

# LATE CAMBRIAN EUCONODONTS FROM SWEDEN

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The apparent derivation of several eucodont lineages from different paraconodonts suggests that crown tissue was incipient in paraconodonts although not as a mineralized tissue prone to fossilization. The earliest species of *Proconodontus*, *P. transitans* sp. n., is recognized. It represents a transitional form from paraconodonts to euconodonts from which most later euconodonts stem. The earlier proposed origination of *Cordylodus andresi* from *Proconodontus serratus* is confirmed. A conodont-based correlation of the uppermost Cambrian of Sweden with North America and Estonia is proposed. Earlier reports of the *Proconodontus* Zone in Estonia are questioned. The uppermost Cambrian conodont zone, *Cordylodus proavus*, is not known in Sweden.

**Key words:** Conodonts, evolution, stratigraphy, Cambrian, Sweden.

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## INTRODUCTION

The Upper Cambrian deposits of the Baltoscandian Platform are composed of black bituminous shales ("Alum Shales") with beds and lenses of gray or dark bituminous limestones ("Stinkstones" or "Orsten"). The deposits were formed in shallow waters, under generally stable conditions in poorly oxidized environments. They are rich in organic admixtures (up to 20%), pyrite, phosphate and trace elements, mainly uranium and vanadium (see BERGSTRÖM and GEE 1985). The whole series is considerably condensed and has many local gaps. The stinkstones, especially the light-colored ones, are very fossiliferous, but the fauna is taxonomically restricted. Arthropods, brachiopods and conodonts predominate. The stratigraphy is well established, mainly on the basis of trilobites. The sequence is known from many outcrops in southern Sweden, the Oslo region, and the isle of Bornholm, as well as from the subsurface of the Baltic Sea and northern Poland.

Conodonts are very abundant and well preserved in the stinkstone intercalations throughout the sequence. Paraconodonts are particularly numerous and taxonomically diversified. They comprise the main material for the first systematic description (MÜLLER 1959) and structural study (MÜLLER and NOGAMI 1971) of Cambrian conodonts. However, paraconodonts have as yet not been used in Scandinavia for stratigraphy (MÜLLER and HINZ 1991).

In the upper part of the sequence, all of the three structural groups of conodonts, proto- para- and euconodonts, occur together. The association was first reported by ANDRES (1981, 1988) and was described

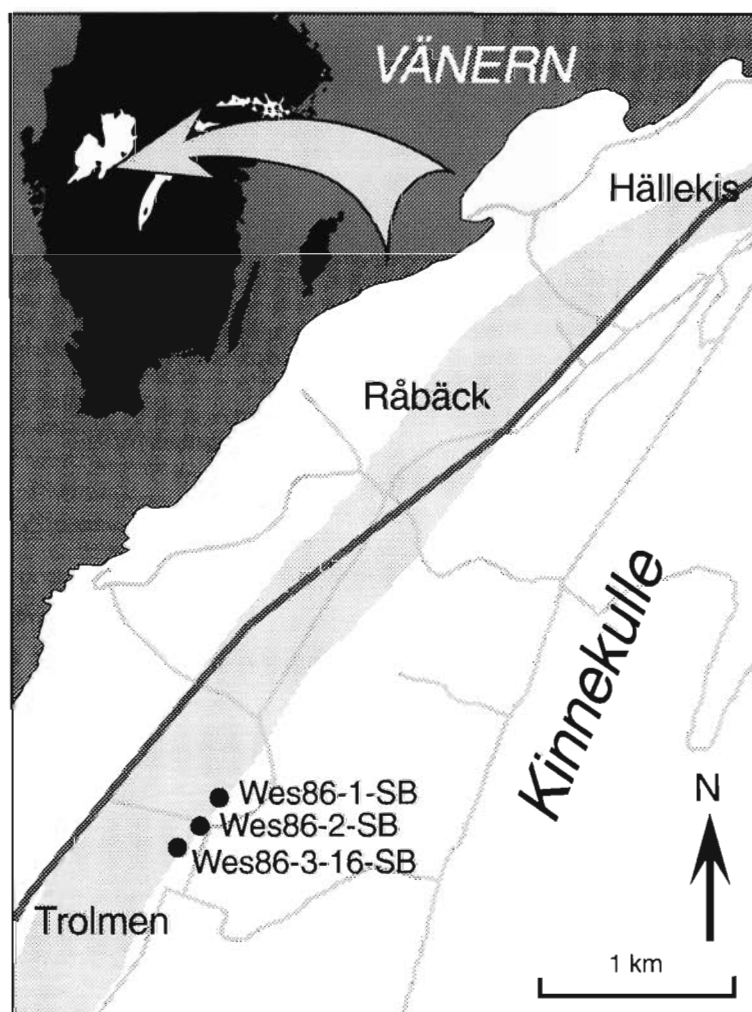


Fig. 1

Map showing the three collecting spots in the Råbäck and Trolmen quarries. The broad grey band shows the outcrop of alum shale in the region (after HOLM 1901). The thin grey lines are roads, and the thicker dashed line shows the railroad.

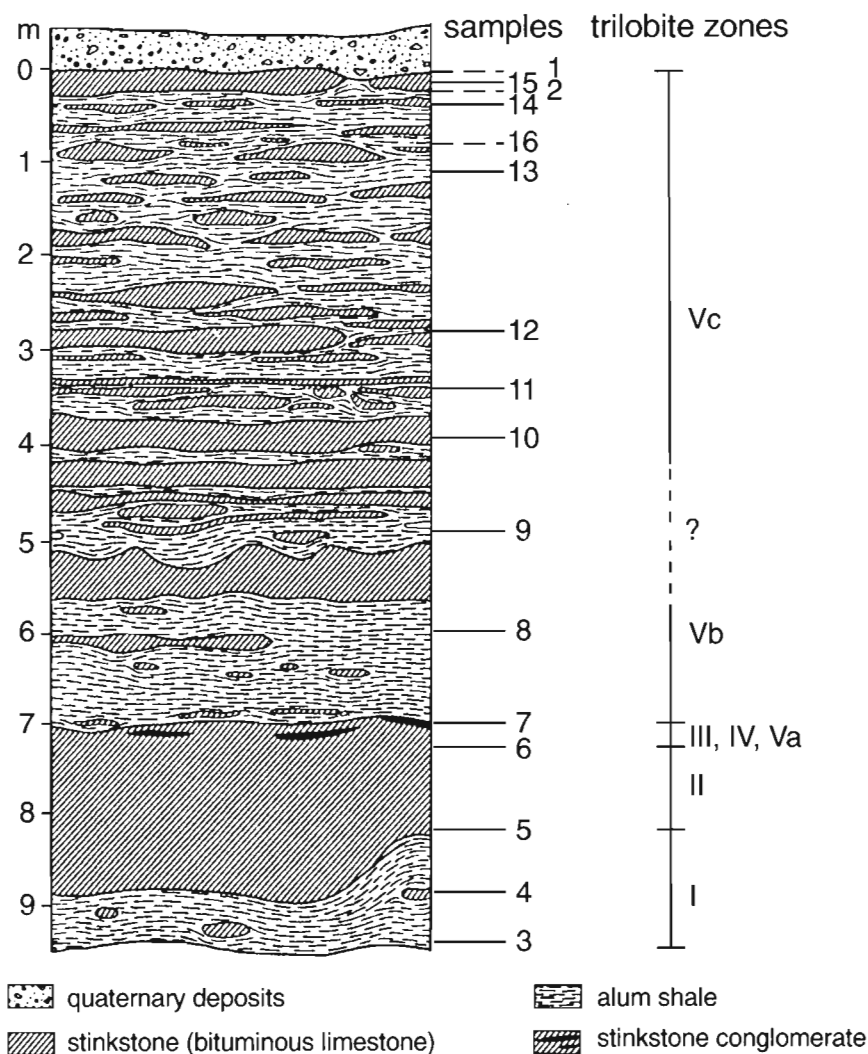


Fig. 2

Diagrammatic section of the Upper Cambrian sequence at Råbäck quarry, after WESTERGÅRD (1922) and approximate position of the investigated samples from Råbäck and Trolmen quarries. I – *Agnostus pisiformis* Zone, II – *Olenus* Zone, III – *Parabolina spinulosa* Zone, IV – *Leptoplastus* Zone, V – *Peltura* Zone, Va – *Protopeltura praecursor* Subzone, Vb – *Peltura minor* Subzone, Vc – *Peltura scarabaeoides* Subzone. The sample 1 (full designation: Wes86-1-SB) has been collected from the Råbäck quarry and all the rest from the adjacent Trolmen quarry, see Fig. 1.

taxonomically by MÜLLER and HINZ (1991). The euconodonts belong to the earliest evolutionary forms of that structural group. Most of them are excellently preserved, include basal bodies, and are not altered thermally. Their most characteristic feature is the sharp contrast between the colorless, translucent crown and the dark basal body. The good preservation of the partly organic basal bodies is probably due to anaerobic conditions of sedimentation and very quick postmortem phosphatization. The latter process has been documented also for the small, spectacularly well-preserved arthropods occurring in the same beds (MÜLLER 1985).

