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The Ordovician conodont *Semiacontiodus cornuformis* (SERGEEVA, 1963) and related species in Baltoscandia

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with 3 text-figures and 2 plates

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Semiacontiodus cornuformis (SERGEEVA, 1963) was probably derived from Laurentian forms such as *Semiacontiodus nogamii* MILLER, 1969, or *Teridontus nakamurai* (NOGAMI, 1967). It had a seximembrate apparatus with Pa, Pb, Sa, Sb, Sc and Sd elements. Its oldest occurrences are encountered at the base of the *Microzarkodina parva* Zone. The elements of its inferred ancestors, appearing immediately below this level, are morphologically simpler, resembling *S. nogamii.* Elements of the lineage then rapidly attained the typical morphology of *S. cornuformis* which spread over the Baltoscandian shelf during the late Arenig. In the early Kunda it was joined by *Semiacontiodus davidi* n. sp. which initially also seems to have resembled *S. nogamii* and is probably a descendant of a new immigrant to the area. Less specialized taxa of Laurentian origin apparently established themselves a number of times in Baltoscandia and evolved into taxa adapted to the deep and cold environment on that platform. Later Ordovician representatives of this conodont group are less widely known in Baltoscandia, but they also appear to differ from Laurentian forms of similar age, thus confirming the general picture of Baltoscandia as a local centre of evolution for the group.

Semiacontiodus cornuformis (SERGEEVA 1963) und die nahe verwandte Art *Semiacontiodus davidi* n. sp. haben wahrscheinlich ihren Ursprung in Formen aus Laurentia, wie *Semiacontiodus nogamii* MILLER 1969 oder *Teridontus nakamurai* (NOGAMI 1967). Sie haben einen seximembraten Apparat mit Pa, Pb, Sa, Sb, Sc und Sd Elementen. Ihr frühestes Auftreten wird von der Basis der *Microzarkodina parva*-Zone erwähnt. Die Elemente ihrer vermuteten Vorgänger, die unmittelbar unter diesem Niveau erscheinen, haben eine einfachere Morphologie, ähnlich *S. nogamii.* Die Elemente dieser Entwicklungsreihe zeigten dann bald die typische Morphologie von *S. cornuformis*, der sich während des späten Arenig über dem baltoskandischen Schelf ausbreitete. Im frühen Kunda wurde er begleitet von *Semiacontiodus davidi* n. sp., der anfangs auch *S. nogamii* zu ähneln schien und der Nachfahre eines neuen Einwanderers in dieses Gebiet ist. Weniger spezialisierte Taxa laurentischer Herkunft haben sich scheinbar mehrmals in Baltoskandia etabliert und Taxa hervorgebracht, die der tieferen und kühleren Umwelt auf dieser Plattform angepasst waren. Spätordovizische Vertreter sind in Baltoskandia weniger weit bekannt, aber auch sie scheinen sich von laurentischen Formen ähnlichen Alters zu unterscheiden. Baltoskandia wird daher als ein lokales Zentrum für die Evolution dieser Gruppe aufgefasst.

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Introduction

A very characteristic conodont species, *Scolopodus cornuformis*, was described by S.R. SERGEEVA in 1963 from beds of Volkhov and Kunda (mid- to late Arenig and early Llanvirn) age along the River Volkhov near St Petersburg. The taxon has later been reported from the mid-Arenig to mid-Llanvirn over much of Baltoscandia, and its first appearance and co-occurrence with two other species has been used to characterize the *Microzarkodina parva* Assemblage Zone (LINDSTRÖM 1971). "*Scolopodus*" *cornuformis* has, however, also been reported from considerably older beds as in Korea and S China, which taken together with the fact that "*S.*" *cornuformis* has not been found below the Kunda in some Baltoscandian areas (see for instance, STOUGE 1975: 35) has led to doubts about its stratigraphic usefulness (STOUGE 1989). A general survey of first and last appearances of "*S.*" *cornuformis* has now been undertaken to investigate this in greater detail, and some probable predecessors have been identified.

My search for the ancestry of "*Scolopodus*" *cornuformis* also led to an analysis of the morphologies and apparatus reconstructions of similar older and younger taxa elsewhere, and of the possible relations between these and "*Scolopodus*" *cornuformis*. It seems to most closely resemble *Semiacontiodus*, and as has been previously suggested by various authors I recommend that "*S.*" *cornuformis* should be transferred to that genus.

I have also investigated some younger related species in Baltoscandia. In particular *Semiacontiodus davidi* n. sp., which first appeared in the early Kunda and co-occurs with *S. cornuformis* through that stage, has been treated. It is described and the apparatus morphology and environmental preferences are compared with those of *S. cornuformis*.

Localities, samples and material

Material for this investigation of *Semiacontiodus cornuformis* (SERGEEVA, 1963), *S. davidi* n. sp. and their closest relatives has been collected from Gillberga and Sandvik on N Öland; Gullhögen (Skövde) and Hällekis in Västergötland; Lanna in Närke; the Finngrundet drill core from the Gulf of Bothnia; Rävanäs, Kårgärde and Leskusänget in Dalarna; and Kloxåsen, Lunne, Gusta, Gärde and Kalkberget in Jämtland. Locations and further references can be found in LÖFGREN (1995: 696, fig. 2), and in LÖFGREN (1978) for the Jämtland sections. A few samples collected from the Hälludden and Haget sections, N Öland (locations in BOHLIN 1949), and the Tamsalu drill core, central Estonia (for location, see PUURA 1986: fig. 1.1, bore hole no 565), have also proved highly informative. Information concerning some older and younger related taxa derived from the literature has also been included.

The conodont elements are reasonably well to very well preserved, and only those from Jämtland and some from Västergötland show an increase in CAI (conodont Color Alteration Index, EPSTEIN et al. 1977) indicating higher thermal maturation. The Jämtland elements have a CAI of between 3 and 4, while elements from the upper parts of the Gullhögen section (Billingen) I investigated have a CAI of 2, or even lower in most of the samples (cf. BERGSTRÖM 1980: 389). All specimens from Hällekis (Kinnekulle) had a CAI of less than 1.5.

The conodont samples vary in size; all except those from Jämtland have been treated in buffered acetic acid (method according to JEPPSSON et al. 1985) and washed through a 63 µm sieve, and the residues in most cases concentrated by magnetic separation. The Jämtland samples, which were treated earlier, had been dissolved in non-buffered acetic acid and the residue washed through a 90 µm sieve, dried and separated in bromoform. In these samples, some of the original smaller elements may have been lost in the washing process, and some elements could possibly have been corroded by acid, so the results may not be directly comparable.

Repository: The conodont elements illustrated in this paper are deposited in the type collection, Department of Geology, Lund University, Lund, Sweden (prefix LO).

Scolopodontids in Baltoscandia

Conodonts of the lineage in which "*Scolopodus*" *cornuformis* holds a central place (group here loosely referred to as scolopodontids) were established over Baltoscandia in late Volkhov, Kunda and Aseri times in all but the deepest marine environmental settings. Where did these taxa come from? A survey shows that similar taxa were common and had diversified as early as the early Tremadoc in Laurentia and its Asian counterparts (N China and Korea). These areas were then characterized by fairly shallow equatorial seas, whereas Baltica occupied higher latitudes with an epicontinental sea which for most of the time was deeper. We should therefore expect these scolopodontid conodonts to occur mainly in the regressive parts of the sequence in Baltoscandia.

The first regression that led to the introduction of scolopodontids in Baltoscandia was the Ceratopyge Regressive Event (CRE) of ERDTMANN (1986), also known as the Kelly Creek Eustatic Event based on Australian sections (NICOLL et al. 1992). During this major regression "*Oneotodus*" *variabilis* LINDSTRÖM, 1955 appeared in the *Paltodus deltifer* Zone in Sweden (cf. LINDSTRÖM 1955; LÖFGREN 1996). It has not been found in the top part of that zone, and was possibly replaced by a related taxon (LÖFGREN 1996: 181). "*Oneotodus*" *variabilis* also occurred in deeper water in Laurentia, as in western United States (J. REPETSKI, pers. comm. 1995), so this species may be a true immigrant to Baltoscandia. When analysed in detail, "*Oneotodus*" *variabilis* displays a seximembrate apparatus model (LÖFGREN, REPETSKI and ETHINGTON in manuscript) resembling that described by NICOLL (1994) in a (late) population of *Teridontus nakamurai* (NOGAMI, 1967) from Queensland, Australia. This is probably the basic type of apparatus structure in "scolopodontids".

Teridontus nakamurai gave rise to the *Semiacontiodus* lineage, the oldest species of which is *S. nogamii* MILLER, 1969 (MILLER 1980; JI & BARNES 1994a). The oldest elements of *Semiacontiodus* differ from those of *Teridontus* for instance in not being circular in cross-section (MILLER 1980) and in having a slightly expanded base and either well-developed shallow lateral grooves or a posterior carina (JI & BARNES 1994a). According to JI & BARNES (1994a) the *Semiacontiodus* lineage soon died out, having given rise in late Tremadoc times to the *Variabiloconus* and *Polycostatus* lineages both of which appear to have considerably more advanced apparatuses than *Semiacontiodus*. In the environmental analysis presented by JI & BARNES (1994b), *Variabiloconus* and *Polycostatus* were described as inhabiting shallower waters than did *Teridontus* and *Semiacontiodus*. It thus seems to me more convincing to consider that emigrant scolopodontids, like "*Oneotodus*" *variabilis* and the ancestors of later Baltoscandian scolopodontids, were direct descendents of *Teridontus* or *Semiacontiodus nogamii*. In fact, as will be seen below, there are reports of less advanced, *S. nogamii*-like elements from the Tremadoc and throughout the Arenig from various parts of the world that support this idea. In central North America, however, shallow-water scolopodontids with more derived apparatuses prevailed after the late Tremadoc.

After the deposition of the Ceratopyge Limestone (Björkåsholmen Formation) there were few incursions of scolopodontids in the central Baltoscandian sequence until the mid-Arenig, an exception being a few indeterminate elements of *Semiacontiodus* found in the lower *Paroistodus proteus* Zone at Storeklev at Hunneberg, Västergötland (LÖFGREN 1993: text-fig. 6).

In the early to mid-Arenig in Baltoscandia the scolopodontid niche in general was occupied by *Scolopodus rex*

LINDSTRÖM, with hyaline elements, possibly conspecific with *Scolopodus quadratus* PANDER (see FÅHRÆUS 1982), but probably not closely related to later scolopodontids such as *S. cornuformis*. According to the sea-level curve presented by NIELSEN (1992: text-fig. 1), the early Arenig up to approximately the lower *Paroistodus originalis* Zone is mainly characterized by a sea-level highstand.

There was a limited influx of scolopodontids (here referred to as *Semiacontiodus* sp. aff. *S. nogamii*) in the *Baltoniodus triangularis* and *B. navis* Zones at Lanna, Närke (LÖFGREN 1995: text-fig. 6), in phase 2 of the *Paroistodus originalis* Zone on Öland (LÖFGREN 1995: text-fig. 4), and phase 3 of the same zone at Leskusänget in Dalarna (LÖFGREN 1995: text-fig. 8). These are, indeed, intervals of transgression or relative highstand rather than regression, and few elements were actually found. These elements, however, seem to have belonged to the vanguard of a more enduring establishment of scolopodontids in Baltoscandia (cf. Text-fig. 1). Just below the base of the *Microzarkodina parva* Zone such populations (here referred to as *Semiacontiodus* cf. *S. cornuformis*) apparently evolved into *Semiacontiodus cornuformis*. That taxon then spread to other relatively shallow parts of the epicontinental sea during the *M. parva* Zone period and to areas with formerly deeper waters at the time of the lowstand at the base of the *Asaphus expansus* trilobite Zone (cf. NIELSEN 1992), approximately at the base of the *E.? variabilis* Zone (see discussion in LÖFGREN 1995: 706-707).

In the Gillberga section (N Öland), where the stratigraphic distribution of *S. cornuformis* has been studied in some detail, it is joined by a similar taxon, *Semiacontiodus davidi* n. sp., at the base of the *A. expansus* Zone. In a few samples found just below this level a probable ancestor of *S. davidi* occurs, here treated under the name of *Semiacontiodus* cf. *S. davidi*, that has elements of a simpler morphology than those of *S. cornuformis* and *S. davidi*. *Semiacontiodus davidi* and *S. cornuformis* co-occur through much of the upper part of the Gillberga sequence. In some of the sections from northern Sweden, which extend into even younger strata, *Semiacontiodus bulbosus*, a close relative to these two species, was found. A few specimens of probably related taxa, referred to as *Semiacontiodus*? sp. A and *Semiacontiodus*? sp. B were also found, and are described in the systematic section.

