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An Early to Middle Ordovician succession of conodont faunas at Mäekalda, northern Estonia

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Abstract – The Mäekalda section presents a *c.* 12 m thick succession of mainly limestones, dolomites and siltstones of late Tremadoc to late Llanvirn age, exposed on the eastern outskirts of Tallinn, northern Estonia. The condensed sequence is rich in well-preserved conodont elements that provide the basis for detailed biozonation. In the Baltoscandian zonation, beds from the upper Varangu *Paltodus deltifer* Zone up to the lower Aseri *Eoplacognathus foliaceus* Subzone have been identified. In all, the conodont faunas exhibit a close resemblance to Swedish faunas. Many intervals can also be compared with coeval strata in western Russia. The presence at some levels of representatives of Laurentian conodont lineages provides an unusual opportunity for correlating Baltoscandian sequences with sequences in North America, especially in the lower Arenig part of the succession. The middle Volkhov (upper middle Arenig) *Paroistodus originalis* Zone at Mäekalda is remarkably complete bearing in mind the highly condensed nature of the section as a whole. The details of this zone can be correlated with the equivalent intervals in Swedish sections. In the upper Volkhov–lower Kunda beds there is a considerable stratigraphic gap in the section, but the upper Kunda has provided an excellent series of successive populations of *Eoplacognathus*, indicating that in this part the section is virtually complete.

1. Introduction

The Mäekalda section in northern Estonia provides a link between outcrops in Scandinavia and in Russia. Preliminary examination of conodont faunas from Mäekalda also demonstrated the presence of Laurentian elements which are not normally present in Scandinavia. Thus, the Mäekalda section and other northern Estonian sections could provide important links to wider correlations.

The first lithological description of the Mäekalda section was written by Silvi Mägi for an excursion guide book (Mägi, 1990). In connection with the Third Baltic Stratigraphic Conference in Tallinn, 1996, Viive Viira added information on the conodont ranges (in Einasto, Puura & Viira, 1996), and some additional conodont samples from the Päite Member were also collected at that time. The 51 samples available to us had been processed (dissolved and picked over) at the Institute of Geology in Tallinn. Eighteen of these samples, representing the entire *Paroistodus originalis* Zone, together with two samples just below and two just above this zone formed the basis for a report at Lund University, written by Jenny Wickström and supervised by Anita Löfgren (Wickström, 1999). Our paper was written by Viive Viira and Anita Löfgren in cooperation, with contributions from the other two authors, and with most of the planning, element counting and photographic work carried out by V. V. and A. L. during V. V.'s visit to Lund in March 2000.

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2. Geological setting and previous studies

The Mäekalda section is situated in the western part of the continuous outcrop belt of Ordovician rocks that extends from west to east through northern Estonia and the St Petersburg region (Fig. 1). Tremadoc, Arenig and Llanvirn sediments crop out in the Baltic–Ladoga Klint (escarpment) and consist of highly fossiliferous shallow-water deposits. The upper Tremadoc Varangu Formation consists of silty clay and sands with glauconitic grains. The lowermost Arenig Leetse Formation is characterized by poorly lithified glauconitic siltstones and sands (Klooga and Joa members) and calcareous glauconitic sandstones (Mäeküla Member). From the Päite Member (Toila Formation) upwards, the Volkhov Stage is represented by various partly dolomitized glauconitic limestones. The Kunda Stage is characterized by oolitic, clayey and glauconitic limestones. The Kunda beds decrease in thickness towards northwestern Estonia, mostly owing to decreasing thickness in the lower part. This Lower Ordovician sedimentary sequence characterizes the shallowest part of the epicontinental palaeobasin where changes in sea-level took place repeatedly. Sea-level lowstands are commonly represented by numerous discontinuity surfaces which in some cases are

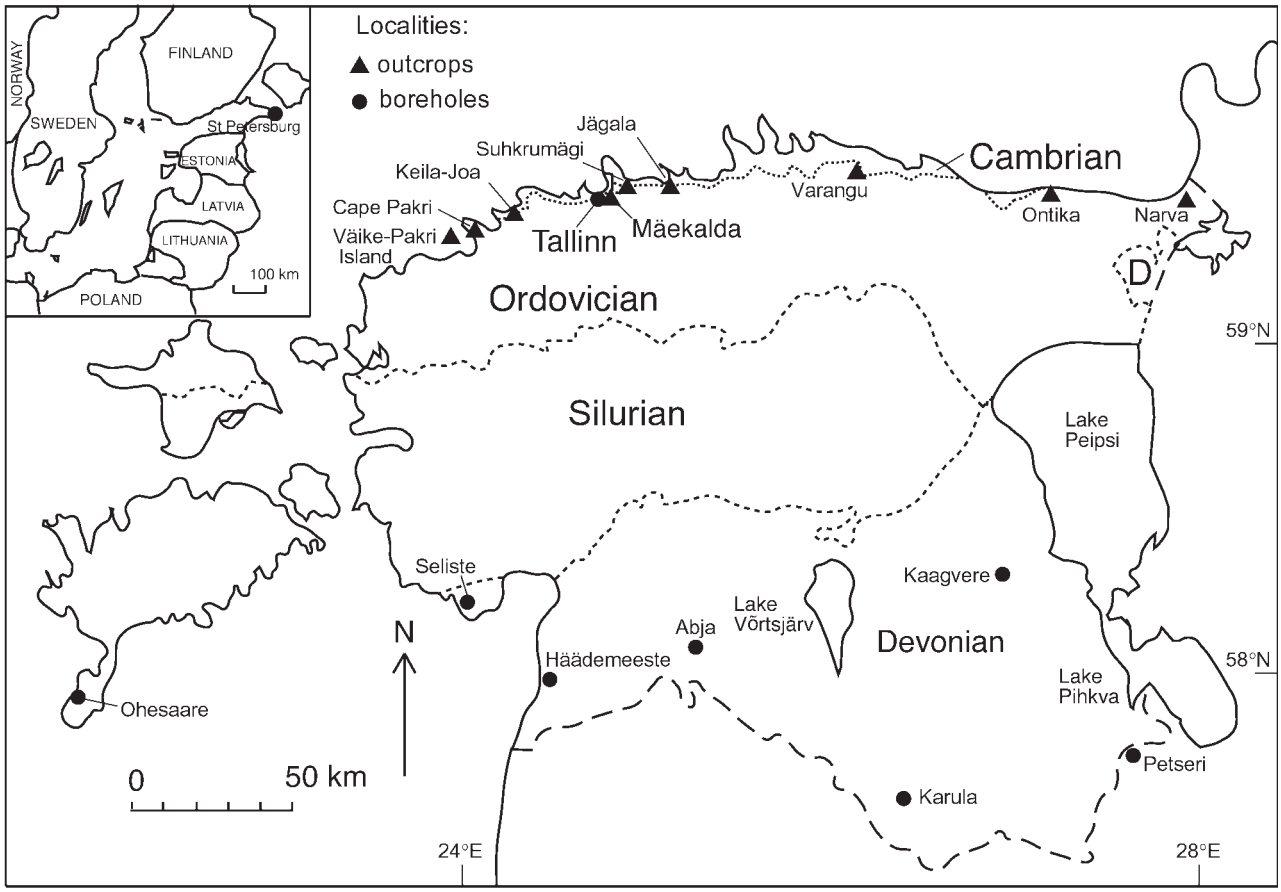

Figure 1. Map of Estonia, showing extent of Palaeozoic rocks and location of the Mäekalda section.

regarded as boundaries between stratigraphic units (Orviku, 1960*b*). The facies differentiation is pronounced, with the lithofacies and biofacies arranged in belts. The biogeographic and facies differences within the Ordovician Palaeobasin of Baltoscandia are expressed in the confacies belt concept (Jaanusson, 1976), Estonia being divided between the North Estonian and the Central Baltoscandian Confacies belts.

Good exposures have made it possible to study the Ordovician sediments of the northern Estonian Klint (escarpment) since the nineteenth century. K. Orviku carried out comprehensive lithostratigraphic investigations in the carbonate-rich Arenig–Llanvirn part of the sequence (Orviku, 1940, 1960*a*,*b*), while the terrigenous part of the lower Arenig has been subjected to lithological and biostratigraphic studies by S. Mägi (Mägi, 1970, 1984; Kleesment & Mägi, 1975; Mägi & Viira, 1976; Mägi, Viira & Aru, 1989). Drilling performed by the Estonian Geological Survey in central and southern Estonia enabled R. Männil to present a comprehensive picture of the evolution of the Ordovician Baltic Basin (Männil, 1966). In recent years, results of new investigations have been published, in particular with reference to the Volkhov Stage in Estonia (Meidla, Ainsaar & Tinn, 1998; Dronov *et al.* 2000).

The Mäekalda sequence, extending from the Lower Cambrian Tiskre Formation to the Middle Ordovician Uhaku Stage, has been exposed in a road cutting since 1986. The Cambrian part of the section was described by Mens *et al.* (1989). About 500 m eastwards along the road, the upper Pakerort Stage to the Aseri Stage is exposed (the part investigated here), while the Lasnamägi and Uhaku stages are exposed in a road cutting further to the east. A detailed description of the lithologies in the Mäekalda section with a list of fossil occurrences extracted from other localities in the Tallinn area has been presented by Mägi (1990). The first fossil data obtained directly from the Mäekalda section were reported during the Third Baltic Stratigraphic Conference (Einasto, Puura & Viira, 1996).

3. Methods and repository

The conodont samples, weighing from *c.* 300 to *c.* 1000 g, were dissolved in (unbuffered) dilute acetic acid and the residue washed and decanted repeatedly to remove the clay fraction. The remaining fraction was picked over for conodonts. The elements in the samples were then sorted and their numbers counted for the semi-quantitative plots in Figures 4 and 7. All conodont elements are thermally unaltered with a

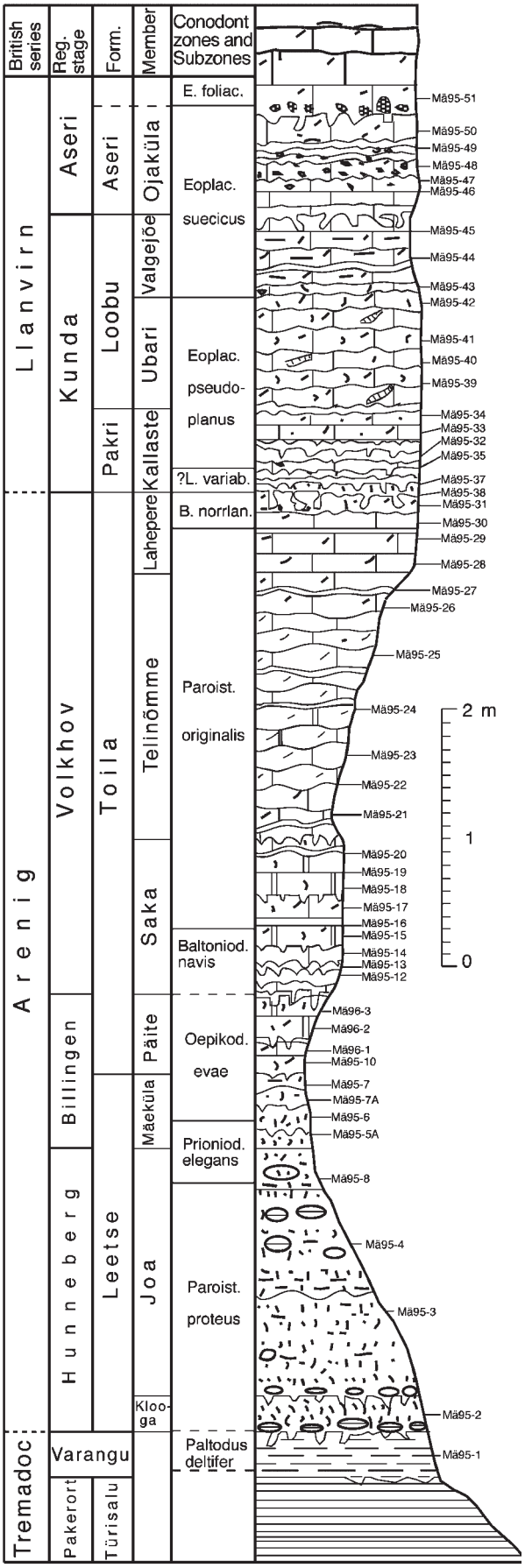

Figure 2. The section at Mäekalda (after Mägi, 1990), showing sampled levels and stratigraphic subdivisions. Sample Mä95-32 has been lost.