Because of the good preservation and the co-occurrence with ancestral forms, the euconodonts present a valuable opportunity for structural and biological studies. Based on this material, ANDRES (1988) and SZANIAWSKI and BENGTSON (1993) documented a transformation of paraconodonts to euconodonts and the origin of the euconodont crown.

The euconodonts have not been used widely for stratigraphic correlations of the Cambrian in Baltoscandia up till now. Our present investigation shows that they comprise more taxa than hitherto known and that they may be of greater stratigraphic use. Recognition of the earliest forms of the *Proconodontus* lineage also permits a better understanding of conodont evolution.

Table 1  
Element distribution in the investigated section.

Sample	12	13	16	14	2	15	1	Total
<i>P. transitans</i>	37	4	108	206	24?			379
<i>P. muelleri</i>			12?	22?	490	170	210	904
<i>P. tenuiserratus bicostatus</i>					3	18		21
<i>P. serratus</i>					8	12	93	113
<i>C. andresi</i>							188	188
<b>Total</b>	37	4	120	228	525	200	491	1605

The approximate average weight of the samples 1, 2 and 15 was about 4 kg, and of the samples 12, 13, 14 and 16, was about 2 kg. (Full designation of the samples as in Fig. 2).

All the material for the study has been obtained from the section outcropping in two neighbouring old quarries, Trolmen and Råbäck, in the Kinnekulle region, Västergötland, Sweden (Fig. 1). The section has been investigated stratigraphically by WESTERGÅRD (1922) and sedimentologically by DVORATZEK (1987). Of the 16 samples processed euconodonts were found in the upper seven (Fig. 2, Table 1). In all about 1600 identifiable elements belonging to five species and two genera, *Proconodontus* and *Cordylodus*, were collected. The collection is deposited at the Swedish Museum of Natural History (SMNH), Stockholm, repository numbers X2159–X2229 and X2241–X2344. The numbers within brackets after the individual museum numbers indicate the SEM stub number and specimen number as used by us (e.g., “(113.6)” means specimen no. 6 on stub no. 113).

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## EVOLUTION

The evolutionary origin of at least most euconodonts from Late Cambrian paraconodonts seems to be sufficiently documented by histological evidence (SZANIAWSKI and BENGTON 1993). Some of the Upper Cambrian paraconodont elements are more rich in calcium phosphate than others. As a result, they approach euconodont elements in their mode of preservation and can be difficult to identify without specific structural studies. On the other hand, some of the earliest euconodonts, having a very small crown, can be distinguished from paraconodonts only under high magnification and when preservation is good. The conodonts from the Baltic region have an excellent preservation for such studies.

According to MÜLLER and HINZ (1991) already in the early Late Cambrian (*Agnostus pisiformis* Zone), three species of alleged euconodonts occur in Sweden: *Acodus cambricus* NOGAMI, *Cambropustula kinnekullensis* MÜLLER and HINZ and *Coelocerodontus bicostatus* VAN WAMEL. However, the internal structure of the elements and the relationship with other conodonts are not yet known. Even if they have the same structure as later euconodonts, they do not belong to the same lineage as *Proconodontus* and appear not to have left many descendants. The elements assigned to *Acodus cambricus* (MÜLLER and HINZ 1991: pl. 12: 20, 21) are different from all Ordovician elements of the genus and most probably are not closely related to them. According to SWEET (1988) *Acodus* should be treated as *nomen dubium*. No descendants or ancestors of *Cambropustula kinnekullensis* are known. The elements of *Coelocerodontus bicostatus*\*, encountered by us in the uppermost Cambrian, differ in preservation from all co-occurring euconodonts, and their euconodont nature is in our opinion doubtful. They have unusually thin walls, with no trace of a basal body. Contrary to other euconodonts, they often occur in clusters. ANDRES (1988) assigned *C. bicostatus* to paraconodonts. It is interesting, however, that the apparatus of the species is composed of several distinct types of elements, which is known neither in paraconodonts nor in the earliest proconodontids.

\* BAGNOLI, BARNES and STEVENS (1987) erected for the species new genus, *Diaphonodus*, but MÜLLER and HINZ (1991) included the name to the synonymy of *Coelocerodontus*. It is out of the scope of the present paper to discuss taxonomic assignment of the species.

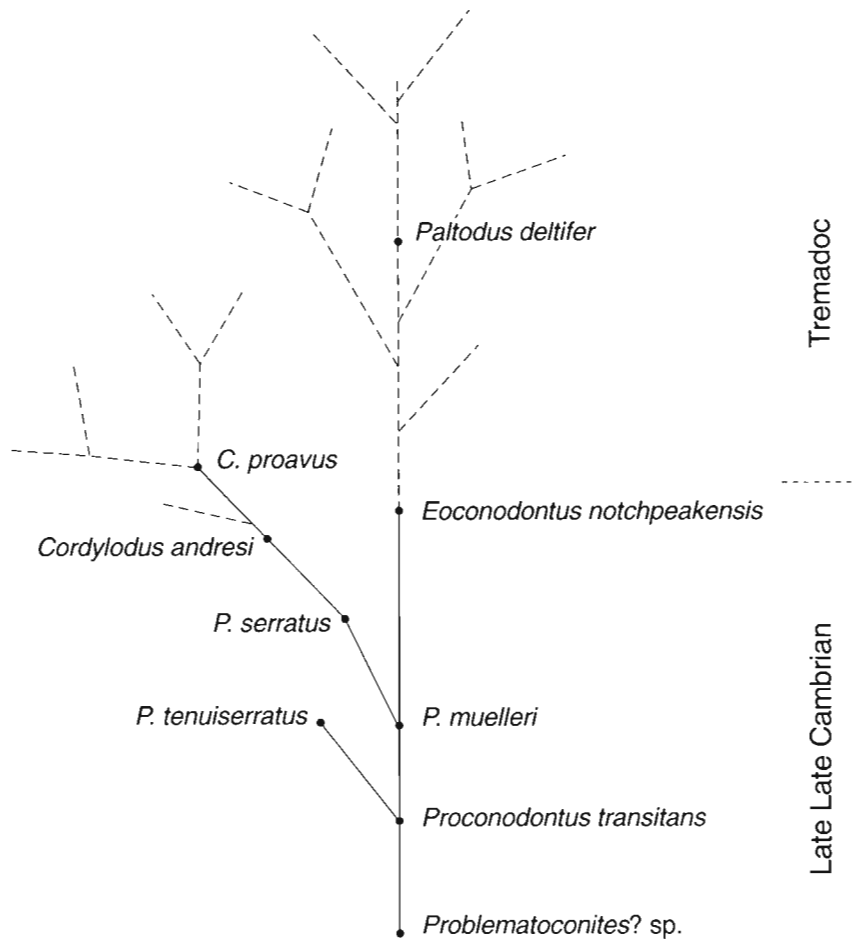


Fig. 3  
Evolution of the *Proconodontus* lineage.

The proconodontids were the first euconodonts to reach evolutionary success and gave rise to many later conodonts (Fig. 3). The earliest and the most primitive of them, *Proconodontus transitans* sp. n., most probably originated from a form close to *Problematoconites* (ANDRES 1988; SZANIAWSKI and BENGTON 1993), but the direct ancestral species is not known. MILLER (1984) assumed that *Proconodontus* evolved from an unnamed genus of euconodonts which originated from *Prooneotodus rotundatus* (DRUCE and JONES). However, this assumption is based only on morphological similarity. The internal structure of *P. rotundatus* is not known. The structure of the type species of *Prooneotodus*, *P. gallatini*, is less similar to that of proconodontids (ANDRES 1988; SZANIAWSKI and BENGTON 1993) than is the structure of *Problematoconites* representatives.

The apparatus of the first proconodontid species was composed of only slightly differentiated elements. The apparatuses of its ancestors are not known, but most probably they were composed of even more similar elements. Many clusters of incomplete paraconodont apparatuses are known (ANDRES 1981; SZANIAWSKI 1987; MÜLLER and HINZ 1991), and these are composed of two, three or four very similar elements differing mainly in size. The rapid morphological differentiation of the elements within apparatuses in the *Proconodontus* lineage began after their phosphatic crown evolved. This is because it is much easier to modify shape for elements growing by deposition over the whole surface (euconodonts) than for those growing only basally (paraconodonts) (BENGTON 1976). In *Proconodontus* the differentiation was rapid. Already in *P. muelleri*, the elements were quite strongly differentiated. Probably simultaneously with differentiation in shape, the elements began to fulfil slightly different functions in the apparatus, and as a result separate morphological types were formed. However, in none of the species of *Proconodontus* are there well-defined discrete types of elements, and intermediate forms between them occur. In addition, there was a strong infraspecific variability of the elements.

