formerly referred to as the *Pentamerus* Limestone, and correlated with similarly named strata in Wales and Estonia (Nestor 1972).

Depending on geographic region, the Rytteråker Formation is underlain by the Solvik Formation or by the Sælabonn Formation. In some areas, the middle-upper parts of the latter units contain the Aeronian *Proatrypa-Cryptothyrella* brachiopod fauna (Worsley 1982), which is similar to that reported from the Ede Quartzite (Boucot & Johnson 1964; G. Baarli pers. comm. 2003). Based on brachiopods from Norderön (Fig. 1), Boucot and Johnson (1964) assigned an Early Silurian age to the Ede Quartzite. Later, after consideration of the revised position of the global Ordovician–Silurian boundary (Holland & Bassett 1989), Karis (1998, p. 34) referred the same fauna to the latest Ordovician. The Aeronian age suggested by the Ede brachiopods is in agreement with the age interpretations by Thorslund (1943, 1960). It is also consistent with the new conodont data, which indicate that the fauna from the Upper Ede Quartzite is early–middle Aeronian in age and that this unit is coeval with the upper part of the Sælabonn and Solvik formations in Norway (Figs. 2, 6).

Based on brachiopods, Baarli *et al.* (2003, fig. 3) recognised a marked diachroneity between the base of the Rytteråker Formation in the Ringerike area and the Oslo region but, if real, this age difference is not obvious in the conodont record. In this connection it is also of interest to note that Aldridge & Mohamed (1982) recorded a primitive form of *Distomodus staurognathoides*, the index of the late Aeronian–early Telychian *D. staurognathoides* Zone, just below the top of the Solvik Formation in the Asker area in the Oslo region. This suggests that most, if not all locally, of the Rytteråker Formation is referable to this conodont zone (cf. Nakrem 1986). Although *D. staurognathoides* has not yet been found in Jämtland, this record may be taken as an indication that most of the Berge Limestone will prove to represent this conodont zone (Fig. 6).

The Sælabonn and Solvik formations consist mainly of shale and subordinate, more or less nodular limestone and sandstone, and their dominant lithology differs markedly from that of the Ede Quartzite. However locally, as in Ringerike, the Sælabonn Formation is dominated by sandstone. In the Mjøsa district in the northern part of the Oslo region, the Sælabonn includes a basal part referred to as the Helgøya Quartzite Member (Skjeseth 1963) that exhibits a much closer lithological similarity to the Ede Quartzite. This 6–10 m-thick unit, which rests unconformably on the conspicuously karsted top surface of the much older (Middle Ordovician) Mjøsa Limestone (Bergström *et al.* 1998a), comprises quartzitic sandstones and shales with fossiliferous calcareous interbeds, especially in the upper part of the member. Interestingly, a sample from a sandy limestone bed in the middle of the unit at the top of steep wall in the well-known Stein Quarry at Furuberget about 4 km north of Hamar produced a collection of about 125 black, small but relatively well-preserved, conodont elements (Bergström, unpubl.). This collection includes, among others, *Distomodus kentuckyensis*, *Ozarkodina oldhamensis*, and *Icriodella* sp. but lacks *Pranognathus tenuis*. It has a typical Silurian aspect and is likely to be coeval with, or possibly slightly older than, that of the Upper Ede Quartzite. Presumably based on undocumented fossils, Skjeseth (1963) referred the Helgøya Quartzite Member to Etage 6c, that is, early Aeronian in current standard terminology, which is in general agreement with the conodont evidence. He, as well as other authors, placed the Ordovician–Silurian boundary at the unconformity at the base of the unit. However, further studies are needed to clarify if this is correct, or if the lowermost part of the Helgøya Quartzite Member (below the conodont sample), which at Furuberget is 2–3 m thick and consists of thin-bedded limestones and dark shales, may be of Ordovician age and correspond to the Lower Ede Quartzite. At any rate, there is little doubt that the conodont fauna from the Helgøya Quartzite Member represents the same shallow-water biofacies as the fauna from the Ede Quartzite.

7.3. Estonia

Rhuddanian and Aeronian strata have been extensively studied in both outcrops and numerous drill-cores in Estonia, where they are classified into the Juuruan, Raikkülan, and lowermost Adaveran stages and several formations. The Juuruan Stage is characterised by micritic limestones, marl- and mudstones, and various types of grainstones (Nestor & Einasto 1997). The Raikkülan Stage includes micritic and bioclastic limestones, marl- and mudstones, and dolomites. Low-diversity graptolite faunas show that this stage ranges from the late Rhuddanian to the middle Aeronian. The overlying, richly fossiliferous, Adaveran Stage is of late Aeronian and Telychian age and contains a diverse shelly fossil fauna.

Samples from the Juuruan Stage have only produced a low-diversity conodont fauna that includes *Distomodus kentuckyensis*, *Ozarkodina* cf. *oldhamensis* and coniform taxa such as *Dapsilodus* and *Decoriconus* (Männik & Viira 1990). Conodonts from the lower to middle part of the overlying Raikkülan Stage are more diverse taxonomically and include, among others, *Icriognathus cornutus*, *Kockelella? manitoulinensis*, *Ozarkodina excavata puskuensis*, *Oz.* aff. *oldhamensis*, *Oz.* aff. *hassi* Rexroad and *Pranognathus tenuis* (Fig. 6). The interval in the lower–middle part of the Raikkülan Stage containing this fauna is distinguished as the *Pranognathus tenuis* Zone (Viira & Männik 1997). This zone is overlain by

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the *Distomodus staurognathoides* Zone of late Aeronian to early Telychian age.

Based on the close similarity in the conodonts faunas, it is obvious that the Ede–lowermost Berge succession corresponds to the Estonian *P. tenuis* Zone (Fig. 6). Also, it appears that the Estonian and Swedish conodont faunas represent the same conodont biofacies. Nestor & Einasto (1997, fig. 140) interpreted the depositional environment of the Raikkülan Stage in northern Estonia as representing lagoon–shoal–open shelf, hence quite shallow water, which is consistent with the preferred environment of this biofacies elsewhere.