CAI (conodont colour alteration index) well below 1.5. For an explanation of CAI, see Epstein, Epstein & Harris (1977). The illustrated elements are deposited in the type collection at the Institute of Geology, Technical University of Tallinn.

4. Conodont biozonation

A dark brown kerogenous argillite belonging to the Türisalu Formation of the Tremadocian Pakerort Regional Stage is overlain by *c.* 0.25 m of the argillitic Varangu Formation from which sample Mä95-1 derives (Figs 2, 3). *Paroistodus numarcuatus* (Lindström, 1955) was reported from this interval by Einasto, Puura & Viira (1996), and in our investigation *Drepanoistodus* cf. *D. nowlani* Ji & Barnes, 1994 was encountered there. The interval probably represents the *Paltodus deltifer* Zone. Part of this Tremadocian unit appears to have been eroded, since *P. numarcuatus* and some other conodonts of Tremadoc age appear as redeposited elements in the Joa Member above. The basal Arenig is, however, represented by *c.* 0.2 m of the glauconitic, silty Klooga Member of the Leetse Formation, and sample Mä95-2 from this unit belongs to the *Paroistodus proteus* Zone (cf. Fig. 4), as does all but the uppermost part of the overlying glauconitic sand of the Joa Member, represented by samples Mä95-3 and Mä95-4. In addition to the zonal index fossil, the fauna in these three samples includes *D.* cf. *nowlani, Drepanodus arcuatus* Pander, 1856, *Tripodus* sp. A, *Paltodus deltifer deltifer* (Lindström, 1955), *P. d. pristinus* (Viira, 1970), *Juanognathus*? sp. A, *Cordylodus* spp., *Scandodus? subarcuatus* (Furnish, 1938) and, in the uppermost part, *Paltodus subaequalis* Pander, 1856 and *Oelandodus elongatus* (Lindström, 1955). Some of these taxa do not occur naturally together, so redeposition from eroded Tremadocian strata nearby must be inferred.

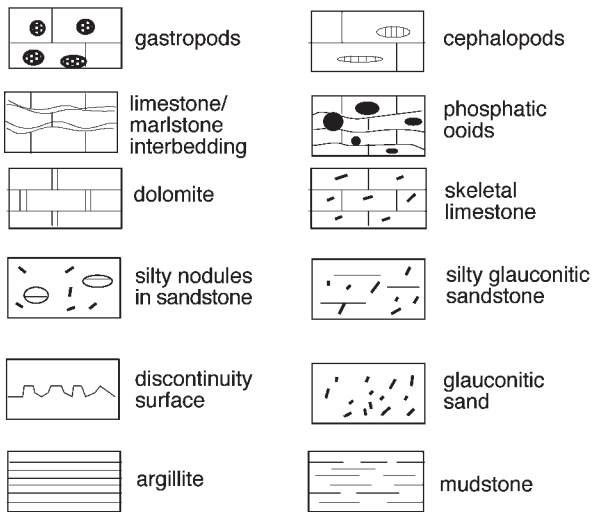

Figure 3. Legend to symbols used in the stratigraphic column of the Mäekalda section in Figure 2.

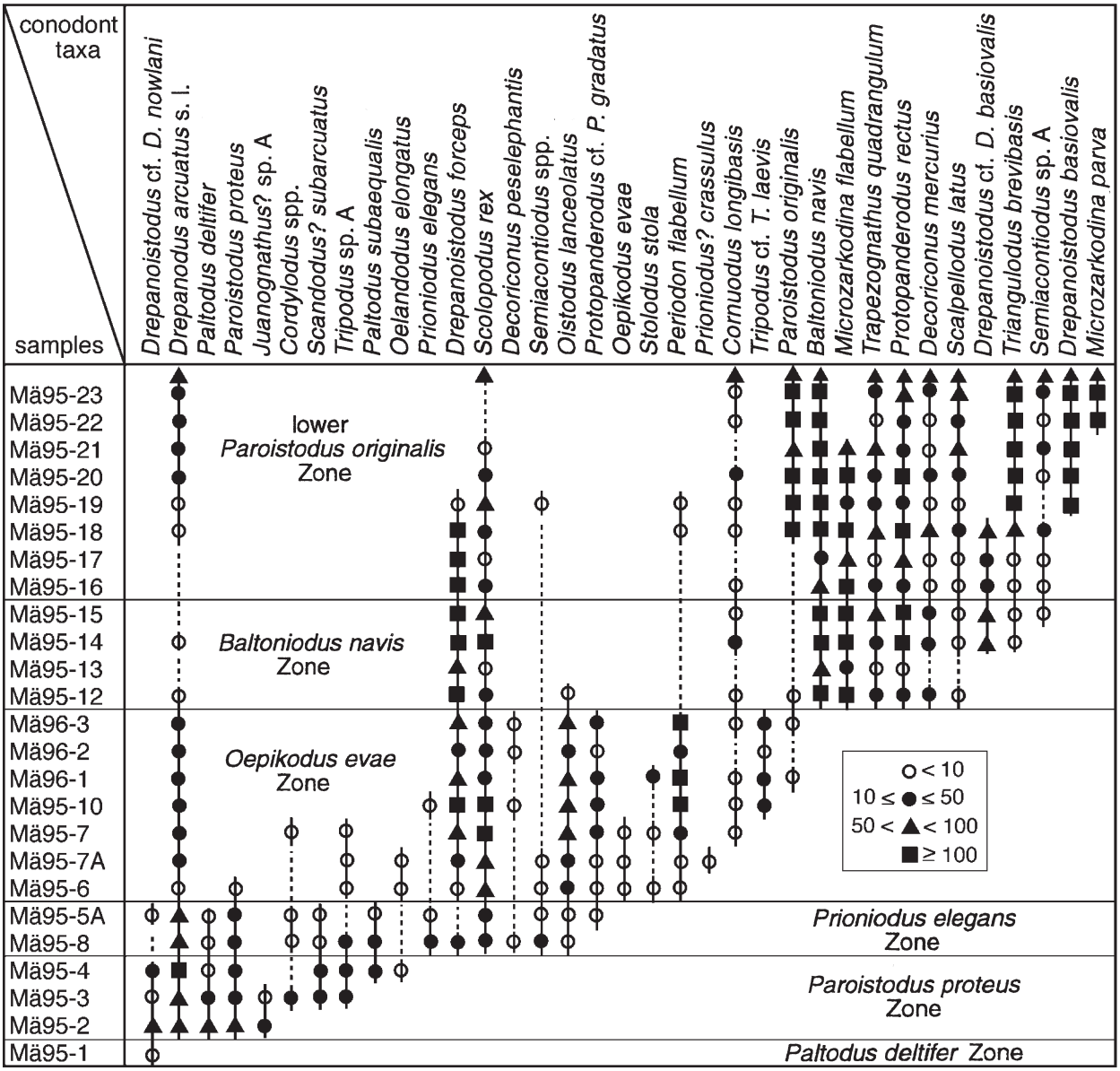

Figure 4. Semi-quantitative representation of the distribution of conodont taxa in samples from Mäekalda ranging from the *P. deltifer* Zone to the middle part of the *P. originalis* Zone. Some rare taxa have been left out but are commented on in the text.

Illustrations of conodonts from this zone can be found in Figure 5.

It has not been possible to estimate which part of the *P. proteus* Zone is represented in the basal part of the Leetse Formation. Since the Tremadoc–Arenig boundary lies in the upper part of this zone (cf. Maletz, Löfgren & Bergström, 1996) it has tentatively been taken to lie at the local base of the *P. proteus* Zone at Mäekalda.

The uppermost, silty, transitional *c.* 0.20 m of the Joa Member, represented by sample Mä95-8 and probably also the basal glauconitic sandstone of the overlying Mäeküla Member, represented by sample Mä95-5A, belongs to the *Prioniodus elegans* Zone. The first specimens of *Prioniodus elegans* Pander, 1856, *Drepanoistodus forceps* (Lindström, 1955), *Scolopodus rex* Lindström, 1955 and *Oistodus lanceolatus* Pander, 1856 were also found at the base of this interval in addition to a few specimens of *Decoriconus peselephantis* (Lindström, 1955), *Protopanderodus* cf. *P. gradatus* Serpagli, 1974, *Acodus deltatus* Lindström, 1955 and *Semiacontiodus* sp. Several taxa that had been found in the lower Joa were also retrieved here, some of which, notably *Cordylodus* spp., must be regarded as redeposited.

The glauconitic packstone of the middle and upper parts of the Mäeküla Member (samples Mä95-6, -7A and -7) as well as the grey, dolomitized packstone of the Päite Member (basal member of the Toila Formation: samples Mä95-10, Mä96-1, -2 and -3) belong to the *Oepikodus evae* Zone *sensu lato*, in all measuring *c.* 1 m. Thus, in addition to the lower part of the zone, containing the zonal index (samples Mä95-6, -7A and -7), there is also an upper part,

which lacks the zonal index species, up to the base of the *Baltoniodus triangularis–B. navis* zones. Recently, Bagnoli & Stouge (1997) distinguished the upper part of the *O. evae* Zone *sensu lato* as the *Trapezognathus diprion* Zone and the *Microzarkodina* sp. A Zone, but since neither of these zonal indicators were present in our samples, we could not adopt this improved biozonation. The most numerous taxa in the interval are *D. forceps*, *S. rex*, *O. lanceolatus* and, particularly in the upper part, *Periodon flabellum* (Lindström, 1955). Less common are *Acodus deltatus, Scandodus furnishi* Lindström, 1955, *Toxotodus gabriellae* Löfgren, 1998 and others listed in Figure 4. The occurrence of a few elements of *Cordylodus* spp. indicates that redeposition was a factor even in the middle part of this zone but appears to be of considerably less importance than in the lower parts of the section.

From sample Mä95-12, the lowermost available sample from the dolomitic and glauconitic Saka Member, onwards, there is a considerable change in the conodont fauna. There are numerous discontinuity surfaces at the base of the Saka Member, indicating breaks and condensation in the succession, and we have not been able to identify the *Baltoniodus triangularis* Zone in the section. Sample Mä95-12 is instead regarded as the lowermost sample of the *Baltoniodus navis* Zone, which we consider ends with sample Mä95-15, thus being less than 1 m thick in the section. Six species have their lowermost occurrence in sample Mä95-12: the zonal index species, *B. navis* (Lindström, 1955), together with *Microzarkodina flabellum* (Lindström, 1955), *Trapezognathus quadrangulum* (Lindström, 1955), *Protopanderodus rectus* (Lindström, 1955), *Decoriconus mercurius* (Löfgren, 1998) and *Scalpellodus latus* (van Wamel, 1974). The most abundant taxa are *D. forceps*, *B. navis*, *M. flabellum*, *S. rex* and, in the upper part, *P. rectus*. It should be noted that throughout this zone there is a gap in the distribution of *Periodon flabellum* and that *D. arcuatus* and *P. originalis* are almost totally lacking, indicating that the sea was slightly shallower than previously. Conodont palaeoecological studies in general support of this have been presented by Pohler, Barnes & James (1987) and Pohler (1994). Reviews of sea-level changes in the interval and higher up in the succession have been published by Nielsen (1992) and Nicoll *et al.* (1992). In sample Mä95-14 *Drepanoistodus* cf. *D. basiovalis* (Sergeeva, 1963) and, sparsely, *Triangulodus brevibasis* (Sergeeva, 1963) first appear. *Semiacontiodus* sp. A occurs sparsely in sample Mä95-15. Conodonts from the *B. navis* Zone and the overlying *P. originalis* Zone are illustrated in Figure 6.