Element designations and apparatus reconstructions

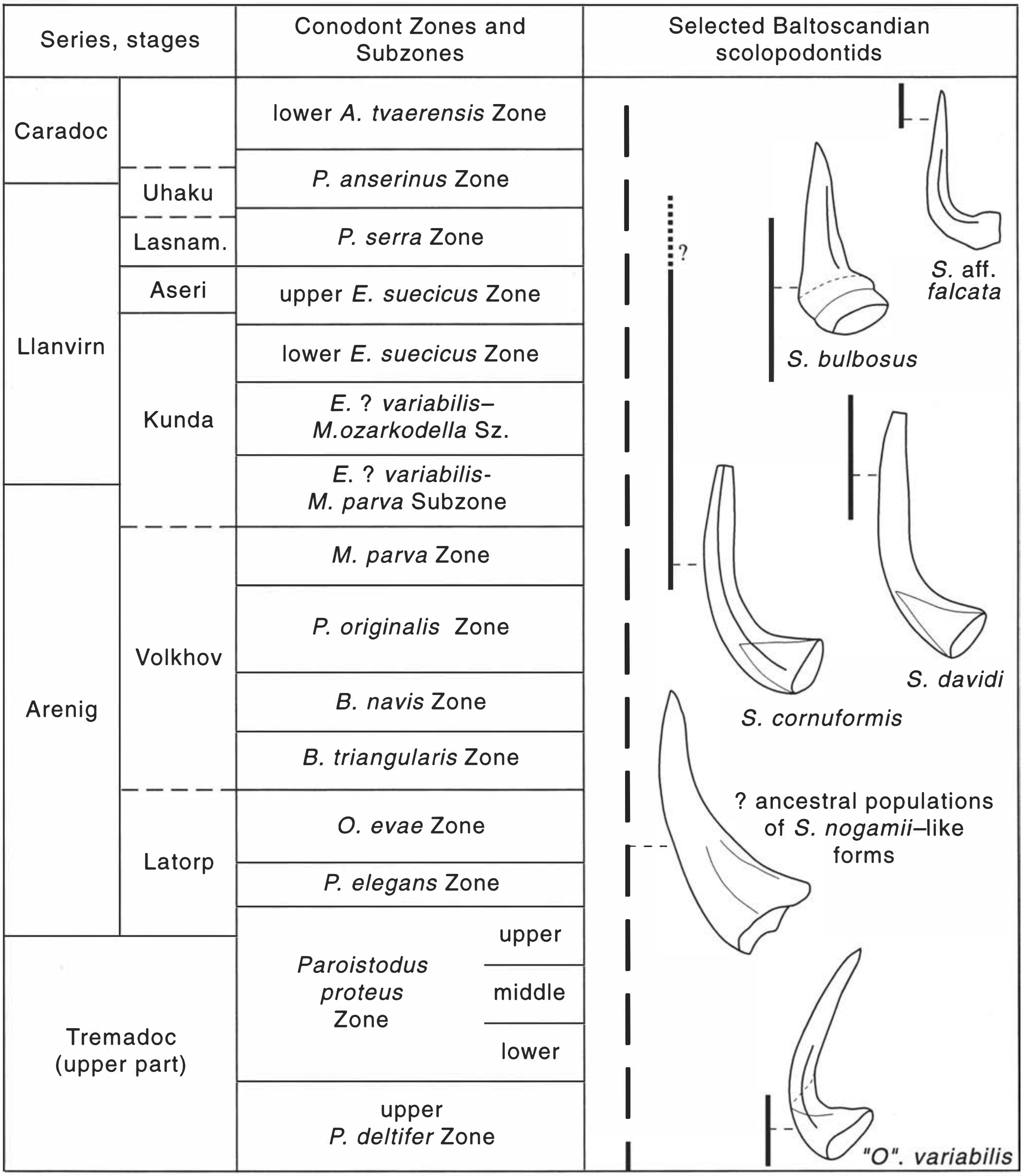
Among previously described apparatus designs for coniform elements, that suggested for *Teridontus nakamurai* (NOGAMI, 1967) by NICOLL (1994) best fits my collections of *Semiacontiodus cornuformis* and its closest relatives. NICOLL (1994) found a common pattern in the seximembrate apparatus design of *T. nakamurai* and other taxa with coniform elements referred to the Order Protopanderodontida as defined by SWEET (1988). It is also possible to find similarities of detail in the element types distinguished in these apparatuses and six of the seven element types in the earliest conodont genus with denticulated elements, *Cordylodus* PANDER, 1856, as described by NICOLL (1990). NICOLL (1990, 1994) thus used the same designations for these sets of elements and the same locational system (M, P and S) that had previously been used for later (prionioodontid) apparatuses (see SWEET 1988). It may not have been proved that element locations in some coniform and non-coniform apparatuses are sufficiently alike to permit the use of the same notational system for them. However, the similarities in apparatus structure between many early genera with coniform elements and those with non-coniform elements are so striking that I consider that this use is appropriate. Alternative systems (such as that of BARNES et al. 1979 and JI & BARNES 1994a) tend to obscure some obvious similarities which are traceable among the earliest of all conodont lineages and are probably thus fundamental. Consequently, I have used the same element designations here (cf. Text-fig. 2) for *Semiacontiodus cornuformis* and its closest relatives (e.g. *S. davidi* n. sp.) as NICOLL (1994) used for *Teridontus nakamurai*.

The six element types distinguished in these two species are: Sa, Sb, Sc, Sd, Pa and Pb. No M element has been found. The base is shorter in the Pa and Pb elements than in the S elements; the Pa element is more asymmetrical (concavo-convex) than the Pb element. The Sa element resembles the rest of the S-series, but there is no morphological intergradation with Sb or Sc elements. This condition seems to be intermediate between that in *Paltodus* LINDSTRÖM, 1971, for instance, where the erect Sa element is an entirely separate entity morphologically (see LÖFGREN 1997b for further description of the *Paltodus* apparatus) and *Paroistodus* LINDSTRÖM, 1971, where the recurved Sa element is clearly a morphologically integrated part of the S-series (see LÖFGREN 1997a for further description). The Sb and Sd elements are proclined with a long, straight base and the cusp twisted in relation to the base; the Sd element is the most asymmetrical. The Sc element is almost symmetrical with a suberect cusp. More detailed descriptions of each element appear under Systematic Palaeontology.

As noted by DZIK (1991: 288), the frequency of the symmetrical (Sa) element type seems to be too high in many collections of *Semiacontiodus* to represent only one medial location. A similar phenomenon was ascribed to the presence of two symmetrical element types in some species of the scolopodontid genera *Glyptoconus/Colaptoconus* KENNEDY, and *Striatodontus* JI & BARNES, 1994, by JI & BARNES (1994a).

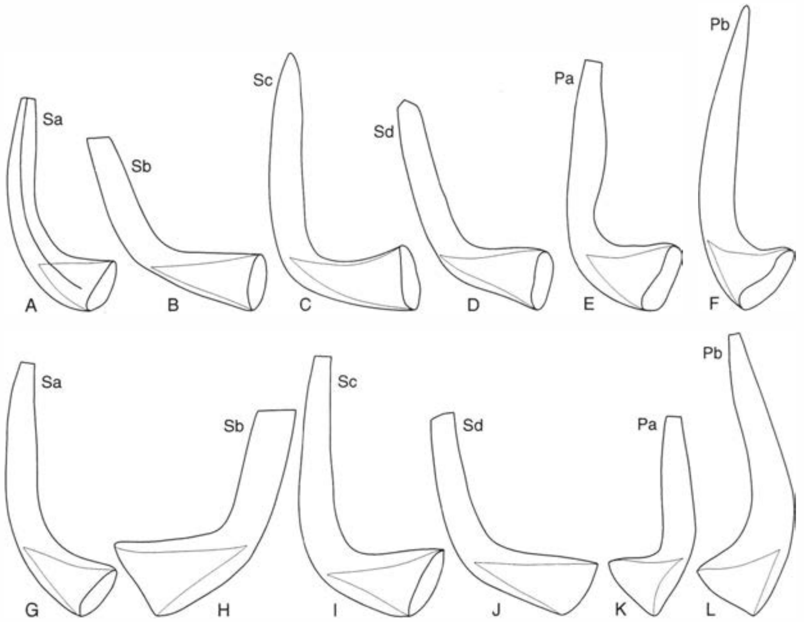
In my collections of *Semiacontiodus* the element ratios are variable. The proportion of Sa elements in particular varies widely between samples. This could to some degree be attributed to the more isolated position of the Sa element in the apparatus, suggesting that it may have had a separate taphonomic history from the rest of the apparatus. That this would almost invariably result in the overrepresentation of Sa elements, is, however, difficult to believe.

I have selected samples with many well-preserved elements as a basis for calculating the numerical proportions between the element types. The best numerical fit for most samples is with two Sa elements, and I have tentatively included this as a possibility for the apparatus reconstruction. NICOLL (1994: 371), however, only recovered sufficient Sa elements from his collection of *Teridontus nakamurai* to account for one Sa element in each apparatus. In most of my samples the Sb+Sc+Sd elements were not sorted separately, but where I did this there were about the same number of Sb elements as Sc and Sd elements taken together. The higher proportion of Sb elements is consistent with that found in apparatuses of *Paroistodus* LINDSTRÖM, 1971, for instance (apparatus reconstruction according to LÖFGREN 1997a).



Text-fig. 1: Stratigraphic relations between Baltoscandian scolopodontids. Note that in the "Series, stages" column, the modern British usage (FORTEY et al. 1995) has been used, extending the Llanvirn upwards to include the former Llandeilo Stage as well.

Among the selected samples, Öl87-4 from Gillberga is typical of *Semiacontiodus davidi* with 45 Pa, 82 Pb, 32 Sa and 158 Sb+Sc+Sd elements, corresponding to 2 Pa, 4 Pb, 1 (or 2)Sa, 4 Sb, 2 Sc and 2 Sd elements. In the sample that yielded the type of the species, HK88-2 from Hällekis, the proportions are almost the same: 23 Pa, 73 Pb, 18 Sa and 108 Sb+Sc+Sd elements. Sample Öl94-201 from Gillberga is typical of *S. cornuformis* with 93 Pa, 157 Pb, 83 Sa and 403 Sb+Sc+Sd elements, corresponding to a proportion of 2 Pa, 4 Pb, 2 (or 1) Sa, and 10 (or 8) Sb+Sc+Sd elements. As regards the other taxa dealt with here, too few elements were retrieved to justify any calculation of element proportions.



Text-fig. 2: Sketches of *Semiacontiodus* elements traced from camera lucida drawings. All x90. **A–F**: *Semiacontiodus cornuformis* from sample Öl87-3, middle part of the *E.*? *variabilis–M. parva* Subzone, Gillberga quarry, Öland. **A:** LO 7787t; **B:** LO 7788t; **C**: LO 7789t; **D**: LO 7790t; **E**: LO 7791t; **F**: LO 7792t. **G–L**: *Semiacontiodus davidi* from sample HK88-2, *E.*? *variabilis–M. parva* Subzone, Hällekis quarry, Västergötland. **G:** LO 7793t; **H:** LO 7794t; **I**: LO 7795t; **J**: LO 7796t; **K**: LO 7797t; **L**: LO 7798t.

Distribution of *Semiacontiodus cornuformis* in Baltoscandia and other areas

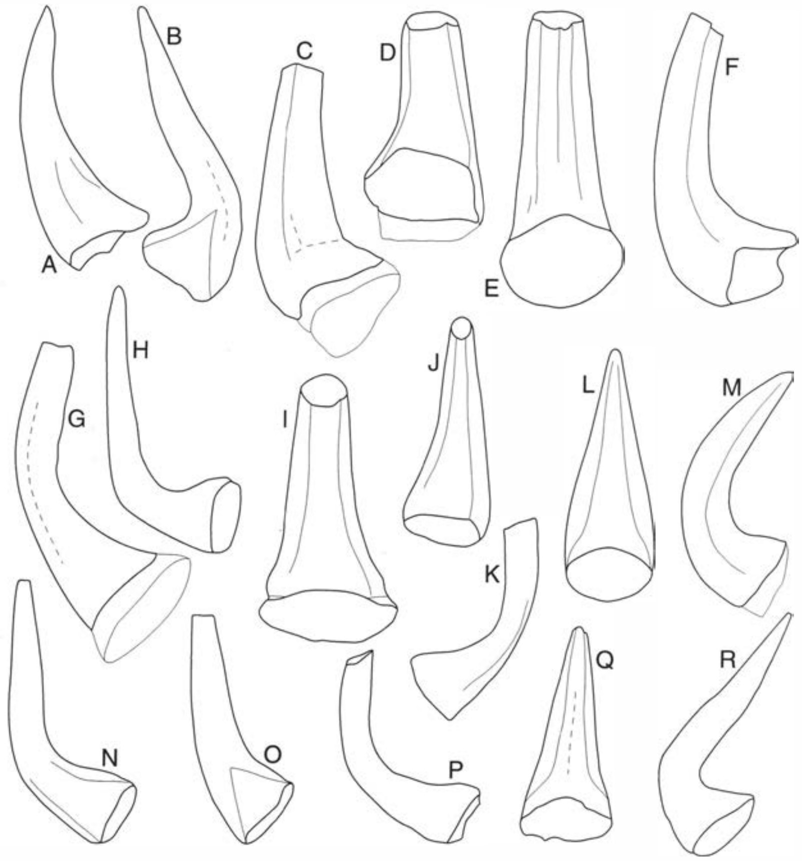
In addition to comparing the structure of the apparatus of the *S. cornuformis* lineage with that of similar, possibly related, taxa it is necessary to investigate its stratigraphic and geographic occurrence in as much detail as possible so that the phylogeny can be correctly interpreted. I have therefore examined the literature and also searched through my own extensive collections of Lower Ordovician conodonts for first occurrences of this species and related taxa as well as for unusual, "out of normal range", occurrences that could reveal dispersal patterns within the scolopodontid group. Occurrences within Baltoscandia will be dealt with first, followed by reports from other parts of the world.

There is perfect, or virtually perfect, correspondence between the first appearance of *S. cornuformis* and that of *Baltoniodus norrlandicus* in all sections I have investigated, including those from Jämtland in the west. RASMUSSEN (1994) reported the same phenomenon from one of his Jämtland sections (Andersön A) in the easternmost part of the allochthonous succession. Further to the west, however, (Andersön B, Steinsodden, in RASMUSSEN 1994) and in the Slemmestad section in the Oslo region (RASMUSSEN 1991) there is an obvious gap in time between the first appearance of *B. norrlandicus* and that of *S. cornuformis*. Caution should thus be observed in using the first appearance of *S. cornuformis* as a stratigraphic marker. The type of potential miscorrelation would be an overestimation of the time of first appearance in areas with an initial deep-water setting. Is there a similar risk of underestimating the time of first occurrence in shallow-water environments? "*Scolopodus cornuformis* SERGEEVA" and similar taxa have in fact been reported from many areas outside Baltoscandia and from beds usually older than those normally yielding this taxon.

One of the forms most closely resembling *S. cornuformis* that has been reported from outside Baltoscandia is *S. cornuformis* from S China (Text-fig. 3G–K), illustrated by AN (1987: pl. 7 figs. 10, 11, 13–16), from beds of approximately the same age as those of the *Baltoniodus navis* Zone (lower Volkhov). The Chinese specimens represent at least three element types and differ only slightly from Baltoscandian elements from the upper Volkhov, though their bases are more bulbous. Without access to the specimens it is impossible to say whether there are other differences and whether the entire set of elements closely resembles that of the Baltoscandian species.

