Apparatus of the conodont *Scolopodus striatus* Pander, 1856 and a re-evaluation of Pander's species of *Scolopodus*

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The Lower Ordovician conodont *Scolopodus striatus* Pander, 1856 (= *Scolopodus rex* Lindström, 1955) has an apparatus composed of five element morphotypes: acontiodiform, subrounded, compressed paltodiform, paltodiform, and scandodiform. The identification of the morphotypes is based on the general asymmetry of elements and shape of their bases. The elements are variable within each morphological group and form a continuous transition series generally reflected in differences in the depth of the basal cavity, height and degree of lateral compression of the base. The new collection from the localities near St. Petersburg, the type area of the first investigations on conodonts by Christian Pander in 1856, was examined and species of *Scolopodus* named by him are revised. All Pander's species with the exception of the type species *Scolopodus sublaevis* are identified as a single species of *Scolopodus* that was named 99 years later as *Scolopodus rex*. The *S. sublaevis* sensu formae was not recognised in collections studied and its validity is questionable. *S. striatus* is the most easily recognisable among Pander's species of *Scolopodus* and is here proposed to be a senior synonym of *S. rex*.

Key words: Conodonta, apparatus, Ordovician, East Baltic, Estonia, Russia.

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Introduction

Scolopodus striatus Pander, 1856 (= *Scolopodus rex* Lindström, 1955) is a distinctive hyaline conodont species that has a wide distribution through the Lower Ordovician, ranging from the uppermost part of the *Paroistodus proteus* Zone up to the *Microzarkodina parva* Zone (Löfgren 1978; Stouge and Bagnoli 1990). In most Swedish sections it is rare and usually makes up less than 1% of the total number of conodont species in the assemblages (Stouge and Bagnoli 1990; Löfgren 1994, 1995). In the East Baltic, however, and in Estonia especially, *S. striatus* elements are more abundant and in places compose up to 8% of the assemblages at some levels within the *Oepikodus evae* Zone.

Scolopodus striatus was described by Pander (1856) from the Lower Ordovician in the vicinity of St. Petersburg almost one hundred years before the studies of Lindström (1955). Unfortunately, the original collection has been lost. Moreover, all the *Scolopodus* species, including the type species *S. sublaevis* described and illustrated by Pander, were not identified by Lindström (1955) among *Scolopodus* elements from the Scandinavian Lower Ordovician. Thus, Lindström (1955) erected the new species *S. rex* and *S. rex* var. *paltodiformis*, and emended the diagnosis of *Scolopodus* Pander, 1856. In later studies by Lindström (1971) and Löfgren (1978), the elements within the *S. rex* apparatuses were subdivided into symmetrical and asymmetrical elements. Later, a more advanced reconstruction was made by Fåhræus (1982) who was the first to revise *S. rex* Lindström, 1955. Fåhræus (1982) identified five *Scolopodus* element morphotypes and subdivided them into: *S. sublaevis* Pander, 1856 and *S. quadratus* Pander, 1856. However, he studied only the Swedish collection of *Scolopodus* elements, and did not obtain samples from the type area. Bergström (1988) studied conodonts from Pander's sections on the Tosna and Popowka rivers (Fig. 1), but did not discuss the species of *Scolopodus* in detail.

A small conodont collection represented by two small test tubes that both contain approximately 500 conodont elements was recently found in the museum of the Mining Institute in St. Petersburg. It is believed that the conodonts in the tubes were collected by Christian Pander and represent the unillustrated part of his type collection (Tolmacheva 2004). Studies of the newly found collection and arguments that it was collected by Pander are in progress, but, even now, it is evident that the collection contains a conodont assemblage almost identical to that described by Pander. Among the other conodonts the collection includes 54 elements of *Scolopodus*. All of them belong to the widely known *Scolopodus* taxon that was named by Lindström (1955) as *Scolopodus rex*. If it turns out to be clearly evident that the newly found collection belongs to Pander, it can be considered as a paratype collection, even though there are no documents providing information on the sampled locality or conodont identification.

The aim of this paper is to analyse the elemental morphology and composition of the apparatus of *Scolopodus striatus* Pander, 1856 and to re-describe and revise Pander's species