From sample Mä95-16 upwards in the section, the Saka Member has fewer discontinuities and *T. brevibasis* is represented by considerably more numerous specimens (0.1% in samples Mä 95-14 and -15, as compared with 0.6% in Mä 95-16, and between 2 and 11% higher up in the interval). The lower boundary of the *Paroistodus originalis* Zone is taken to lie just below sample Mä95-16, although the zonal denominator, *P. originalis*, is actually lacking in this part of the sequence, reappearing in sample Mä95-18. At the lower zonal boundary *Drepanoistodus forceps* is still the dominant taxon (about 40%), as in the upper *B. navis* Zone. There is a small percentage of *Periodon flabellum* in samples Mä95-18 and Mä95-19, indicating the presence of a brief transgressive interval (for conodont palaeoecology, see Pohler, 1994), which is probably equivalent to the onset of 'phase 2' in the informal subdivision of the zone outlined for Swedish sections by Löfgren (1995). In sample Mä95-19, *Drepanoistodus basiovalis* replaces *D. forceps* as the most abundant species, and at the same level *B. navis* increases from *c.* 10% to *c.* 20%. The conodont fauna in the *P. originalis* Zone at Mäekalda is diverse, and in 'phase 1' and 'phase 2' (samples Mä95-16 to Mä95-21) *Protopanderodus rectus* is particularly abundant with a maximum of 18% in sample Mä95-17. With sample Mä95-21 begins the grey, fine-grained, seminodular packstone of the Telinõmme Member of the Toila Formation.

Microzarkodina parva Lindström, 1971 replaces its predecessor, *M. flabellum*, from sample Mä95-22 upwards indicating the beginning of 'phase 3' in the informal subdivision of the *P. originalis* Zone of Löfgren (1995). In the zonation introduced by Bagnoli & Stouge (1997) this would denote the lower boundary of the *M. parva* Zone. The remaining portion of the *P. originalis* Zone (Fig. 7) represents 'phase 3' and probably also 'phase 4' in the upper part. The top of the zone is represented by the lower part of the dolomitized packstone of the Lahepere Member. As in the Gillberga section in northern Öland, the uppermost *P. originalis* Zone at Mäekalda has yielded early specimens of *Semiacontiodus cornuformis* (Sergeeva, 1963) (cf. Löfgren, 1999), and also a few specimens of *Protopanderodus calceatus* Bagnoli & Stouge, 1997. The *P. originalis* Zone measures *c.* 3 m at Mäekalda.

From sample Mä95-30, *Baltoniodus norrlandicus* (Löfgren, 1978) begins to replace *Baltoniodus navis*. This is indicative of the base of the *B. norrlandicus* Zone *sensu* Bagnoli & Stouge (1997) and Löfgren (2000*a*), which is thus situated in the middle part of the Lahepere Member. Bagnoli & Stouge (1997) subdivided the overlying interval into a lower *B. norrlandicus* Zone and an upper *Lenodus antivariabilis* Zone. *Trapezognathus quadrangulum,* which has its last occurrence in their lower zone, is present in all three samples representing the *B. norrlandicus* Zone at Mäekalda (Mä95-30, -31 and -38), the entire thickness of which is less than 0.3 m. It can thus be concluded that the uppermost Volkhov–lowermost Kundan *L. antivariabilis* Zone of Bagnoli & Stouge (1997), or the *L. antivariabilis* Subzone *sensu* Löfgren (2000*a*), is lacking in the section. Between samples Mä95-38 and Mä95-37, at the boundary between the Lahepere Member of the Toila Formation and the Kallaste

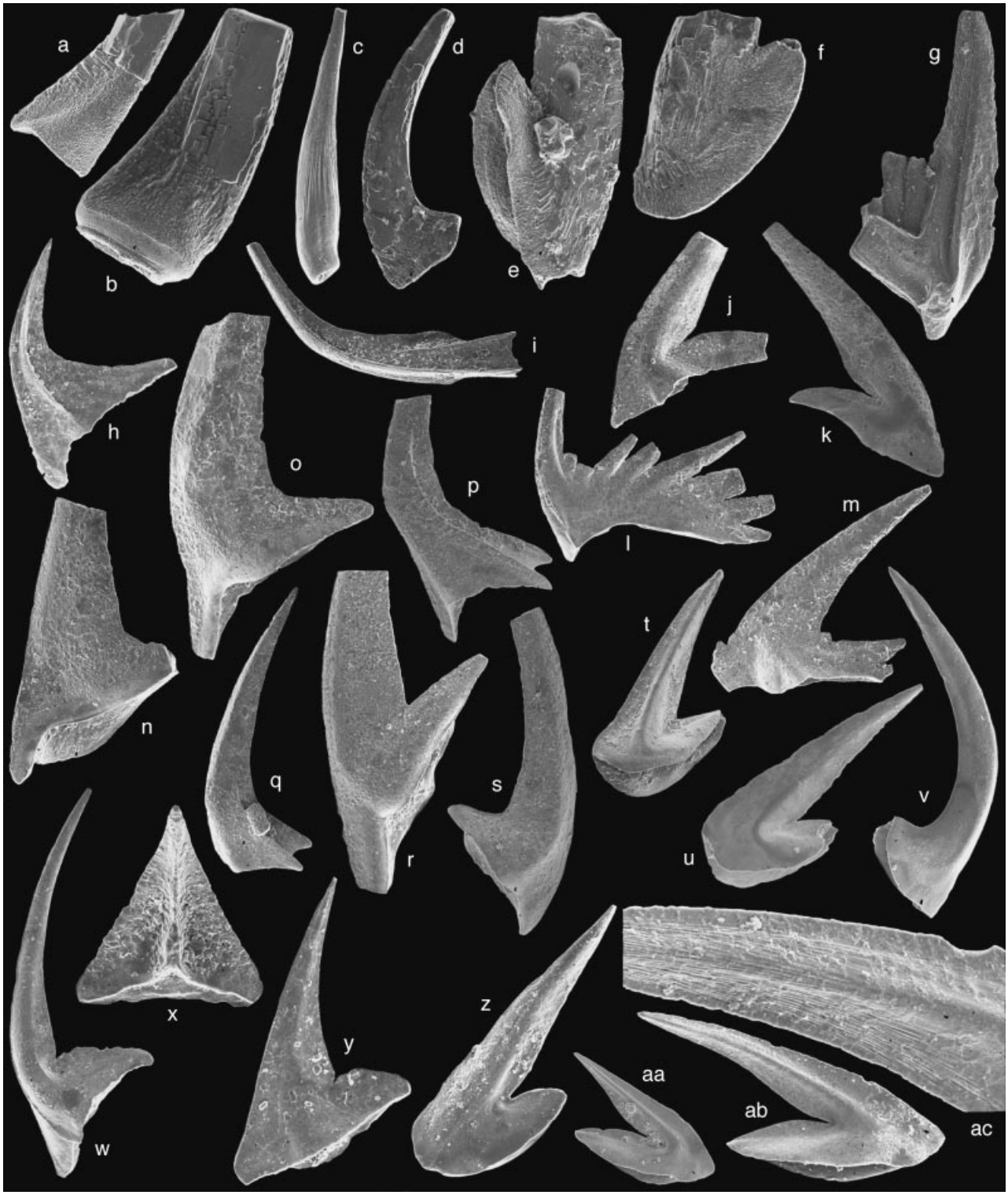

Figure 5. Conodont elements from the *P. proteus* Zone to the *B. norrlandicus* Zone. (a, b) *Juanognathus?* sp. A from sample Mä95-2, *P. proteus* Zone; note recrystallization. (a) ×85, Cn 1631. (b) ×115, Cn 1632. (c) *Toxotodus gabriellae* Löfgren from sample Mä95-10, upper *O. evae* Zone, ×85, Cn 1633. (d–f) *Drepanoistodus* cf. *D. nowlani* Ji & Barnes from sample Mä95-2, *P. proteus* Zone, ×70. (d) S? element, Cn 1652. (e) M element, inner side, Cn 1653. (f) M element, outer side, Cn 1654. (g) *Oepikodus evae* (Lindström), P element from sample Mä95-7A, *O. evae* Zone, ×90, Cn 1634. (h, i) *Stolodus stola* (Lindström) from sample Mä96-1, uppermost *O. evae* Zone. (h) P element, ×100, Cn 1635. (i) S element, ×75, Cn 1636. (j) *Prioniodus? crassulus* (Lindström), M element from sample Mä 95-7A, *O. evae* Zone, ×65, Cn 1637. (k–m) *Periodon flabellum* (Lindström) from sample Mä96-1, uppermost *O. evae* Zone. (k) M element, ×50, Cn 1638. (l) S element, ×70, Cn 1639. (m) P element, ×65, Cn 1640. (n–s) *Tripodus* cf. *T. laevis* Bradshaw from sample Mä96-1, uppermost *O. evae* Zone. (n) P? element, ×70, Cn 1641. (o) Sc? element, ×70, Cn 1642. (p) Sb? element, ×85, Cn 1643. (q) Sb? element, ×55, Cn 1644. (r) M element, ×65, Cn 1645. (s) ?P element, ×55, Cn 1646.(t) *Drepanoistodus* aff. *D. basiovalis* (Sergeeva) from sample Mä95-31, *B. norrlandicus* Zone, ×60, Cn 1680. (u)

Member of the Pakri Formation, there is thus a considerable stratigraphic gap in the succession, since the basal Pakri includes at most 0.1 m of the combined upper Volkhov–lower Kunda up to the base of the *Eoplacognathus pseudoplanus* Zone represented by sample Mä95-35. The interval in the Gillberga section in northern Öland, which corresponds to this gap, is at least 7.9 m thick (Löfgren, 2000*b*).

The conodont fauna in the *B. norrlandicus* Zone at Mäekalda is dominated by *Baltoniodus*, *D. basiovalis* and *M. parva*. *Baltoniodus norrlandicus* first totally replaces *B. navis* in the uppermost sample, Mä95-38. Other fairly common species are *Scalpellodus latus*, *Triangulodus brevibasis* and *Semiacontiodus cornuformis*. In addition to *B. navis* and *B. norrlandicus*, *M. parva*, *T. quadrangulum*, *D. mercurius*, *S. latus*, *T. brevibasis*, *P. originalis* and *Protopanderodus calceatus* last occur in the section in this zone. In younger beds of the section *Protopanderodus rectus* is succeeded by a taxon which resembles it morphologically, but their taxonomical relations are unclear.

Sample Mä95-37, from the base of the fine-grained grey limestone of the Kallaste Member is the only sample representing the upper Volkhov–lower Kunda Stage. It yielded few conodont specimens and only five taxa; the presence of *Baltoniodus medius* (Dzik, 1976) in particular and of *Scalpellodus gracilis* (Sergeeva, 1974) indicates a Kundan age. The sample has tentatively been referred to the *Lenodus variabilis* Zone.

The following sample, Mä95-35, is also rather poor in conodonts. A few elements of *Eoplacognathus pseudoplanus* (Viira, 1974) found there places it in the *E. pseudoplanus* Zone in the lower Llanvirn. In the next sample analysed, Mä95-33, the first elements of *Microzarkodina ozarkodella* Lindström, 1971 were already met with, denoting the upper *E. pseudoplanus* Zone, *M. ozarkodella* Subzone. Approximately from this level upwards in the section, the beds lack the numerous discontinuity surfaces which characterize the interval below from the middle *B. norrlandicus* Zone upwards. The upper *E. pseudoplanus* Zone thus comprises the grey, thick-bedded skeletal packstone of the upper Kallaste Member as well as the darker grey packstone of the Ubari Member of the succeeding Loobu Formation; it is represented by seven samples (Mä95-33 to Mä95-42), and is *c.* 1 m thick.

The conodont fauna of the upper *E. pseudoplanus* Zone is dominated by *Baltoniodus medius*, *Semiacontiodus cornuformis* and *Scalpellodus gracilis*. *Drepanoistodus basiovalis* occurs in all samples but is considerably less common than in the Volkhov part of the section. *Parapanderodus quietus* Bagnoli & Stouge, 1997, *Microzarkodina bella* Löfgren (2000*b*) and *Dapsilodus viruensis* (Fåhræus, 1966) each occur in only one sample. For illustrations of conodonts from the *E. pseudoplanus* Zone to the *E. foliaceus* Zone, see Figures 8 and 9.

In sample Mä95-43 from the base of the light grey, fine-grained, thick-bedded Valgejõe Member of the Loobu Formation, the first specimens of *Eoplacognathus suecicus* Bergström, 1971 were found, denoting the base of the *E. suecicus* Zone. In the succeeding sample, Mä95-44, *Panderodus sulcatus* (Fåhræus, 1966) and *Oslodus semisymmetricus* (Hamar, 1966) first appear. The zone, which is *c.* 1.5 m thick, extends to the uppermost part of the overlying fine-grained packstone of the Ojaküla Member, and the Kunda–Aseri boundary has been placed between the Valgejõe and the Ojaküla members on macrofossil evidence. This agrees well with the conodont ranges: *Panderodus sulcatus* first appears in the uppermost Kunda in northern Sweden (cf. Löfgren, 1978).