7.4. United Kingdom

Modern regional work on Silurian conodonts in the United Kingdom was initiated by Aldridge (1972), who monographed Llandovery and Lower Wenlock collections from Wales and the Welsh Borderland. Although he used single-element taxonomy, Aldridge's detailed conodont data can easily be transferred into multi-element taxonomy and his work remains a basic reference on British Llandovery conodonts. No Rhuddanian conodonts were recovered by him and conodonts of that age remain very poorly known in Great Britain (cf. Aldridge, 1985), but Aldridge (1972) obtained taxonomically diverse Aeronian and Telychian faunas (Fig. 7). Of special interest in this study is the species association of his *Icriodella discreta-I. deflecta* Assemblage Zone that includes, apart from the zone indices, *Distomodus kentuckyensis*, *Kockelella? manitoulinensis* (=*Spathognathodus abruptus* Aldridge, 1972, cf. Männik, 1992b), *Ozarkodina hassi*, *O. oldhamensis*, *Pranognathus siluricus*, and *Pranognathus tenuis* (Fig. 6). This zone, which has the same upper limit (FAD of *Distomodus staurognathoides*) as the Estonian *P. tenuis* Zone but may extend lower stratigraphically, is of early–middle Aeronian (B$_2$–C$_1$) age. The recently recorded *Pranognathus tenuis* fauna from the middle Aeronian Skomer Volcanic Group in Wales (Aldridge 2002) is of very similar composition and age. The close resemblance between these British species associations and that of the Ede–lowermost Berge interval in Jämtland confirms the early–middle Aeronian age of the latter succession (Fig. 6).

Some of the earliest work on Llandovery conodont palaeoecology was carried out in Great Britain (Aldridge 1972, 1976, 1985; Aldridge *et al.* 1981; Aldridge & Jeppsson 1984). The *I. discreta–I. deflecta* Zone faunas originated from the Venusbank Formation and Pentamerus Beds, two units considered to have been deposited in relatively shallow water (depth zones of the *Eocoelia* to *Stricklandia* communities; cf. Cocks *et al.* 2003, fig. 5). Based on collections from sites with depth-diagnostic brachiopods, Aldridge (1972, 1976, 1985) and Aldridge & Jeppsson (1984) concluded that *Icriodella* and *Pranognathus*, in association with *Distomodus*, are particularly well represented in strata representing high-energy, near-shore environments and decrease in frequency in rocks deposited in deeper water. The preferred near-shore, shallow-water habitat of *Pranognathus tenuis* and its associated taxa is also shown by their Skomer Volcanic Group occurrence that represents a relatively high-energy, near-shore environment characterised by the very shallow-water *Lingula–Eocœlia* brachiopod communities (Aldridge 2002) which represent the Benthic Assemblages 1–2 of Boucot (1975). This ecological preference seems to fit well with the conditions in Baltoscandia.

7.5. North America

Llandovery sediments are very widely distributed in North America with particularly important outcrop areas in the Great Lakes region in north–central U.S.A. and southern Canada, New York State, Québec, and the Great Basin in Nevada and Utah (Berry & Boucot 1970). Conodonts of this age have been described from many areas during the last few decades, the most important of which for the present study are the Cincinnati region in Ohio, Kentucky, and Indiana, the Great Lakes region (especially northern Michigan-Illinois-Wisconsin, and Manitoulin Island and adjacent part of Ontario and New York State), and the Anticosti Island in Québec (Fig. 8).

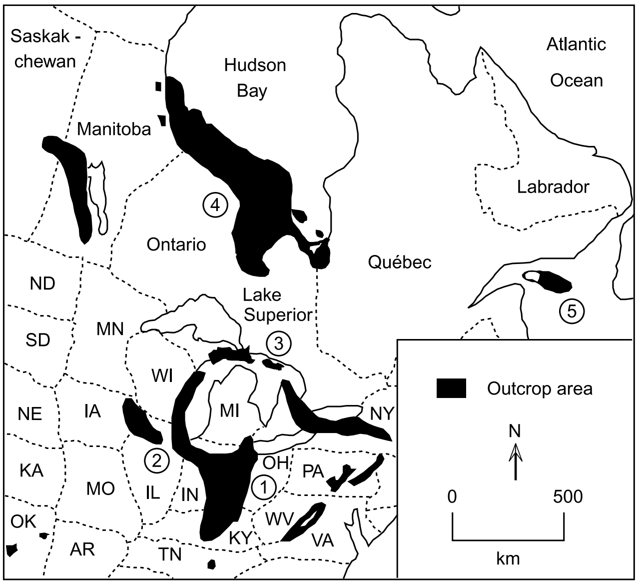

Figure 8 Sketch-map of the North American Midcontinent and adjacent regions showing major Llandovery outcrop areas (black). Figures in circles denote: (1) The Cincinnati region in Ohio, Kentucky, and Indiana; (2) Northern Illinois, Iowa and eastern Wisconsin; (3) Manitoulin Island and Bruce Peninsula in southern Ontario; (4) Hudson Bay lowlands; and (5) Anticosti Island, Québec.

Important data on the Llandovery conodont biostratigraphy in the Cincinnati region have been published by, amongst others, Rexroad (1967), Cooper (1975), and Kleffner (1994, 2000). A unit of particular interest for the present study is the Brassfield Limestone that has been referred to the *Distomodus kentuckyensis* Zone (Cooper 1975). The Brassfield Limestone includes relatively pure grainstones and packstones with occasional chert nodules and it contains quite a diverse macrofossil fauna. It appears to represent an offshore, open-marine shelf environment with moderate water depth (Benthic Assemblages 2–3 of Boucot, 1975; cf. Johnson 1987, fig. 6). Important taxa in its conodont fauna include, apart from the zone index, *Icridella deflecta*, *I. discreta*, *Ozarkodina hassi*, *Oz. oldhamensis* and a variety of coniform conodonts. The Brassfield Limestone has generally been referred to the Aeronian *Distomodus kentuckyensis* Zone (see, e.g., Cooper 1975). The Aeronian age is consistent with the fact that Grahn (1985) and Grahn & Bergström (1985) recorded in the lower and middle Brassfield Limestone several chitinozoan species characteristic of the latest Rhuddanian to Aeronian *C. electa* and *A. convexa* chitinozoan zones (Nestor 1990) in Estonia. Hence, one might expect that equivalents of the Aeronian Ede–lowermost Berge stratigraphic interval in Jämtland would be present in the Brassfield Limestone. This has recently been confirmed by the discovery of *Pranognathus tenuis* in the upper Brassfield Limestone in western Ohio (M. Kleffner, pers. comm. 2005). It should be noted that the major part of the Brassfield Limestone was referred to the Rhuddanian in a recent summary paper by Brett *et al.* (1998, fig. 29), who apparently overlooked the chitinozoan and conodont studies referred to above. The chitinozoan and conodont dating of the Brassfield Limestone is also supported by the fact that the index of the