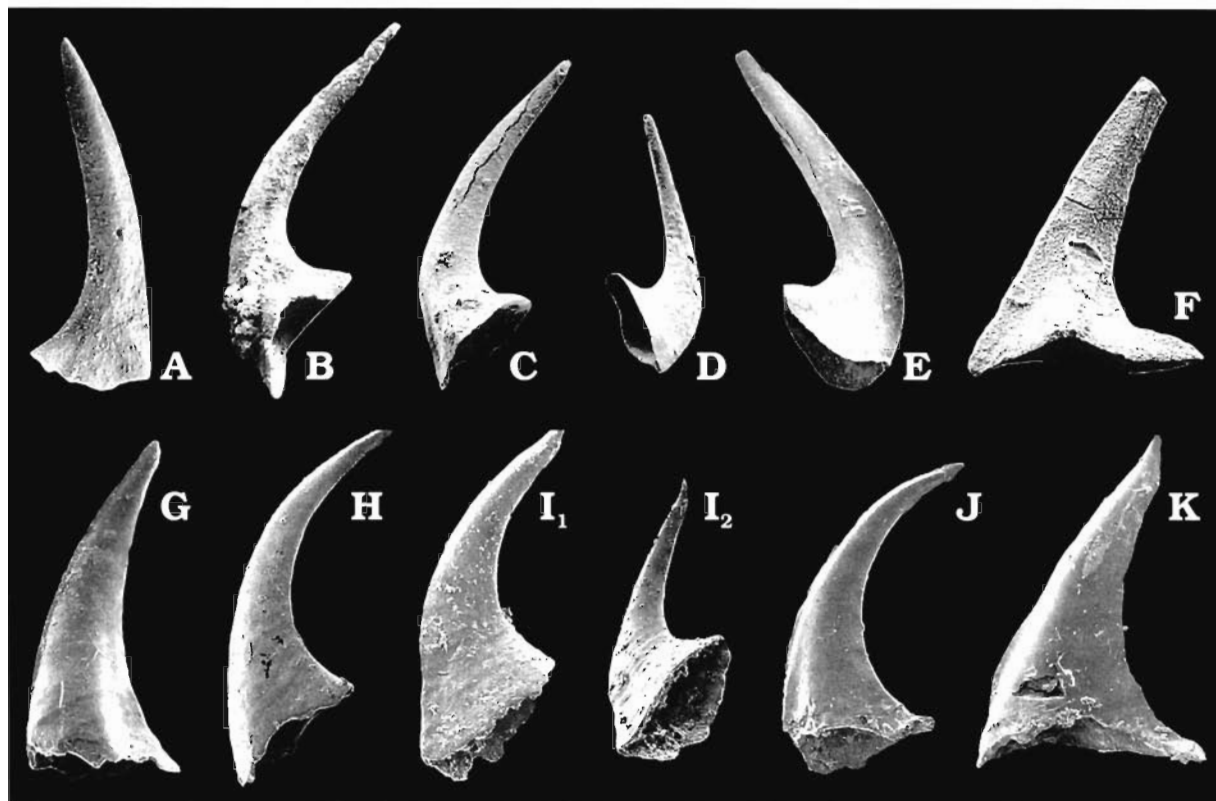


Fig. 4

Comparison of selected elements of *Paltodus deltifer pristinus* (VIIRA) (A–F) and *Proconodontus muelleri* MILLER (G–K). A–F. Upper Tremadoc, Poland, Holy Cross Mountains, Wysoczki, chalcedony beds; A, C–E  $\times 90$ , B, F  $\times 120$  (after SZANIAWSKI 1980). G–K. Upper Cambrian, collection described in this paper; G – SMNH X2186 (102.11),  $\times 100$ ; H – SMNH X2246 (103.34),  $\times 100$ ; I – SMNH X2343 (115.9),  $\times 100$ , I<sub>1</sub> – lateral view, I<sub>2</sub> – basal view; J – SMNH X2244 (103.18),  $\times 80$ ; K – SMNH X2243 (103.13),  $\times 80$ ; G and J, K – sample Wes86-2-SB (Trolmen), H, I – sample Wes86-1-SB (Råbäck).

The evolution of the early euconodonts was rapid. Within one trilobite subzone, *Peltura scarabaeoides*, at least five species and two genera of the *Proconodontus* lineage originated. Directly from *Proconodontus* evolved the first genus with elements having a denticulate process, *Cordylodus* PANDER (*C. andresi* VIIRA et SERGEEVA, see discussion on p. 17), and soon thereafter a second genus with coniform elements, *Eoconodontus* MILLER. *Eoconodontus* differs from *Proconodontus* in having a better developed, distally longer crown, which indicates its further evolutionary advancement from paraconodonts. Its apparatus is not well known. MILLER (1980) has recognized two types of elements in *E. notchpeakensis*, rounded and compressed, but the elements illustrated by him (fig. 3D, E; pl. 1: 10–12) differ greatly in depth of basal cavity, and their conspecificity seems uncertain.

NICOLL (1992: p. 106) supposed that all the three genera, *Proconodontus*, *Eoconodontus* and *Cordylodus*, "... are similar with a septimembrate apparatus structure". The *Eoconodontus* apparatus, according to him (NICOLL 1990: p. 530), "... includes geniculate elements earlier assigned to the genus *Cambrooistodus*". However, he only presented documentation for the apparatus of *Cordylodus*.

Further evolutionary steps can be traced in two separate branches, *Cordylodus* and a lineage of simple cones. We confirm here our earlier suggestion (SZANIAWSKI and BENGTON 1993) that the earliest species of the *Cordylodus* branch, *C. andresi*, originated from *Proconodontus serratus*. MILLER (1969, 1980) and NICOLL (1990, 1992) were convinced that *Cordylodus* evolved from *Eoconodontus notchpeakensis*, but at that time the earliest species of the genus, *C. andresi*, was not yet well known. *C. andresi* has a less well-developed crown and a larger basal cavity than *E. notchpeakensis*, which suggest that it is evolutionarily less advanced and could not originate from the latter species. The further evolution of *Cordylodus* has been the subject of several analyses in recent years (see e.g., NICOLL 1992).

The early evolution of simple-cone conodonts is not well understood, because of the weaker morphological differentiation of the elements. Furthermore, in the Baltic region the transition from *Proconodontus* to *Eoconodontus* and to later simple-cone genera cannot be readily studied because of stratigraphic hiatuses. However, the similarity of the elements of *P. muelleri* to those of the Late Tremadoc *Paltodus deltifer pristinus* (Fig. 4) suggest their close relationship. Most probably, the family Drepanoistodontidae, as well as many later conodonts, evolved from the *Proconodontus* stem lineage. SWEET (1988) suppose that the family Drepanoistodontidae belongs to the separate lineage which originated from *Teridontus*. It is quite possible that in addition to the *Proconodontus* lineage there were other euconodont lineages that originated directly from paraconodonts. This may be true of the *Teridontus* lineage (see MILLER 1984; SWEET 1988) and some other possible lineages. The transition from paraconodonts to euconodonts in these lineages is not documented, however, and most probably they did not have so many and so diversified descendants.

The strong possibility that several euconodont lineages, in addition to the *Proconodontus* one discussed herein, originated separately from paraconodonts, suggests that the crown, the distinguishing feature of euconodonts, represents the visible development of a feature that was widespread already in paraconodonts. This incipient crown would have the propensity for developing into the thicker, apatite crust suitable for morphological diversification that we see in euconodonts.

## STRATIGRAPHIC CONCLUSIONS

Stratigraphic correlation of Cambrian–Ordovician boundary beds in Sweden, as on the entire Baltic Platform, is difficult because of hiatuses in the sections and the common occurrence of mixed faunas of slightly different ages (LÖFGREN 1996). The stratigraphy of the Swedish Upper Cambrian is based mainly on trilobites; conodonts have not been much used until now. However the present state of knowledge of early euconodont evolution, as well as new data on their distribution in Sweden, permits an attempt to use them for stratigraphy and for correlations with other regions (Fig. 5). We correlate the uppermost Cambrian of Sweden with North America, where conodont stratigraphy of corresponding strata is well established (MILLER 1984; 1988), and with Estonia, where, despite the location in the same Acado-Baltic Province, the Upper Cambrian is developed in different facies. In Estonia, trilobites are not preserved and the conodonts presently serve as the main tools for Upper Cambrian stratigraphic subdivision (KALJO *et al.* 1986; VIIRA *et al.* 1987; MENS *et al.* 1993, 1996).

We do not use paraconodonts for this purpose, because their stratigraphic significance is still not well known. Paraconodont zones have been proposed for the Late Cambrian in Iran (MÜLLER 1973), the Middle and most of the Upper Cambrian in China (AN 1982; WANG CHENG-YUAN and WANG ZHI-HAO 1983; AN and MEI 1994), and for the Upper Cambrian in Estonia and the St. Petersburg region (KALJO *et al.* 1986), but the broader applicability of these zones has not yet been confirmed. MÜLLER and HINZ (1991), in their monograph on Upper Cambrian conodonts (mainly paraconodonts) of Sweden, preferred not to use them for stratigraphy as yet. In the present paper, only euconodonts of the *Proconodontus*–*Cordylodus* lineage are taken into account in the stratigraphic discussion.