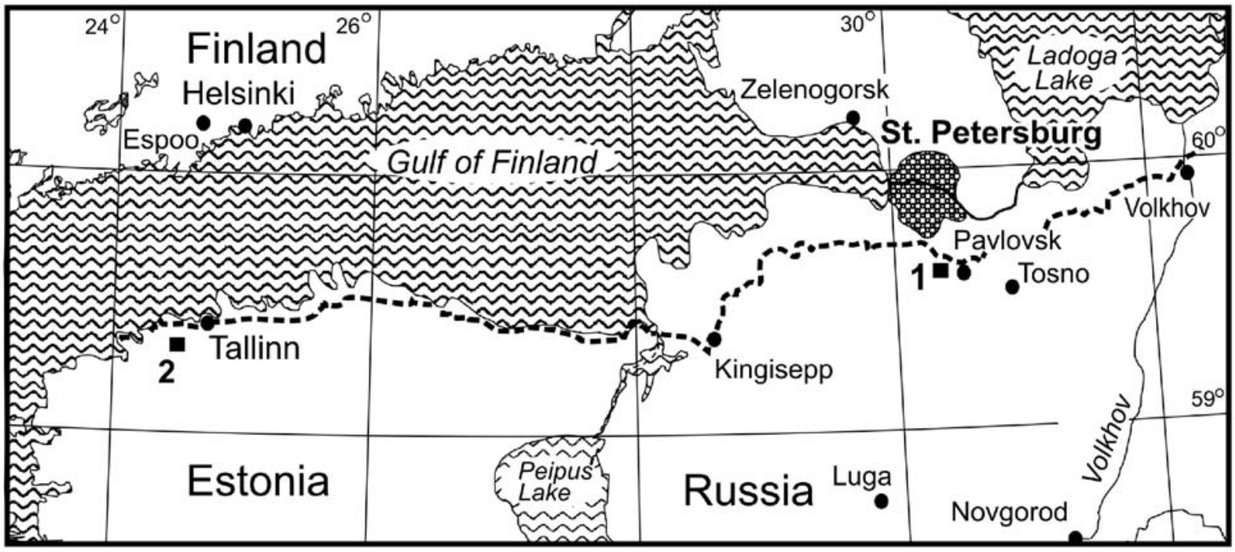

Fig. 1. Location of the Harku section in Estonia and the Popowka River section in Russia. Legend: 1, the Popowka section; 2, the Harku section; dash line marks the Baltic-Ladoga Klint.

of *Scolopodus* on the basis of the collection that presumably belonged to Pander, as well as of the new samples from one of Pander's original localities on the Popowka River, St. Petersburg district (Fig. 1).

Institutional abbreviation.—PMU, Palaeontological Museum, Uppsala University, Sweden.

Material

The outcrops of Lower Ordovician glauconitic limestones on the left bank of the Popowka River were among the localities around St. Petersburg listed by Christian Pander in the first report on conodonts (Pander 1856). Unfortunately, he did not give any precise geographic and stratigraphic position of the described and illustrated conodont elements. However, the description of the sampled beds and the list of characteristic taxa imply that he studied the lowermost bed of the Ordovician glauconitic sandstones that yields a conodont assemblage of the uppermost *Prioniodus elegans* Zone. This is the most unconsolidated bed within the section; thus, it is possible to extract conodonts simply by washing with water (Pander did not use acid extraction). The material for this study was collected from this bed and prepared in this way.

Conodont elements are numerous in the sample residue, but their preservation is rather poor. Most of the elements have broken cusps and truncated edges of the base. *Scolopodus* elements are not abundant and comprise not more than a few percent of the whole assemblage. More than one hundred S*colopodus* elements were picked from the sample and compared with the *Scolopodus* species described and illustrated by Pander in 1856. Unfortunately, imperfect preservation and the low number of specimens obtained from the disscussed locality, make recognition of different morphotypes, as well as any statistical analysis, hardly possible. For these purposes, a supplementary collection of some ten thousand conodont elements sampled from the lower part of the *Baltoniodus navis* Zone of the Harku section (northern Estonia) has been investigated. The collection yielded more than 600 complete elements of *S. striatus* showing much better preservation. Conodont element damage is insignificant and the thermal alteration is minimal (CAI <1.5).

The elements were measured under reflected light using a Leitz 2000 microscope with a precision scale in the reticle. The scale resolution under the 80× magnification is 0.03 mm, so the precision of conodont measurement was approximately 8–10%. Drawings were traced from conodont specimens using camera lucida.

Element designation and apparatus composition of *Scolopodus striatus*

The apparatus of *Scolopodus* can be assigned to the unimembrate apparatus type (Sweet 1981) or to the apparatus of Type IA (Ji and Barnes 1996) that contains coniform nongeniculate elements extremely similar in their morphology. The most obvious difference between the simple cone costate elements is the degree of their asymmetry that is usually expressed in the classifications of *Scolopodus* elements (Ji and Barnes 1996; Stouge and Bagnoli 1990; Stait and Druce 1993). The first separation of *S. striatus* elements in terms of multielemental taxonomy was also based on the symmetrical and asymmetrical forms (Löfgren 1978; Bergström 1988; Lindström 1971; Fig. 2). The transitional series