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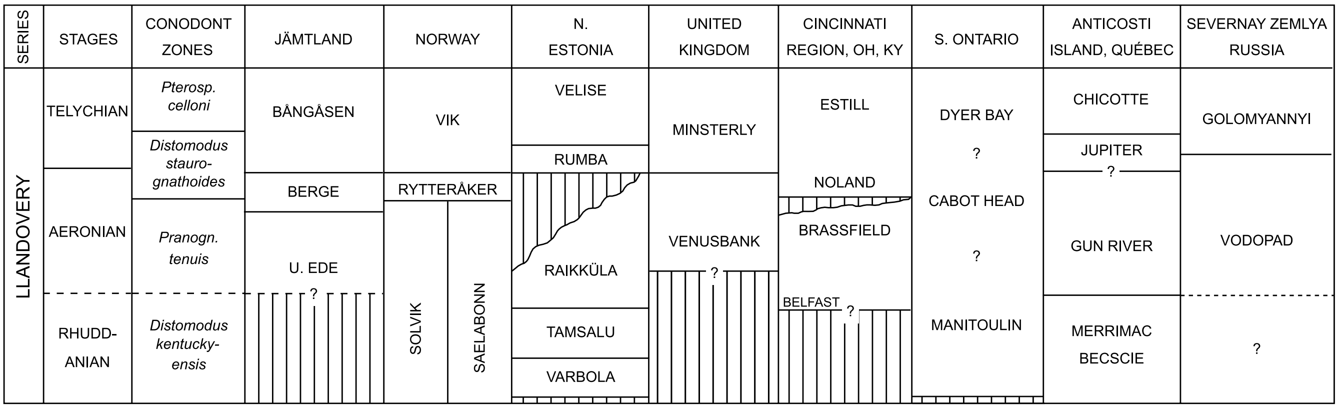

Figure 9 Correlation of the Ede–Berge interval with coeval strata in some regions of northern Europe and North America.

late Aeronian *Distomodus staurognathoides* Zone appears in the very topmost part of the Brassfield Limestone, the Lee Creek Member (Nicoll & Rexroad 1969; Cooper 1975).

The Brassfield conodont species assemblage differs from the Jämtland fauna in having much more abundant representation of species of *Distomodus*, *Ozarkodina*, *Oulodus*, and *Rexroadus* but fewer specimens of *Icriodella* and *Pranognathus*. This difference is attributed to the fact that most of the Brassfield fauna represents a biofacies that is characteristic of deeper water than the habitat of the Ede–lowermost Berge conodonts.

Very shallow-water, proximal shelf carbonates of early and middle Llandovery age are widely distributed in the Great Lakes region in southern Ontario, Michigan, Illinois, Ohio, and adjacent areas (Berry & Boucot 1970). Conodonts are generally sparse in these strata, especially in the lowermost part of the Silurian succession. The conodont fauna of the Manitoulin Dolomite, which is the oldest formation in large parts of the region, and of somewhat younger strata, is best known from northern Michigan, and from Manitoulin Island and Bruce Peninsula in southern Ontario (Pollock *et al.* 1970; Barnes *et al.* 1978; Barnes & Bolton 1988). It includes, amongst others, *Distomodus kentuckyensis*, *Icriodella discreta*, *I. deflecta*, *Kockelella? manitoulinensis*, *Ozarkodina hassi*, and *Oz. oldhamensis*. Although *Pranognathus tenuis* has not been recorded, this fauna, which is referred to the *Distomodus kentuckyensis* Zone, is evidently equivalent to, or slightly older than, that of the Ede-lowermost Berge interval (Fig. 9). From presumed intertidal strata of the Aeronian lower Severn River Formation in the Hudson Bay region, LeFèvre *et al.* (1976) reported similar sparse faunas including *Kockelella? manitoulinensis*.

Pranognathus tenuis, associated with *D. kentuckyensis* and species of *Icriodella*, *Oulodus*, and *Ozarkodina*, was recently recorded from the Hickory Corners Member of the Reynales Limestone in the Niagara region of New York State (Kleffner 2004). This occurrence is of special importance in that it provides a biostratigraphic age of the basal portion of the well-known Clinton Group, which is the lowest part of the Niagaran Series in the classical standard classification of the North American Lower Silurian.

The approximately 565 m-thick, dominantly calcareous, richly fossiliferous succession on Anticosti Island in Québec (Fig. 8) is in several respects one of the finest, if not the finest, Llandovery successions in the world. It contains diverse and excellently preserved conodonts of Rhuddanian through Telychian age (Uyeno & Barnes 1983; Fåhraeus & Barnes 1981; Zhang & Barnes 2002a, b, c). The Rhuddanian–Aeronian conodont faunas, which represent an outer shelf biofacies, are dominated by taxa of *Distomodus*, *Ozarkodina*, *Oulodus*, and *Rexroadus* along with numerically abundant coniform conodonts. Although present, platform genera such as *Icriodella* are less well represented. This makes it difficult to recognise precisely widely used standard zones based on platform taxa, and this may be the principal reason why a new Rhuddanian–Aeronian conodont zone succession was recently proposed by Zhang & Barnes (2002a; Fig. 7). Unfortunately, some of their zonal indices are not as widely distributed outside Anticosti Island as would be desirable in a standard zone succession, and this makes it difficult to apply these zones to successions representing a different biofacies, such as that in Jämtland. However, the stratigraphic interval in the Anticosti Island succession corresponding broadly to that studied in Jämtland can be recognised (Fig. 9). The distinctive *Distomodus staurognathoides*, which elsewhere appears in the upper Aeronian, ranges through the upper Gun River Formation (Zhang & Barnes, 2002a, fig. 8). Its first appearance is just below the disappearance of *Icriodella deflecta*, *Kockelella? manitoulinensis*, and *Ozarkodina oldhamensis*. However, because the Pa elements referred to *D. staurognathoides* from the upper Gun River are all fragmentary and the associated Pb elements are atypical of this species, the presence of this zone index in the Gun River needs confirmation, especially as pentamerid brachiopods from the topmost part of the formation were considered to be of mid-Aeronian (B_3) age by Jin & Copper (2000) and Dewing (1999) dated the diverse strophomenid brachiopod fauna from the lowermost part of the overlying Jupiter Formation as late Aeronian in age. Although *Icriodella discreta* is restricted to the Becscie Formation, which underlies the Gun River Formation, and *Pranognathus tenuis* has not been reported from Anticosti Island, it appears likely that the Jämtland formations studied are equivalent to the middle part of the Gun River Formation. This is consistent with the fact that graptolites from the lower Gun River Formation suggest an age no younger than the early Aeronian *triangulatus*–*pectinatus* Zone and *Monograptus sedgwickii* and other graptolites of the late Aronian *sedgwickii* Zone are present in the lower part of the Jupiter Formation. In the zone terminology of Zhang & Barnes (2002a), the Jämtland interval would correspond to the lower part of the *Ozarkodina clavula* Zone.