We propose herein the ***Proconodontus transitans* Subzone** of the *Proconodontus* Zone as the lowermost conodont-based stratigraphic unit (our samples Wes86-12, 13, 16, 14-SB in the Trolmen section). Its lower limit corresponds to the first appearance of the nominal species, and its upper limit marks the appearance of *P. muelleri*. *P. transitans* sp. n. is presently known only from Sweden and North America?, but its evolutionary development shows clearly that it is the earliest of all *Proconodontus* species. Lack of the subzone as well as of the whole *Proconodontus* Zone in many sections hitherto investigated for conodonts in Sweden (ANDRES 1988; MÜLLER and HINZ 1991), is best explained by their incompleteness. The uppermost Cambrian trilobite zone, *Acerocare* is preserved only in one of the sections. It is very probable that the hiatus comprises also the uppermost part of the *Peltura scarabaeoides* Subzone, which corresponds to the whole *Proconodontus* Zone. In the one investigated section in which the *Acerocare* Zone is preserved (ANDRES 1988), in the Grönhögen quarry on the isle of Öland, *P. muelleri* also has been found lower down, in the *Peltura scarabaeoides* Subzone (ANDRES 1988).

On the eastern part of the Baltic shield, in Estonia and in the St. Petersburg region, the uppermost Cambrian is developed mainly as sandstones with thin clay interbeddings. KALJO *et al.* (1986), POPOV *et*

REGIONAL STAGE	NORTH AMERICA after MILLER (1988a)		SWEDEN		TRILOBITE ZONES	ESTONIA (compiled)	REGIONAL STAGE
	Subzone	Zone	Subzone	Zone		Zone	
SKULL ROCKIAN	<i>Clavohamulus elongatus</i>	<i>Cordylodus proavus</i>	hiatus ?			<i>Cordylodus proavus</i>	PAKERORT
	<i>Fryxellodontus inornatus</i>						
	<i>Hirsutodontus hirsutus</i>						
TREMPEALEUAN	<i>Cambrooistodus minutus</i>	<i>Eoconodontus</i>	<i>Cordylodus andresi</i>		<i>Acerocare</i>	<i>Cordylodus andresi</i>	
	<i>Eoconodontus notchpeakensis</i>						
	<i>Proconodontus muelleri</i>	<i>Proconodontus</i>	hiatus				
	<i>Proconodontus posterocostatus</i>						
<i>Proconodontus tenuiserratus</i>							
FRANCONIAN	NO ZONATION ESTABLISHED		<i>Proconodontus transitans</i>		<i>Peltura</i> uppermost part		
NO ZONATION							

Fig. 5

Conodont zonation of the uppermost Cambrian of Sweden and its correlation with North America and Estonia.

*al.* (1989), and MENS *et al.* (1993) distinguished a “*Proconodontus* Subzone” as the upper part of the *Westergaardodina* Zone, which, according to the zonation of those authors, occurs there below the *Cordylodus andresi* Zone. In our opinion, however, this is a misunderstanding caused by an incorrect taxonomic designation. Both of the two “*Proconodontus*” species cited from the sections, *P. primitivus* (MÜLLER) and *P. rotundatus* (DRUCE *et al.* JONES), are in fact paraconodonts. The first is *Furnishina primitiva* MÜLLER, a long-ranging species appearing in many other sections much earlier than the real proconodontids. The affinity of the second one is less clear. MILLER (1984: p. 46) assigned it to *Prooneotodus* MÜLLER. It occurs earlier than the proconodontids and differs from them at least by lack of keels. Most probably, there is a long gap in this region between the Tsitre Formation, in which only proto- and paraconodonts were found, and the overlying Kallavere Formation (Lower Pakerort), at the base of which in some places *Cordylodus andresi* occurs.

The next subzone, *Proconodontus muelleri*, in the Trolmen section (samples 2 and 15) is characterized by the occurrence of *P. muelleri*, *P. transitans*, *P. serratus*, and *P. tenuiserratus bicostatus*. The first of these is most abundant, the second occurs mainly in the lower part of the subzone, and the third and fourth occur sparsely in the upper part. Most of the *P. serratus* elements occurring in the subzone have poorly developed serration. The subzone ends with the first appearance of *Cordylodus andresi*. The differences with North America and other regions in sequence of occurrence, i.e. the earlier appearance of *P. muelleri* compared with *P. tenuiserratus*, might be due to redeposition of the Västergötland conodonts from neighbouring layers, but this is not necessarily the case. It is possible that the earliest forms of *P. muelleri*, which are small and have a poorly developed crown, were not recognized in the other regions because of different preservation. The specimens from the Swedish stinkstones are especially easy to identify because of the sharp contrast in color of their basal body and crown. Moreover, in North America, *Eoconodontus notchpeakensis* appears earlier than *P. serratus*, but this may not reflect evolutionary succession, as *E. notchpeakensis* appears to be more advanced than *P. serratus* and *C. andresi*. Our collection contains transitional forms between *P. muelleri* and *P. serratus* (Pl. 4:13) but it is possible that the early representatives of *P. serratus* are not known in North America.



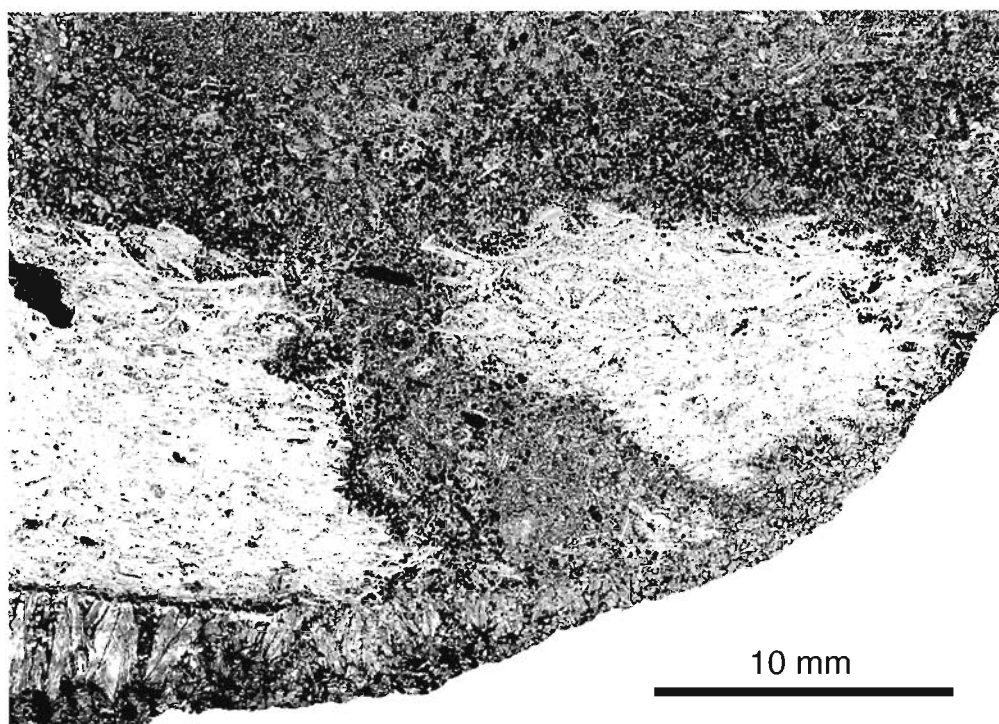


Fig. 6

Thin section of sample Wes86-1-SB showing the lithologic relationship between the lighter limestone clasts (older) and the dark limestone (younger).

The *Cordylodus andresi* Zone was proposed by KALJO *et al.* (1986) on the basis of the occurrence of the nominal species on Öland (ANDRES 1981), in north Estonia, and in the St. Petersburg region. The zone ends with the first appearance of *C. proavus*. LÖFGREN (1996) considered the specimens of *C. andresi* from Estonia and NW Russia to be redeposited. This seems unlikely, however, because the zone in Estonia has been recognized in five outcrops and one borehole (MENS *et al.* 1993). In some other sections in that region, the zone is lacking (see e.g., MENS *et al.* 1996), but *C. andresi* occurs in the higher, *C. proavus* Zone, and there it may possibly be redeposited. The problem is important, because the *C. andresi* Zone in Estonia defines the base of the Pakerort Regional Stage (MÄNNIL 1990).

In Sweden, *C. andresi* is known from the upper part of the *Acerocare* Zone in the Grönhögen section on Öland (ANDRES 1981, 1988) and from the *Peltura scarabaeoides* Subzone in several localities in Västergötland and Öland (MÜLLER and HINZ 1991; SZANIAWSKI and BENGTSON 1993). From Grönhögen it was first described as *C. sp.* (ANDRES 1981) and later as *C. proavus* (ANDRES 1988). It occurs there in black, impure stinkstone, and no other euconodonts co-occur with it. We have encountered the species in the uppermost bed of the Cambrian section in the Råbäck quarry at Kinnekulle (sample 1), which is regarded as the upper part of the *P. scarabaeoides* Subzone (WESTERGÅRD 1922). The layer is composed of black, coarsely crystalline, clayish stinkstone with much lighter fossiliferous stinkstone occurring as partly broken-up, lenticular intercalations in the dark matrix (Fig. 6). It is interesting that *C. andresi* occurs exclusively in the black rock, while the light rock contains numerous *P. muelleri* and *P. serratus* (the reverse was accidentally stated by SZANIAWSKI and BENGTSON 1993). Both of the *Proconodontus* species occur also in association with *C. andresi* in the black rock but are not as abundant. It is possible that the black rock represents somewhat younger strata that may already belong to the *Acerocare* Zone. Trilobites of the *Acerocare* Zone were not found in the section, but the black stinkstone is in general not very fossiliferous. Unfortunately, the conodont distribution in the *Acerocare* Zone in Scandinavia is difficult to recognize, because the sequence consists mainly of shales. Except for the above-mentioned investigations of the Grönhögen section on Öland, only one section in Scandinavia, in the Oslo region, Norway, has been successfully studied for conodonts (BRUTON *et al.* 1988). From the stinkstone concretions of the *Acerocare ecorne* Subzone, *C. proavus* and *Eoconodontus notchpeakensis* were found. The specimens are

poorly preserved, however, and their basal bodies are not clearly visible. It is possible that the specimens assigned to *C. proavus* in fact belong to *C. andresi*, which at that time was not well known.