Pander (1856)	Lindström (1955)	Löfgren (1978)	Fåhræus (1982)		Stouge and Bagnoli (1990)	This paper	
Single element species		Multielement species					
		Scolopodus rex	*Scolopodus sublaevis*	*Scolopodus quadratus*	*Scolopodus rex*	*Scolopodus striatus*	
Scolopodus quadratus		Symmetrical elements		Symmetrical elements	Symmetrical elements	Acontiodiform elements (P)	
Scolopodus costatus				Asymmetrical elements I			
Scolopodus aequilateralis	*Scolopodus rex*		Symmetrical elements			Subrounded elements (Sa)	
Scolopodus semicostatus		Slightly asymmetrical elements		Near symmetrical elements	Asymmetrical elements	Compressed paltodiform elements (S)	Short-based variant
Scolopodus striatus							
Scolopodus costatus							
Scolopodus aequilateralis			Asymmetrical elements II				Long-based variant
Scolopodus semicostatus		Asymmetrical elements	Scandodiform elements	Asymmetrical elements II		Paltodiform elements (S)	Short-based variant
			Asymmetrical elements I				Moderate-based variant
	Scolopodus rex var. *paltodiformis*		Scandodiform elements			Scandodiform elements (M)	

Fig. 2. Terminology used by previous authors to describe the *Scolopodus* apparatuses and the notation system used herein. The descriptive nomenclature used here is based on Stait and Druce (1993) and Ji and Barnes (1994), the analogous locational system is based on Sweet (1981). Hatched space indicates that authors did not illustrate the particular element.

of symmetrical and slightly asymmetrical elements were originally described as *S. rex* Lindström, 1955 and the more asymmetrical elements as *S. rex* var. *paltodiformis* Lindström, 1955. Later, *S. rex* var. *paltodiformis* was assigned to *S. rex* apparatuses as the most asymmetrical element (Lindström 1971). Fåhræus (1982: table 1) subdivided *S. rex* into two species and recognised symmetrical, near-symmetrical, two types of asymmetrical elements and the most asymmetrical or scandodiform elements. In fact, Fåhræus recognised all the morphotypes of *S. striatus* that are described in this paper but shared different morphotypes between two different species. Four morphotypes were assigned to the apparatus of *S. sublaevis* and five morphotypes to *S. quadratus*. The most asymmetrical scandodiform elements were included into apparatuses of both his S*colopodus* species.

Examination of the collection of *S. striatus* elements from the Harku sample resulted in the recognition of five major morphotype groups (Fig. 3). These groups are characterised by their distinctive morphology and transitions between the groups of elements are absent. Identification of the morphotype groups was based on several morphological features, including the degree of the elements' torsion; the asymmetry of costae, and the shape of the base with a reference to the ratio of the base length versus the basal cavity depth. The element morphotypes are designated in the descriptive nomenclature (Stait and Druce 1993; Ji and Barnes 1994), but the analogues' locational nomenclature (Löfgren 1998; Purnell et al. 2000) is also employed to interpret the possible homology between the different coniform apparatuses. As the detailed description of the *S. striatus* elements is given in the section Systematic Palaeontology, only a brief description is provided below:

(1) Acontiodiform elements are costate symmetrical and nearly symmetrical elements with low, slightly bloated bases and reclined cusps (Fig. 3A).

(2) Subrounded elements are costate symmetrical elements that have high bases with round cross-section and almost straight reclined cusps (Fig. 3H).

(3) Compressed paltodiform elements form a morphotype group consisting of costate slightly asymmetrical ele-

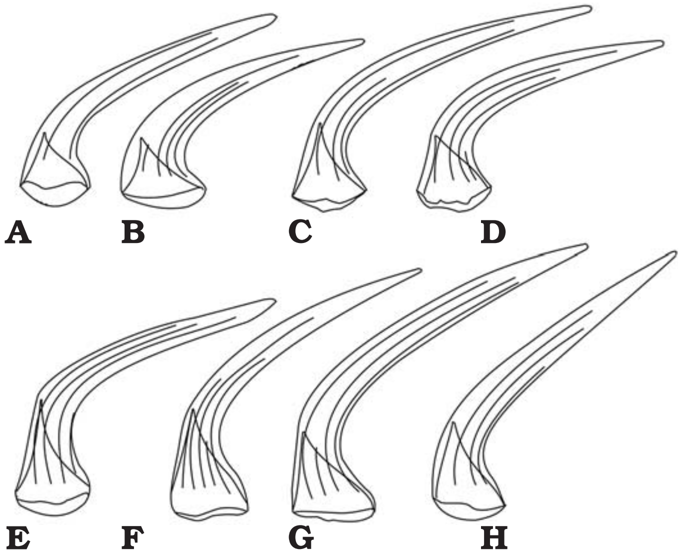

Fig. 3. Schematic drawings of *Scolopodus striatus* Pander, 1856 element morphotypes. **A**. Acontiodiform element (P). **B**. Scandodiform element (M). **C**, **D**. Paltodiform elements (S). **C**. Medium-based variant. **D**. Short-based variant. **E**–**G**. Compressed paltodiform elements (S). **E**. Long-based variant. **F**, **G**. Short-based variant. **H**. Subrounded element (Sa).

ments having curved cusps and bases of variable height (Fig. 3E–G).