7.6. Other regions

The early–middle Llandovery conodont faunas from Greenland described by Armstrong (1990) contain *Kockelella? manitoulinensis* but lack *Icriodella* and *Pranognathus* and are not closely similar to the Jämtland faunas. They apparently represent another biofacies, which resembles that of the coeval Anticosti Island faunas. Closer similarity to the Jämtland faunas is shown by the conodont collections from the lower–

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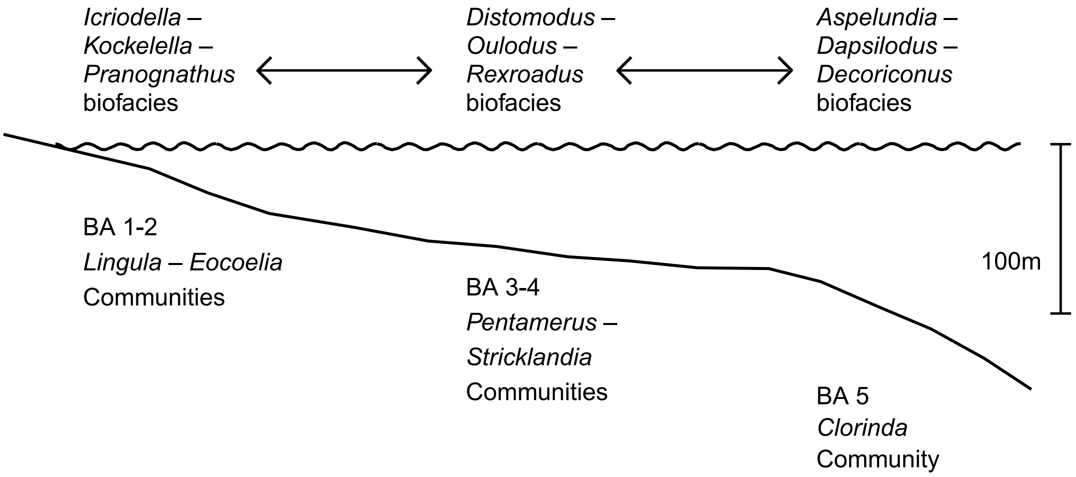

Figure 10 Diagrammatic illustration of the relations between Aeronian conodont biofacies, inferred water depth, benthic assemblages (BA) of Boucot (1975), and brachiopod communities (Ziegler *et al.* 1968). Note that the Ede–lowermost Berge succession contains conodonts representing the *Icriodella–Kockelella–Pranognathus* biofacies that is characteristic of shoreface–very shallow subtidal environments.

middle part of the dolomitic Vodopad Formation of Severnaya Zemlya in the Arctic Ocean of Russia reported on by Männik (1983). This fauna includes, amongst others, *Icridella* cf. *deflecta*, *Distomodus* cf. *kentuckyensis*, *Ozarkodina oldhamensis*, *Pranognathus tenuis*, and *Rexroadus kentuckyensis* and is clearly referable to the *Pranognathus tenuis* Zone. This is in agreement with Männik's (1983) interpretation that this part of the Vodopad Formation is of early–middle Aeronian age. Many other Aeronian conodont faunas from other parts of the world were discussed briefly by Männik (1992b) but most of these do not closely resemble that of the Ede–lowermost Berge interval.

8. Conodont biofacies and water depth

The described Llandovery conodont faunas, as well as the associated macrofossil faunas, show far less provincial differentiation than the Late Ordovician faunas (Bergström 1990), and many conodont genera, and also conodont species, have a pandemic distribution. A possible reason for this apparent palaeobiogeographic uniformity may be that by Early Silurian time, most regions, from which conodonts have been described, were located in the tropical zone (Fig. 1b). However, even if showing a general similarity between different regions, the Llandovery conodont faunas exhibit some differences that are interpreted as reflecting the fact that many taxa had a preferred habitat, especially in terms of water depth and factors related to water depth. Hence, different depositional environments had their characteristic associations of species. Following the practice of Sweet (1988) in the Ordovician, such apparently ecologically controlled species associations are referred to as different conodont biofacies. Also in the Aeronian, it is possible to distinguish a shoreface-offshore faunal differentiation into a succession of apparently depth-related, intergrading biofacies (Fig. 10).

We recognise the shallowest of these as the *Icriodella–Kockelella–Pranognathus* biofacies. This is characteristic of proximal shelf-lagoonal, shoreface to tidal flat to proximal shelf, low to high energy, environments such as that of the Ede Quartzite and lower–middle Raikkülan Stage in Estonia (Viira & Männik 1997). In a pioneer study of the paleoecology of Aeronian conodonts in the Oslo region, Idris (1984, pp. 183–187) recognised a biofacies of this type (but without *Pranognathus tenuis*) in strata characteristic of the very shallow-water *Lingula-Eocœlia* communities (Benthic Assemblage 1–2 of Boucot, 1975). Unfortunately, the collections made by Idris (1984) did not cover the 'shallowest' part of the upper Sælabonn Formation that yields *P. tenuis* (Aldridge & Mohamed 1982) and is the likely equivalent to the Upper Ede–lowermost Berge sequence.

Because recent cross-bedding like that in the Ede Quartzite generally occurs at a water depth of <15 m (Brett *et al.* 1993), this provides an approximate depth figure of the habitat of this biofacies in Jämtland. In the Aeronian of Great Britain, Aldridge (1976, 2002) recorded a species association, including *Ozarkodina hassi* and *Pranognathus tenuis*, which is most common in strata of the shallowest-water *Lingula*/*?Rostricellula* brachiopod community. From tidal flat to shallow shelf strata (Benthic Assemblage 1–2 of Boucot, 1975) of the Aeronian Byron and Hendricks Dolostones in eastern Wisconsin, Harris *et al.* (1998) reported sparse conodonts, including *Icriodella deflecta*, *I. discreta*, *Kockelella? manitoulinensis*, and *Ozarkodina oldhamensis*, hence a closely similar species association as that described by Pollock *et al.* (1970) from coeval and lithologically similar stratigraphical units in Michigan and southern Ontario. These records are in good agreement with the inferred very shallow-water environment of deposition of the Upper Ede Quartzite and lowermost Berge Limestone, and this distinctive conodont biofacies is evidently widely distributed geographically.