SEO et al. (1994) reported *Scolopodus cornuformis* SERGEEVA from even older beds in Korea that have been interpreted as corresponding to the *O. evae* Zone. The specimens illustrated show less resemblance to Baltoscandian *S. cornuformis* than the Chinese specimens discussed above, in that the lateral grooves are deeper and the carinae sharper (Text-fig. 3C). They are probably not conspecific with *S. cornuformis*.

"*Semiacontiodus*" *cornuformis* (SERGEEVA, 1963) sensu LEHNERT (1995) from Argentina as well as *Scolopodus euspinus* JIANG & ZHANG, 1983 and *Scolopodus opimus* JIANG (Text-fig. 3D), both sensu AN & ZHENG (1990) from N China are probably *not* closely related to *S. cornuformis* in the sense used here. The most obvious difference is that all or most of the elements illustrated by LEHNERT (1995) and AN & ZHENG (1990) seem to be provided with a fairly deep, *Panderodus*-type lateral groove. A similar specimen (here called *Semiacontiodus?* sp. B) was found in the *M. parva* Zone at Gullhögen (Skövde). Alternatively, it is possible to place such forms at or near the origin of *Panderodus*.



Text-fig. 3: Scolopodontid specimens redrawn from previously published reports. Not to scale. **A–B**: *Semiacontiodus nogamii* MILLER (from MILLER 1980: pl. 2 figs. 10, 12 and text-fig. 4W); Sa and ?Pa elements with "generalized" appearance. **C**: "*Scolopodus cornuformis* SERGEEVA" (from SEO et al. 1994: text-fig. 10:37); Sa element with sharp lateral carina. **D**: *Scolopodus opimus* JIANG (from AN & ZHENG 1990: pl. 2 fig. 18); Sa element with deep lateral groove. **E–F**: "Scolopodiform D" (from ETHINGTON & CLARK 1982: text-fig. 30); Sa element with deep posterior groove. **G–K**: "*S. cornuformis* SERGEEVA 1963" (from AN 1987: pl. 7 figs. 10–11, 13–14, 16); ?Sb, ?Pa and Sa elements; probably homeomorphs of elements of the Baltoscandian taxon. **L–M**: "Scolopodiform F" (from ETHINGTON & CLARK 1982: text-fig. 32); Sa element with wide lateral "wings". **N–O**: *Semiacontiodus carinatus* DZIK (from DZIK 1976: text-figs. 13n, o); ?Sd and ?Pa elements of taxon resembling *S. davidi* n. sp. **P–R**: "*Staufferella* sp." (from BAUER 1987: pl. 5 figs. 12–14), ?Sb, Sa and Pa elements resembling those of *Semiacontiodus cornuformis*.

Another report of "*S.*" *cornuformis* from Argentina is more problematic. The specimen illustrated (ORTEGA et al. 1995: pl. 5 fig. 13) is far from typical but could lie just within the limits of variation for the Baltoscandian taxon. The Argentinian specimens were found co-occurring with *Ansella jemtlandica*, *Periodon flabellum* and others in an interval interpreted as uppermost Arenig. They thus probably lie within the stratigraphic range of *S. cornuformis* in Baltoscandia.

From Canada *Scolopodus* sp. aff. *S. cornuformis* was reported by FÅHRÆUS & ROY (1993). The specimens, from the upper Tremadoc, are morphologically simple. They may not be particularly closely related to Baltoscandian forms, but show that populations of this kind were present in western Newfoundland.

BAUER (1987) described specimens referred to *Staufferella* sp. from beds of *Pygodus serra* Zone age from the Mc Lish and Tulip Creek Formations in Oklahoma. The specimens illustrated could lie within the limits of variation of *S. cornuformis* (Text-fig. 3P–R), although the posterior groove in the Sa element appears to be deeper than in the corresponding Baltoscandian elements that I have seen.

Scolopodus paracornuformis ETHINGTON & CLARK, 1982 from the Wah Wah Formation in Utah resembles the morphologically simple immediate predecessors of *S. cornuformis* in Baltoscandia and is probably only slightly older than these. Only the Sa element has been identified, and was described as "unquestionably hyaline throughout" (ETHINGTON & CLARK 1982: 102). I therefore regard it as not conspecific with *S. cornuformis*, but rather as a possible ancestor.

Some other forms resembling *S. cornuformis* were described and illustrated as "Scolopodiform D" (Text-fig. 3E–F) and "Scolopodiform F" (Text-fig. 3L–M) from the Pogonip Group in Utah (ETHINGTON & CLARK 1982). Both forms represent Sa elements, but "D" seems to have deeper posterior grooves and "F" wider lateral carinae than the Baltoscandian taxon.

Other taxa that are morphologically less differentiated are *Scolopodus staufferi* (FURNISH, 1938) sensu DRUCE & JONES (1971) from the upper Tremadoc of Queensland, Australia, and *Scolopodus acontiodiformis* REPETSKI, 1982 from pre-*O. evae* Zone, Arenig strata of the El Paso Group in Texas and New Mexico. They less obviously resemble the Baltoscandian forms than *S. paracornuformis* does, but are nevertheless interesting in that they demonstrate the continued presence of populations with simple morphologies from the Tremadoc into the Arenig.

Australian counterparts to *S. cornuformis* were reported by COOPER (1981) from the mid-Arenig Horn Valley Siltstone of central Australia, some as *Protopanderodus primitus* DRUCE and some as *Scalpellodus latus* (van WAMEL), and from slightly younger beds (mid- to late Arenig) in the Georgina Basin of central Australia as "conical elements" by STAIT & DRUCE (1993). However, none of these resemble the Baltoscandian taxon as closely as some of the North American taxa treated above.

My conclusion is that the presumed transition from *Semiacontiodus* cf. *S. cornuformis* to *S. cornuformis* observed in the Gillberga sequence probably represents the "birth" of *S. cornuformis*, while reports of occurrences in older beds refer to homeomorphs. The younger Baltoscandian scolopodontid taxa have not been reported from other realms, so they, too, must be considered indigenous, a possible exception being *Semiacontiodus* aff. *falcata* from the Caradoc, but this taxon lies outside the scope of this report.

Environmental preferences of Baltoscandian scolopodontids

As discussed in connection with the geographical distribution of *Semiacontiodus cornuformis*, most scolopodontids are considered as having preferred shallow-water settings. A possible exception is *Scolopodus rex* LINDSTRÖM, 1955 (sensu lato) which occurs rarely from the uppermost *P. proteus* Zone (Talubäcken section, see BERGSTRÖM 1988), and in Sweden more commonly from the *O. evae* Zone onwards. What is probably the same taxon has also been found in western U.S.A. (ETHINGTON 1972) and in Korea (SEO et al. 1994) and it thus appears to be widespread. In Baltoscandia the elements are consistently hyaline.

In the *O. evae* Zone and the *B. triangularis* and *B. navis* Zones *S. rex* attains its highest frequencies, though the relative abundance rarely lies above 3%. Some of the faunas richest in *S. rex* come in fact from my Jämtland sections (LÖFGREN 1978). In the *P. originalis* Zone, *S. rex* becomes even less common, rarely attaining a relative abundance of 1%, four samples from Jämtland with c. 2.5% being among the few exceptions.

At the beginning of its stratigraphic range *Semiacontiodus cornuformis* sometimes alternates with *S. rex* from sample to sample. The two taxa co-occur in a few samples, as in Öl94-7, Öl94-6 and Öl93-1 from the base of the *M. parva* Zone at Gillberga. No specimens of *S. rex* were found at Gillberga above the *Scalpellodus latus* - *S. gracilis* boundary (within the *M. parva* Zone), nor in the Tamsalu and Finngrundet drill cores or the sections at Kårgärde and Gullhögen (Skövde). At Lanna, Hällekis and Leskusänget and in the Jämtland sections investigated, *S. rex* was not found above the *P. originalis* Zone. Nor were any specimens of *Scolopodus rex* found in the few samples of appropriate age investigated by RASMUSSEN (1991, 1994) from more westerly sections in Sweden and in Norway.

If *S. rex* can be considered a Baltoscandian counterpart to the Laurentian scolopodontids, its ecological requirements appear to differ slightly. The geographical range seems to be wider than that of *S. cornuformis*. These differences are perhaps connected with the histology of its elements.

Hyaline elements have been considered to be particularly common in some extreme environments, such as those with very high salinity. Since such environments are almost invariably associated with high water temperatures, it is possible that it is the higher temperature rather than the degree of salinity that favours the occurrence of conodonts with hyaline elements, in which case it could explain why pelagic taxa with hyaline elements could thrive in shallow waters as well as in more open oceanic environments. Some such taxa are among the most widespread in the upper part of the Lower Ordovician. BARNES & FÅHRÆUS (1975) interpreted some conodonts with hyaline elements as euryhaline, which accords well with this suggestion. Among scolopodontid taxa there is a mixture of genuinely hyaline forms such as *S. rex*, and those that are almost entirely albid such as *Glyptodontus* JI & BARNES, 1994a. According to JI & BARNES (1994a: 60) *Semiacontiodus nogamii* (Text-fig. 2A–B) has albid elements. In adult specimens of *Semiacontiodus cornuformis* and *S. davidi* the elements are of intermediate type. In my collections the immediate ancestors of *S. cornuformis* and of *S. davidi* tend to have hyaline elements, which could, however, be attributed to the fact that many of them are not fully mature. On the whole it seems as if many species with hyaline elements were more widespread than those with genuinely albid ones, and this applies not only to scolopodontids. It would not be surprising, therefore, if the immigrant predecessors of *S. cornuformis* and *S. davidi* proved to have had hyaline elements. It should also be noted that at least one of the Arenigian scolopodontids from North America with less specialized morphology, *Scolopodus paracornuformis*, was described as having thoroughly hyaline elements (ETHINGTON & CLARK 1982).

Frequencies of *S. cornuformis*

The appearance of the direct predecessors of *S. cornuformis* in phase 2 of the *P. originalis* Zone (see LÖFGREN 1995), an interval of deepening water or increased oceanic influence, is followed by the establishment of the lineage under shallower-water conditions. It is notable that during the "founding interval", the *Periodon*-yielding (presumedly deeper water) samples Öl88-1 and -2 (cf. LÖFGREN 1995: text-fig. 4) at Gillberga lack *Semiacontiodus* cf. *S. cornuformis*.

Initially, relative frequencies of *S. cornuformis* were low, not exceeding 5% until c. 0.3 m below the lower boundary of the Kunda (*A. expansus* trilobite Zone) at Gillberga. About 0.5 m higher up it attains c. 10% in a few of the samples. From about 2.5m above the lower boundary of the Kunda relative abundance almost invariably exceeds 13% in the samples, with a maximum of 32.4% in Öl93-10C at the top of an interval where the relative frequencies of *S. cornuformis* generally exceed 25%, but where *S. davidi* is lacking. NIELSEN's (1992) sea-level curve indicates extreme lowstand during the early Kunda, except for a brief highstand in the early Llanvirn.

The highest absolute frequencies of *S. cornuformis* at Gillberga are found in samples from the upper (Llanvirnian) part of the section, such as sample Öl93-9 from the just described interval that lacks *S. davidi*, where the relative frequency is c. 27% and the absolute abundance about 1,000 specimens per kg rock. Another example is Öl74-100 from a level at the beginning of the range of *Microzarkodina ozarkodella*, where the relative frequency of *S. cornuformis* is c. 24% and the absolute abundance about 1,000 specimens per kg rock.

In the Kårgärde and Rävanäs sections from Dalarna and in my sections from Jämtland, *S. cornuformis* rarely attains a frequency of 10% except in one sample from Kårgärde (H11) where it made up almost 20%. In samples from the Finngrundet core most of the frequencies of *S. cornuformis* are slightly higher though they only occasionally reach 20%. In the more westerly sections from Västergötland, Gullhögen (Skövde) and Hällekis, the abundance of *S. cornuformis* was well below 10% in all the samples investigated, generally below 5%.

Semiacontiodus plays a part in the characterization of the shallowest biofacies distinguished by RASMUSSEN (1994) and RASMUSSEN & STOUGE (1995). The Correspondence Analysis technique used by them does not, by definition, allow samples other than those used in the original calculation to be included. Some informal comparisons can, however, be of interest.

The shallowest of RASMUSSEN & STOUGE's (1995) biofacies types is the *Scalpellodus* biofacies with 5–10% *Semiacontiodus cornuformis*. At most, 5 of the 55 samples from Gillberga which are young enough to have the potential to be assigned to that biofacies can be placed there. All of these 5 samples are near the lower Kunda boundary (*A. expansus* Zone). *Baltoniodus* makes up more than 20% in most of my Gillberga samples, which agrees with the characterization of the *Baltoniodus* biofacies of RASMUSSEN & STOUGE (1995) in general terms (high frequency of *Baltoniodus*; usually 20–40%). However, their biofacies model cannot be directly applied to the Gillberga section. Most environments represented there probably lie within the shallowest part of the biofacies spectrum of RASMUSSEN & STOUGE (1995) or may be even shallower.

Most of the samples from Gillberga that have yielded *Semiacontiodus davidi* represent a biofacies that is probably shallower than any of those described by RASMUSSEN & STOUGE (1995) for the Baltoscandian platform margin in western Jämtland and in Norway. Samples with *S. davidi* generally contain between 10 and 30% of *S. cornuformis*, which holds for the Estonian samples and for the samples from Skövde, Kårgärde, Rävanäs and Leskusänget as well. *Semiacontiodus davidi* thus seems to characterize a fairly distinct biofacies in a shallow, but not extremely shallow, marine environment. In the samples from Kinnekulle (Hällekis) high frequencies of *S. davidi* are associated with frequencies of *S. cornuformis* below 5%, indicating a separate kind of occurrence there, possibly coupled with a more "oceanic" location. Also, except for 2 samples from Estonia, 4 out of 35 from Gillberga and 1 from Kårgärde, the samples that include *S. davidi* all yielded more than 7% of *Drepanoistodus basiovalis*. Of even greater significance, samples that contained less than 7% of *D. basiovalis* lacked *S. davidi* even when *S. cornuformis* made up between 10 and 30%.