The conodont fauna in the *Eoplacognathus suecicus* Zone at Mäekalda is dominated by *Baltoniodus medius* and *Semiacontiodus cornuformis*. *Semiacontiodus davidi* Löfgren, 1999 is very rare in the interval. Of particular interest are the finds of *Sagittodontina* sp., *Complexodus* sp. and *Triangulodus* cf. *T. maocaopus.* Rare elements of *Sagittodontina* have previously been found in the Llanvirn of Baltica and southern China (Dzik, 1994) and *Complexodus* has been retrieved from the slightly younger *Eoplacognathus reclinatus* Zone in southern China (Chen & Zhang, 1984). *Triangulodus maocaopus* was first described from beds of early Llanvirn age in south-central China (Zhang, 1998*b*), and one element has been reported (as an unknown species, related to '*S.' brevibasis*) from northern Sweden (Löfgren, 1978, p. 104).

In the uppermost sample from Mäekalda, Mä95-51, two diagnostic species appear for the first time: *Baltoniodus prevariabilis* (Fåhræus, 1966) and *Eoplacognathus foliaceus* (Fåhræus, 1966). This denotes the base of the *E. foliaceus* Zone, indicating that the argillaceous, medium-bedded limestone of the Rebala Member of the Väo Formation, from which this sample derives, belongs to this zone.

Drepanoistodus cf. *D. basiovalis* (Sergeeva) from sample Mä95-14, upper *B. navis* Zone, ×80, Cn 1681. (v) *Drepanoistodus* aff. *D. suberectus* (Branson & Mehl) from sample Mä95-10, upper *O. evae* Zone, ×60, Cn 1647. (w–y) *Oistodus lanceolatus* Pander from sample Mä96-1, uppermost *O. evae* Zone. (w) P element, ×70, Cn 1648. (x) Sa element, ×110, Cn 1649. (y) Sc? element, ×110, Cn 1650. (z) *Drepanoistodus basiovalis* (Sergeeva) from sample Mä95-24, middle *P. originalis* Zone, ×90, Cn 1682. (aa–ac) *Drepanoistodus forceps* (Lindström). (aa) From sample Mä95-14, upper *B. navis* Zone, ×60, Cn 1683. (ab, ac) From sample Mä95-10, upper *O. evae* Zone, Cn 1651. (ab) ×85. (ac) Detail of cusp of specimen in (ab); note striations, ×300.

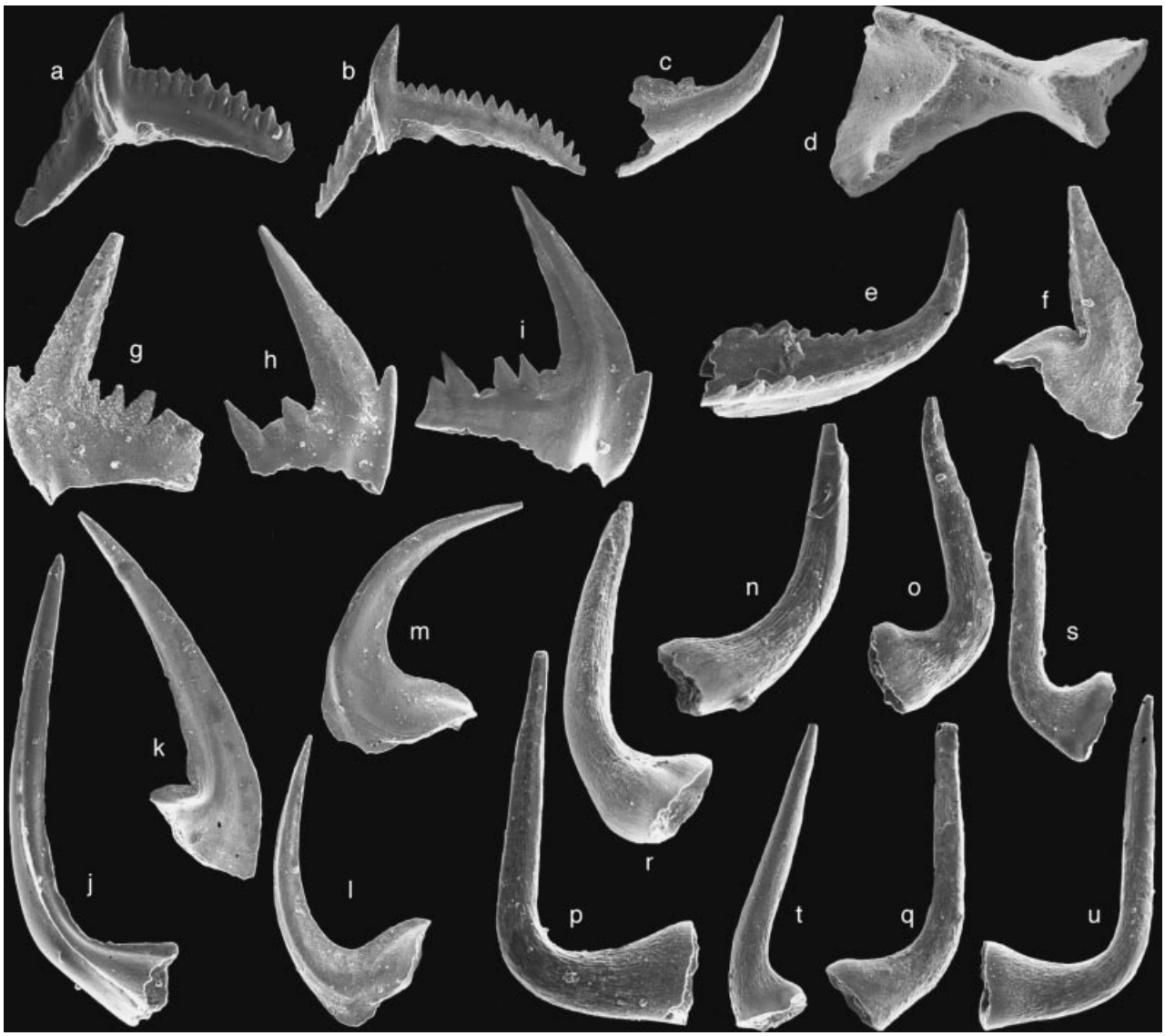

Figure 6. Conodonts from the *B. navis* and *P. originalis* zones. (a, b) *Baltoniodus navis* (Lindström) from sample Mä95-24, *P. originalis* Zone. (a) Adult Pa element, ×56, Cn 1684. (b) Juvenile Pa element, ×60, Cn 1685. (c–f) *Trapezognathus quadrangulum* Lindström. (c, f) From sample Mä95-16, basal *P. originalis* Zone. (c) Sc element, ×65, Cn 1686. (f) M element, ×100, Cn 1687. (d, e) From sample Mä95-15, top *B. navis* Zone. (d) Pa element, ×100, Cn 1688. (e) Sb element, ×120, Cn 1689. (g) *Microzarkodina flabellum* (Lindström) from sample Mä95-14, upper *B. navis* Zone, P element, ×95, Cn 1690. (h, i) *Microzarkodina parva* Lindström from sample Mä95-23, middle *P. originalis* Zone. (h) Juvenile P element, ×80, Cn 1691. (i) Adult P element, ×85, Cn 1692. (j, k) *Triangulodus brevibasis* (Sergeeva) from sample Mä95-24, middle *P. originalis* Zone, ×80. (j) ?Sb element, Cn 1693. (k) ?M element, Cn 1694. (l, m) *Paroistodus originalis* (Sergeeva). (l) Sb element from sample Mä95-18, lower *P. originalis* Zone, ×60, Cn 1695. (m) Sd element from sample Mä95-22, middle *P. originalis* Zone, ×75, Cn 1696. (n–q) *Semiacontiodus* sp. A from sample Mä95-18, lower *P. originalis* Zone. (n) Sa element, ×130, Cn 1697. (o) Pa element, ×100, Cn 1698. (q) Pb element, ×115, Cn 1699. (p) Sb element, ×125, Cn 1700. (r–u) *Semiacontiodus cornuformis* (Sergeeva) from sample Mä95-28, top *P. originalis* Zone. (r) Sa element, ×115, Cn 1701. (s) Pa element, ×90, Cn 1702. (t) Pb element, ×70, Cn 1703. (u) Sd element, ×110, Cn 1704.

5. Comparison with other East Baltic sections

Apart from the classical study by Pander (1856), investigations on conodonts from the East Baltic sections of the St Petersburg region were initiated by Sergeeva (Sergeeva, 1962, 1963, 1966, 1974), and from sections in Estonia by Viira (Viira, 1966, 1967, 1974). Conodont data from some northern Estonian outcrops (Väike-Pakri Island, Cape Pakri, Jägala, Narva) and from boreholes in southern Estonia (Kaagvere, Petseri, Karula, Abja, Seliste, Häädemeeste, Ohesaare) that are used for this comparison (for locations, see Fig. 1) have not previously been published.

Regardless of changes in conodont taxonomy most of the three zones and seven subzones established by Sergeeva (1966) for conodont faunas from the Latorp,

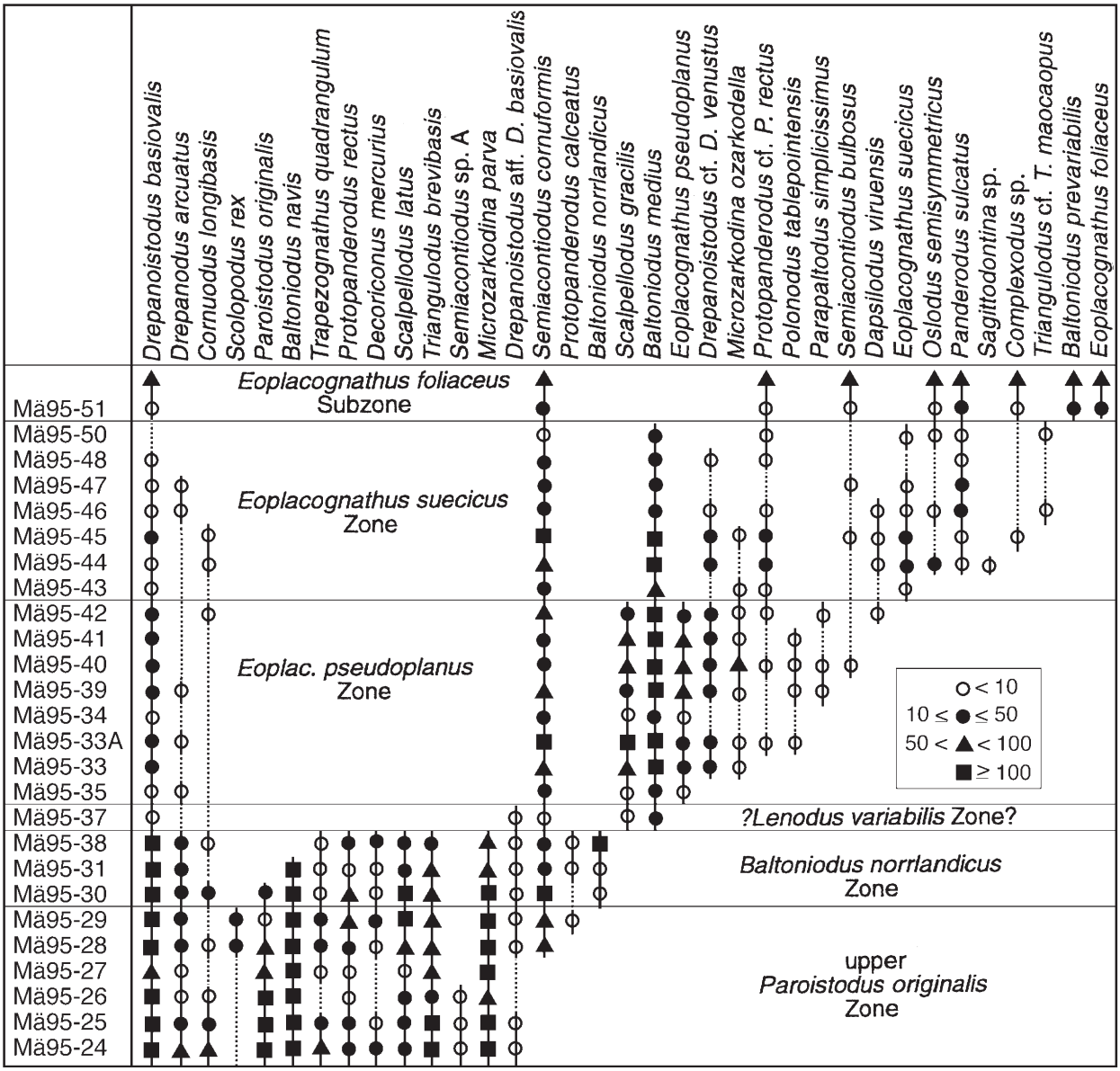

Figure 7. Semi-quantitative representation of the distribution of conodont taxa in samples from Mäekalda ranging from the middle part of the *P. originalis* Zone to the *E. foliaceus* Zone. A few rare taxa have been left out but are commented on in the text.