Deeper water on the open shelf was characterised by the *Distomodus–Oulodus–Rexroadus* biofacies (Fig. 10). Idris (1984, figs. 4–5) illustrated graphically the relative frequency of the various species of this biofacies in Aeronian strata in the Oslo region. Most of his collections represent the *Stricklandia* community (Benthic Assemblage 3–4 of Boucot, 1975). Coeval faunas of this biofacies are known in North America from, for instance, the Brassfield Limestone (Cooper 1975) of the Cincinnati region and the Gun River Formation of Anticosti Island (Zhang & Barnes 2002a). In a detailed palaeoecological analysis, Zhang & Barnes (2002c) recognised three conodont communities in the early Aeronian part of the Gun River Formation that consists of mudstones, wackestones, and lenticular grainstones deposited on a low-energy shelf ramp at an estimated depth of 50–80 m (Zhang & Barnes 2002b). The same biofacies is present in the underlying Becscie Formation, which is interpreted to have been deposited at a water depth of 30–70 m (Zhang & Barnes 2002b). Hence, the typical depth range of this biofacies may be from approximately 20–80 m.

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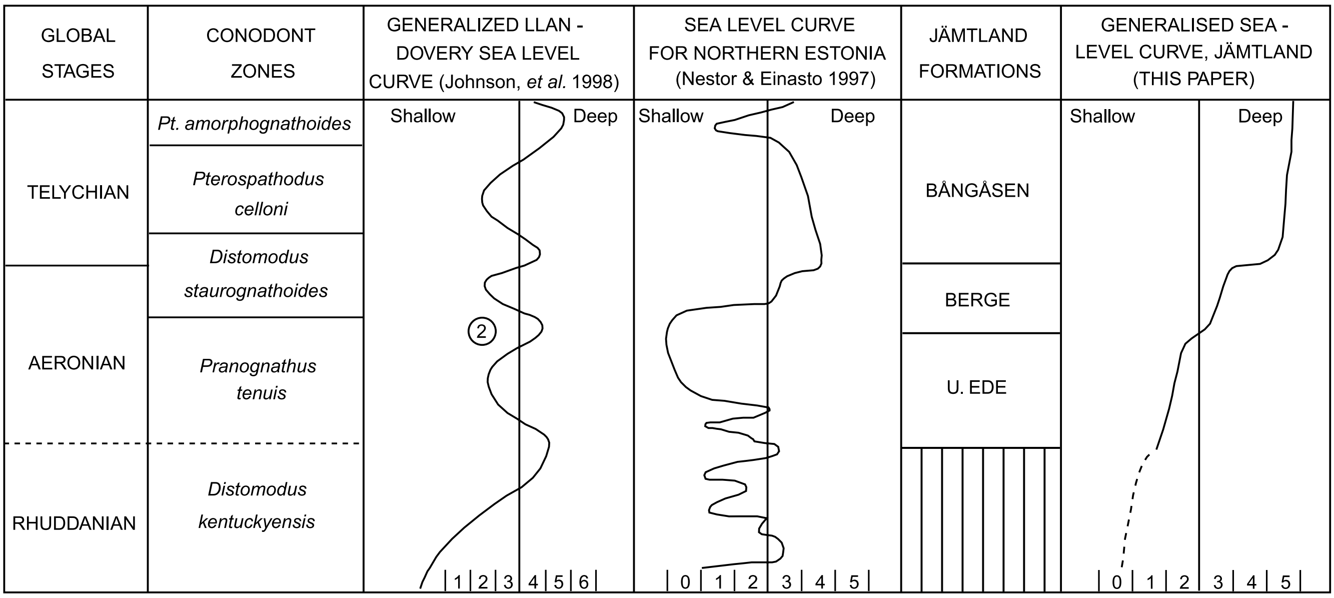

Figure 11 Comparison between a generalised global sea level curve for the Llandovery (after Johnson *et al.* 1998, fig. 2), a sea level curve proposed for northern Estonia (redrawn from Nestor & Einasto 1997, fig. 140), and the position of the stratigraphic interval of the Upper Ede Quartzite–lowermost Berge Limestone advocated in the present study. Note that the transgressive Jämtland succession appears to correspond to a shallowing episode prior to the well-documented late Aeronian sea level rise (Second Silurian transgression of Johnson *et al.* 1998). Figures at the bottom of the sea level curve columns refer to Benthic Assemblages of Boucot (1975) (global column) and corresponding depositional environments (Estonian column).

Still deeper water, in some cases more than 100 m deep, on the outer shelf and upper slope, was characteristically inhabited by a species association here referred to as the *Aspelundia–Dapsilodus–Decoriconus* biofacies (Fig. 10). This biofacieshas been documented previously from northern Greenland (Armstrong 1990) and is also represented by faunas from, for instance, the Motala Formation of south-central Sweden (Bergström & Bergström 1996), and the late Aeronian–Telychian Jupiter Formation of Anticosti Island (Zhang & Barnes 2002b). The latter has been interpreted to have been deposited at a water depth of 80–115 m. The Aeronian conodont faunas present in still deeper environments (lower slope and basin) remain too poorly known to permit any conclusions regarding possible biofacies differentiation.

The deposition of the Upper Ede–lowermost Berge succession clearly represents a transgressive event following a major regression and a substantial period of non-deposition. An obvious way to attempt to clarify whether or not this is a local event is to make a comparison with the many sea level curves that have been published in recent years. Several such curves (Zhang & Barnes 2002b, figs 13, 14) show a eustatic sea level peak in the latest Rhuddanian followed by a lowering of the sea level in the early–middle Aeronian, and a new sea level rise in the latest Aeronian–early Telychian. Such a sea-level curve has been published for northern Estonia (see, e.g., Nestor & Einasto 1997, fig. 140; Fig. 11). However, as clearly shown by the many sea level curves in this interval recently presented by Landing & Johnson (2003), there is a great deal of variation in different regions of Europe and North America and, for instance, Zhang & Barnes (2002b, fig. 10) show a rather flat sea level curve for the Aeronian of Anticosti Island. The latter may possibly be due to the fact that the Aeronian water depth in this region was too great to permit the establishment of a clear sedimentary record of relatively modest sea level changes.