Summing up, *Semiacontiodus* appears to characterize some fairly shallow to shallow biofacies types on Öland. The investigation of differences in frequency at species level also appears to be of value in detecting variations in biofacies. In addition, other factors have probably influenced the Öland biofacies as much as, or more than, water depth.

Generic and suprageneric assignment of the Baltoscandian scolopodontids

The Baltoscandian scolopodontids differ from typical albid coniforms of Baltoscandia, as for instance *Paroistodus*, in having elements with thicker-walled bases that are rarely laterally compressed. In this they somewhat resemble some early albid or hyaline Laurentian taxa whose apparatus also typically lacks the M element. As we have seen, it is probable that these Baltoscandian scolopodontids were derived from *Semiacontiodus* immigrants from Laurentia with simple element shapes and an apparatus design resembling that of *Teridontus nakamurai*. However, according to JI & BARNES (1994a) *Semiacontiodus* became extinct in the late Tremadoc and was replaced by descendants with more specialized element types in the Laurentian realm. Could any of these genera also have included the Baltoscandian scolopodontids?

One of these Laurentian genera, *Colaptoconus* KENNEDY, 1994 (formerly *Glyptoconus* KENNEDY, 1980) has prominently grooved, finely striated elements. The numerous species of this genus described in detail by JI & BARNES (1994a) all have at least one element type with deeper grooves and/or sharper costae than in any of the Baltoscandian forms found so far. According to JI & BARNES' (1994b) environmental analysis, *Colaptoconus* was typically peritidal, thus occupying a habitat that differed considerably from those normally provided by the Baltoscandian sea which were on the whole much deeper. It also seems less probable that a conodont taxon specialized for life in warm shallow seas would migrate to deeper, colder waters and there revert to forms with more simply shaped elements like those of its ancestors. By reasoning along similar lines, *Polycostatus* and probably also *Variabiloconus* can be excluded from the ancestry of "*Scolopodus*" *cornuformis*. There are also some other, mainly Laurentian, genera which may or may not be closely related to "*S.*" *cornuformis*.

ETHINGTON & AUSTIN (1991) discussed various scolopodid and similar genera and assigned *S. cornuformis* SERGEEVA to *Parapanderodus* STOUGE, 1984. However, the type species of *Parapanderodus*, *P. arcuatus*, includes elements with a narrow, deep *Panderodus*-like posterior groove, whereas no elements of *S. cornuformis* or its close relatives have such a groove. Even though they have symmetrical element types that are morphologically close, I consider it warrented to retain *P. arcuatus* and *S. cornuformis* in separate genera.

Aloxoconus SMITH, 1991, is another Lower Ordovician "scolopodontid" genus that must be considered. Only one element type (symmetrical) can with certainty be distinguished in species of *Aloxoconus* (SMITH 1991). These elements have deeper posterior grooves than any of the Baltoscandian forms under consideration.

Lumidens ETHINGTON, DROSTE & REXROAD, 1986, is a Middle Ordovician taxon with hyaline elements (symmetrical and asymmetrical) which from the published illustrations appear to have sharper "marginal shoulders" (lateral carinae) than the Baltoscandian scolopodontids. From their association with other conodont taxa and the rock types in which they were found it can be deduced that these elements derive from deposits laid down in extremely shallow water (ETHINGTON et al. 1986). It is thus hardly likely that *Lumidens* is closely related to Baltoscandian taxa.

The name *Staufferella* was first given by SWEET, THOMPSON & SATTERFIELD (1975) to apparatuses including symmetrical elements with "basally alate lateral costae", as well as slightly asymmetrical and decidedly asymmetrical element types, all with faint longitudinal striations. It is obvious that this description fits at least some Baltoscandian forms reasonably well. However, few if any collections with a fair number of all element types of the type species of *Staufferella*, *S. falcata* (STAUFFER, 1935), have been described. It is thus almost impossible to decide whether *Staufferella* had a reduced (3-element) apparatus or whether in fact it has a "full" set (6 element types) as, for instance, *S. cornuformis* has. In addition to this, the most characteristic element type (Sa) of *S. falcata* is provided with wide lateral costae on the base, a feature lacking in the Baltoscandian scolopodontids under consideration. It would perhaps be better to treat *Staufferella* as another specialized Laurentian taxon, and somewhat similar forms in Baltoscandia, such as "*Distacodus*? *falcatus*" of BERGSTRÖM (1962) (= *Semiacontiodus* aff. *falcata* in Text-fig. 1), as homeomorphs.

This leaves us, as far as I can see, with *Semiacontiodus* as the only available alternative name for apparatuses with a "full" set of fairly simple elements (6 element types) like those from Baltoscandia discussed here. DZIK (1991, 1994) also preferred this generic designation for these forms.

Semiacontiodus was originally described as a subgenus of *Acontiodus* PANDER. LINDSTRÖM (1973) ranked it as a genus and this procedure has been followed by most subsequent authors. MILLER (1980) emended the diagnosis to include conodonts with an albid cusp, and an apparatus consisting of antero-posteriorly slightly compressed symmetrical elements as well as asymmetrical elements with a costa on one side. JI & BARNES (1994a) emended the diagnosis to include four element types: two symmetrical types (a and c), one asymmetrical element type with a lateral costa (b), and one asymmetrical element type with a compressed, keeled cusp (e).

It is not entirely clear how this arrangement could be reconciled with the apparatus reconstruction that I favour for Baltoscandian scolopodontids. However, only one element type (c) of JI & BARNES (1994a) appears to be entirely symmetrical and thus a candidate for the Sa position. Possibly, the a elements of JI & BARNES (1994a) in *S. nogamii* match the Sb+Sc+Sd series in my interpretation of *S. cornuformis*, while their b and e elements could represent Pb and Pa elements.

The difficulty of comparing *S. cornuformis* element by element with *S. nogamii* may simply be an indication that the latter is too advanced morphologically to be an ancestor of the *S. cornuformis* lineage whose origins should then be sought closer to *Teridontus*. Alternatively, Baltoscandian scolopodontids may in actual fact differ too much from their putative Laurentian ancestors to allow them to be included in any genus based on a Laurentian species. This would require giving them a new generic name as suggested by STOUGE & BAGNOLI (1990). In my opinion, however, representatives of the Baltoscandian *S. cornuformis* lineage sufficiently resemble Laurentian representatives of *Semiacontiodus* in general element morphology to allow them to be retained in the same genus, at least until differences in their apparatus architectures can be demonstrated.

The suprageneric assignment of the Baltoscandian scolopodontids is also somewhat problematic. If they are placed in *Semiacontiodus* they would be classified together with older taxa such as *Oneotodus* and *Monocostodus* in Oneotodontidae MILLER, 1981. If instead they are placed together with younger taxa such as *Scolopodus* and *Staufferella* they would belong in Scolopodontidae BERGSTRÖM, 1981. A third possibility is to put them in Protopanderodontidae LINDSTRÖM, 1970, to which SWEET (1988) referred among others *Oneotodus, Monocostodus, Semiacontiodus, Staufferella, Variabiloconus* and *Glyptoconus* (now *Colaptoconus*) together with *Protopanderodus*. DZIK (1991) also included *Drepanodus* in Protopanderodontidae. This association is probably too extensive to be phylogenetically meaningful. I thus prefer to regard *Semiacontiodus* (as interpreted here) as belonging to Scolopodontidae together with *Scolopodus* and *Staufferella*, for instance.

Systematic Palaeontology

Scolopodontidae BERGSTRÖM, 1981

Semiacontiodus MILLER, 1969

Type species (by original designation): *Acontiodus (Semiacontiodus) nogamii* MILLER, 1969.

Semiacontiodus bulbosus (LÖFGREN, 1978)

Text-fig. 1

1974 *Scolopodus cornuformis* SERGEEVA. – VIIRA, Ordov. Conod. E Baltic: text-fig. 161 É.

1978 *Scolopodus bulbosus* n. sp. LÖFGREN, Jämtland conod.: 107, pl. 7 figs. 7–8, pl. 8 figs. 3A–B.

Description: The holotype is an Sa element and the additional material studied adds nothing to the previous description of this element type (LÖFGREN 1978: 107). The Sa element is the most characteristic, with a short, straight, stout cusp without lateral grooves or sharp edges, but with a shallow posterior groove. Most of the "scandodontiform" elements of LÖFGREN (1978) are either Pa or Sd elements, which have the most conspicuous lateral flange on the cusp starting abruptly above the point of maximum curvature, and displaced to the inner side in Pa elements (e.g. pl. 8 fig. 3B in LÖFGREN 1978) and to the outer side in Sd elements (e.g. pl. 8 fig. 3A in LÖFGREN 1978). The other element types are less characteristic; most of them were erroneously referred to *S. cornuformis* in LÖFGREN (1978), and 49 specimens previously reported as belonging to that species have been reassigned to *S. bulbosus* here (see below). In the two samples from Kårgärde (DLK86-H1 and Vg90-3) that have provided the additional material of *S. bulbosus* for this investigation *S. cornuformis* is lacking, so the characteristics of all element types of *S. bulbosus* can be more precisely defined.

In both Pa and Pb elements the base is short. The Pa element is the more concavo-convex of the two, with a faint anterior edge displaced to the inner side and a more distinct lateral flange on the cusp. The cusp of the Pb element is straighter and the base almost symmetrical, but there is a laterally directed flange on the (presumed) inner side of the cusp. Sb, Sc and Sd elements are more difficult to differentiate; the base is shorter and more bulbous than in the homologous elements of *S. cornuformis*, and the posterior edge of the cusp has a flange displaced to the outer side (but posteriorly directed). The cusp of the Sc element is almost erect and the element is subsymmetrical. The Sd element has the most pronounced flange and is distinctly asymmetrical.

Discussion: *Semiacontiodus longicostatus* (DRYGANT, 1974) is a similar, slightly younger taxon in which the Sa element also lacks lateral alae (grooves and carinae; DZIK 1994: 67). All element types of this taxon illustrated by DZIK (1994) have wrinkles on the base, and since this is never so in my *S. bulbosus* collections, there is good reason to treat them as belonging to a separate, although probably closely related species. The lateral flange in Pa and Sd elements also seems to be more sharply delimited proximally in *S. bulbosus* than in *S. longicostatus*. Faunas from the upper Llanvirn need to be studied in greater detail so that the exact relationship between *S. bulbosus* and *S. longicostatus* can be determined. They are either ancestor and descendant, or both daughter species of *S. cornuformis*.

Occurrence: Middle Llanvirn.

Material: From Kårgärde 131 specimens: 25 Pa, 19 Pb, 8 Sa, 79 Sb+Sc+Sd elements. From Jämtland (LÖFGREN 1978) 213 specimens: 45 Pa, 21 Pb, 39 Sa, 108 Sb+Sc+Sd elements.

Semiacontiodus cornuformis (SERGEEVA, 1963)

Pl. 1 figs. 1–6, 8, 10–14, 16–19, 23–24; text-figs. 1, 2A–F

1963 *Scolopodus cornuformis* sp. nov. SERGEEVA, Leningrad region conod.: 93, pl. 7 figs. 1–3; text-fig. 1.
1978 *Scolopodus cornuformis* SERGEEVA. – LÖFGREN, Jämtland conod.: 105–107, pl. 7 figs. 1–6, 9–12, pl. 8 figs. 1–2, 4–6 (with synonymy to 1978).
? 1987 *Scolopodus cornuformis* SERGEEVA. – AN, South China conod.: 183, pl. 7 figs. 10-11, 13-16.
1990 "*Semiacontiodus*" *cornuformis* (SERGEEVA). – STOUGE & BAGNOLI, Hagudd. (Öland) conod.: 26, pl. 9 figs. 14–18, 20–25.
1991 *Semiacontiodus cornuformis* (SERGEEVA 1963). – DZIK, Evol. Oral app.: text-fig. 7A.
non 1991 *Parapanderodus cornuformis* (SERGEEVA). – ETHINGTON & AUSTIN, Dounans Ls conod.: pl. 1 figs. 2, 9.
1994 *Semiacontiodus cornuformis* (SERGEEVA, 1963). – DZIK, Mojcza Ls conod.: 66, pl. 13 figs. 7–10, text-fig. 7a.
non 1995 "*Semiacontiodus*" *cornuformis* (SERGEEVA 1963). – LEHNERT, Argentina conod.: 125, pl. 7 fig. 22, pl. 8 fig. 5, pl. 9 figs. 14, 21–22, pl. 12 figs. 18–19, 21, 23–24.
1997 "*Semiacontiodus*" *cornuformis* (SERGEEVA, 1963). – BAGNOLI & STOUGE, Horns Udde (Öland) conod.: 159.

Element descriptions: Much of the basic morphology and variation in elements of *S. cornuformis* has already been described by LÖFGREN (1978). The following is an update according to a seximembrate apparatus plan, and based on more material from a number of areas in Sweden (and the Tamsalu drill-core, Estonia).

Sa element: The cusp is proclined to slightly recurved with a rounded anterior face (Pl. 1 fig. 2). There is a lateral groove on each side, posteriorly directed, not quite reaching the aboral margin, and delimited in anterior direction by a carina (Pl. 1 fig. 10). The posterior side is flat to rounded basally, in some specimens even with a weak central groove; on the cusp the posterior margin becomes sharper. The elements are fairly variable in length of base, inclination of cusp and in depth of lateral grooves, which with some exceptions become more pronounced in stratigraphically younger forms.

Sb element: Cusp proclined to almost erect, less than twice the length of base with a sharp posterior margin distally which is slightly twisted to the outer side (Pl. 1 fig. 1). The base of the stratigraphically younger specimens is generally shorter and the posterior edge of the cusp more "wing-like" (Pl. 1 fig. 13).

Sc element: Cusp erect, about twice as long as the base with a fairly sharp posterior margin distally which in most specimens is not developed into a "wing" (Pl. 1 figs. 6, 18). The element is almost symmetrical except in that the inner side of the base is slightly flatter than the outer one.