Recently LÖFGREN (1996) reported two specimens of *C. andresi* from Upper Tremadoc beds of the *Paltodus deltifer* Zone in the Orreholmen section, Västergötland. These were interpreted as redeposited from the underlying Cambrian beds.

The *Cordylodus proavus* Zone is well known in many regions of the world (see MILLER 1984; LEHNERT 1994), but it is not recognized in Sweden. As has been already mentioned, the "*C. proavus*" specimens found in the *Acerocare* Zone of Öland (ANDRES 1988) are presently assigned to *C. andresi*. ANDRES (1988) described *C. proavus* also from the Middle Tremadoc of the Äleklinta section on Öland, but his specimens occur together with *C. intermedius*, *C. lindstroemi*, and *C. angulatus* (representing higher zones) and may be redeposited.

In Scandinavia the *C. proavus* Zone has been reported from the Oslo region only (BRUTON *et al.* 1988), where it corresponds to the upper part of the *Acerocare trilobite* Zone. As mentioned above, preservation of the conodonts is not good there and some of the designations are uncertain.

According to LENDZION (1983) the *C. proavus* Zone occurs in the subsurface of north-eastern Poland, but in that time the species *C. andresi* was not known and the concept of *C. proavus* was broader.

The time span of the *C. proavus* Zone in Sweden probably corresponds to the border beds of the *Acerocare* Zone and Lower Tremadoc *Dictyonema* Shales, but there are many local hiatuses in this diapason and possibly there are no continuous sections at all.

In Estonia, the *C. proavus* Zone has been reported from many sections (see MENS *et al.* 1993, 1996) in the Maardu Member of the Kallavere Formation (lower part of the Pakerort Regional Stage). In addition to the index species, *C. primitivus*, *C. andresi* and *Eoconodontus notchpeakensis* were also encountered in these strata.

Recently LÖFGREN (1997: fig 2), on the basis of earlier papers, correlated the uppermost Cambrian trilobite zone *Acerocare* with three conodont zones: *Proconodontus*, *Cordylodus andresi*, and *Cordylodus proavus*. Her paper concerns Late Tremadoc conodonts, however, and the Cambrian correlations are neither documented nor discussed therein.

## SYSTEMATIC PALEONTOLOGY

### Genus *Cordylodus* PANDER

Type species: *Cordylodus angulatus* PANDER 1856.

#### *Cordylodus andresi* VIIRA *et* SERGEEVA, 1986

(Pl. 1: 4–6, 8–15; Pl. 2: 1–3)

1981. *Cordylodus* sp.; ANDRES: p. 23, figs 11–19.

1986. *Cordylodus andresi* VIIRA *et* SERGEYEV; KALJO *et al.*: p. 103, pl. 2: 1–6, 9–10

1987. *Cordylodus andresi* VIIRA *et* SERGEYEV; VIIRA, SERGEYEV and POPOV: p. 147, pl. 1: 1–8, pl. 3: 1, 2, 4, fig. 2: 18, 33–36, 42–49, fig. 4: 28.

1988. *Cordylodus proavus* MÜLLER; ANDRES: p. 129, figs 26–34, pl. 13: 1, 2; not fig. 35.

1991. *Cordylodus primitivus* BAGNOLI, BARNES *et* STEVENS; MÜLLER and HINZ: p. 54, pl. 43: 4, 5, 8–15.

**Material.** — About 190 elements.

**Remarks.** — The specimens described by ANDRES (1981, 1988), first as *Cordylodus* sp. and later as *C. proavus* MÜLLER, from the uppermost Cambrian (*Acerocare* Zone) of Öland, are very similar to those of our collection. Some of them differ only in having a slightly better-developed crown. The specimens described by MÜLLER and HINZ (1991) are from the same stratigraphic horizon as ours (*Peltura scabraeoides* Zone).

According to VIIRA *et al.* (1987: p. 146), the earliest species of the genus *Cordylodus*, "... *C. andresi*, and *C. proavus* are three-element apparatuses with symmetry transition from rounded to twisted forms". According to NICOLL (1990: p. 529), the genus has "... a septimembrate apparatus containing **M**, **S**, and **P** elements". In addition to MILLER's (1980) different types, i.e. rounded (**S**) and compressed (**P**) elements with a denticulate posterior process, NICOLL (1990) also distinguished "makellate" elements (**M**) with a lateral process that

“may or may not be denticulate”. JI and BARNES (1994: p. 31), based on their own observations and the illustrations of ANDRES (1988) (which shows variable shape of the elements of *C. andresi*, fig. 26, and *C. proavus*, fig. 35), came to the conclusion that “...*Cordylodus* contains three elemental morphotypes...”: “subrounded” with two variants, “suberect” and “compressed” with two variants.

In our collection, the elements of *C. andresi* are very diversified. Typical rounded and compressed elements occur, but there are many transitional forms between them, and none of the intermediate forms can be regarded as a separate morphotype. Most probably, the diversification is due to the great infraspecific variability rather than to the differentiation of element types in the apparatus. *Cordylodus andresi* was one of the earliest euconodont species, and different types of elements of its apparatus were not yet well defined. ANDRES (1981) described a cluster composed of seven juvenile elements that are very similar to each other and differ mainly in size.

New material confirms our earlier supposition (SZANIAWSKI and BENGTSON 1993) that the direct ancestor of *Cordylodus andresi* was *Proconodontus serratus*. There are transitional forms between the rounded elements of the two species (Pl. 1: 3–4), and in some cases it is even difficult to decide to which of the species they should be assigned.

MENS *et al.* (1996: p. 13) argued that *Cordylodus primitivus* BAGNOLI, BARNES *et* STEVENS is not a junior synonym of *C. andresi* but a separate species, which differs by possession of white matter. In our opinion, *C. primitivus* may be a separate species, though not because of the white matter (which occurs also in some specimens of *C. andresi*) but because of the slightly different shape of the elements. The occurrence and distribution of white matter in conodont elements depend partly on their ontogenetic stage and preservation and should not be used as the decisive diagnostic feature.

#### Genus *Proconodontus* MILLER, 1969

Type species: *Proconodontus muelleri* MILLER, 1969.

**Emended diagnosis.** — Multielement apparatus composed of slightly diversified simple-cone elements with transition series. Crown of elements thin; basal body funnel-shaped, extending almost to the tip; basal cavity of basal body very large and deep; cross section nearly round or oval, more compressed from one side; keels on anterior or posterior edge, or both; compressed elements slightly asymmetrical owing to lateral curvature.

**Remarks.** — In addition to the differentiation of elements within one apparatus there is apparently a great infraspecific variability in the studied population. This causes great difficulties for reconstructions. The elements of a species differ mainly in cross section, posterior arching and lateral curvature. Transitional forms between all of them exist, and components of the apparatus are thus not distinct morphologically. Only the extreme forms of the rounded and compressed elements are clearly differentiated. Apart from the cross section, they differ in symmetry. The rounded elements are nearly symmetrical, while the compressed forms are laterally curved. In *P. muelleri*, which is most numerous in the collection and has the most diversified elements, nearly geniculate elements also can be recognized.

On the inner surface of the basal body of well-preserved specimens, small pits, longitudinal grooves and horizontal ridges are visible.

MILLER (1969), in the original definition of the genus, wrote that the basal body of the elements is white. The elements from Sweden have a colorless and quite translucent crown, and the basal body is usually dark or brown, often also partly translucent. Some of the elements, however, have a nearly black basal body. The differences in color preservation are related to host-rock lithology and diagenetic history.

In transmitted light, fractured tips can be seen in most of the elements. The crown is usually regenerated, but not the basal body.

#### *Proconodontus muelleri* MILLER 1969

(Pl. 2: 4–17, Fig. 4: g–k)

1969. *Proconodontus mülleri mülleri* n. sp., n. subsp.; MILLER: p. 437, pl. 66: 34–40, fig. 5h, not pl. 66: 31?, 32–33.

1980. *Proconodontus muelleri* MILLER; MILLER: p. 29, fig 4C, pl. 1: 7.

1991. *Proconodontus muelleri* MILLER; MÜLLER and HINZ: p. 56, pl. 42: 1, 3–9, not pl. 42: 2?, 10?, 11, 14, 15, 16? See for more complete synonymy.