It is currently difficult to establish a reliable global sea level curve, although that of Johnson *et al.* (1998; Fig. 11) is probably based on most observations from many parts of the world. Several authors, including Johnson *et al.* (1998), have recognised a sea level high-stand in the late Aeronian (second Silurian high-stand of Johnson *et al.* 1998; Fig. 11) and this may well be reflected in the deposition of a part of the Berge Limestone. The early–middle Aeronian low-stand, which may be associated with the first Silurian glaciation in South America (Grahn & Caputo 1992; Caputo 1998), does not fit well with the Upper Ede transgressive deposition in Jämtland (Fig. 11). Although similar transgressive events are known from coeval sequences in the North American Midcontinent (e.g., the Brassfield Limestone) and in Great Britain (e.g., the Venusbank Formation and the Pentamerus Limestone), perhaps the more likely interpretation is that the Ede–Berge transgression is not primarily related to any global eustatic sea level rise but to a tectonically-induced deepening of the Jämtland foreland basin in early–middle Aeronian time. This is consistent with the fact that the Early Silurian was the beginning of a tectonically active period in the orogenic history of the Caledonides, which was referred to as an early phase of the Scandian tectonism by Bassett (1985). In this connection it is also appropriate to draw attention to the suggestion by Baarli (1990) that the formation of the Ordovician–Silurian stratigraphic gaps in some of the western and northern parts of the Oslo region was due to the advancement of a peripheral bulge in front of the Caledonian nappes that led to the emergence of local or regional areas in the Early Llandovery. The progressive movement of such a peripheral bulge onto the craton is thought to have been followed by subsidence and foreland basin development. Although such a scenario cannot be ruled out as an explanation of the formation of the apparently significant gap between the Lower and Upper Ede Quartzite and the subsequent basin development, further work is needed to clarify the possible relations between such an advancing bulge and the Early Silurian depositional pattern in Jämtland.

9. Summary of conclusions

The principal results of the present study may be summarised as follows:

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1. Based on lithology and the presence of an unconformity about 1/3 from the base of the unit, the shallow-water Ede Quartzite can be subdivided into two parts, the Lower and Upper Ede Quartzite.
2. The somewhat unexpected find of moderately common and biostratigraphically diagnostic conodonts in calcareous interbeds in the Upper Ede Quartzite makes it possible to refer this unit, as well as the lowermost part of the overlying Berge Limestone, to the *Pranognathus tenuis* Zone, which is of early–middle Aeronian age. This clarifies for the first time the previously controversial age of the Upper Ede Quartzite.
3. The apparently identical composition of the conodont faunas from the Upper Ede Quartzite and lowermost Berge Limestone, as well as the gradational contact between these units, indicate that they are of approximately the same age. Corals from the Berge Limestone indicate a Raikkülan–Adaveran (late Aeronian) age (Mõtus 2004). This is consistent with the fact that graptolites from the basal part of the Bångåsen Shale that rests on the Berge Limestone are of earliest Telychian age.
4. In the absence of calcareous interbeds suitable for conodont extraction, the Lower Ede Quartzite remains undated by conodonts, and no other fossils have been found in the unit. However, lithological and sedimentological indications, and the fact that a Late (but not latest) Ordovician *Hirnantia* shelly fauna is present in the uppermost part of the subjacent Kogsta Siltstone, suggest that the Lower Ede Quartzite is of latest Ordovician age and that the unconformable contact between the Lower and Upper Ede Quartzite represents the Ordovician/Silurian boundary. The stratigraphic gap associated with the unconformity in the Ede Quartzite corresponds to at least the Rhuddanian Stage.
5. A regional comparison shows that the Ede–lowermost Berge conodont faunas exhibit close similarity to coeval faunas from Estonia, Norway, United Kingdom, North America, and Russia. These conodont faunas are referred to the *Pranognathus tenuis* Zone that occupies a lower–middle Aeronian (B_1–C_1) interval below the *D. staurognathoides* Zone and above a slightly restricted *D. kentuckyensis* Zone. As far as the present authors are aware, *P. tenuis* has not yet been recorded from the very lowermost Aeronian (B_1), but pending further study, they tentatively place the base of the *P. tenuis* Zone at the base of the Aeronian (cf. Aldridge & Schönlaub 1989, p. 278). This interval correlates broadly with the *triangulatus*–lower *sedgwickii* Zones in the graptolite zone succession (see, e.g., Worsley 1989, fig. 77).
6. Based on inferred water depths in the habitats of early–middle Aeronian conodont faunas in Europe and North America, three intergrading conodont biofacies are recognised. These represent the shoreface–tidal–lagoonal, open shelf, and outer shelf-upper slope environments, respectively. Each of these is characterised by the co-occurrence of several typical conodont taxa, and these biofacies can be recognised both in northern Europe and North America. Amongst these, the Jämtland conodonts represent the one characteristic of the shallowest water. This biofacies differentiation makes it difficult to use the same conodont zone scheme everywhere and, for correlation purposes, two of more zone schemes may be required to properly date successions, or part of successions, representing different biofacies.
7. The Ede–lowermost Berge transgressive event does not fit well into most published global sea level curves and is interpreted to represent a local deepening of the Jämtland foreland basin associated with active tectonism in the Caledonides and the possible migration of a peripheral bulge.
8. Although the studied Jämtland succession differs in some respects in lithologic development from that in the Oslo region of Norway, the overall similarity in faunas and stratigraphic sequence suggests that these sequences might have been deposited in the same elongate trough or foreland basin along the Caledonide orogen.