Sd element: Cusp fairly strongly proclined, less than twice as long as the length of base, with a sharp posterior "wing-like" edge displaced to the outer side (Pl. 1 fig. 4). The element is more twisted, i.e., more asymmetrical than the Sb element which it resembles.

Pa element: Cusp recurved, usually 2–3 times longer than the base, laterally compressed, and with a posterior "wing-like" extension distally, directed outwards (Pl. 1 fig. 11). The base is rounded anteriorly and posteriorly at the aboral margin. The anterior margin of the base can be quite sharp and is often slightly flexed to the inner side.

Pb element: Cusp proclined to erect, 2–3 times longer than the base, rounded anteriorly and with a sharp posterior edge, slightly displaced to the outer side, but without a "wing-like" extension (Pl. 1 fig. 19). Posterior half of cusp usually delimited by a faint longitudinal groove on each side (Pl. 1 fig. 3). Anterior margin meeting aboral margin at an angle of about 90°. Oral margin rounded in side view, meeting the aboral margin at an acute angle.

Microstructure: Elements of *S. cornuformis* have a micro-ornamentation of fibre-like striae except anteriorly, as described by LÖFGREN (1978: 106). This surface pattern is visible in most of the specimens of *S. cornuformis* illustrated in Pl. 1, and can also be discerned in the other, closely related, taxa in Pl. 1 and Pl. 2. It is also possible to observe this fine striation under a light microscope at a lower magnification (c. x40) in well-preserved specimens.

Discussion: The type material derives from beds of Kundan age along the River Volchov. The holotype as well as other material used by SERGEEVA (1963) in the original description comprises symmetrical (Sa) elements. The base is almost as long as the cusp and the lateral carinae are strong. The posterior side is fairly flat on the base and lower part of the cusp, more convex or even sharp on the distal part of the cusp. SERGEEVA (1963) did not report a central groove on the posterior side in any of her specimens.

DZIK (1976: text-figs. 13g–l) combined five different elements from one sample representing all element types of *S. cornuformis* except Sb into the same apparatus. He later recognized sp (Pa), tr (Sa), hi (Sc) and ne (M) elements in the apparatus (DZIK 1991: text-fig. 7A, 1994: text-fig. 7a), his sp element being apparently equivalent to my Pb element and his ne element to my Pa element.

LÖFGREN (1978) described the Sa element as "cornuform", the Pa element as "scandodontiform element B", the Pb element as "scandodontiform element A", but did not distinguish between Sb, Sc and Sd elements, lumping them together under the designation "scandodontiform element C". A fair amount of mostly non-temporal variation among collections was also described.

STOUGE & BAGNOLI (1990) distinguished between symmetrical (Sa), long-based reclined (Sc), long-based proclined (Sd and probably also Sb), short-based proclined (Pa), and scandodiform (Pb) elements in their illustrations of *S. cornuformis*, but they did not describe the element types in any detail. STOUGE & BAGNOLI (1990) and BAGNOLI & STOUGE (1997) also described the variation that they had encountered in samples from N Öland. In these, the variation was interpreted as (mainly) temporal, with weaker grooves and costae in stratigraphically older forms. Based on considerably more material from a more extensive geographical area, I have interpreted similar variation in the earlier part of the stratigraphic range of *S. cornuformis* as part of a much more complex interaction between temporal, geographical and (for the greater part) ecological variation in populations of the species. My Öland collections of *S. cornuformis* show a considerable degree of morphological variation between samples. It is also usual to find a number of slightly differing element morphotypes (e.g. with shallower or deeper grooves, or with longer or shorter bases) in the same sample. This phenomenon is of course much easier to detect in samples with several hundred *S. cornuformis* elements (as in many of my samples) than in samples containing fewer elements of *S. cornuformis*. My samples also most certainly represent many more biofacies types than those investigated by STOUGE & BAGNOLI (1990) and BAGNOLI & STOUGE (1997), and also include a greater part of the stratigraphic range of *S. cornuformis*. Thus, I have seen evidence that certain morphotypes of that taxon have appeared, disappeared and reappeared as the environmental conditions varied. When these conditions have been investigated in greater detail, it will probably be possible to understand these morphological "shifts" better and even to make use of them in biofacies interpretations. However, I consider some of the morphological variation to be stratigraphically related, as described below.

In two samples taken from the Gillberga quarry and separated vertically by only a few centimetres it is possible to observe what is probably the transition between the predecessor of *S. cornuformis* and early representatives of *S. cornuformis* itself. The collection of *Semiacontiodus* elements from the older sample, Öl88-3, agrees with what is occasionally found in even slightly older beds and has here been assigned to *S.* cf. *S. cornuformis*. The morphology of these elements is simpler, resembling that of much older species such as the Tremadocian *Semiacontiodus nogamii* (cf. Text-figs. 3A–B) or even older species of *Teridontus*. One Sa element in particular, (Pl. 1 fig. 16) from the younger of the two samples, Öl94-7, could well have been assigned to *S. nogamii* had it been encountered in much older strata. Occurring together with this Sa element in Öl94-7 are specimens (cf. Pl. 1 fig. 8) that are clearly recognizable as Sa elements of *S. cornuformis*, but in which the posterior grooves are shallower than in later representatives (as Pl. 1 fig. 10).

Other element types have apparently evolved in a similar manner: in Pb elements of *S.* cf. *S. cornuformis* the oral margin is longer and the cusp less erect than in slightly younger specimens (compare Pl. 1 fig. 20 with fig. 19) while Pa elements evolve into more concavo-convex forms (compare Pl. 1 fig. 22 with figs. 23 and 11). Sb, Sc and Sd elements are so generalized that they are almost indistinguishable in Öl88-3, but the characteristic base-cusp bend and straight cusp in some of these specimens (cf. Pl. 1 fig. 21) reveals that they are Sc elements (cf. Pl. 1 figs. 18 and 6 for younger forms).

Occurrence: Upper Volkhov (upper middle Arenig) and at least to the upper Llanvirn. *Semiacontiodus cornuformis* has been encountered in all areas investigated. In Lanna (Närke) and in the Öland sections its predecessors, with elements of very simple shape, appear in the uppermost *P. originalis* Zone. A few "intermediate" populations (i.e. probably the direct ancestors of *S. cornuformis*) have been distinguished as *Semiacontiodus* cf. *S. cornuformis* (see below). In the other areas investigated, sampling has not yet revealed transitional forms. In the Gullhögen (Skövde) and Hällekis quarries, the Rävanäs, Leskusänget, Kårgärde and Jämtland sections and the Finngrundet and Tamsalu drill cores *S. cornuformis* is first encountered at the base of the *Microzarkodina parva* Zone, coinciding with the first occurrence of *Baltoniodus norrlandicus*, or nearly so. From the Hälludden and Haget sections on N Öland only samples from the *E.? variabilis-M. parva* Subzone were available.

The last specimens of *S. cornuformis* probably occur in the upper Llanvirn, or possibly higher (DZIK 1994). In its upper range the taxon is replaced by, and sometimes co-occurs with, *S. bulbosus* in some of the samples investigated.

A few elements from the Finngrundet drill core previously assigned to *S. cornuformis* (LÖFGREN 1985) have been reassigned to *S. davidi* (see discussion of *S. davidi*) and some from my Jämtland sections (LÖFGREN 1978) reassigned to *S. bulbosus*. Otherwise the sample to sample distribution of *S. cornuformis* is as previously stated (Lanna and Leskusänget sections in LÖFGREN 1995).

Material: 27,226 specimens: 3,132 Pa, 4,591 Pb, 3,250 Sa and 16,253 Sb+Sc+Sd elements.

Semiacontiodus cf. *S. cornuformis* (SERGEEVA, 1963)

Pl. 1 figs. 9, 20–22

Description: The elements differ from their counterparts in *S. cornuformis* in the more rounded cross-sections of the cusp and base and the consequently less conspicuous grooves and carinae. The Sa element is more compressed anteriorly-posteriorly than in *S. cornuformis*. For comparisons see also *S. cornuformis* under Discussion.

Discussion: Elements designated *S.* cf. *S. cornuformis* belong to the immediate predecessors of *S. cornuformis* and have been retrieved from the N Öland sections Gillberga and Sandvik and from the Lanna quarry in Närke (LÖFGREN 1995). For a treatment of the stratigraphic relations between these two taxa see *S. cornuformis* under Discussion.

Occurrence: Rare in the upper *Paroistodus originalis* Zone, middle Arenig.

Material: 105 specimens: 17 Pa, 24 Pb, 8 Sa, 56 Sb+Sc+Sd elements.

Semiacontiodus davidi n. sp.

Pl. 2 figs. 1–8, 11–13, 15–16, 18–22; Pl. 1 fig. 15; text-figs. 1, 2G–L

1980 *Drepanoistodus forceps* (LINDSTRÖM). – MERRILL, Finland conod.: text-fig. 6:24 (Pa element).

1990 "*Semiacontiodus*" *cornuformis* (SERGEEVA). – STOUGE & BAGNOLI, Hagudd. (Öland) conod.: pl. 9 fig. 21 (Pb element).

Derivation of name: Named for my colleague David J. KENNEDY, Thorold, Canada, who has provided excellent descriptions of scolopodontids.

Holotype: LO 7840T from sample HK88-2, *E.? variabilis-M. parva* Subzone (see Pl. 2 fig. 7).

Type locality: Hällekis quarry, Kinnekulle, Västergötland (see THORSLUND & JAANUSSON 1960).

Type stratum: 0.6 m above the base of the c. 1.2 m grey interval in the basal part of the Holen Limestone above the red Lanna Limestone.

Diagnosis: A scolopodontid species with a seximembrate apparatus with elements lacking costae and with only faint carinae and grooves and cusps that are laterally compressed distally with at least one sharp edge.

Element descriptions: The descriptions below are based on material from a number of areas. There is a little morphological variation in this species as compared with that in *S. cornuformis*.

Sa element: The cusp is fairly strongly proclined, making an angle of c. 130° with the oral margin (Pl. 2 fig. 7). Distally it is compressed laterally and both the anterior and posterior edges are sharp. Proximally the cusp is rounded in cross-section (Pl. 2 fig. 18) with faint lateral carinae. The oral margin has a thin, sharp edge that does not reach the aboral margin (Pl. 2 fig. 22). The basal cavity is almost twice as deep as wide and only slightly widened laterally (Pl. 2 fig. 18).

The Sa element differs from that of *S. cornuformis* in lacking most anterio-posterior compression of the base, in being less curved, and in having a deeper basal cavity and sharper anterior and posterior edges of the cusp.

Sb element: The base is short, less than half as long as the length of the cusp, which is proclined, forming an angle of about 120° with the base (Pl. 2 figs. 1, 13). Proximally the cusp is round in cross-section, but distally it is compressed with a sharp posterior edge with a wing-like extension in mature specimens (Pl. 2 fig. 13). The oral margin is slightly keeled.

The element differs from the Sb element of *S. cornuformis* in being flatter, in the shorter base, in the sharper edge of the oral margin and in the less conspicuous wing-like flange on the cusp.

Sc element: The base is fairly short (Pl. 2 fig. 2), approximately half the length of the cusp, and although the element is laterally compressed the sides are rounded. The base and cusp meet at an angle of about 90°. Proximally the cusp is rounded in cross-section, being widest anteriorly. Distally there is a sharp posterior edge, with a wing-like, inwards-directed extension.

The element differs from the Sc element in *S. cornuformis* in being more compressed laterally, with a shorter base.

Sd element: The base is flattened and fairly long, more than half as long as the cusp (Pl. 2 figs. 11, 12). The cusp is slightly proclined, forming an angle of 100–120° with the base, which is sharply keeled orally and slightly concave on the inner side. The cusp is flattened laterally with sharp edges and an indistinct posterior "wing", and is slightly twisted.

The element differs from the Sd element in *S. cornuformis* in the keeled oral margin and in being more flattened laterally.

Pa element: This element is scandodontiform, with the outer side convex (Pl. 2 fig. 15) and the inner side concave. The maximum concavity is posteriorly, between the cusp and base where there is a thin, crescent-shaped area posterior to the bulging basal cavity (cf. Pl. 2 fig. 6). The anterio-basal corner is rounded in side view. The depth of the basal cavity is about 1.2 times the width; the apex is long and very slender, and placed close to the anterior margin. The cusp is flattened and slightly proclined. The posterior edge is thin and sharp, the anterior edge blunter (Pl. 2 fig. 19); in cross-section the maximum width is anteriorly.

The element differs from its equivalent in *S. cornuformis* among other things in the flatter cusp and the less bulging basal cavity.

Pb element: The cusp is erect to slightly proclined (cf. Pl. 2 figs. 3–5, 21) and the oral edge very short and sharp. The cusp is laterally flattened; the edge of the posterior margin being sharper than that of the anterior margin. There is a flattish anterior carina on each side, delimited by a thin, faint groove (Pl. 2 figs. 3–5). The basal cavity is slightly deeper than wide; its oral outline is almost circular. It bulges towards the inner side, making the whole element slightly asymmetrical (Pl. 2 fig. 21).

The element differs from the Pb element in *S. cornuformis* in the flatter cusp and the less bulging base.

Microstructure: All the elements are finely striated. On the posterior, straight parts of the cusp the striae are long and uninterrupted, and are 3–4 µm wide. The cusp striae are confined to the central part of the lateral sides and the unkeeled, posterior proximal part, while the anterior margin and the distal posterior edge are smooth in adult specimens. On the base, particularly where there is a change in convexity, such as posterior to the carinae, the striae are short and intertwining. In many specimens there are also faint striae rather far anteriorly on the base, but there is a wide unstriated zone all around the aboral margin in all element types.

The striation agrees well with that observed in *S. cornuformis* by LÖFGREN (1978: 106), the main difference being that the flatter anterior side of Sa elements of *S. cornuformis* is completely lacking in striae.