(4) Paltodiform elements have costate inner sides and sometimes smooth outer sides, curved cusps and variable heights of the base (Fig. 3C, D).

(5) Scandodiform elements are strongly asymmetrical elements with twisted and keeled cusps as well as low bases. Only the inner sides of these elements are costate (Fig. 3B).

S. striatus elements are variable in the depth of the basal cavity, in the height of the base and in the degree of its lateral compression, thus forming a continuous transition series of elements within each morphotype group. However, the acontiodiform, the symmetrical subrounded and the scandodiform elements are less variable in morphology, whereas the asymmetrical compressed paltodiform and the paltodiform elements vary significantly within the groups.

Good preservation of conodont elements in the collection makes it possible to carry out quantitative analyses of the morphological variations and ontogenetic growth of different morphotypes. To this end, more than 500 elements were measured (Fig. 4). The overall proportions of the elements can be expressed by two variables—the depth of the basal cavity and the length of the base. The depth of the basal cavity was estimated as the distance between the anterior angle of the basal margin and the tip of the basal cavity, whereas the length of the base was estimated as the distance between the anterior and posterior basal angles (Fig. 4). The height of the cusps is a rather variable feature and does not characterise any particular morphotype group. Moreover, the cusps are commonly broken and subsequently regenerated. It is obvious that the *S. striatus* elements of all morphotypes have a similar isometric mode of basal cavity growth during ontogeny, and the adult elements are characterised by having a relatively shallow basal cavity when compared with juveniles. Scandodiform elements have the highest growth rates of the base length in contrast to basal cavity depth, and are characterised by having the shallowest basal cavity among all adult elements of any morphotypes. Acontiodiform and scandodiform elements are relatively short-based morphotypes, whereas compressed paltodiform and subrounded elements are assigned to a group of long-based morphotypes. Paltodiform elements have the most variable depth of the basal cavity (Fig. 4) and occupy an intermediate position as compared with scandodiform elements.

Compressed paltodiform elements are the most abundant elements in the studied collection from the Harku section (206 elements); there are also 160 acontiodiform elements, 103 scandodiform elements, 32 subrounded elements, and 82 paltodiform elements.

Nomenclature of elements of coniform conodonts

The element morphotypes of all coniform taxa are generally similar. Moreover, elements of coniform apparatuses show subtle changes in morphology, particularly in large collections, and it is often not easy to reconstruct the composition of apparatuses, or to distinguish between inter- and intraspecific characters. Consequently, many coniform apparatuses with similar morphotypes were previously considered as "monoelemental". Later, it has been found that each coniform taxon may be composed of elements of different morphotypes that are distinctive in their shape and degree of symmetry. Recently, different morphotypes are recognised among the elements of the majority of Ordovician coniform taxa (Nicoll 1994; Sansom et al. 1995; Löfgren 1999).

The locational nomenclature introduced by Sweet (1981) is started to be commonly used for the designation of elements of coniform morphology (Nicoll 1994; Löfgren 1998, 1999). However, it basically expresses the morphology of coniform elements rather than their position in the apparatuses or their actual homology with the elements of other coniform and pectiniform-ramiform apparatuses. In terms of Sweet's conception coniform elements are usually subdivided into the transition series of S elements and morphologically different P and M elements.

It has been proposed that the most asymmetrical or scandodiform elements is the P elements in the majority of scolopodontid apparatuses reconstructions (Stait and Druce 1993; Löfgren 1998). However, scandodiform elements differ from paltodiform and compressed paltodiform elements mainly by a more significant degree of asymmetry. Thus, they might occupy a morphologically marginal position in the transition series of S elements. On the other hand acontiodiform elements are remarkably different in their mor-