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Figure 12 SEM micrographs of selected conodont taxa from the Ede Quartzite. (a–b) *Icriodella discreta* Pollock, Rexroad & Nicoll, 1970: (a) OSU 52135, upper view of Pa element, × 80, sample J-02-13; (b) OSU 52136, lateral view of Pa element, × 75, sample J-02-13. (c–e) *Pranognathus siluricus* (Pollock, Rexroad & Nicoll, 1970): (c) OSU 52137, lateral view of Pa element, × 66, sample J-O2-14; (d) upper view of same specimen as in (c), × 90; (e) OSU 52138, lateral view of Pa element, × 75, sample J-02-14. (f) *Ozarkodina oldhamensis* (Rexroad, 1967), OSU 52139, lateral view of fragmentary Pa element, × 100, sample J-02-25. (g–h) *Icriognathus cornutus* Männik, 1992: (g) OSU 52140, lateral view of Pa element, × 65, sample J-02-20; (h) OSU 51141 upper view of Pa element, × 65, sample J-02-20. (i–j) *Kockelella? manitoulinensis* (Pollock, Rexroad & Nicoll, 1970): (i) OSU 52142, upper view of Pa element, × 85, sample J-01-64; (j) same specimen as (i), lateral view, × 85. (k) *Rexroadus* sp., OSU 52143, inner-lateral view of P element, × 85, sample J-02-15. (l), *Distomodus kentuckyensis* Branson & Branson, 1947, OSU 52144, posterior view of S element, × 75, sample J-02-20. (m) *Panderodus recurvatus* (Rhodes, 1953), OSU 52145, lateral view, × 100. (n–o) *Panderodus unicostatus* (Branson & Mehl, 1933): (n) OSU 51146, lateral view of broad element, × 70, sample 92B26-1; (o) OSU 52147, lateral view of elongate element, × 70, sample 92B26-1. (p-aa) *Pranognathus tenuis* (Aldridge, 1972): (p) OSU 52148, lateral view of Sb element, × 130, sample J-02-20; (q) OSU 52149, upper view of Pc element, × 115, sample J-02-20; (r) OSU 52150, lateral view of M(?) element, × 130, sample 92B26-1; (s) OSU 52151, lateral view of Sc element, × 130, sample 92B26-1; (t) OSU 52152, lateral view of Sa element, × 130, sample J-02-14; (u) OSU 52153, antero-lateral view of Pc element, × 130, sample 92B26-1; (v) OSU 52154, anterior view of Pb element, × 100, sample J-02-14; (x) OSU 52155, anterior view of Pb element, × 80, sample J-02-15; (y) OSU 52156, upper view of Pa element, × 130, sample J-02-15; (z) OSU 51157, lower view of Pa element, × 85, sample J-02-14; (aa) OSU 52158, upper view of Pa element, × 85, sample J-02-15.

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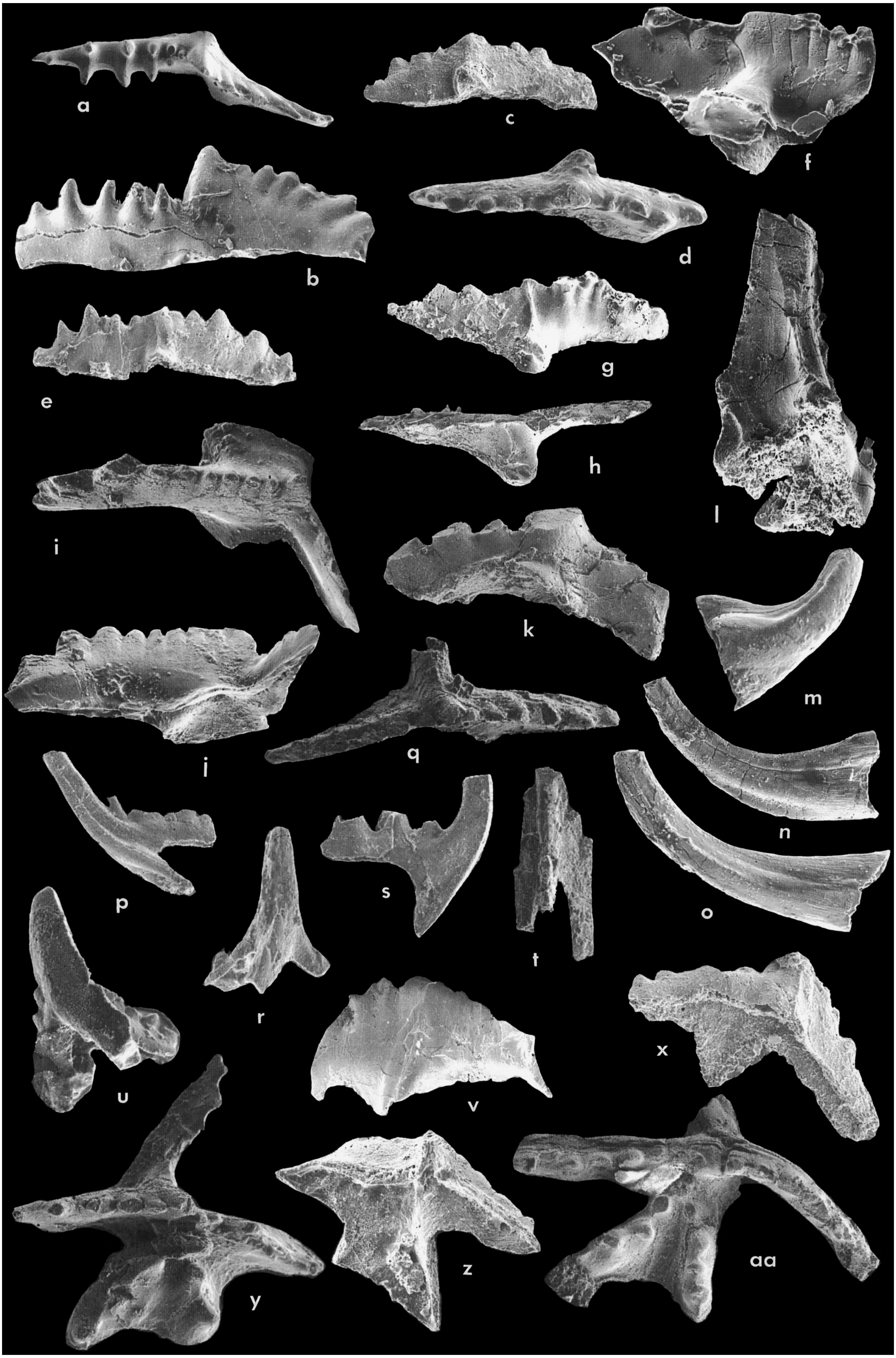

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11. Appendix 1. Comments on the taxonomy and distribution of conodont taxa

In comparison with many described Silurian conodont collections, the present one, which includes slightly less than 850 identified specimens, is not large. Furthermore, it is dominated by elements of the ubiquitous genus *Panderodus* (42·2%), the state of preservation of most specimens is less than perfect, and the taxa present have been adequately described in the recent literature. In view of this, extensive taxonomic comments and detailed morphologic descriptions are not warranted and we restrict ourselves to brief comments on the identified taxa. The collection is currently housed in the Micropaleontological Collections, Department of Geological Sciences, The Ohio State University, Columbus, Ohio and illustrated specimens are filed under OSU numbers in the type collection of the Orton Geological Museum at the same university.