Discussion: In the samples Öl92-1 and Öl93-5 collected from Gillberga c. 0.5 m below where the stratigraphically oldest sample containing *S. davidi* was taken, some elements, here referred to as *S.* cf. *S. davidi*, were found. They occur together with "normal" *S. cornuformis* elements and are morphologically simpler than these. They are also simpler in shape than homologous elements of *S. davidi*. I presume that *S. davidi* evolved from predecessors with such elements rather than from *S. cornuformis*. This probably implies repeated invasions of ancestral populations that adjusted to different available niches in Baltoscandia.

Previous finds of elements that can be referred to *S. davidi* are from Öland (STOUGE & BAGNOLI 1990) and from the Åland islands in the central part of the Baltic Sea (MERRILL 1980). Both these occurrences probably lie within the stratigraphic boundaries of *S. davidi* on Öland, although MERRILL (1980) considered his specimens to be slightly younger.

A younger species resembling *S. davidi* is *Semiacontiodus carinatus* DZIK, 1976, found in a glacial boulder (of Baltoscandian origin) from the upper Llanvirnian *E. robustus* Zone. The illustrated specimens of *S. carinatus* (DZIK 1976: text-fig. 13 m–o) are of the same general appearance as Sa, Pa and Sd elements of *S. davidi* (presumed Pa and Sd elements sketched as Text-fig. 3N–O). However, the lateral carinae, or in this case, costae, of the Sa element are much more prominent in *S. carinatus* which is a probable successor of *S. davidi*.

Occurrence: Kunda (upper Arenig–lower Llanvirn). *Semiacontiodus davidi* has been encountered in the Gillberga and Hälludden sections in N Öland, at Gullhögen and Hällekis in Västergötland, Lanna in Närke, Finngrundet in the Gulf of Bothnia, Rävanäs, Leskusänget and Kårgärde in Dalarna and in the Tamsalu drill core, north-central Estonia. For some of these sections the sample by sample element distribution has been reported before, e.g. for Lanna and Leskusänget (in LÖFGREN 1995: text-figs. 6, 8), where *S. davidi* was called "*Semiacontiodus* sp. A".

The first occurrence of *S. davidi* in the Gillberga quarry section coincides with the base of the Kunda (base of *A. expansus* trilobite Zone), and it almost coincides with the first occurrence of *E.? variabilis* sensu stricto. At Gillberga the last specimens of *S. davidi* were encountered about 1.5 m from the top of the section, in the *E.? variabilis-M. ozarkodella* Subzone. Most of the occurrences from other areas are from the *E.? variabilis-M. parva* Subzone, but in one sample from Kårgärde and two from Tamsalu (Estonia), *S. davidi* was also retrieved from the *E.? variabilis-M. ozarkodella* Subzone.

In the Finngrundet drill core, *S. davidi* is restricted to the lower *E.? variabilis-M. parva* Subzone, an interval of c. 4.5 m (31.00 m – 35.50 m), from slightly above the first appearance of *A. expansus* to slightly above the first appearance of *A. raniceps* (cf. TJERNVIK & JOHANSSON 1980; LÖFGREN 1985). Most of the elements in the Finngrundet samples now referred to *S. davidi* had previously been assigned to *S. cornuformis*. A few poorly preserved Sc elements were erroneously assigned to *Scalpellodus latus* and some broken S elements to *S. gracilis*. In all, 74 elements from 9 Finngrundet samples have thus been reassigned.

Material: 2,134 specimens: 222 Pa, 631 Pb, 202 Sa and 1,079 Sb+Sc+Sd elements.

Semiacontiodus cf. *S. davidi* n. sp.

Pl. 2 figs. 9–10, 14, 17

Description: Sa elements in *S.* cf. *S. davidi* have a slightly shorter and wider base than those in *S. davidi*, but lack the lateral carinae and posterior grooves characteristic of *S. cornuformis* (cf. Pl. 2 fig. 17 with Pl. 2 fig. 18 and Pl. 1 figs. 2, 24). Probable Pb elements belonging to *S.* cf. *S. davidi* (Pl. 2 fig. 14) were found in the same samples as the Sa elements. The base is longer than is typical of the Pb elements of *S. davidi* and *S. cornuformis*. Thus also the Pb elements are morphologically more "generalized" than elements of these taxa. Specimens probably representing Sb, Sc and Sd elements of *S.* cf. *S. davidi* (Pl. 2 figs. 9, 10) also occur in the same samples as the other elements referred to this taxon. Their bases are longer than in corresponding elements of *S. davidi*. The cusp/base angle, however, approaches what is usual in *S. davidi*, being wider than in *S. cornuformis*.

Discussion: As was seen in the description of *S. davidi*, *S.* cf. *S. davidi* is the presumed ancestor of *S. davidi*. It has only been found in samples from a level c. 0.5 m below the first occurrence of *S. davidi* in the Gillberga quarry.

Occurrence: Less than 0.5 m below the base of the Kunda (*A. expansus* trilobite zone), uppermost *Microzarkodina parva* Zone, Gillberga quarry.

Material: 43 specimens: 5 Pa, 12 Pb, 7 Sa and 19 Sb+Sc+Sd elements.

Semiacontiodus sp. aff. *S. nogamii* (MILLER, 1969)

Occurrence and discussion: A few specimens from the *Baltoniodus triangularis* and *B. navis* Zones at Lanna (Närke) and the *Paroistodus originalis* Zone at Leskusänget (Dalarna) and the Gillberga quarry, N Öland, have been designated *Semiacontiodus* sp. aff. *S. nogamii*. Both base and cusp of these elements are rounded in cross-section. The only identified Sa element has an anterio-posteriorly compressed cusp. Elements of the rest of the S-series have a nearly erect cusp that is circular in cross-section and with a slight S-bend distally. In this they resemble some illustrated specimens of *Semiacontiodus nogamii* (e.g. MILLER 1980: pl. 2 fig. 12, redrawn here as Text-fig. 3B). The best-preserved of the elements can be seen to be hyaline.

Elements of *S.* sp. aff. *S. nogamii* are here interpreted as representatives of a long-lived lineage of scolopodontids with simple element morphology which at intervals invaded Baltoscandian waters but did not become established here until late *P. originalis* Zone times, when one such population of immigrants evolved into *S. cornuformis* (cf. Text-fig. 1).

Material: 11 specimens: 1 Sa and 10 unspecified S elements.

Semiacontiodus? sp. A

Pl. 1 fig. 7

Description: Only one element type, symmetrical (Sa element?) is known. The oral margin is extremely short or totally lacking and the posterior margin of cusp and base thin and sharp. The anterior side is well rounded with faint anterio-lateral carinae, so that the cusp is drop-shaped in cross-section. The basal cavity is fairly shallow; the apex is anterior. With other well-preserved elements here referred to *Semiacontiodus*, elements of *S.* sp. A share the fibre-like microornamentation noted in the description of *S. davidi*.

Discussion: The element somewhat resembles the specimen of *Ulrichodina abnormalis* (BRANSON & MEHL) from Newfoundland illustrated by STOUGE & BAGNOLI (1988: pl. 16 fig. 16) as seen in posterio-lateral view. My elements lack the anterior basal fold typical of *Ulrichodina*, however, and instead have tentatively been referred to *Semiacontiodus*. No other elements consistently co-occur with *S.*? sp. A, although *S. davidi* has a similar range and occurrence.

Occurrence: The stratigraphically oldest of the elements occur just below and at the lower boundary of the range of *Baltoniodus medius* (Dzik) within the *E.? variabilis-M. parva* Subzone in samples from the Gillberga quarry, Gullhögen (Skövde) quarry, Rävanäs and Leskusänget sections and the Finngrundet drill core. In the Kårgärde section the taxon has also been found in the basal part of the *E.? variabilis-M. ozarkodella* Subzone.

Material: 14 specimens.

Semiacontiodus? sp. B

Description: One specimen seems to agree closely with elements referred to "*Semiacontiodus*" *cornuformis* (SERGEEVA) by LEHNERT (1995: e.g. pl. 5 fig. 5). The striation is coarser than that found in (other) elements of *Semiacontiodus* in my collections and there appears to be a narrow furrow along one side.

Occurrence: *Microzarkodina parva* Zone. The single element in my collection was found in one of the very few samples within the range of *S. cornuformis* where that taxon is lacking.

Material: 1 specimen from sample GB81-1300, Gullhögen (Skövde) quarry, Västergötland.

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Literature

AN Tai-Xiang (1987): The lower Paleozoic conodonts of south China. – 238 pp., 35 pls.; Beijing (Publishing House of Geology). [in Chinese]

AN Tai-Xiang & ZHENG Zhao-Chang (1990): The conodonts of the marginal areas around the Ordos Basin, North China. – 210 pp., 17 pls.; Beijing (Science Press). [in Chinese with English summary]

BAGNOLI, Gabriella & STOUGE, Svend (1997): Lower Ordovician (Billingenian – Kunda) conodont zonation and provinces based on sections from Horns Udde, north Öland, Sweden. – Bolletino della Società Paleontologica Italiana **35** (2): 109–163, 7 text-figs., 8 pls.; Modena.

BARNES, Christopher R., KENNEDY, David J., MCCRACKEN, Alexander D., NOWLAN, Godfrey S. & TARRANT, Glen A. (1979): The structure and evolution of Ordovician conodont apparatuses. – Lethaia **12**: 125–151, 9 text-figs.; Oslo.

– & FÅHRÆUS, Lars E. (1975): Provinces, communities and the proposed nekto-benthic habit of Ordovician conodontophorids. – Lethaia **8**: 133–149; Oslo.

BAUER, Jeffrey A. (1987): Conodonts and conodont biostratigraphy of the McLish and Tulip Creek Formations (Middle Ordovician) of south-central Oklahoma. – Oklahoma Geological Survey Bulletin **141**: 1–58, 8 text-figs., 5 pls.; Tulsa, Okla.

BERGSTRÖM, Stig M. (1962): Conodonts from the Ludibundus Limestone (Middle Ordovician) of the Tvären area (S.E. Sweden). – Arkiv för mineralogi och geologi **3** (1): 1–61, 5 text-figs., 5 pls.; Uppsala.

– (1980): Conodonts as paleotemperature tools in Ordovician rocks of the Caledonides and adjacent areas in Scandinavia and the British Isles. – Geologiska Föreningens i Stockholm Förhandlingar **102**: 377–392, 8 text-figs.; Stockholm.

– (1981): Family Scolopodontidae. – In: ROBISON, Richard A. (ed.): Treatise on invertebrate paleontology. Part W, Supplement 2. Conodonta. – W141; Boulder, Colo., Lawrence, Kans. (Geological Society of America, University of Kansas Press).

– (1988): On PANDER's Ordovician conodonts: distribution and significance of the *Prioniodus elegans* fauna in Baltoscandia. – Senckenbergiana lethaea **69**: 217–251, 9 text-figs., 3 pls.; Frankfurt am Main.

BOHLIN, Birger (1949): The Asaphus Limestone in Northernmost Öland. – Bulletin of the Geological Institutions of the University of Uppsala **33**: 529–570, 1 pl.; Uppsala.

COOPER, Barry J. (1981): Early Ordovician conodonts from the Horn Valley Siltstone, central Australia. – Palaeontology **24**: 147–183, 6 text-figs., 7 pls.; London.

DRUCE, Edward C. & JONES, Peter J. (1971): Cambro-Ordovician conodonts from the Burke River Structural Belt, Queensland. – Bureau of Mineral Resources, Geology and Geophysics, Bulletin **110**: 1–159, 20 pls.; Canberra.

DRYGANT, Daniel M. (1974): Novije sredneordovikskije konodontij severo-zapadnoj Volijni (New Middle Ordovician conodonts from the North-Western Volhynia). – Paleontologicheskij sbornik **11**: 54–58; Lvov.

DZIK, Jerzy (1976): Remarks on the evolution of Ordovician conodonts. – Acta Palaeontologica Polonica **21**: 395–455, 36 text-figs., 1 tab., 4 pls.; Warszawa.

– (1991): Evolution of oral apparatuses in the conodont chordates. – Acta Palaeontologica Polonica **36**: 265–323, 18 text-figs.; Warszawa.

– (1994): Conodonts of the Mojcza Limestone. – In: DZIK, Jerzy, OLEMPSKA, Ewa & PISERA, Andrzej (eds.): Ordovician carbonate platform ecosystem of the Holy Cross Mountains. –

Palaeontologica Polonica **53**: 43–128, 32 text-figs., 11 tabs., 14 pls.; Warszawa.

EPSTEIN, Anita G., EPSTEIN, Jack B. & HARRIS, Leonard D. (1977): Conodont color alteration – an index to regional metamorphism. – U.S. Geological Survey, Professional Paper **995**: 1–27, 20 text-figs.; Washington.

ERDTMANN, Berndt-Dieter (1986): Early Ordovician eustatic cycles and their bearing on punctuations in early nematophorid (planktic) graptolite evolution. – In: WALLISER, Otto, H. (ed.): Global Bio-Events. Lecture Notes in Earth Sciences **8**: 139–152, 4 text-figs.; Berlin (Springer-Verlag).

ETHINGTON, Raymond L. (1959): Conodonts of the Ordovician Galena Formation. – Journal of Paleontology **33**: 257–292, 2 text-figs., 3 pls.; Tulsa, Okla.

– (1972): Lower Ordovican (Arenigian) conodonts from the Pogonip Group, central Nevada. – Geologica et Palaeontologica, Sonderband **1**: 17–28, 1 pl.; Marburg.

ETHINGTON, Raymond, L. & AUSTIN, Ronald, L. (1991): Conodonts of the Dounans Limestone, Highland Border Complex, Scotland. – Journal of Micropalaeontology **10**: 51–56, 1 pl.; London.

ETHINGTON, Raymond, L. & CLARK, David L. (1982): Lower and Middle Ordovician conodonts from the Ibex Area Western Millard County, Utah. – Brigham Young University, Geological Studies **28**: 1–160, 35 text-figs., 14 pls.; Provo, Ut.

ETHINGTON, Raymond, L., DROSTE, John B. & REXROAD, Carl B. (1986): Conodonts from subsurface Champlainian (Ordovician) rocks of eastern Indiana. – Indiana Geological Survey Special Report **37**: 1–32, 5 text-figs., 2 pls.; Bloomington, Ind.