**Material.** — About 900 elements.

**Remarks.** — Apparatus composed of at least three types of elements: comparatively slender and rounded in cross section, slightly wider and compressed from one side, and nearly geniculate. The nearly

geniculate elements are comparatively rare. There is a transition series from compressed elements to the nearly geniculate ones.

The original concept of the species (MILLER 1969) was very broad. In 1980 MILLER, excluded from it the former subspecies *P. muelleri serratus* and established two new species of the genus, *P. posterocostatus* and *P. tenuiserratus*. The new species described herein, *P. transitans*, further restricts the original concept of *P. muelleri*. Nevertheless, it is still broad, and elements assigned to the species are very diversified. However, it is not easy and probably not necessary to split it into several species, because transition series between the elements exist. The variation within each of the element types is mainly expressed in the cross section, degree of posterior arching, length-to-width ratio, and development of the keels. Usually either the anterior or posterior keel is better developed. Specimens with short posterior keel and weakly developed anterior keel are very similar to *P. posterocostatus* MILLER.

*Proconodontus serratus* MILLER, 1969  
(Pl. 1: 1–3, 7; Pl. 4: 9–10, 13, 17–19)

1969. *Proconodontus muelleri serratus* n. subsp.; MILLER: p. 438, pl. 66:1–44.

1980. *Proconodontus serratus* MILLER; MILLER: p. 31, fig. 4D, pl. 1: 13.

1991. *Proconodontus serratus* MILLER; MÜLLER and HINZ: p. 56, pl. 42: 17–21, pl. 43: 1–3, 6, 7; fig. 22A. See for more complete synonymy.

**Material.** — About 110 elements.

**Remarks.** — In our collection, two types of elements can be differentiated: rounded, nearly symmetrical ones and compressed ones which are asymmetrical because of compression from one side and lateral bending. The compressed elements predominate. Nearly geniculate, unserrated elements may also belong to the apparatus.

The elements are comparatively large but not numerous. Differentiation within each of the two serrated types of elements mainly comprise width/length proportions and development of serration. In the primitive forms, occurring mainly in the samples Wes86-15-SB, and Wes86-2-SB, the serration is very irregular and developed usually in the basal part (Pl. 4: 13). There are also elements of the same shape as those of *P. serratus*, with both keels well-developed but without serration (Pl. 2: 9). These are most probably intermediate forms between *P. serratus* and *P. muelleri*, from which *P. serratus* evidently evolved. On the other hand, some of the advanced elements (from the sample Wes86-1-SB) with comparatively long denticles (Pl. 1: 3) are difficult to distinguish from some elements of *Cordylodus andresi* (Pl. 1: 4), which is thought to have evolved from *P. serratus* (SZANIAWSKI and BENGTON 1993).

*Proconodontus tenuiserratus* MILLER, 1980

**Emended diagnosis.** — Apparatus composed of at least two types of curved simple-cone elements, rounded and compressed in cross section. In both types posterior keel small and finely serrate, developed mainly in the apical portion; anterior keel present or absent. Rounded elements nearly symmetrical; compressed ones flattened from one side and slightly bent laterally.

**Remarks.** — The populations in which all elements have only posterior keel developed, as in the type material described by MILLER (1980), are treated here as the nominative subspecies *Proconodontus tenuiserratus tenuiserratus*.

*Proconodontus tenuiserratus bicostatus* subsp. n.  
(Pl. 4: 11–12, 14–16)

Holotype: The specimen SMNH X2215 (103.38), figured on Pl. 4: 16.

Type horizon: Upper Cambrian, *Proconodontus muelleri* Subzone.

Type locality: Sweden, Kinnekulle, Trolmen quarry.

Derivation of name: Latin *bicostatus* = two-costate; the elements have sharp edges along anterior and posterior margins (= keels).

**Diagnosis.** — *P. tenuiserratus* in which both of the known elements have posterior and anterior keel developed; the anterior one is usually wider and extends much further to the base.

**Material.** — 21 elements.

**Remarks.** — Rounded elements of the new subspecies correspond in shape to the type material of the nominative subspecies. The only difference is that in addition to the small, serrated posterior keel, elements

of the new subspecies possess an anterior keel. This keel extends from the apical part of the element nearly to its base. The compressed elements are similar in shape to the rounded ones but are flattened from one side. They probably correspond to the rare elements that are "oval near base", mentioned by MILLER (1980: p. 31) in the original description of the species. In the new subspecies the compressed elements are also more rare than the rounded ones.

The serration of the posterior keel can be very faint, visible only in high magnification, as in the nominative subspecies. The number of denticles varies from 2 to 12, but in some specimens the number is difficult to estimate because the apical portion of the elements has been fractured and regenerated. None of our specimens has serration developed on the regenerated part of the cusp. *P. tenuiserratus* has not been known in the North Atlantic Province until now. In the studied section, it occurs only sparsely in *P. muelleri* Subzone.

*Proconodontus* cf. *tenuiserratus bicostatus* subsp. n.  
(Pl. 4: 7–8)

**Material.** — Six elements.

**Remarks.** — The collection contains elements that are very similar to those of the new subspecies but do not have serration on the short posterior keel. The species assignment of these elements is not clear.

*Proconodontus transitans* sp. n.  
(Pl. 3: 1–12; Pl. 4: 1–6)

1969. *Proconodontus mülleri mülleri* n. sp., n. subsp.; MILLER: p. 347, pl. 66: 31?, 32–33?, not pl. 66: 34–40, fig. 5h.

1991. *Proconodontus muelleri* MILLER; MÜLLER and HINZ: p. 56, pl. 42: 2?, 10, 11, 14, 15, 16?, not pl. 42: 1, 3–9.

1993. *Proconodontus* sp.; SZANIAWSKI and BENGTSON: fig. 1: 1–3, 8–12; fig. 2: 1–2, 5–6; fig. 3: 5–10.

Holotype: The specimen SMNH X2247 (104.3), figured on Pl. 3: 1.

Type horizon: *Peltura scarabaeoides* trilobite subzone, lower part of the *Proconodontus* conodont Zone.

Type locality: Sweden, Kinnekulle, Trolmen quarry.

Derivation of name: Latin *transitans* – passing through, refers to the transitional form of the elements from paraconodonts to euconodonts.

**Diagnosis.** — Apparatus composed of small, slender, slightly arched and comparatively weakly differentiated elements; crown very thin, developed mainly around the apical portion of the cusp; very narrow keel on the posterior or on both edges, disappearing toward the base; wall of basal body thin; basal cavity extending almost to the tip; lateral curvature comparatively small.

**Material.** — About 380 elements, mostly well preserved.

**Description.** — Average length of elements 550 µm; maximum width, at the base, about one-fourth of the length. Base not differentiated from cusp. Only rounded and compressed elements can be recognized. The compressed elements are asymmetrical, slightly laterally curved. They are usually also a little wider at the base.

The posterior keel is often better developed but shorter than the anterior one. The tip is in most of the specimens fractured, its crown usually regenerated but basal body not. The basal body in cross section narrows posteriorly.

Intraspecific variability of the elements involves their posterior arching, lateral curvature and width at the base.

**Remarks.** — In the lowermost sample of the species' occurrence (Wes86-12-SB), most of the elements are very small, slender and weakly differentiated. Their crown is very thin, developed mainly in the apical part and in the keels, which usually do not reach the base. In the higher samples (Wes86-14-SB and Wes86-16-SB), the difference between the rounded and compressed elements is greater. Within each morphotype a greater differentiation also exists. Because of greater asymmetry in the compressed elements, their left and right forms are easily recognizable. Some of the compressed elements are more erect and longer, some are strongly curved posteriorly (Pl. 3: 12). The rounded elements are usually more erect. In the even higher samples (Wes86-15-SB and Wes86-2-SB), the differentiation is even greater, but *Proconodontus muelleri* also occurs in these samples and it is not possible to distinguish some elements of the new species from those of juvenile *P. muelleri*.

The new species differs from *P. muelleri* in having smaller and more slender elements, smaller morphological differentiation, and weaker development of the crown. The holotype of *P. muelleri* (MILLER 1969: pl. 66: 37–39) is a comparatively large and wide specimen with both keels well developed, but the

specimens illustrated in the same paper on pl. 66: 30–33 as paratypes of *P. muelleri* and transitional to *Euconodontus nothchpeakensis* (MILLER) are very similar to the new species and probably belong to it. They are not from the same section as the holotype. Elements of *E. notchpeakensis*, if their basal cavity is not clearly visible, can be easily confused with the new species.

Some of the elements from our collection, which have the posterior keel developed only in the apical part and the anterior keel developed very weakly, are very similar to *P. posterocostatus* (Pl. 3: 10).

*P. transitans* is the earliest species of *Proconodontus* in the studied section.