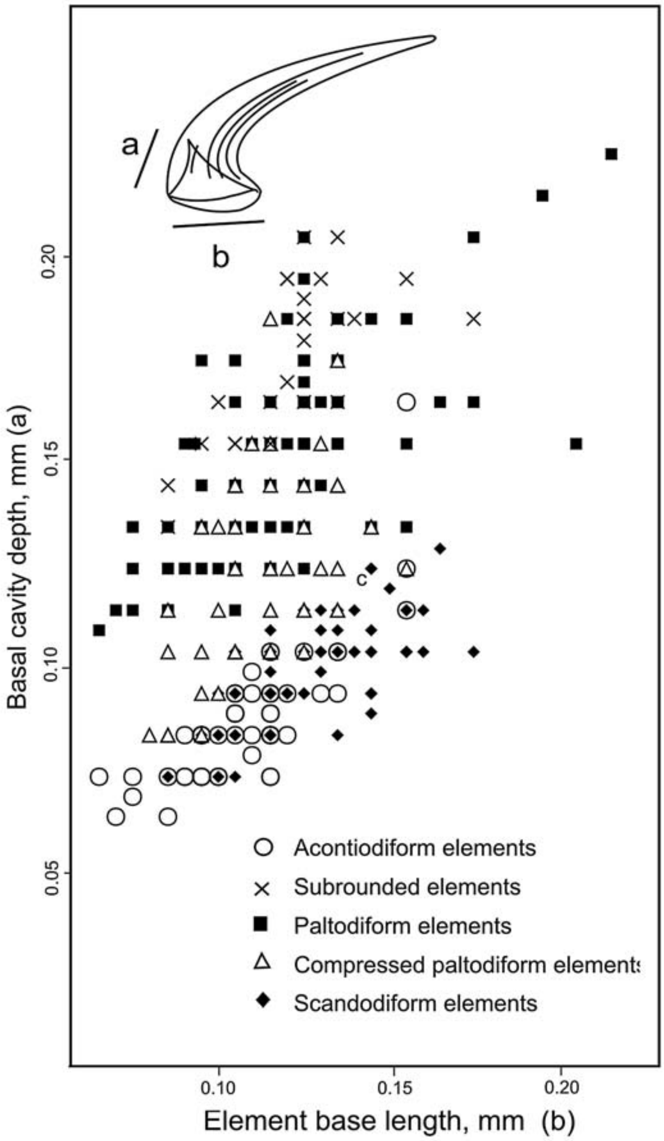

Fig. 4. Scatter diagram showing the ratio between base length and depth of the basal cavity for element morphotypes.

phology from other elements of *S. striatus*. Moreover, the numerical ratio of the acontiodiform elements is very close to the proportion of P elements in the septimembrate apparatuses. Therefore, acontiodiform elements are interpreted here as being P elements, and scandodiform elements as M elements and the rare symmetrical subrounded elements as Sa elements. Symmetrical acontiodiform elements are considered to be P elements, and symmetrical subrounded elements are assigned to Sa elements. Paltodiform and compressed paltodiform elements represent a transition series of S elements. The absence of M elements is considered to be typical for scolopodontid apparatuses (Stait and Druce 1993; Löfgren 1998). It is possible, however, that scandodiform elements may occupy M positions.

All the morphotype groups that were identified in the Harku sample have also been recognised in all the samples from the available collections from Russia, Estonia, and Sweden. The numerical ratios of different element morphotypes in all samples are almost identical; the paltodiform and compressed paltodiform are more abundant whereas subrounded elements are rare.

Coniform costate elements with a general morphology typical of *Scolopodus* have been reported from almost all continents (Serpagli 1974; Löfgren 1978; Ji and Barnes 1994; Stait and Druce 1993; Zhang 1998). Reconstructions of apparatus compositions of different *Scolopodus* species from outside of Baltoscandia are also based on the morphological characters mainly connected with the degree of asymmetry of their elements (Stait and Druce 1993; Ji and Barnes 1994). In spite of similarity in general concept of element assignment the different reconstructions of *Scolopodus* and other coniform apparatuses are contradictory mainly in the positional homology of the most asymmetrical element morphotype group.

Stait and Druce (1993) recognised six morphotypes of elements in their Australian species of *Scolopodus*: laterally compressed paltodontiform (Sc) elements, planoconvex (Sb) elements, acontiodontiform (Sa) elements, equidimensional paltodontiform (Sd) elements, scandodontiform (Pa) and posteriorly keeled scandodontiform (Pb) elements. It was proposed that the most asymmetrical scandodiform elements occupied the P position. Their reconstruction of *S. subrex* apparatus differs from the reconstruction proposed here by the presence of one symmetrical morphotype group homological to the Sa elements, whereas two symmetrical morphotypes (acontiodiform and subrounded elements) were identified among the *S. striatus* elements.

Ji and Barnes (1994) emended the diagnosis of *Scolopodus* by adding the description of apparatus composition. They proposed the existence of four element morphotypes in species of *Scolopodus*: subrounded (a), transitional (b), and compressed (e) elements that can be associated with suberect staufferiform (c) and suberect (f) elements in some species. *S. subrex* was described by them as most similar to *S. striatus* in containing subrounded scolopodiform (a), transitional paltodiform (b), compressed scandodiform (e), and symmetrical ulrichodiniform (f) elements. The recognised morphotypes of *Scolopodus* elements are almost the same as those identified among *S. striatus* elements. The only difference is in the transitional paltodiform morphotype that is separated into compressed paltodiform and paltodiform elements in *S. striatus* apparatuses.