ETHINGTON, Raymond L. & SCHUMACHER, Dietmar (1969): Conodonts of the Copenhagen Formation (Middle Ordovician) in central Nevada. – Journal of Paleontology **43**: 440–484, 5 text-figs., 2 pls.; Tulsa, Okla.

FÅHRÆUS, Lars E. (1982): Recognition and redescription of PANDER's (1856) *Scolopodus* (form) species – Constituents of multi element taxa (Conodontophorida, Ordovician). – Geologica et Palaeontologica **16**: 19–28, 2 pls.; Marburg.

– & ROY, Kaustuv (1993): Conodonts from the Cambro-Ordovician Cooks Brook and Middle Arm Point Formations, Bay of Islands, western Newfoundland. – Geologica et Palaeontologica **27**: 1–53, 5 text-figs, 6 tabs., 5 pls.; Marburg.

FORTEY, Richard A., HARPER, David A.T., INGHAM, J. Keith, OWEN, A.W. & RUSHTON, Adrian, W.A. (1995): A revision of Ordovician series and stages from the historical type area. – Geological Magazine **132**: 15–30, 1 text-fig.; Cambridge.

FURNISH, William M. (1938): Conodonts from the Prairie Du Chien (Lower Ordovician) beds of the Upper Mississippi Valley. – Journal of Paleontology **12**: 318–340, 2 text-figs., 2 pls.; Tulsa, Okla.

JEPPSSON, Lennart, FREDHOLM, Doris & MATTIASSON, Bo (1985): Acetic acid and phosphatic fossils – a warning. – Journal of Paleontology **59**: 952–956; Tulsa, Okla.

JI Zailiang & BARNES, Christopher R. (1994a): Lower Ordovician conodonts of the St. George Group, Port au Port Peninsula, western Newfoundland, Canada. – Palaeontographica Canadiana **11**: 1–149, 38 text-figs., 25 pls.; Toronto.

– & – (1994b): Conodont paleoecology of the Lower Ordovician St. George Group, Port au Port Peninsula, western Newfoundland. – Journal of Paleontology **68**: 1368–1383, 15 text-figs.; Lawrence, Kans.

KENNEDY, David J. (1980): A restudy of the conodonts described by BRANSON & MEHL, 1933, from the Jefferson City Formation, Lower Ordovician of Missouri. – Geologica et Palaeontologica **14**: 45–76, 2 text-figs., 2 pls.; Marburg.

– (1994): *Colaptoconus* (Conodonta), a replacement name for *Glyptoconus* KENNEDY, 1981, non *Glyptoconus* von MOELLENDORFF, 1894. – Journal of Paleontology **68**: 1417; Lawrence, Kans.

LEHNERT, Oliver (1995): Ordovizische Conodonten aus der Präkordillere Westargentiniens: Ihre Bedeutung für Stratigraphie und Paläogeographie. – Erlanger geologische Abhandlungen **125**: 1–193, 26 text-figs., 20 pls.; Erlangen.

LINDSTRÖM, Maurits (1955): Conodonts from the lowermost Ordovician strata of south-central Sweden. – Geologiska Föreningens i Stockholm Förhandlingar **76**: 517–604, 6 text-figs., 2 tabs., 7 pls; Stockholm.

– (1970): A suprageneric taxonomy of the conodonts. – Lethaia **3**: 427–445, 9 text-figs.; Oslo.

– (1971): Lower Ordovician conodonts of Europe. – Geological Society of America Memoir **127**: 21–61, 20 text-figs., 1 pl.; Boulder, Colo.

– (1973): *Semiacontiodus*. – In: ZIEGLER, Willi (ed.): Catalogue of Conodonts **1**: 437; Stuttgart (Schweizerbart'sche Verlagsbuchhandlung).

LÖFGREN, Anita (1978): Arenigian and Llanvirnian conodonts from Jämtland, northern Sweden. – Fossils and Strata **13**: 1–129, 41 text-figs., 16 pls.; Oslo.

– (1985): Early Ordovician conodont biozonation at Finngrundet, south Bothnian Bay, Sweden. (Geology of the southern Bothnian Sea. Part III.). – Bulletin of the Geological Institutions of the University of Uppsala, N.S. **10**: 115–128, 4 text-figs.; Uppsala.

– (1993): Conodonts from the Lower Ordovician at Hunneberg, south-central Sweden. – Geological Magazine **130**: 215–232, 9 text-figs.; Cambridge.

– (1994): Arenig (Lower Ordovician) conodonts and biozonation in the eastern Siljan district, central Sweden. – Journal of Paleontology **68**: 1350–1368, 8 text-figs.; Lawrence, Kans.

– (1995): The middle Lanna/Volkhov Stage (middle Arenig) in Sweden and its conodont fauna. – Geological Magazine **132**: 693–711, 9 text-figs.; Cambridge.

– (1996): Lower Ordovician conodonts, reworking, and biostratigraphy of the Orreholmen quarry, Västergötland, south-central Sweden. – Geologiska Föreningens i Stockholm Förhandlingar **118**: 169–183, 9 text-figs.; Stockholm.

– (1997a): Reinterpretation of the Lower Ordovician conodont apparatus *Paroistodus*. – Palaeontology **40**: 913–929, 5 text-figs., 1 pl.; London.

– (1997b): Conodont faunas from the upper Tremadoc at Brattefors, south-central Sweden, and reconstruction of the *Paltodus* apparatus. – Geologiska Föreningens i Stockholm Förhandlingar **119**: 257–266, 6 text-figs.; Stockholm.

MERRILL, Glenn K. (1980): Ordovician conodonts from the Åland Islands, Finland. – Geologiska Föreningens i Stockholm Förhandlingar **101**: 329–341, 6 text-figs.; Stockholm.

MILLER, James F. (1969): Conodont fauna of the Notch Peak Limestone (Cambro-Ordovician), House Range, Utah. – Journal of Paleontology **43**: 413–439, 5 text-figs, 4 pls.; Tulsa, Okla.

– (1980): Taxonomic revisions of some Upper Cambrian and Lower Ordovician conodonts with comments on their evolution. – University of Kansas Paleontological Contributions, Paper **99**: 1–44, 6 text-figs., 2 pls.; Lawrence, Kans.

– (1981): Family Oneotodontidae. – In: ROBISON, Richard A. (ed.): Treatise on invertebrate paleontology. Part W, Supplement 2. Conodonta. – W117; Boulder, Colo., Lawrence, Kans. (Geological Society of America, University of Kansas Press).

NICOLL, Robert S. (1990): The genus *Cordylodus* and latest Cambrian-earliest Ordovician conodont biostratigraphy. – BMR Journal of Australian Geology & Geophysics **11**: 529–558, 23 text-figs.; Canberra (Bureau of Mineral Resources, Geology and Geophysics).

– (1994): Seximembrate apparatus structure of the Late Cambrian coniform conodont *Teridontus nakamurai* from the Chatsworth Limestone, Georgina Basin, Queensland. – BMR Journal of Australian Geology & Geophysics **15**: 367–379, 15 text-figs.; Canberra (Bureau of Mineral Resources, Geology and Geophysics).

NICOLL, Robert S., LAURIE, John R., SHERGOLD, John H. & NIELSEN, Arne T. (1992): Preliminary correlation of latest Cambrian to Early Ordovician sea level events in Australia and Scandinavia. – In: WEBBY, Barry D. & LAURIE, John D. (eds.): Global perspectives on Ordovician Geology. – 381–394; Rotterdam (Balkema).

NIELSEN, Arne T. (1992): Intercontinental correlation of the Arenigian (Early Ordovician) based on sequence and ecostratigraphy. – In: WEBBY, Barry D. & LAURIE, John D. (eds.): Global perspectives on Ordovician Geology. – 367–379, 1 text-fig.; Rotterdam (Balkema).

NOGAMI, Yasou (1967): Kambrische Conodonten von China, Teil 2. Conodonten aus den hoch oberkambrischen Yencho-Schichten. – Memoirs of the College of Science, University of Kyoto, Series B, Geology and Mineralogy **33**: 211–218, 3 text-figs., 1 pl.; Kyoto.

ORTEGA, Gladys, ALBANESI, Guillermo L. & HÜNICKEN, Mario A. (1995): Bioestratigrafia en base a conodontes y graptolitos de la Formaciones San Juan (Techo) y Gualcamayo (Arenigiano-Llanvirniano) en el Cerro Potrerillo, Precordillera de San Juan, Argentina. – Boletin de la Academia Nacional de Ciencias, Cordoba, Argentina **60**: 317–364, 4 text-figs., 6 pls.; Cordoba.

PANDER, Christian H. (1856): Monographie der fossilen Fische des Silurischen Systems der Russisch-Baltischen Gouvernements. – i–x, 1–91; St. Petersburg (Akademie der Wissenschaften).

PUURA, Väino (1986): Geology of the Kukersite-bearing beds of the Baltic oil shale basin. – 77 p., 20 text-figs.; Tallinn (Valgus Publishers).

RASMUSSEN, Jan A. (1991): Conodont stratigraphy of the Lower Ordovician Huk Formation at Slemmestad, southern Norway. – Norsk Geologisk Tidsskrift **71**: 265–288, 8 text-figs., 1 app.; Oslo.

– (1994): Stratigraphy, conodont faunas and depositional setting of the Lower Allochthon limestones within the Scandinavian Caledonides [Ph. D. thesis]. – København Universitet, 244p., 40 text-figs., 9 app., 19 pls.; København.

RASMUSSEN, Jan A. & STOUGE, Svend (1995): Late Arenig - Early Llanvirn conodont biofacies across the Iapetus Ocean. – In: COOPER, John D., DROSER, Mary, L. & FINNEY, Stanley C. (eds.): Ordovician Odyssey: Short Papers for the Seventh International Symposium on the Ordovician System. – SEPM, Pacific Section, Book **77**: 443–447, 3 text-figs.; Fullerton, Cal.

REPETSKI, John E. (1982): Conodonts from El Paso Group (Lower Ordovician) of westernmost Texas and southern New Mexico. – New Mexico Bureau of Mines and Mineral Resources, Memoir **40**: 1–120, 8 text-figs., 1 tab., 28 pls.; Socorro, N.Mex.

SEO, Kwang-Soo, LEE, Ha-Young & ETHINGTON, Raymond E. (1994): Early Ordovician conodonts from the Dumugol Formation in the Baegunsan Syncline, eastern Yeongweol and Samcheog areas, Kangweon-Do, Korea. – Journal of Paleontology **68**: 599–616, 11 text-figs.; Lawrence, Kans.

SERGEEVA, Svetlana P. (1963): Konodontij iz niznego ordovika Leningradskoj oblasti. [Conodonts from the Lower Ordovician in the Leningrad region]. – Akademia Nauk SSSR. Paleontologicheskij Zhurnal **1963**: 93–108, 11 text-figs., 2 pls.; Moskva. [in Russian]

SMITH, M. Paul (1991): Early Ordovician conodonts of East and North Greenland. – Meddelelser om Grønland. Geoscience **26**: 1–81, 42 text-figs., 4 app.; København.

STAIT, Kathi & DRUCE, Edward C. (1993): Conodonts from the Lower Ordovican Coolibah Formation, Georgina Basin, central Australia. – BMR Journal of Australian Geology and Geophysics **13**: 293–322, 22 text-figs; Canberra (Bureau of Mineral Resources, Geology and Geophysics).

STAUFFER, Clinton R. (1935): Conodonts of the Glenwood beds. – Geological Society of America Bulletin **46**: 125–168, 4 pls.; New York.

STOUGE, Svend (1975): Conodontzonerne i orthoceratitkalken (Nedre Ordovicium) på Bornholm og ved Fågelsång. – Dansk geologisk forening, Årsskrift for **1974**: 32–38; København.

– (1984): Conodonts of the Middle Ordovician Table Head Formation, western Newfoundland. – Fossils and Strata **16**: 1–145, 28 text-figs., 18 pls., 8 app.; Oslo.

– (1989): Lower Ordovician (Ontikan) conodont biostratigraphy in Scandinavia. – Eesti NSV Teaduste Akadeemia Toimetised, Geoloogia **38**: 68–72, 1 text-fig.; Tallinn.

STOUGE, Svend & BAGNOLI, Gabriella (1988): Early Ordovician Conodonts from Cow Head Peninsula, western Newfoundland. – Palaeontographia Italica **75**: 89–179, 7 text-figs., 16 pls.; Pisa.

– & – (1990): Lower Ordovician (Volkhovian-Kundan) conodonts from Hagudden, northern Öland, Sweden. – Palaeontographia Italica **77**: 1–54, 4 text-figs., 1 app., 10 pls.; Pisa.

SWEET, Walter C. (1988): The Conodonta. Morphology, taxonomy, paleoecology and evolutionary history of a long-extinct animal Phylum. – 212 pp., numerous text-figs.; New York (Oxford University Press).

SWEET, Walter C., THOMPSON, Thomas L. & SATTERFIELD, Ira R. (1975): Conodont stratigraphy of the Cape Limestone (Maysvillian) of eastern Missouri. – Studies in Stratigraphy: Missouri Geological Survey, Department of natural resources, Report Inv. **57**: 1–59, 4 text-figs., 1 tab., 3 pls.; St. Louis, Mo.

THORSLUND, Per & JAANUSSON, Valdar (1960): The Cambrian, Ordovician and Silurian in Västergötland, Närke, Dalarna, and Jämtland, central Sweden. Guide to Excursions Nos. A23 and C18. – International Geological Congress, XXI Session, Norden 1960, Sweden, Guide-book e: 1–51; Stockholm.

TJERNVIK, Torsten E. & JOHANSSON, Jan V. (1980): Description of the upper portion of the drill-core from Finngrundet in the south Bothnian Bay. Geology of the southern Bothnian Sea. Part II. – Bulletin of the Geological Institutions of the University of Uppsala N.S. **8**: 173–204, 10 text-figs.; Uppsala.

VIIRA, Viive (1974): Konodonty Ordovika Pribaltiki [Ordovician conodonts of the east Baltic]. – 142 pp., 165 text-figs., 13 pls.; Tallinn ("Valgus").