Volkhov and Kunda stages are comparable to zones still used in biostratigraphy (cf. Fig. 10). Her subzones of *Drepanodus proteus, Prioniodus elegans* and *P. evae* correspond to the zones of *Paroistodus proteus, Prioniodus elegans* and *Oepikodus evae* currently in use in the same interval. The Volkhov Stage is comparable to the *Cordylodus perlongus* (=*Microzarkodina flabellum*) Zone *sensu* Sergeeva (1966). *Microzarkodina flabellum* is particularly characteristic of this stage in the northern East Baltic region. Within this zone the *Oistodus parallelus* (=*Paroistodus originalis*) Subzone of Sergeeva (1966) comprises the later-established *Baltoniodus navis* and *Paroistodus originalis* zones. The *Ambalodus planus* Subzone of Sergeeva (1966) in the lower part of the Kunda Stage corresponds to the *Lenodus variabilis* Zone. The holotype of *A. planus* is a Pb element of *L. variabilis*.

At Mäekalda, the *Paltodus deltifer* Zone at the base of the section is extensively eroded and the sediments redeposited, but there are other sections in the northern Estonian outcrop area with representative faunas from this zone. In the Varangu section, which is situated about 90 km east of Mäekalda, a *c.* 2.60 m thick interval represents the lower and upper subzones of the *P. deltifer* Zone with well-preserved conodont faunas (Viira, 1970; Viira, Kivimägi & Loog, 1970). To the west of Mäekalda the *P. deltifer* Zone is found in the Keila-Joa section, on Cape Pakri and Väike-Pakri Island (Mägi & Viira, 1976; Viira, 1996). In the St Petersburg area this zone is established in the easternmost sections of the Baltic–Ladoga Klint area on the Nazya and Lava rivers and in the Putilovo quarry (Nazya Formation) (Popov *et al.* 1989; Dronov *et al.* 1998; Tolmacheva *et al.* 2001). The *P. deltifer* Zone has

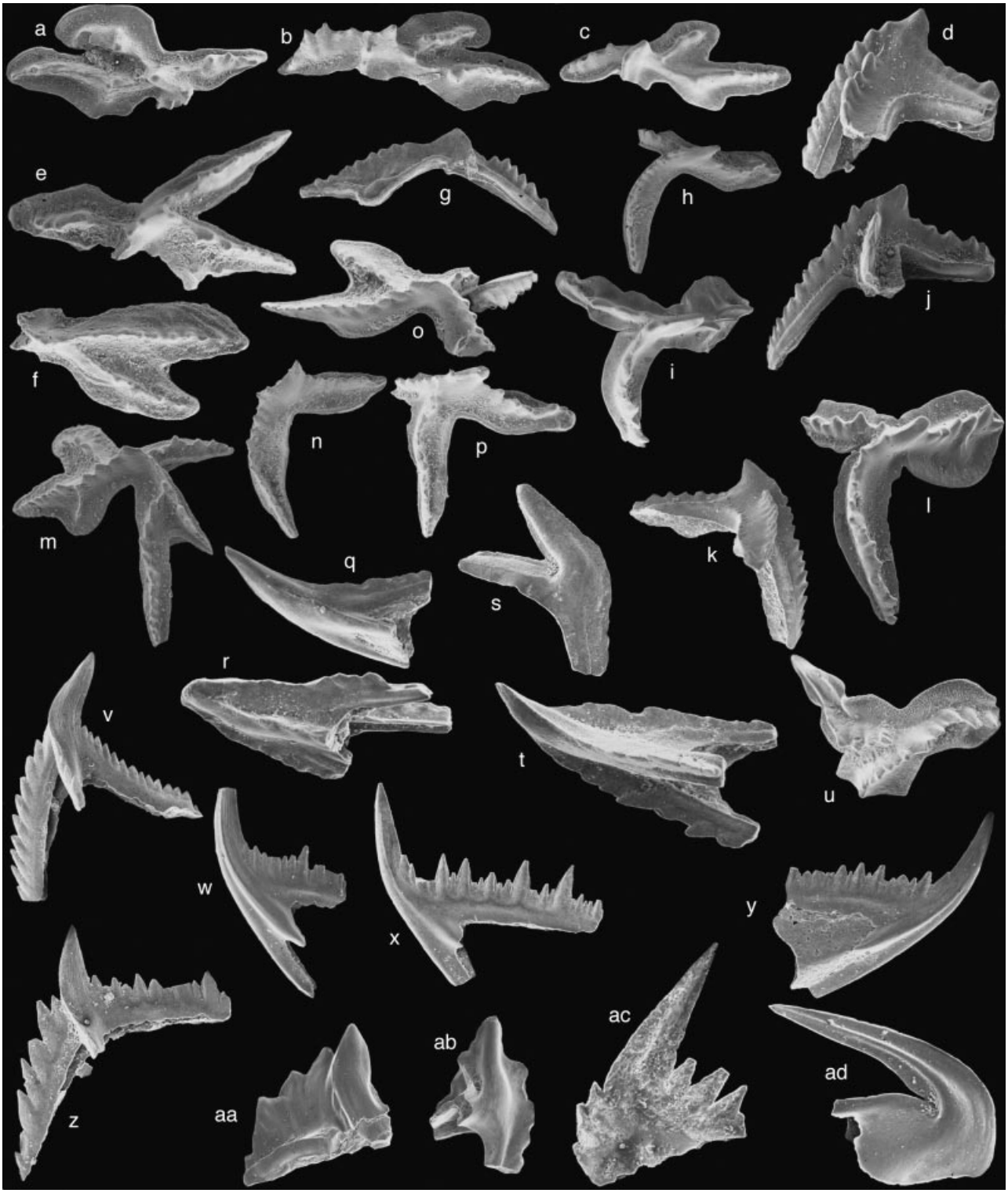

Figure 8. Conodonts with ramiform and platform elements from the *E. pseudoplanus* Zone to the *E. foliaceus* Zone. (a–l) *Eoplacognathus pseudoplanus* (Viira) from the *E. pseudoplanus* Zone, *M. ozarkodella* Subzone; (a, j, l) from sample Mä95-33, (b, d, f–h, k) from sample Mä95-40, (c, e, i) from sample Mä 95-41. (a) Dextral Pa element, ×50, Cn 1705. (b) Sinistral Pa element with high cusp and denticles, ×50, Cn 1706. (c) Sinistral Pa element, ×55, Cn 1707. (d) Juvenile dextral Pb element, lateral view, ×75, Cn 1708. (e) Dextral Pa element, ×70, Cn 1709. (f) Posterior and posterior-lateral processes of dextral Pa element, ×70, Cn 1710. (g) Dextral Pa element, lateral view, note low cusp and denticles, ×45, Cn 1711. (h) Sinistral Pb element, ×50, Cn 1712. (i) Sinistral? Pb element, ×35, Cn 1713. (j) Dextral Pb element, inner lateral view, ×60, Cn 1714. (k) Dextral Pb element, outer lateral view, ×70, Cn 1715. (l) Sinistral Pb element, ×60, Cn 1716. (m–p) *Eoplacognathus suecicus* Bergström from sample Mä95-45, *E. suecicus* Zone. (m) Dextral Pa element, ×80, Cn 1717. (n) Sinistral Pb element, ×55, Cn 1718. (o) Juvenile dextral Pa element, ×90, Cn 1719. (p) Dextral Pb element, ×55, Cn 1720. (q–t) *Eoplacognathus pseudoplanus* (Viira) from the *E. pseudoplanus* Zone, *M. ozarkodella* Subzone, (q, s) from sample Mä95-41, (r, t) from sample Mä95-39. (q) Sc1 element, ×65, Cn 1721.

also been identified in several boreholes (e.g. Sturi, Vergale, Baldone) within the Zebre Formation in the Central Baltoscandian Confacies Belt in Latvia (Ulst, Gailite & Yakovleva, 1982).

At Mäekalda, as well as in other sections in northern Estonia (Keila-Joa, Suhkrumägi, Jägala, Varangu), the *P. proteus* Zone is equivalent to the Klooga Member as well as almost the entire Joa Member of the Leetse Formation (Mägi & Viira, 1976; Viira, 1966). In the easternmost Estonian Narva section the *P. proteus* Zone is absent, as it is to the east of Narva. Only much further to the east, in the Putilovo and Vassilkovo sections in the St Petersburg region, is the zone established in the lower part of the Lakitsky Member (Dronov *et al.* 1998; Tolmacheva *et al.* 2001). The *P. proteus* Zone is found in the Central Baltoscandian Confacies Belt in drill-core samples from southeastern Estonia (Karula 495.3–495.5 m, Petseri 441.0–444.5 m) and northern Latvia (Sturi 1150.0–1154.65 m, Adze 990.3–990.7)(Ulst, Gailite & Yakovleva, 1982; Viira, 1974).

Occurrences of *P. elegans* in northern Estonian sections are not numerous but it is possible to establish the *P. elegans* Zone in many places such as Keila-Joa, Jägala, Varangu, Ontika and Narva (Mägi & Viira, 1976; Mägi, 1984). The *P. elegans* Zone corresponds to the upper part of the Joa Member (Ontika, Narva) or the Mäeküla Member (Suhkrumägi, Jägala, Varangu). As at Mäekalda, *Oistodus lanceolatus, Scolopodus rex* and *Drepanoistodus forceps* also first appear at the lower boundary of the *P. elegans* Zone in other northern Estonian sections. In the Jägala and Varangu sections *Paroistodus parallelus* is found in this zone. In two southern Estonian drill-cores *P. elegans* has been identified occurring together with *O. evae* (Kaagvere 349.9 m and Abja 485.1 m). In northern Latvia *P. elegans* has been found in two drill-core samples, Sturi 1144.55 m and Adze 990.3 m (Ulst, Gailite & Yakovleva, 1982).

In the easternmost St Petersburg region the *P. elegans* Zone corresponds to the upper part of the Lakity Member and to the Mäeküla Member of the Leetse Formation (Dronov *et al.* 1998; Tolmacheva *et al.* 2001). Bergström (1988) found *P. elegans* together with *O. evae* in the upper 30 cm of the Leetse Formation type section on the Tosno River. The entire formation measures only 40 cm. Since it directly overlies the Tremadoc Dictyonema Shale there, Bergström (1988) concluded that the stratigraphic unit with *P. elegans* rested with a pronounced unconformity on the lower Tremadoc in the St Petersburg region and possibly also in Estonia. Conodont studies of many northern Estonian sections have shown that the duration of this stratigraphic gap in fact varies from place to place. The hiatus is maximally developed in the Tosno section in Russia and in the Narva section in easternmost Estonia, and is least at Varangu where the Leetse Formation rests on a complete Varangu Formation. In the western Estonian Cape Pakri and Keila-Joa sections the stratigraphic gap includes the upper part of the Varangu Formation (Mägi & Viira, 1976).

Briefly, conodont studies indicate that the glauconitiferous terrigenous sandy sediments of the Leetse Formation, resembling the lower Tremadoc Obolus sandstones, show evidence of many local unconformities as well as redeposition. As in the lower Tremadoc, the boundaries of the *P. deltifer, P. proteus, P. elegans* and *O. evae* conodont zones do not coincide with boundaries of the lithostratigraphic units. Glauconitic sands of the Leetse Formation with conodonts of the *P. proteus* and *P. elegans* zones occur all along the northern Estonian outcrop area, but owing to local gaps and redeposition the zones may be incomplete. In addition to a gap in the lower part of the Joa Member (at Ontika and Narva), there is a gap at the lower boundary of the Mäeküla Member (at Keila-Joa, Jägala and Varangu) where *S. rex, O. lanceolatus* and *D. forceps* first appear. Co-occurrence of *O. evae* and *P. elegans* is attributed to transgression and redeposition in the upper Mäeküla Member (at Keila-Joa) and in the Päite Member (at Jägala).