The best-known reconstruction of a coniform apparatus is the reconstruction of *Panderodus* (Sansom et al. 1994). It has been studied on the basis of abundant collections of discrete elements as well as in several natural assemblages, which permit formulation of the complete *Panderodus* apparatus as consisting of seventeen elements of six general morphotypes. All morphotypes are recognised on the basis of cusp curvature and cross-sectional symmetry. A suite of compressed elements composed of the most asymmetrical elements in the apparatus (faliciform and tortiform elements) corresponds with the paltodiform and scandodiform elements of *S. striatus*. The graciliform morphotype of *Panderodus* comprises both asymmetric long- and short-based elements; the subsymmetrical long- and short-based forms encompassed into the other suite of elements. The elements of the graciliform morphotype are the most numerous in the apparatus and correspond well with the compressed paltodiform elements of *S. striatus*, which are also very variable morphologically. The arcuatiform and aequaliform elements can be compared with acontiodiform and subrounded elements of *S. striatus*. The truncatiform as the shortest element in apparatuses corresponds with the smallest element of *S. striatus* identified in the compressed paltodiform morphotype group.

The apparatus of *Semiacontiodus cornuformis* (Sergeeva, 1963) was reconstructed by Löfgren (1999), and is composed of P elements that have a short base and series of S elements characterised by different degree of cusp curvature. The Sd elements are the most asymmetrical elements among the S elements. The morphological similarity of *S. cornuformis* P elements with acontiodiform elements of *S. striatus* is obvious. In contrast, the apparatus of *Decoriconus peselephantis* (Lindström, 1955) does not comprise any symmetrical elements, besides Sa elements that are, indeed, symmetrical. The proposed P elements are the most asymmetrical and have a twisted cusp (Löfgren 1998). Symmetrical and laterally compressed elements with a short base are considered to occupy the Sa position in the *D. peselephantis* apparatus.

Identification of Pander's *Scolopodus* species

Scolopodus elements from the Popowka River locality and in the recently found Pander collection were compared with the type specimens of *S. rex* Lindström, 1955, and *S. rex* elements from the Sjurberg and Talubäcken sections, Sweden, and the Harku section, Estonia. All these elements seem to belong to one taxon, since the general morphology of all the elements is identical and all element morphotypes can be identified in the available collections.

The collections of *Scolopodus* elements from the type area have been compared with the species described and illustrated by Pander (1856). At a first glance, Pander's illustrations and descriptions of *Scolopodus* elements seem to be very detailed and accurate, but closer study reveals several problems. Firstly, Pander (1856: 25) stated (in the genus diagnosis) that the elements were white, but the majority of available elements from the region are hyaline and yellow. *Oistodus lanceolatus* Pander, 1856 is another hyaline taxon that occurs in the same sample and its elements are also yellow. A few *Scolopodus* elements from the available conodont collections from the Billingen beds of the studied localities near St. Petersburg have albid, i.e. white bases. The uppermost beds of the Hunneberg Stage from the Lava and Putilovo sections yield a greater number of albid *S. striatus* elements, but even in that case they compose not more than 10% of all *Scolopodus* elements. However, in the collection that is assumed to have belonged to Pander, no less than a quarter of all *Scolopodus* elements are albid. Nevertheless, all other albid conodonts from these assemblages have a more pronounced white colour when compared with the light yellow albid *Scolopodus* elements.

Secondly, almost all conodonts figured by Pander are shorter than the real elements. The specimens in the available collections with relatively short cusps bear traces of breakage and subsequent regeneration. However, it is possible to identify the species illustrated by Pander, since the height of the cusp is not characteristic for any of the morphotypes of *Scolopodus* elements. Additional, but less significant disagreements include the following: (1) Pander claimed that the costae run from the base of the elements up to the tip, whereas the costae on *Scolopodus* elements never run to the very tip of the cusp; all types of elements usually have smooth tips. (2) Some *Scolopodus* elements in the collection from the Popowka locality, as well as the *Scolopodus* elements from Estonia, are characterised by additional short costae intercalated with the main ones, whereas the species figured by Pander show only the main prominent costae of equal length. (3) Four species of the six described by Pander are characterised by costae starting just from the edge of the basal margins, but none of the complete *Scolopodus* elements in the available collection have costae that start from this position; all of them have a small smooth surface or low rim on the base of the elements. Only two of Pander's species (*S. striatus*, Fig. 5A and *S. sublaevis*, Fig. 5C) demonstrate the costae starting slightly above the basal margin.