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## LATE CAMBRIAN EUCONODONTS FROM SWEDEN

## PLATE 1

*Proconodontus serratus* MILLER, 1969 . . . . . 18

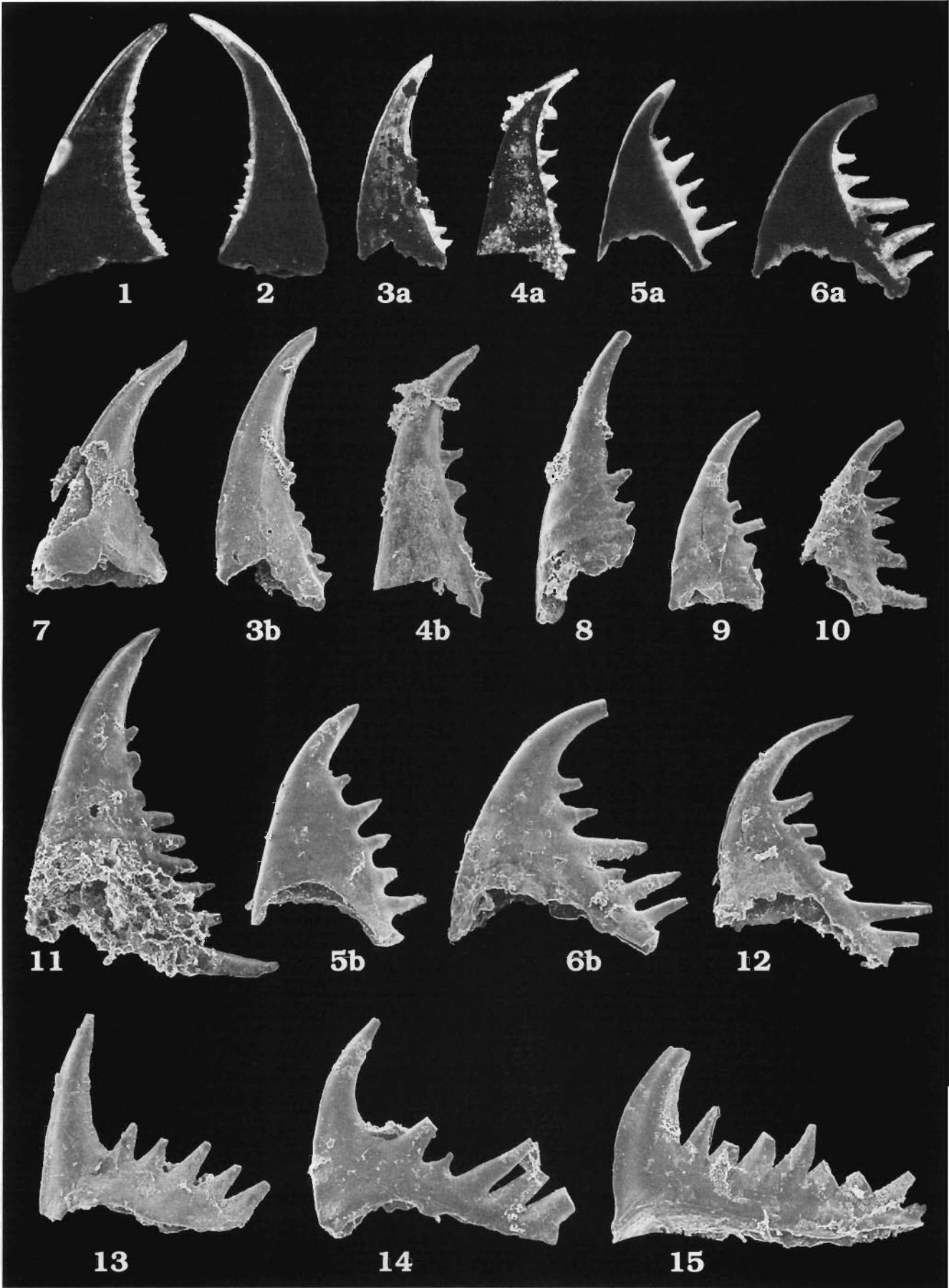
1. Compressed element with well-developed denticulation, SMNH X2303 (113.6). The same specimen is illustrated on Pl. 4: 17.
2. Rounded element with irregular denticulation, SMNH X2302 (113.5).
3. Rounded element, morphologically intermediate between *P. serratus* and *Cordylodus andresi*, SMNH X2318 (113.20).
7. Compressed element with irregular denticulation, SMNH X2304 (113.7).

*Cordylodus andresi* VIIRA et SERGEEVA, 1986 . . . . . 16

4. Rounded element, morphologically intermediate between *P. serratus* and *C. andresi*; SMNH X2267 (112.12).
- 5, 6, 8–11. Rounded elements of different development; SMNH X2309 (113.12), X2312 (113.15), X2298 (113.1), X2270 (112.15), X2271 (112.16), X2301 (113.4), respectively.
12. Element morphologically intermediate between rounded and compressed; SMNH X2310 (113.13).
- 13–15. Compressed elements; SMNH X2280 (112.25), X2278 (112.23), X2256 (112.1), respectively.

1, 2, 3a, 4a, 5a, 6a – photographs taken in transmitted light, by crossed nicols,  $\times 50$ ; all the rest SEM,  $\times 65$ .  
All the specimens are from sample Wes86-1-SB (Råbäck).





## LATE CAMBRIAN EUCONODONTS FROM SWEDEN

## PLATE 2

*Cordylodus andresi* VIIRA et SERGEEVA, 1986 . . . . . 16

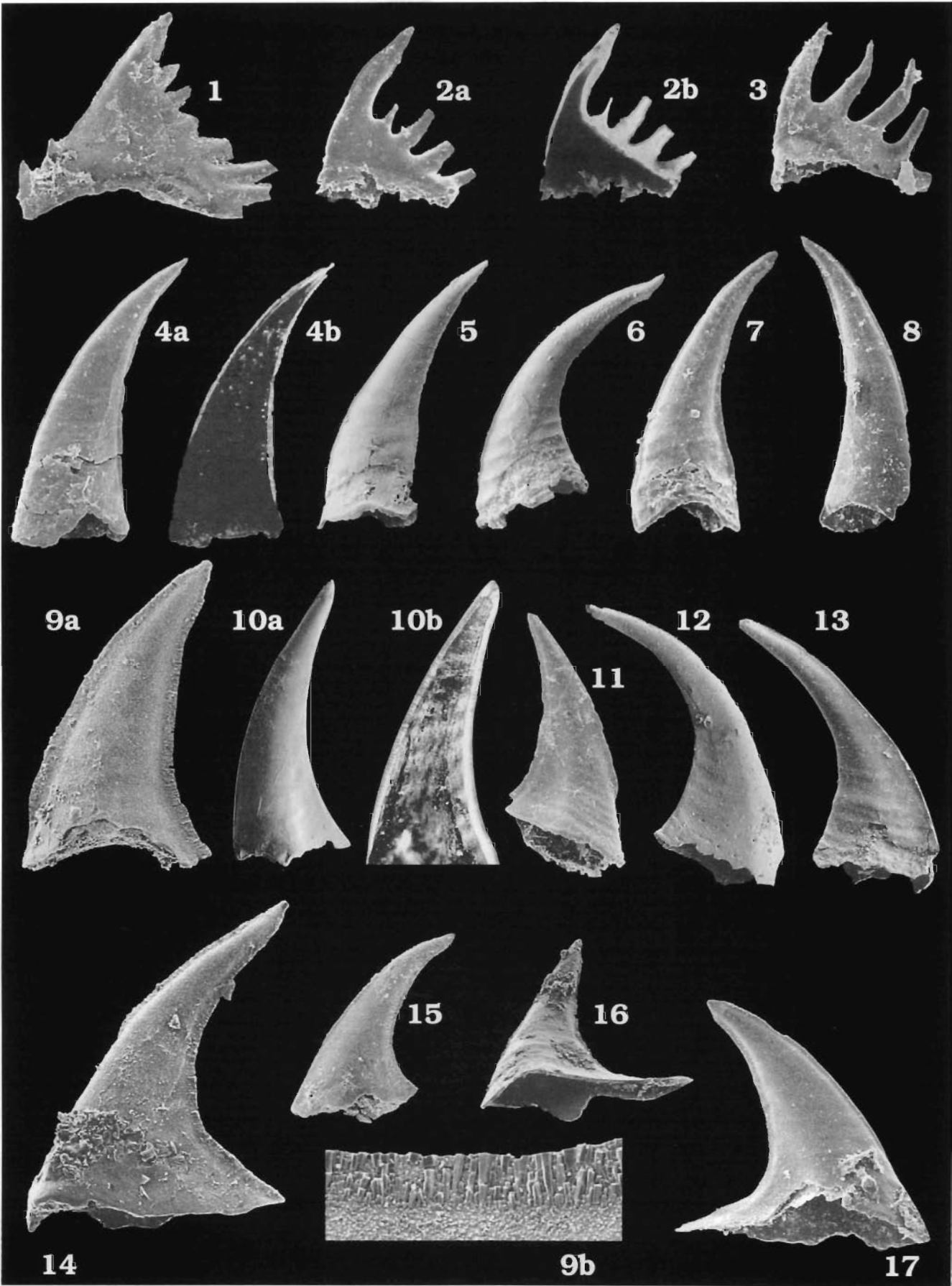
1. Aberrant(?) element with additional anterior, denticulate process; SMNH X2284 (112.29).  
 2–3. Intermediate elements with comparatively short posterior process but long teeth; 2 has unusually well-developed keels on the cusp; 2*b* the same as 2*a* but in transmitted light with crossed nicols; SMNH X 2308 113.11, SMNH X2314 113.17 respectively.