At Mäekalda the *Oepikodus evae* Zone is equivalent to the upper part of the Mäeküla Member and the Päite Member, whereas at Suhkrumägi, Ontika and Narva it occupies the entire Mäeküla and Päite members. In the eastern St Petersburg region (at Putilovo and Vassilkovo) the *Oepikodus evae* Zone *sensu lato* corresponds to the upper part of the Mäeküla, Vassilkovo and Päite members (Dronov *et al.* 1995, 1998). At Putilovo, as in the Estonian sections, the upper part of the zone lacks specimens of *O. evae*, and characteristic species are *Periodon flabellum, Oistodus lanceolatus* and *Protopanderodus rectus*.

Sergeeva (1966) noted the upper ranges of *Distacodus stola* (=*Stolodus stola*), *Distacodus expansus* (=*Paroistodus parallelus*), *Oistodus lanceolatus* and *Scolopodus rex* in the Volkhov Stage, but except for *S. rex* the corresponding ranges end with the Päite Member in northern Estonia (Viira, 1974). In south-

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(r) Sb element, ×85, Cn 1655. (s) M element, ×65, Cn 17212. (t) Sc2 element, ×100, Cn 1656. (u) *Eoplacognathus foliaceus* (Fåhræus), sinistral? Pb element from sample Mä95-51, *E. foliaceus* Zone, ×65, Cn 1657. (v–z) *Baltoniodus medius* (Dzik), (v–x, z) from sample Mä95-41, *E. pseudoplanus* Zone, (y) from sample Mä95-45, *E. suecicus* Zone. (v) Pb element, ×65, Cn 1723. (w) Sc1 element, ×60, Cn 1724. (x) Sc2 element, ×90, Cn 1725. (y) Sc2 element, ×70, Cn 1658. (z) Pa element, ×75, Cn 1726. (aa) *Complexodus* sp., Pa element from sample Mä95-45, *E. suecicus* Zone, ×40, Cn 1659. (ab) *Sagittodontina* sp., M element from sample Mä95-51, *E. foliaceus* Zone, ×50, Cn 1660. (ac–ad) *Microzarkodina ozarkodella* Lindström from sample Mä95-39, *E. pseudoplanus* Zone, *M. ozarkodella* Subzone, ×125. (ac) P element, Cn 1661. (ad) M element, Cn 1662.

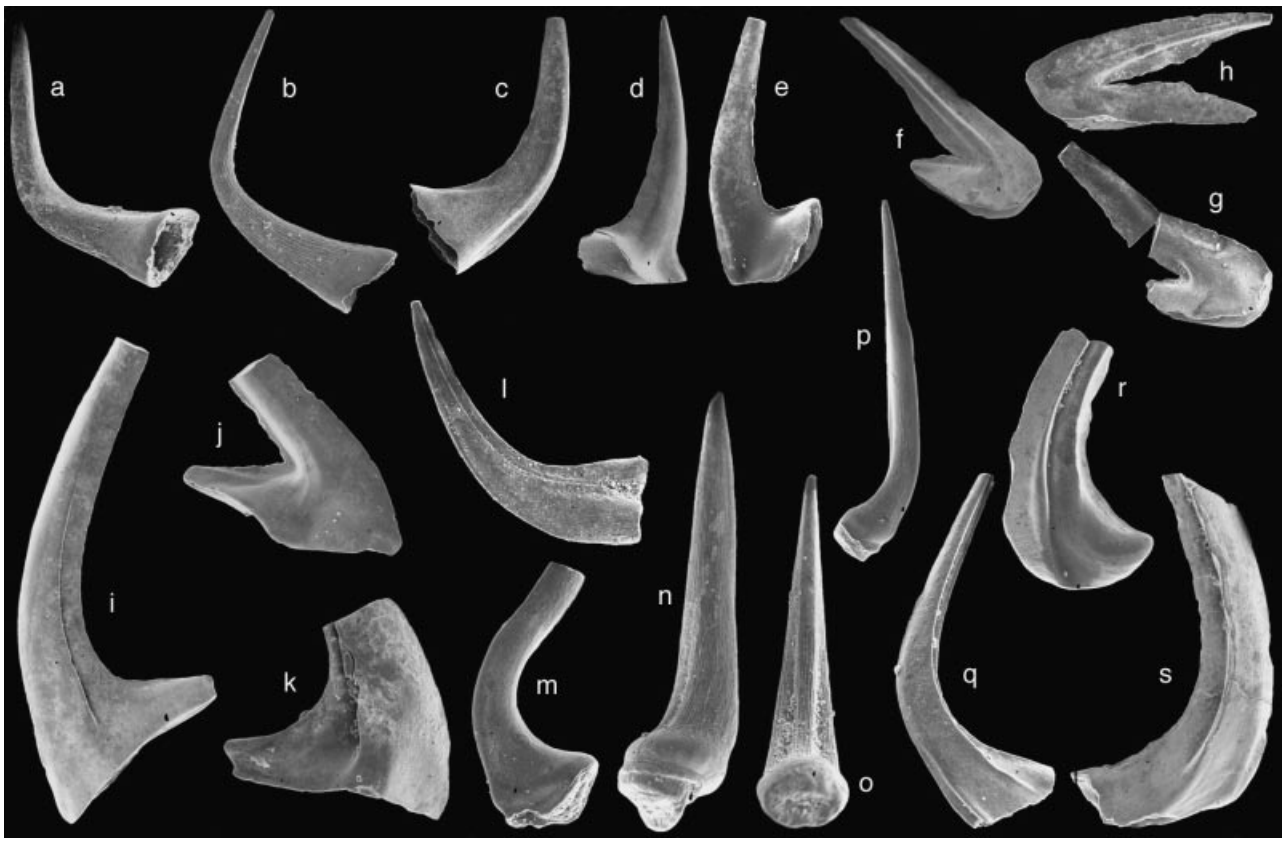

Figure 9. Coniform elements from the upper *E. pseudoplanus* Zone to the *E. foliaceus* Zone. (a–c) *Scalpellodus gracilis* (Sergeeva) from sample Mä95-42, upper *E. pseudoplanus* Zone. (a) Sd? element, ×70, Cn 1663. (b) Sb? element, ×80, Cn 1664. (c) P element, ×65, Cn 1665. (d–g) *Drepanoistodus basiovalis* (Sergeeva), (d, e, g) from sample Mä95-39, upper *E. pseudoplanus* Zone, (f) from sample Mä95-51, *E. foliaceus* Zone. (d) Sa element, ×50, Cn 1666. (e) Sc? element, ×50, Cn 1667. (f) M element, ×60, Cn 1668. (g) M element, ×70, Cn 1669. (h) *Drepanoistodus* cf. *D. venustus* (Stauffer) from sample Mä95-39, upper *E. pseudoplanus* Zone, ×70, Cn 1670. (i–k) *Oslodus semisymmetricus* (Hamar) from sample Mä95-51, *E. foliaceus* Zone. (i) Sb? element, ×80, Cn 1727. (j) M element, ×70, Cn 1728. (k) P? element, ×115. Cn 1671. (l) *Panderodus sulcatus* (Fåhræus), P element from sample Mä95-47, *E. suecicus* Zone, ×90, Cn 1672. (m–p) *Semiacontiodus cornuformis* (Sergeeva), (m) from sample Mä95-42, upper *E. pseudoplanus* Zone, (n–p) from sample Mä95-45, *E. suecicus* Zone. (m) Pa element, ×70, Cn 1673. (n) Sa element with bulbous base, ×75, Cn 1674. (o) Sa element, ×90, Cn 1675. (p) Sb? element, ×45, Cn 1676. (q) *Protopanderodus* cf. *P. rectus* (Lindström) from sample Mä95-45, *E. suecicus* Zone, ×90, Cn 1677. (r, s) *Protopanderodus* cf. *P. varicostatus* (Sweet & Bergström) from sample Mä95-51, *E. foliaceus* Zone. (r) P? element, ×85, Cn 1678. (s) S element, ×75, Cn 1679.

ern Estonia *P. elegans* and *O. evae* are known to co-occur in the Kaagvere and Abja drill-cores. Within the *O. evae* age interval the transgression widened (cf. Nielsen, 1992) and this zone has been identified in two more southern Estonian drill-cores (Karula 493.1 m and Petseri 443.7 m). In the Ohesaare drill-core from the Island of Saarema, typical conodont species of the upper part of the *O. evae* Zone were found at 518.2 m (Viira, 1967).

The *Baltoniodus triangularis* Zone has not been recognized in Estonia, and the lower boundary of the *B. navis* Zone is well defined on the first occurrence of the index species and also on the appearance of *Microzarkodina flabellum* and the disappearance of *Periodon flabellum* in many Estonian sections. In northern Estonia, species of *Paroistodus* are lacking in the lower part of this zone (Viira, 1974). In many places *Protopanderodus rectus* appears below the *B. navis* Zone: at Jägala in the *P. elegans* Zone, at Varangu in the *O. evae* Zone, in the Karula drill-core below the *O. evae* Zone at 494.6 m, in the Adze drill-core below the *B. navis* Zone at 972.0 m, possibly as the result of a generally very shallow-water environment combined with some breaks in sedimentation. In the western part of the St Petersburg region, in the quarry near Kingisepp, the first occurrences of *Baltoniodus triangularis* and *B. navis* appear to be simultaneous, but in the eastern Putilovo section, *B. navis* appears later (Dronov *et al.* 1998).

The next zonal denominator, *Paroistodus originalis*, was originally described from the middle Volkhov Stage in the Popovka River section (Sergeeva, 1963). Subsequently the *P. originalis* Zone has been identified in several outcrops on the Volkhov, Lopukhinka, Koporka and Tosno rivers and in the Putilovo quarry in the St Petersburg region, whereas the first appearance of

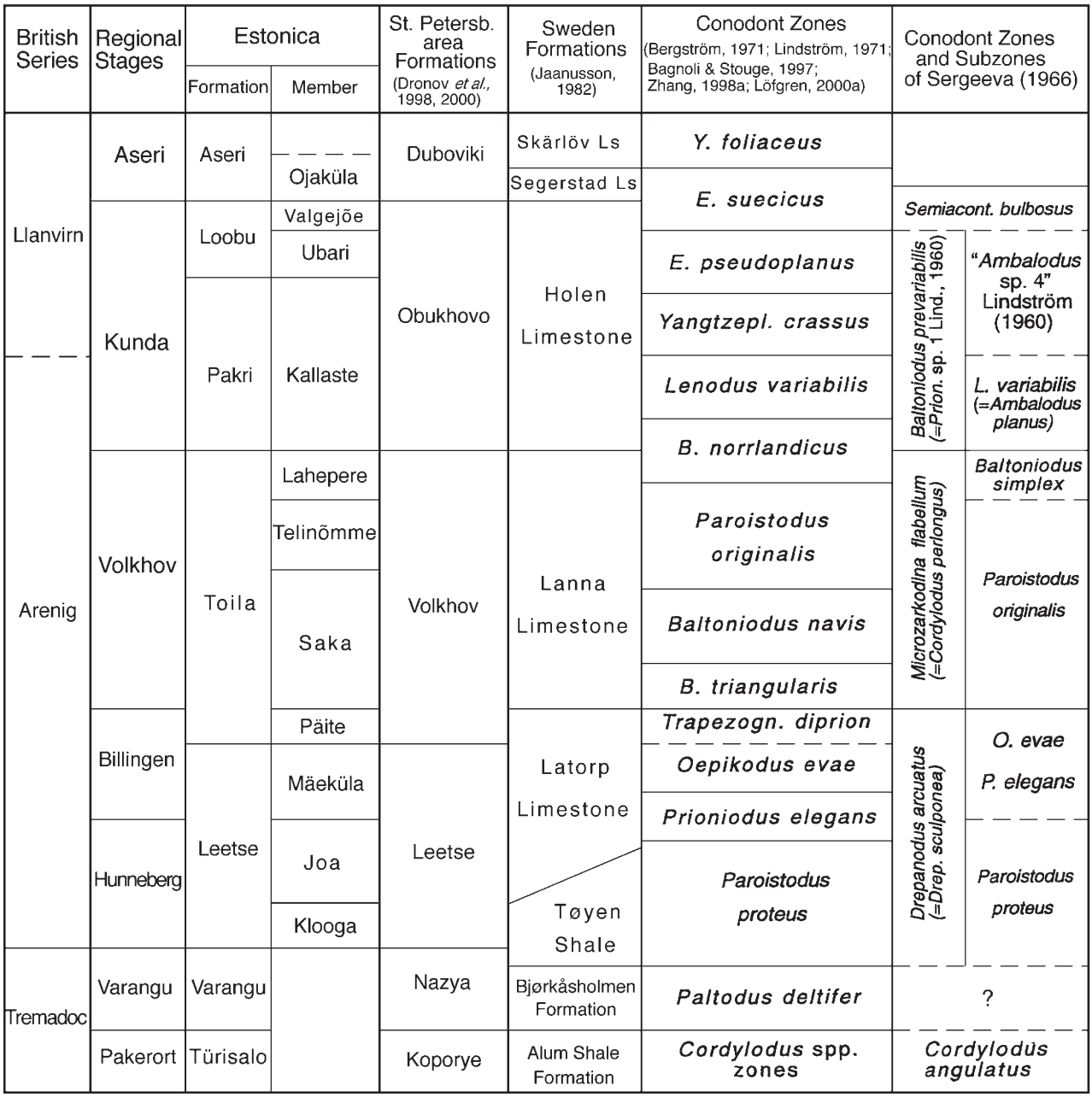

Figure 10. Chronostratigraphic, lithostratigraphic and conodont biostratigraphic units compared. For Sergeeva's (1966) conodont biozonation on the far right, modernized names have been provided as far as possible.

the species has been established in the *B. navis* Zone (Sergeeva, 1966; Tolmacheva, 1997). *Paroistodus originalis* is also found in many drill-cores from southern Estonia (Karula 483.8 m, Petseri 433.9–438.0 m, Kaagvere 346.4–347.7 m, Abja 478.2 m, Ohesaare 516.24–516.94 m, Häädemeeste 536.4 m) and northern Latvia (Adze 966.6–969.9 m).