***Scolopodus sublaevis* Pander, 1986**.—The original description of the type species *Scolopodus sublaevis* Pander, 1986 is as follows: "The cross-section forms a regular oval, the half of which towards the convex margin being somewhat broader than the opposite (half). One lateral face is smooth: a single groove, which starts above the base and continues to the tip, divides the same into two almost equal halves. The opposite lateral surface and the concave margin are, on the other hand, furrowed by numerous similar grooves, through which the surfaces appear ribbed." (Pander 1856: 26, original translation by Fåhræus 1982: 19). As noticed by Fåhræus (1982), there is a disagreement between the illustration and the description of this taxon. The elements are described as asymmetrical, while the drawings indicate symmetry, with the costate posterior margin and lateral margins bearing single grooves. According to Pander's drawings (Fig. 5C), *S. sublaevis* has a relatively low base and strongly recurved cusp that is typical for several *Scolopodus* elements: acontiodiform elements, some varieties of the compressed paltodiform elements and paltodiform elements (Fig. 6B–D). However, the grooves on the

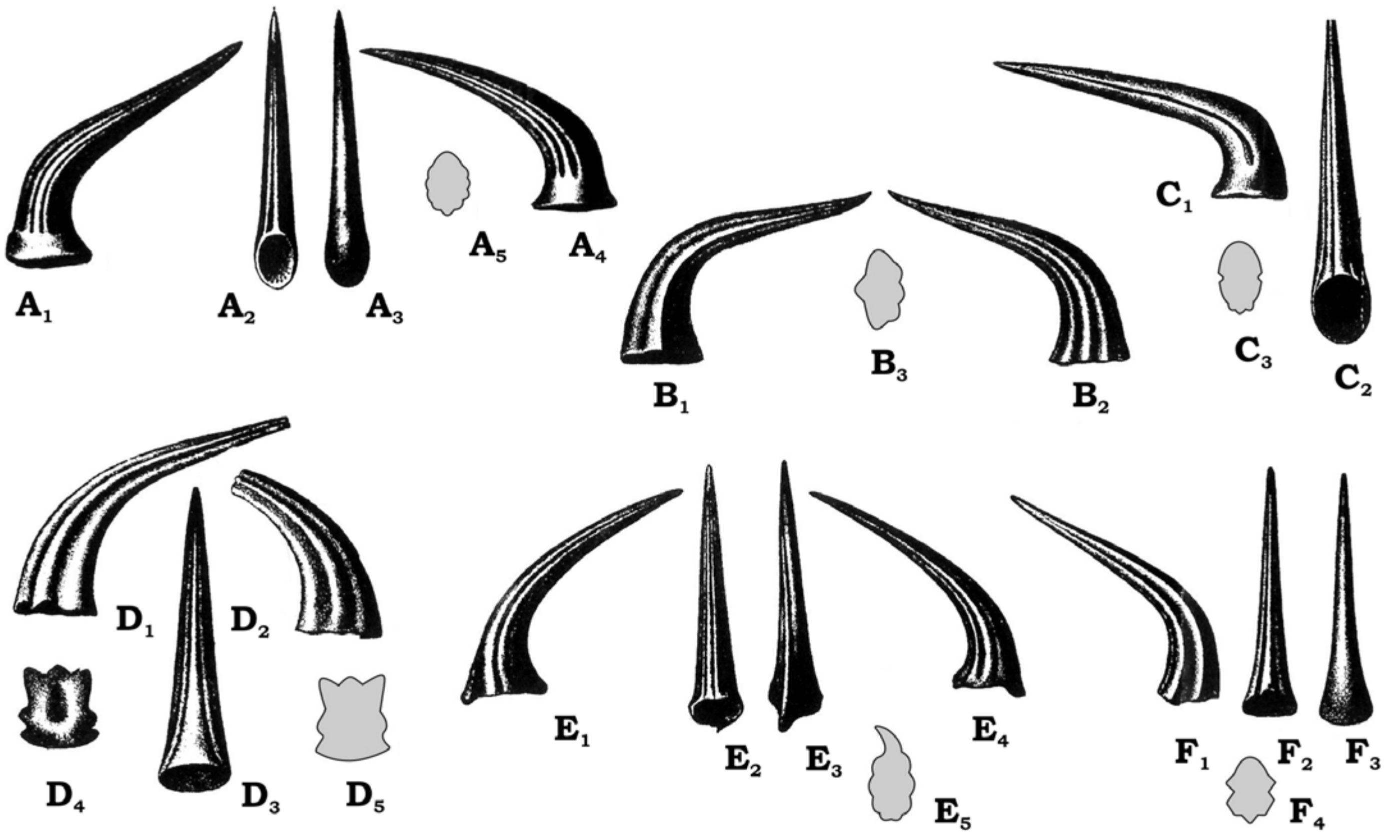

Fig. 5. *Scolopodus* species originally described by Pander. **A**. *Scolopodus striatus* Pander, 1856, in lateral (A_1, A_4), posterior (A_2), and anterior (A_3) views; A_5, cross section of the base (Pander 1856: table 2, fig. 8a–d, table A, fig. 5f). **B**. *Scolopodus semicostatus* Pander, 1856, in lateral views (B_1, B_2); B_3, cross section of the base (Pander 1856: table 2, fig. 4a, b, table A, fig. 5e). **C**. *Scolopodus sublaevis* Pander, 1856, in lateral (C_1) and posterior (C_2) views; C_3, cross section of the base (Pander 1856: table 2, fig. 3a, b, table A, fig. 5e). **D**. *Scolopodus quadratus* Pander, 1856, in lateral (D_1, D_2), posterior (D_3), and lower (D_4) views; D_5, cross section of the base (Pander 1856: table 2, fig. 6a–c, table A, fig. 5e). **E**. *Scolopodus costatus* Pander, 1856, in lateral (E_1, E_4), posterior (E_2), and anterior (E_3) views; E_5, cross section of the base (Pander 1856: table 2, fig. 7a–d, table A, fig. 5e). **F**. *Scolopodus aequilateralis* Pander, 1856, in lateral (F_1, posterior (F_2), and anterior (F_3) views; F_4, cross section of the base (Pander 1856: table 2, fig. 5a–c, table A, fig. 5e).

lateral sides that were described and illustrated by Pander are not characteristic of any available *Scolopodus* element. Based on the assumption, that a single major costa on the one lateral margin of *S. sublaevis* sensu formae could have been mistakenly interpreted by Pander (1856) as a groove, Fåhræus (1982) identified *S. sublaevis* s.f. as an asymmetrical element I in the apparatus of *S. sublaevis* Pander, 1856. However, *S. sublaevis* is the only one of Pander's species of *Scolopodus* that was described as having grooves but not costae thus it was considered that Ch. Pander set apart these morphological characters. *S. sublaevis* Pander, 1856 s.f. bearing grooves was not found in the studied collections from the Popowka River and Harku localities.