*Proconodontus muelleri* MILLER, 1961 . . . . . 17

- 4–8. Rounded elements, SMNH X2261 (112.6), X2294 (103.5), X2180 (103.6), X2258 (112.3), X2292 (112.37) respectively, 4*b* the same as 4*a* but in transmitted light with crossed nicols.  
 9–13. Compressed elements, 9 element morphologically similar to *P. serratus*, probably intermediate form; SMNH X2324 (114.6), X2186 (102.11), X2257 (112.2), X2229 (102.1), X2295 (104.17) respectively; 9*b* magnification of anterior keel of 9*a*; 10*b* the same as 10*a* but in transmitted light and without basal part.  
 14–17. Nearly geniculate elements; SMNH X2321 (114.3), X2288 (112.33), X2320 (114.2), 2282 (112.27) respectively.

Magnifications: 1–4, 7, 11 × 65; 16 × 80; 5–6, 10*a*, 12 × 90; 8, 15, 17 × 100; 9*a*, 10*b*, 13, 14 × 150; 9*b* × 600.

Provenance of specimens: 1–4, 7–9, 11, 14–17 from sample Wes86-1-SB (Råbäck); 7–8, 10, 12–13 from sample Wes86-2-SB (Trolmen).



## LATE CAMBRIAN EUCONODONTS FROM SWEDEN

## PLATE 3

*Proconodontus transitans* sp. n. . . . . 19

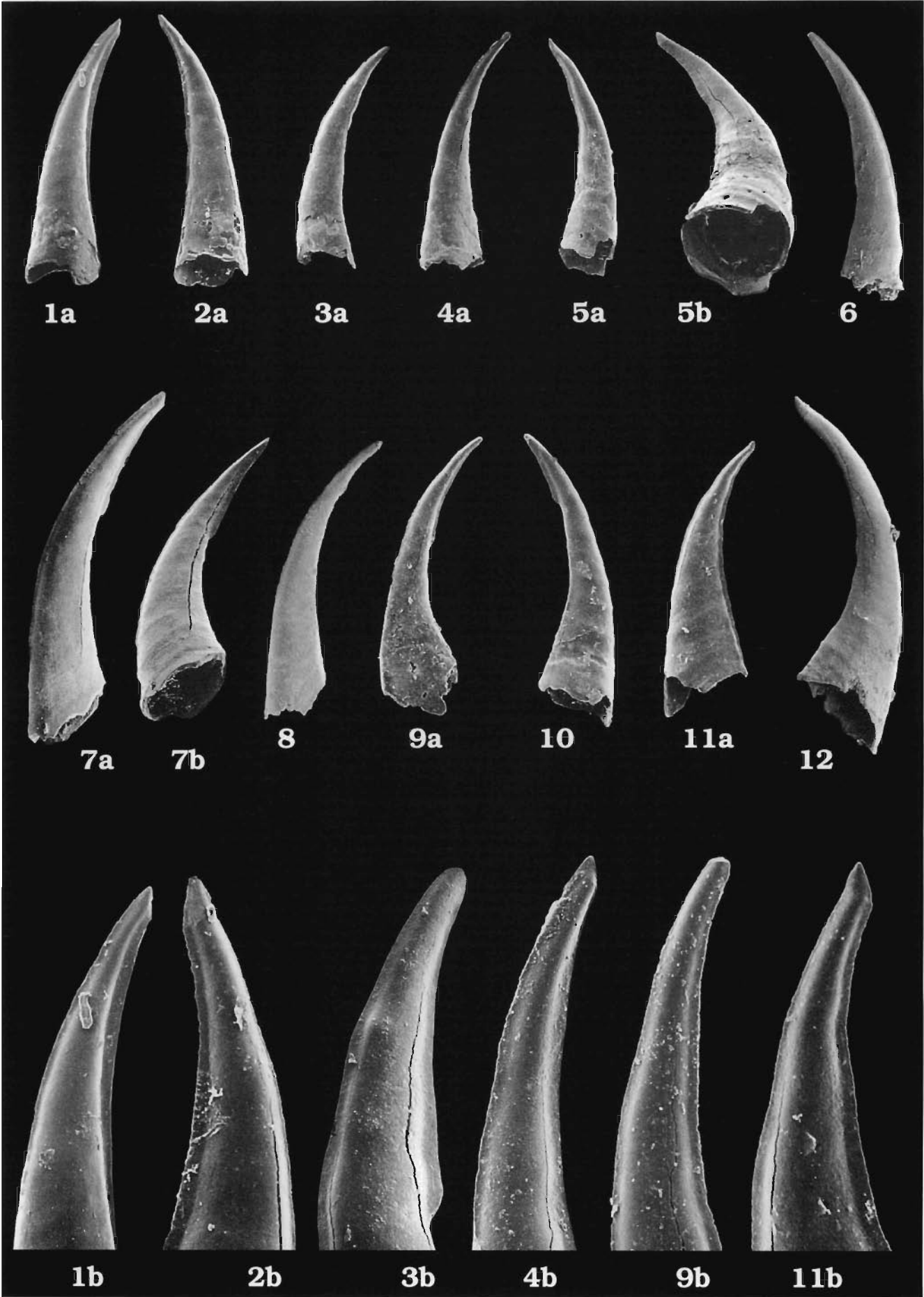
1–6. Rounded elements; SMNH X2247 (104.3) holotype, X2329 (114.11), X2166 (104.6), X2248 (104.4), X2328 (114.10), X2178 (102.6) respectively.

7–12. Compressed elements; SMNH X2167 (104.1), X2159 (102.29), X2334 (114.16), X2330 (114.12), X2331 (114.13), X2161 (102.24).

Magnifications: 1a, 2a, 5a, 7a, 8, 9a, 10, 11, 12  $\times$  110; 3a, 4a, 7b  $\times$  125; 5b  $\times$  200; 6  $\times$  160; 1b  $\times$  250; 2b, 3b  $\times$  420; 4b  $\times$  380; 9b, 11b  $\times$  330.

Provenance of specimens: 8, 12 from sample Wes86-14-SB (Trolmen); all the rest from Wes86-12-SB (Trolmen).

Specimens 6 and 8 are illustrated also on Pl. 4: 6, and 4: 1, respectively.



## LATE CAMBRIAN EUCONODONTS FROM SWEDEN

## PLATE 4

- Proconodontus transitans* sp. n. . . . . 19
- 1–6. Different elements in transmitted light, all but 1 with crossed nicols; 4 has basal part broken off; 6b magnification of the central part of 6a; SMNH X2159 (102.29), X2200 (102.27), X2241 (102.9), X2163 (102.31), X2199 (102.7), X2178 (102.6), respectively.
- Proconodontus* cf. *tenuiserratus bicostatus* subsp. n. . . . . 19
7. Compressed element morphologically characteristic of *P. tenuiserratus bicostatus* but with single denticle(?) or fragment of fractured posterior keel; in this specimen the comparatively large apical part was fractured; SMNH X2255 (111.7).
8. Element morphologically characteristic of *P. tenuiserratus bicostatus* but without serration, intermediate form(?) to *P. muelleri* or to *P. posterocostatus* Miller, 1980; SMNH X2228 (103.7).
- Proconodontus serratus* MILLER, 1969 . . . . . 18
- 9, 10, 17, 19. Compressed elements; 9 with slim and strongly arched cusp; 10 with irregular denticulation; 17b fragment of 17a showing arrangement of crystals in denticles; 17c fragment of 17a in transmitted light, crossed nicols; 19 aberrant(?) element with pustules on the denticulate part of the posterior keel; SMNH X2322 (114.4), X2266 (112.11), X2303 (113.6), X2293 (103.12) respectively.
- 13, 18. Rounded elements; 13 element with poorly developed denticulation, intermediate to *P. muelleri*; SMNH X2306 (103.9), X2168 (112.13), respectively.
- Proconodontus tenuiserratus bicostatus* subsp. n. . . . . 18
11. Fragment of a specimen fractured during preparation, in transmitted light, crossed nicols; note comparatively wide anterior keel; SMNH X2207 (104.25).
- 12, 14, 16. Rounded elements; 16 holotype, SMNH X2252 (111.4), X2245 (103.23), X2215 (103.38), respectively.
15. Compressed element; SMNH X2249 (111.1).
- Magnifications: 1–6a  $\times 100$ ; 6b  $\times 240$ ; 7, 10, 12, 14, 15, 17a, 18  $\times 65$ ; 8, 13, 19  $\times 90$ ; 9  $\times 80$ ; 11  $\times 300$ , 17b  $\times 600$ ; 17c  $\times 140$ .
- Provenance of specimens: 1, 2, 4 Wes86-14-SB (Trolmen); 3, 8, 13, 19 Wes86-2-SB (Trolmen); 5, 6, Wes86-12-SB (Trolmen); 7, 11, 12, 14–16 Wes86-15-SB (Trolmen); 9–11, 17, 18 Wes86-1-SB (Råbäck).