The *B. norrlandicus* Zone corresponds to the *'Falodus' simplex* Subzone in the upper part of the Volkhov Stage in Sergeeva's (1962, 1963, 1966) studies, since *'F.' simplex* probably belongs to the *Baltoniodus norrlandicus* apparatus. In the Putilovo quarry the lower boundary of the *Microzarkodina parva* Zone (upper Volkhov) is distinguished on the first appearance of *B. norrlandicus* (Tolmacheva *et al.* 2001).

The *Lenodus variabilis* Zone [=*Ambalodus planus* Subzone of Sergeeva, 1966] corresponds to the lower and middle Obukhov Formation of the Kunda Stage in the St Petersburg region (Dronov *et al.* 1998). Specimens of *L. variabilis* (*sensu lato*) have been found in some southern Estonian and Latvian drill-cores (Kaagvere 335.2–339.8 m, Abja 472.2–480.9 m, Seliste 448.4–451.9 m, Häädemeeste 527.5–528.6 m, Adze 938.2–945.7 m, Sturi 1071.6–1088.8 m) (Viira, 1974). The stratigraphic range and distribution of the zonal indices *L. variabilis* and *Eoplacognathus pseudoplanus*

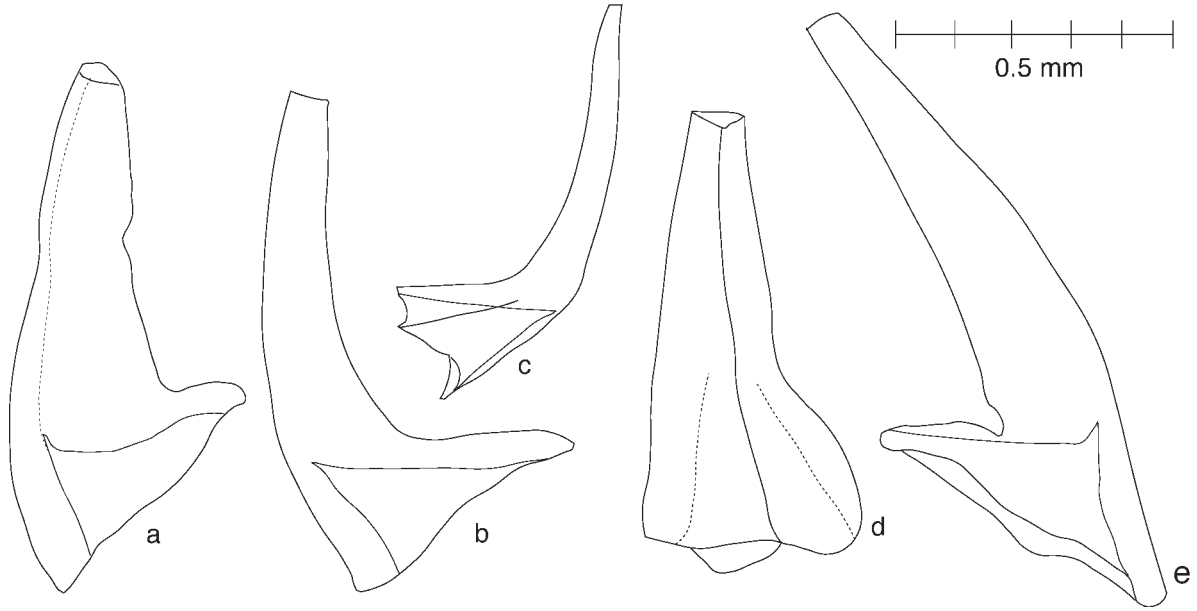

Figure 11. Camera lucida drawings of *Tripodus* cf. *T. laevis* (Bradshaw, 1969) from sample Mä96-1, upper *O. evae* Zone, Mäekalda section. (a) P element, Cn 1729. (b) Sc? element, Cn 1730. (c) Sb? element, Cn 1731. (d) Sa element, Cn 1732. (e) M element, Cn 1733.

need to be investigated in greater detail in view of developments in the apparatus concept.

6. Comparison with Swedish sequences

Beginning with the upper Tremadoc part of the Mäekalda section where our investigation starts, the typical equivalent in Scandinavia is the often glauconitic limestone of the Bjørkåsholmen Formation (previously = the Ceratopyge Limestone)(cf. Fig. 10). For basic correlations between this unit and Estonian equivalents, see Mägi & Viira (1976). The conodont fauna of the Bjørkåsholmen Formation includes a number of faunal elements from Laurentian bioprovinces (Löfgren, 1996, 1997; Löfgren, Repetski & Ethington, 1999). The limited collections from Mäekalda available to us indicate that this is also so in the upper Varangu Formation and the overlying Arenig Leetse Formation there. Erosion and redeposition of conodont elements in these units makes detailed comparison with the Swedish faunal succession in the *Paroistodus proteus* Zone (cf. Löfgren, 1993, 1994) difficult.

The *Prioniodus elegans* Zone is probably represented by two samples at Mäekalda. This zone is usually very thin or completely eroded in most Swedish sections (Lindström, 1971). The combination of early *Protopanderodus* and *Semiacontiodus* present at Mäekalda can also be found in the Siljan district in central Sweden (Bergström, 1988; Löfgren, 1994).

The *Oepikodus evae* Zone begins with a transgression and is represented in many Swedish areas by a rich and characteristic conodont fauna (Lindström, 1971; van Wamel, 1974; Löfgren, 1978; Bagnoli, Stouge & Tongiorgi, 1988; Löfgren, 1993; Bagnoli & Stouge, 1997). In Sweden there are usually hundreds of specimens of *Oepikodus evae* in each sample from the lower part of the zone. In the Mäekalda section we have only retrieved four elements of the zonal fossil, *O. evae,* which indicates that the basal part of the zone may be lacking, particularly since there is a conspicuous discontinuity surface at the lower boundary. In the second lowermost sample, Mä95-7A, we found a specimen of *Prioniodus? crassulus* co-occurring with *O. evae*, which is typical of the upper–middle *O. evae* Zone in Sweden (Löfgren, 1993, 1996).

In the upper part of the sequence, which has traditionally been included in the *O. evae* Zone in Sweden (cf. Lindström, 1971; Löfgren, 1993), the zonal indicator is lacking. We are convinced that at least the Päite Member, which we refer to the *Oepikodus evae* Zone *sensu lato* at Mäekalda, belongs to this upper part which corresponds to the trilobite zone of *Megistaspis (Varvaspis) estonica* (cf. Löfgren, 1993, 1994). One reason is that *Paroistodus parallelus*, which is characteristic of the lower and middle parts of the *O. evae* Zone in Sweden (Löfgren, 1993), is lacking at Mäekalda, while *P. originalis*, typical of the upper *O. evae* Zone in Sweden, appears in the Päite Member. *Periodon flabellum* has the highest number of elements of all species in the upper part of the *O. evae* Zone at Mäekalda as in other northern Estonian sections, distinguishing a (local) *P. flabellum* Zone. This is of doubtful value for wider correlation, however, since a *P. flabellum* frequency maximum occurs in other parts of the zone elsewhere, for instance in the middle of the zone in Jämtland, northern Sweden (cf. Löfgren, 1993, p. 199).

Five taxa have their first occurrence in the section together with *Baltoniodus navis* at the base of the *B. navis* Zone, but this may partly be an artefact, since the *B. triangularis* Zone appears to be lacking at Mäekalda. One of them, *Microzarkodina flabellum,* usually first appears within the *B. triangularis* Zone in Sweden (Löfgren, 1993). Another, *Scalpellodus latus*, first appears earlier at Mäekalda than in most Swedish sections. In the Finngrundet drill-core, elements of *Scalpellodus* cf. *S. latus* (cf. Löfgren, 1985, p. 127, fig. 4AQ–AS, AZ, AAA) were found at approximately the same level as the first *Scalpellodus* specimens in the Mäekalda section. The *Scalpellodus* specimens from the *B. navis* Zone at Mäekalda should probably be referred to the same taxon. *Decoriconus mercurius*, which replaces *D. peselephantis* in the middle *B. navis* Zone in Sweden (Löfgren, 1998), appears in the lowermost sample from the *B. navis* Zone at Mäekalda, indicating that this sample represents a level slightly above the base of the zone.

Together with *B. navis*, *Drepanoistodus forceps* and *Microzarkodina flabellum* are the most abundant species in the *B. navis* Zone at Mäekalda. In the upper part of the zone *Protopanderodus rectus* is also numerous. *Baltoniodus navis* is more abundant than in samples of the same age from Sweden (cf. Löfgren, 1985, 1993, 1995, 2000*b*) while *P. rectus* is usually less common than in Sweden, and *Periodon flabellum,* which is found in most Swedish samples from the *B. navis* Zone, is totally lacking in this zone at Mäekalda. On Öland *Periodon* may also be absent in this interval (Bagnoli & Stouge, 1997). Taken together, these facts confirm the model (cf. Jaanusson, 1976, 1995; Nielsen, 1992) of a deeper marine environment in Sweden than in Estonia during Volkhov time as well.

The lower boundary of the *Paroistodus originalis* Zone was taken to be at a level where the relative abundance of *Triangulodus brevibasis* first exceeded 0.3% of the conodont elements, as was proposed for Swedish sections by Löfgren (1995). It coincides with the first occurrence of the species in small to medium collections from Scandinavia. It might be argued that the use of this boundary definition for Estonian sections is more doubtful, particularly since *P. originalis* does not reappear at Mäekalda until sample Mä95-18, *c.* 0.3 m higher up in the section. Other events recorded in the Mäekalda section support our interpretation, however, for instance the re-appearance of *D. arcuatus* and *Periodon flabellum* together with *P. originalis*, indicating the beginning of a transgressive phase there (='phase 2' of Löfgren, 1995). Even after this phase the same order of events and the same 'phases' of the *P. originalis* Zone as those that have been recognized in Sweden can be identified at Mäekalda (see Biozonation, Section 4). It was only 'phase 5', the last phase of the zone in Sweden, that was not found in the Mäekalda section.

The relative abundances of the taxa within the zone are consistent with a shallower environment at Mäekalda than those for investigated sections on the Swedish mainland (cf. Löfgren, 1995). For instance, *T. brevibasis* is generally more abundant and *P. originalis* much less common than in the Swedish samples.

At Mäekalda the *P. originalis* Zone is *c.* 3 m thick, whereas in the Gillberga section on Öland this interval is only slightly more than 1 m thick (Löfgren, 2000*a*). In most sections on the Swedish mainland the *P. originalis* Zone, however, is thicker, for instance 4.6 m at Lanna, Närke (Löfgren, 1995), and between 8 and 9 m at Kalkberget, Jämtland (Löfgren, 1978).