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Plate 1

The Ordovician conodont *Semiacontiodus* in Baltoscandia

Figs. 1-6, 8, 10-14, 16-19, 23-24: *Semiacontiodus cornuformis* (SERGEEVA, 1963). –

1. Sb element, LO 7799t, sample Öl94-7, uppermost *Paroistodus originalis* Zone, Gillberga quarry, Öland; x125.
2. Sa element, posterior side, LO 7812t, sample Öl93-10C, *E.? variabilis – M. parva* Subzone, Gillberga quarry, Öland; x165.
3. Pb element, inner side, LO 7800t, sample EST86-6, *E.? variabilis – M. parva* Subzone, Tamsalu drill core, Estonia; x140.
4. Sd element, outer side, LO 7813t, sample Öl93-10B, *E.? variabilis – M. parva* Subzone, Gillberga quarry, Öland; x110.
5. Sa element with long straight base and basal cone, LO 7801t, sample EST86-6, *E.? variabilis – M. parva* Subzone, Tamsalu drill core, Estonia; x120.
6. Sc element, inner side, LO 7802t, sample EST86-6, *E.? variabilis – M. parva* Subzone, Tamsalu drill core, Estonia.; x120.
8. Sa element, LO 7803t, sample Öl94-7, uppermost *Paroistodus originalis* Zone, Gillberga quarry, Öland; x160.
10. Sa element, LO 7814t, sample Öl93-10B, *E.? variabilis – M. parva* Subzone, Gillberga quarry, Öland; x150.
11. Pa element, inner side, LO 7815t, sample Öl93-10C, *E.? variabilis – M. parva* Subzone, Gillberga quarry, Öland; x150.
12. Sb? element, LO 7816t, sample Öl93-10B, *E.? variabilis – M. parva* Subzone, Gillberga quarry, Öland; x125.
13. Sb element, LO 7804t, sample EST86-6, *E.? variabilis – M. parva* Subzone, Tamsalu drill core, Estonia; x85.
14. Pb element, outer side, LO 7817t, sample Öl93-10B, *E.? variabilis – M. parva* Subzone, Gillberga quarry, Öland; x120.
16. Sa element, posterior side, LO 7805t, sample Öl94-7, uppermost *Paroistodus originalis* Zone, Gillberga quarry, Öland; x190.
17. Sd? element, LO 7806t, sample Öl94-7, uppermost *Paroistodus originalis* Zone, Gillberga quarry, Öland; x120.
18. Sc element, LO 7807t, sample Öl94-7, uppermost *Paroistodus originalis* Zone, Gillberga quarry, Öland; x130.
19. Pb element, LO 7808t, sample Öl94-7, uppermost *Paroistodus originalis* Zone, Gillberga quarry, Öland; x140.
23. Pa element, LO 7809t, sample Öl94-7, uppermost *Paroistodus originalis* Zone, Gillberga quarry, Öland; x140.
24. Sa element, posterior side, LO 7810t, sample EST86-6, *E.? variabilis – M. parva* Subzone, Tamsalu drill core, Estonia; x150.

Fig. 7: *Semiacontiodus*? sp. A. –

Sa element LO 7825t, sample DLK-H11, lowermost *E.? variabilis – M. ozarkodella* Subzone, Kårgärde section, Dalarna; x120.

Figs. 9, 20-22: *Semiacontiodus* cf. *S. cornuformis*. –

9. Sa element LO 7811t with bulbous base and basal cone, sample EST86-6, *E.? variabilis – M. parva* Subzone, Tamsalu drill core, Estonia, x130.
20. Pb element, LO 7818t, sample Öl88-3, upper *Paroistodus originalis* Zone, Gillberga quarry, Öland; x205.
21. Sc element, LO 7819t, sample Öl88-3, upper *Paroistodus originalis* Zone, Gillberga quarry, Öland; x160.
22. Pa element, LO 7820t, sample Öl88-3, upper *Paroistodus originalis* Zone, Gillberga quarry, Öland; x125.

Fig. 15: *Semiacontiodus davidi* n. sp. –

Sa element LO 7836t, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x160.

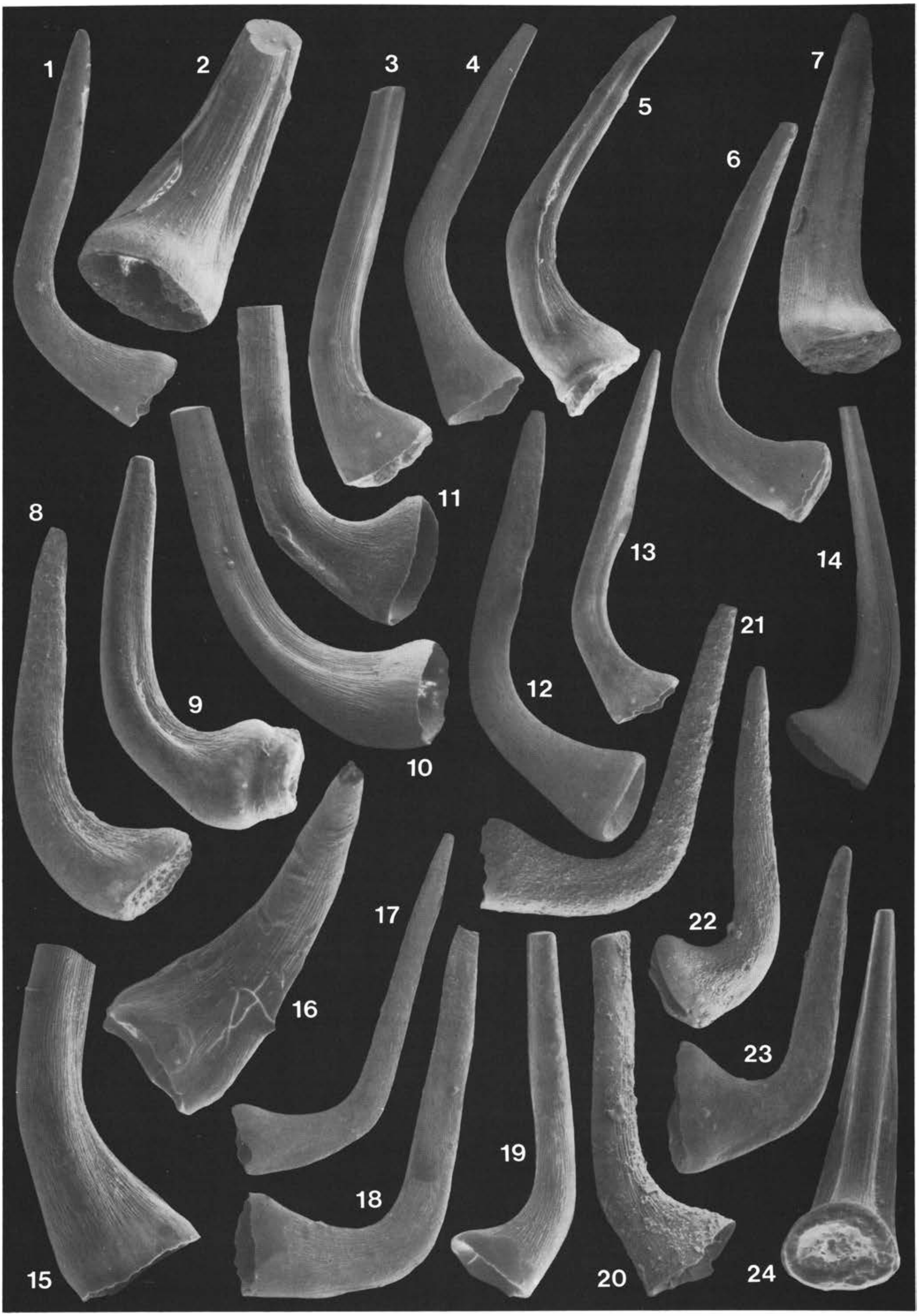
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Plate 2

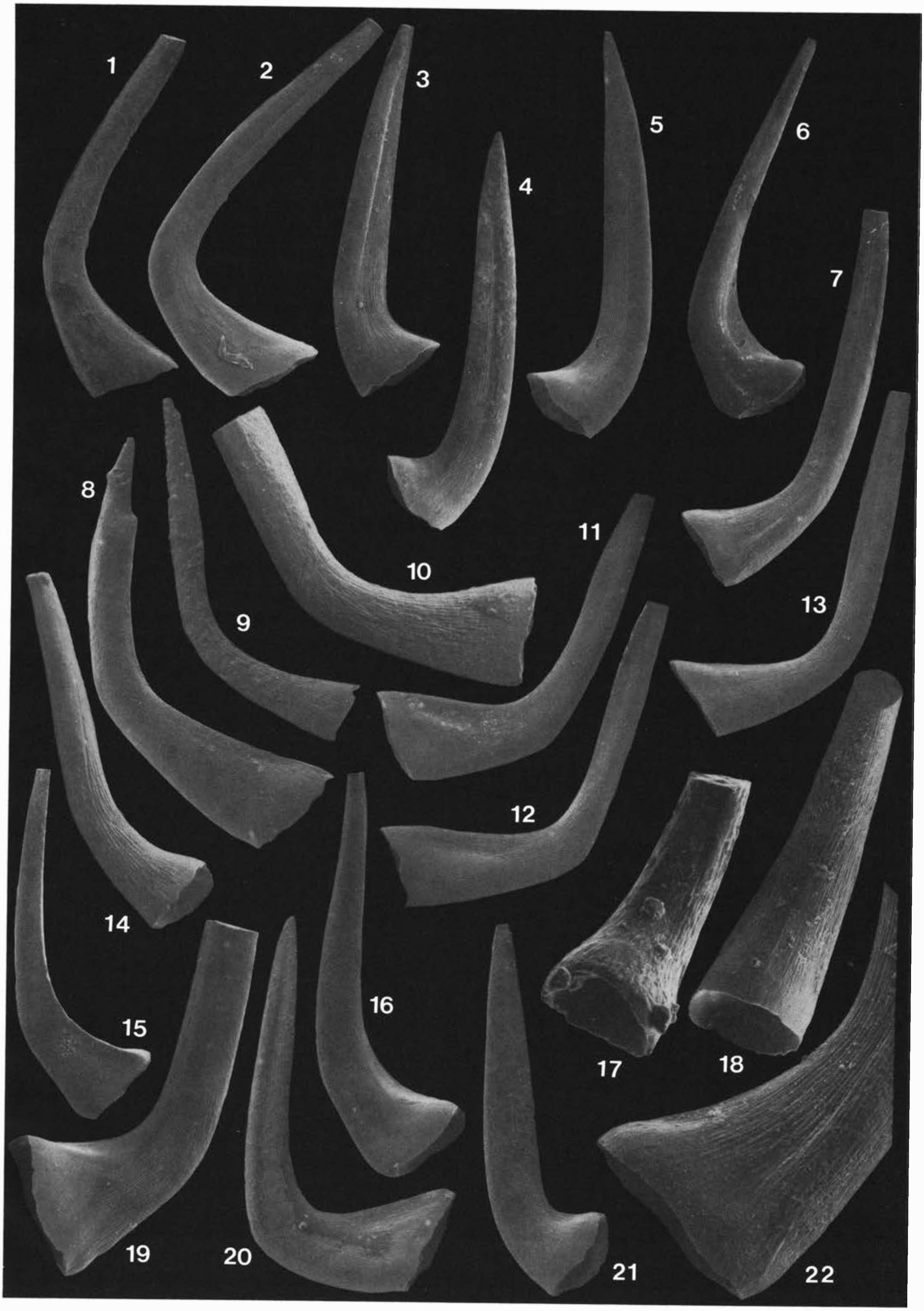
The Ordovician conodont *Semiacontiodus* in Baltoscandia

Figs. 1-8, 11-13, 15-16, 18-22: *Semiacontiodus davidi* n. sp. –

1. Sb element, LO 7826t, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x100.
2. Sc element, LO 7827t, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x100.
3. Pb element, outer side, LO7837t, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x120.
4. Pb element, outer side, LO7838t, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x90.
5. Pb element, inner side, LO 7828t, sample Öl74-100, *E.? variabilis - M. parva* Subzone, Gillberga quarry, Öland; x100.
6. Pa element, LO 7839t, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x110.
7. Sa element, **holotype** LO 7840T, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x100.
8. Sd element, outer side, LO 7829t, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x100.
11. Sd element, inner side, LO 7830t, sample Öl74-100, *E.? variabilis – M. parva* Subzone, Gillberga quarry, Öland; x100.
12. Sd element, outer side, LO 7831t, sample Öl74-100, *E.? variabilis – M. parva* Subzone, Gillberga quarry, Öland; x120.
13. Sb element, LO 7832t, sample Öl74-100, *E.? variabilis – M. parva* Subzone, Gillberga quarry, Öland; x120.
15. Pa element, outer side, LO 7841t, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x110.
16. Pa element, inner side, LO 7833t, sample Öl74-100, *E.? variabilis – M. parva* Subzone, Gillberga quarry, Öland; x125.
18. Sa element, LO 7842t, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x160.
19. Pa element, inner side, LO 7843t, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x150.
20. Sc element, LO 7834t, sample Öl74-100, *E.? variabilis – M. parva* Subzone, Gillberga quarry, Öland; x120.
21. Pb element, inner side, LO 7835t, sample HK88-2, *E.? variabilis – M. parva* Subzone, Hällekis quarry, Västergötland; x90.
22. Sa element (**holotype**); detail of Fig 7; x240.

Figs. 9-10, 14, 17: *Semiacontiodus* cf. *S. davidi*. –

9. Sb? element, LO 7821t, sample Öl92-1, *Microzarkodina parva* Zone, Gillberga quarry, Öland; x150.
10. Sd? element, LO 7822t, sample Öl92-1, *Microzarkodina parva* Zone, Gillberga quarry, Öland; x190.
14. Pb element, LO 7823t, sample Öl92-1, *Microzarkodina parva* Zone, Gillberga quarry, Öland; x180.
17. Sa element, posterior side, LO 7824t, sample Öl92-1, *Microzarkodina parva* Zone, Gillberga quarry, Öland; x265.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