Distomodus kentuckyensis Branson & Branson, 1947 (Fig. 12l). Several samples contain sparse, robust but commonly broken, specimens that appear to represent S elements of *D. kentuckyensis*. Although their poor preservation makes positive identification difficult, they compare well with specimens referred to this species by Bergström & Bergström (1996). There are many records of *D. kentuckyensis* in North America (for references, see Zhang & Barnes 2002a) but the species has been reported also from United Kingdom (Aldridge 1972), Norway (Aldridge & Mohamed 1982), Estonia (Männik 1992b), and Russia (Melnikov 1999). The species has a substantial stratigraphic range, being recorded through most of the Rhuddanian and Aeronian.

Icriodella discreta Pollock, Rexroad & Nicoll, 1970 (Fig. 12a–b). Several *Icriodella* elements are present in one sample (Table 1), but elements of this genus are otherwise absent in most of our samples. With three exceptions, they are incomplete and represent broken processes. The only complete specimens recovered agree in most important respects with *I. discreta*. Although having a denticulation similar to that in *I. deflecta* Aldridge, 1972, the Pa elements lack the strong lateral flange characteristic of this very closely related species (Aldridge 1972, plate 1:4–7). Also, the angle between the blade and the platform is 25–30 degrees in the Ede specimens rather than 40–45 degrees as in typical specimens of *I. deflecta*. Hence, our Pa specimens could in some respects be considered morphologically intermediate between *I. discreta* and *I. deflecta*. Pending further study of these taxa, the oldest name, that is, *I. discreta* is used for the Ede specimens, including the incomplete ones. The present specimens appear to be closely similar to those from the Solvik and Sælabonn Formations of Norway identified as *I. discreta* by Aldridge & Mohamed (1982). Other records of *Icriodella discreta* are from Aeronian strata in Sweden (Bergström & Bergström 1996), the United Kingdom (Aldridge 1972), and several regions in North America (Zhang & Barnes 2002a). It is part of a plexus of Early Silurian platform conodonts that is generally referred to *Icriodella*, the type species of which is *I. superba* Rhodes, 1953 from the Upper Ordovician of the United Kingdom. Although the Pa elements of the Silurian taxa are similar in important respects to those of the latter species, the M and S elements differ appreciably from those in the Ordovician species, and it has not yet been possible to demonstrate that they represent the same evolutionary lineage. If the latter is true, and the Silurian species are not homeomorphs of the Ordovician type species of the genus, *Icriodella* is one of the very few compound conodonts that survived the Late Ordovician extinction event (Barnes & Bergström 1988).

Icriognathus cornutus Männik, 1992a (Fig. 12g–h). Several of our samples contain rare Pa elements that are quite similar to the Pa element of *I. cornutus* except they lack lateral denticles at the end of the anterior process. In his original description of this species, Männik (1992a) indicated that in his collections, specimens without lateral denticles are about as common as the typical representatives of the species. In view of this, we identify these elements with *I. cornutus* but note that they are also reminiscent of the Pa element of *Pranognathus siluricus* (Pollock, Rexroad & Nicoll, 1970). Indeed, we are not convinced that the slight difference in denticulation, which seems variable, justifies separation of *Icriognathus* from *Pranognathus*. Further studies are clearly needed to clarify the relations between these taxa.

Kockelella? manitoulinensis (Pollock, Rexroad & Nicoll, 1970) (Fig. 12i–j). This highly characteristic species is represented by only two Pa specimens in our collections but these elements agree in all details with published descriptions of the species. This species has a wide distribution in Rhuddanian–Aeronian strata and has previously been recorded from several regions of North America (Zhang & Barnes 2002a), Greenland (Armstrong 1990), Estonia (Männik 1992b), and the United Kingdom (Aldridge 1972; referred to as *Spathognathodus abruptus*). As recently noted by Zhang & Barnes (2002a), this species is not a typical representative of *Kockelella*, and we follow these authors in referring it to the latter genus with question.

Ozarkodina oldhamensis (Rexroad, 1967) (Fig. 12e). A few Pa elements in our collections are closely similar to this morphologically somewhat variable species. It has previously been recorded from several regions of North America (Zhang & Barnes 2002a), the United Kingdom (Aldridge 1985), Sweden (as '*Bryantodina*' n. sp. in Bergström 1971), Norway (Aldridge & Mohamed 1982), Russia (Melnikov 1999), and conditionally in Estonia (Männik 1992b).

Panderodus spp. There are many elements of *Panderodus* in our Ede collections but most are broken and also otherwise not well preserved. Such specimens are difficult to identify at the species level. The most common form is a gently curved cone (Fig. 12n,o) that appears to be conspecific with *P. unicostatus* (Branson & Mehl, 1933). Relatively rare, more robust, and more sharply recurved elements (Fig. 12m) are similar to those identified as *P. recurvatus* (Rhodes, 1953) by Zhang & Barnes (2002a, fig. 16) and they are herein referred to that species.

Pranognathus siluricus (Pollock, Rexroad & Nicoll, 1970) (Fig. 12c–e). Slightly more than 100 specimens in our collection compare favourably with published description and illustrations of this species, which has been recorded previously from Aeronian strata in North America (Pollock, Rexroad & Nicoll 1970), Russia (Melnikov 1999), and the United Kingdom (Aldridge 1972; as *Amorphognathus siluricus*).

Pranognathus tenuis (Aldridge, 1972) (Fig. 12p-aa). About 40% of the specimens in our collection are referred to this highly distinctive species. All elements included in the apparatus by Männik & Aldridge (1989, fig. 5) are present. The characteristic Pa and Pb elements are in several morphologic features similar to corresponding elements of the Ordovician genus *Amorphognathus*, but because the other elements of the *Amorphognathus* apparatus differ markedly from those in *Pranognathus tenuis*, which is the type species of *Pranognathus*, there may be no close relationship between these genera. Being a geographically widespread and stratigraphically restricted species, *P. tenuis* appears to be very useful biostratigraphically and it is here recognised as an index of the *P. tenuis* Zone. It has previously been recorded from the United Kingdom (Aldridge 1972, 2002), Norway (Aldridge & Mohamed 1982), Russia (Männik & Aldridge 1989; Melnikov 1999), and North America (Kleffner 2004).

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Rexroadus sp. (Fig. 12k). A few poorly preserved specimens in four of our samples may represent this widespread genus. They are too incomplete for specific identification.

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