The *Baltoniodus norrlandicus* Zone at Mäekalda is equivalent to the lower part of the same zone at the Horns Udde quarry section, the section north of Horns Udde (Bagnoli & Stouge, 1997) and the Gillberga quarry (Löfgren, 2000*a*) on Öland, for instance. Species that have been found in this interval in one or more of the Öland sections but not at Mäekalda are *Scolopodus rex*, *Parapaltodus* sp., *Microzarkodina flabellum* (in sections investigated by Bagnoli & Stouge, 1997) and *Decoriconus mercurius* Löfgren (in the Gillberga quarry, cf. Löfgren, 2000*a*). *Scolopodus rex* is also lacking in the Lanna section in this interval (Löfgren, 1995). *Triangulodus brevibasis* is present in the Öland sections reported by Bagnoli & Stouge (1997) and even has a maximum abundance at Mäekalda, but is entirely lacking in this interval at Lanna in Närke and Gillberga, Öland, where the sea was presumably slightly deeper (Löfgren, 1995).

The paucity of information from the inferred *L. variabilis* Zone and the lower *E. pseudoplanus* Zone at Mäekalda allows no meaningful comparison with other areas. From the upper *E. pseudoplanus* Zone and upwards, however, comparisons are again possible.

The upper part of the *E. pseudoplanus* Zone, which can be *c.* 7 m thick in south-central Sweden (Hällekis section, see Zhang, 1998*a*), and at least 2 m at Gillberga (Löfgren, 2000*b*), measures scarcely more than 1 m at Mäekalda. *Baltoniodus medius* is the most abundant taxon in the last two sections, while *M. ozarkodella*, which is the second most numerous taxon at Gillberga with *c.* 30% attains at most a few per cent at Mäekalda. A substantial part of the fauna in both these sections is made up of *Semiacontiodus cornuformis* and *Scalpellodus gracilis*. *Eoplacognathus pseudoplanus* is more abundant at Mäekalda than at Gillberga where it varies from 1% to 4%. Possibly indicative of greater depositional depth of sediments at Gillberga are the (rare) occurrences of *Periodon* cf. *aculeatus, Ansella* and *Strachanognathus*. These taxa were not found in the Mäekalda section.

The *E. suecicus* Zone is approximately 1.5 m thick at Mäekalda, 3.5 m in the Grötlingbo-1 bore, southern Gotland (Zhang, 1998*a*), and *c.* 5 m at Lunne, Jämtland (Zhang & Sturkell, 1998). *Baltoniodus medius* is generally the most abundant species in all three areas

in this zone, but in Jämtland *Periodon aculeatus* appears in great numbers at a few levels (Zhang, 1998*a*). Only a few *P. aculeatus* elements were recorded from Grötlingbo-1 (Zhang, 1998*a*), and at Mäekalda the taxon is absent. *Semiacontiodus cornuformis* is much more abundant in Estonia than in the Swedish sections, while no elements of the distinctive and diagnostic *Pygodus* species that define the subzones of this zone in Sweden have been retrieved from Mäekalda.

The uppermost sample taken represents the *E. foliaceus* Zone, where *Baltoniodus prevariabilis*, *Semiacontiodus cornuformis*, *Panderodus sulcatus* and *Eoplacognathus foliaceus* are the most abundant taxa. The diversity is lower than in coeval samples from northern Sweden (Löfgren, 1978).

7. Taxonomic comments

In this section and in the figure captions we have chosen to use the Pa, Pb, Sa-Sc terminology for notation of conodont elements in the way suggested by Sweet (1981, p. W19). This 'provides a means of comparing elements in different taxa without indicating homology with better known taxa', as was recommended by Purnell, Donoghue & Aldridge (2000, p. 119).

7.a. *Drepanodus*

We have listed all elements of *Drepanodus* as *D. arcuatus* s.l., but they probably include more than one natural taxon. The Mäekalda collection includes fully hyaline as well as almost totally albid specimens.

7.b. *Drepanoistodus*

In addition to the common Baltoscandian taxa *D. forceps* (Fig. 5aa–ac) and *D. basiovalis* (Figs 5z, 9d–g), the Mäekalda section has yielded an unusual number of what appear to be representatives of the corresponding Laurentian lineage or lineages. In the upper Tremadoc and lowermost Arenig we found a taxon (Fig. 5d–f) with M elements that resemble some illustrations of M elements of *D. nowlani* by Ji & Barnes (1994, pl. 7, figs 16, 17). In the St George Group, western Newfoundland, *D. nowlani* is indicative of the basal Arenig, in an interval equated with the *P. proteus* Zone of Baltoscandia. At Mäekalda the occurrences of *D.* cf. *D. nowlani* pre-date those of *D. forceps*. A possible precursor of *D. basiovalis* has been listed as *D.* cf. *D. basiovalis* (Fig. 5u) and is the same taxon that was called *D.* cf. *D. basiovalis* by Stouge & Bagnoli (1990) and Löfgren (1995). Alternatively this taxon is another Laurentian immigrant related to later *D. suberectus*. A third taxon that is possibly related to American forms occurs sporadically in the middle to upper Kunda sequence at Mäekalda and has been denoted *D.* aff. *D. basiovalis* in the figures. M elements of this taxon (Fig. 5t) are characterized by having a considerably thicker cusp and basal cavity wall than M elements of *D. basiovalis* of the same size. As we are not able to identify the S and P elements of the apparatus with certainty, we prefer to use open nomenclature in this instance. The taxon shows certain similarities to Middle Ordovician *D. suberectus* in North America. The youngest of the species of possible Laurentian affinity is *D.* cf. *D. venustus* (Fig. 9h). Its relations to *D. venustus* (Stauffer, 1935) are far from clear. We have found the M elements of *D.* cf. *D. venustus* invariably associated with characteristic drepanodontiform (S?) elements in Mäekalda samples from the upper Kunda and lower Aseri beds.

7.c. *Complexodus*

A few broken P elements of this genus (Fig. 8aa) have been found in the upper part of our section. We hesitate to assign them to a particular species, although they best agree with *C. originalis* Chen & Zhang, 1984, in both morphology and stratigraphic position.

7.d. *Juanognathus?* sp. A

This taxon includes elements (Fig. 5a, b) resembling those of '*Protopanderodus*? n. sp. 1 s. f.' of Repetski (1982, pl. 18, figs 1, 5) which occur in the El Paso Group of Texas in beds below those yielding *Oepikodus communis*. Beds with *O. communis*, regarded as approximately equivalent in age to the *Prioniodus elegans* Zone of Baltoscandia, have yielded true *Juanognathus* elements. Our specimens were found in the *Paroistodus proteus* Zone and are thoroughly recrystallized, indicating that they may actually derive from even older beds. Strata of approximately the same age in the St Petersburg area have yielded identical specimens (T. Tolmacheva, Uppsala, pers. comm., 2000), making this taxon potentially valuable for correlation in the East Baltic. The simple morphology of the elements is closest to that of some elements of *Juanognathus* Serpagli, 1974, hence our tentative assignment to the genus.

7.e. *Oistodus*

Among the typical elements of *O. lanceolatus* (Fig. 5w–y) in the lower *O. evae* Zone, some specimens were found that have additional small costae or wrinkles on the base, almost as in *Oistodus multicurrugatus* Harris, 1962. We have interpreted this as normal variation within *O. lanceolatus*, since all *Oistodus* elements in these samples agree in colour, mode of preservation, size, etc., indicating that they belonged together.

7.f. *Protopanderodus*

In addition to elements of the Baltoscandian *P. rectus* (paucicostate) and *P. calceatus* (multicostate) we have recovered elements that are more difficult to deter-

mine. Throughout the *Oepikodus evae* Zone, below the first appearance of *P. rectus* at Mäekalda, we infer that *P. gradatus* Serpagli, 1974 is present. Like elements of this taxon from the type area in Argentina, most of our specimens are multicostate. In the Kundan and Aserian parts of our section, above the range of typical *P. rectus* and *P. calceatus*, we have found elements with slightly deviating morphologies, that we have designated *P.* cf. *P. rectus* (Fig. 9q) together with probable *P. varicostatus* (Fig. 9r–s).

7.g. *Sagittodontina*

One characteristic M element (Fig. 8ab), probably of *S. kielcencis* (Dzik, 1976), was found in the lower *E. suecicus* Zone. The taxon and its possible relations have been discussed by Dzik (1994).

7.h. *Scandodus? subarcuatus*

The Mäekalda collection derives from the *P. proteus* Zone, that is, from slightly younger strata than the *S? subarcuatus* elements described by Furnish (1938), but they appear to be closely related to these, and hence of Laurentian affinity.

7.i. *Semiacontiodus*

Elements referable to this genus occur at Mäekalda from the base of the *P. elegans* Zone and up to the top of our section. The oldest representatives have the generalized shape of some early scolopodontids from Laurentia, such as *Semiacontiodus nogami* Miller, 1969. The possible relations of such forms to later Baltoscandian scolopodontids have been discussed by Löfgren (1999). In the uppermost *B. navis* Zone and throughout the lower and middle parts of the *P. originalis* Zone of Mäekalda, specimens of *Semiacontiodus* sp. A (Fig. 6n–q) occur, though never abundantly. This is the same taxon that was designated *Semiacontiodus* cf. *S. cornuformis* by Löfgren (1999, pl. 1, figs 20–22) and which resembles *S. cornuformis* in the general outline of the elements, though the edges of the cusps are blunter and the element types less distinctly defined. The most successful of the scolopodontids in Baltoscandia was *Semiacontiodus cornuformis* (Fig. 6r–u) which first appears in the upper *P. originalis* Zone at Mäekalda and constitutes an important part of the conodont fauna throughout the rest of our section. *Semiacontiodus davidi* Löfgren, 1999, which is the most abundant *Semiacontiodus* species in sediments from deeper water in Baltoscandia in the Kunda, is almost totally lacking in the Mäekalda samples. A few specimens were found in Kundan samples, but have not been specified in Figure 7. *Semiacontiodus bulbosus* (Löfgren, 1978) was found co-occurring with *S. cornuformis* in some samples from the upper *E. pseudoplanus* Zone upwards in the Mäekalda section. Approximately the same distribution prevails in Swedish sections (Löfgren, 1978; Zhang, 1998*a*).

7.j. *Tripodus*

Tripodus sp. A occurs from the upper *P. proteus* Zone to the basal *O. evae* Zone at Mäekalda; in Sweden it is present in the middle *P. proteus* Zone as well as in slightly younger beds (Löfgren, 1994). In the Päite Member, representing the upper *O. evae* Zone *sensu lato*, another *Tripodus* species occurs, here designated *Tripodus* cf. *T. laevis* (Fig. 5n–s, Fig. 11). It is morphologically close to the North American zonal indicator *T. laevis* (cf. Ethington & Clark, 1982), and may be its direct ancestor. Since *T. laevis* has been suggested as a marker for the base of the Whiterockian Series (Ross & Ethington, 1991, 1992), its phylogenetic history is of particular interest and must be studied further.

8. Conclusions

The Mäekalda section includes highly fossiliferous beds ranging in age from the late Tremadoc to the late Llanvirn. In the lowermost part of the section, silty and glauconitic strata prevail, and since repeated erosion and redeposition of sediment has taken place, significant reworking of conodont elements has occurred, sometimes making detailed correlation with other areas difficult. Rare parts of the conodont faunas have Laurentian affinities and make tentative correlation with North America possible. From the *Baltoniodus navis* Zone and throughout the Volkhov the succession at Mäekalda more closely resembles the Swedish succession, the *Paroistodus originalis* Zone in particular being comparable in thickness and conodont fauna to strata from south-central Sweden. Mäekalda and other northern Estonian sections also form a link with successions further to the east extending into the St Petersburg region of Russia. In the uppermost Volkhov and lower Kunda there is a considerable stratigraphic gap at Mäekalda, including most of the interval from the upper *Baltoniodus norrlandicus* Zone to the upper *Eoplacognathus pseudoplanus* Zone, corresponding to a *c.* 8 m thick succession in northern Öland. Above that, the sequence at Mäekalda includes beds from the upper *E. pseudoplanus* Zone to the basal *E. foliaceus* Zone. The interval is rich in conodonts, particularly in platform elements, and the faunas resemble those in Sweden. Some rare faunal components in the Mäekalda sequence also enable long-distance correlation with, for instance, southern China.

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