***Scolopodus striatus* Pander, 1856**.—*S. striatus* was originally described as having: "Oval cross-section. The convex margin is formed by a arched surface, whilst the rest of the entire tooth is covered with fine costae along its entire length." (Pander 1856: 26, original translation of Fåhræus 1982: 20). *S. striatus* Pander, 1856 *sensu formae* (Fig. 5A_1, A_2) appears to be more easily recognised when compared with the other species of *Scolopodus* described by Pander. This fact was commented on by Serpagli (1974), who noticed the general similarity of *Scolopodus* elements from Precordilleran Argentina with *S. striatus* Pander, 1856 s.f. Fåhræus identified *S. striatus* s.f. among the compressed paltodiform elements and placed it as near-symmetrical elements within the apparatus of *S. guadratus* (Fåhræus, 1982). *S. striatus* s.f. is the only one of Pander's *Scolopodus* species whose drawing and description agrees well with the asymmetrical short-based varieties of the compressed paltodiform elements (Figs. 5A, 7M, O, P).

***Scolopodus costatus* Pander, 1856**.—The original description of *S. costatus* is as follows: "Oval cross-section. The entire surface of the tooth is ornamented with prominent costae, which run from above the base to the tip. The most prominent of these is, quite different from all other species of this genus, on the convex margin and projects outward particularly strongly in its lower part." (Pander 1856: 26, original translation of Fåhræus 1982: 20). No specimen in my collection corresponds entirely with the description given above. Some compressed paltodiform and acontiodiform elements bear costae on their anterior margin, but usually these costae are tiny. On the other hand, scandodiform elements with a relatively prominent anterior keel extended to the inner costate side of the elements have a smooth outer side. The only rare exceptions to this are some gerontic specimens, which have weak costae on the outer sides (Fig. $8E_2$). Fåhræus (1982) identified *S. costatus* with acontiodiform elements and included it as the asymmetrical elements I in the S. *quadratus* apparatus. However, he noted that the anterior costa is not so well developed as may be inferred from the original description and illustration.

Scolopodus semicostatus **Pander, 1856**.—The original description of *S. semicostatus* is as follows: "The cross-section is uniform. In the centre of one lateral surface a strong, prominent carina (= costa) runs from the base to the tip, dividing the smooth surface into two equal halves. The opposite lateral surface is ornamented with four costae, which are separated from each other by five-six furrows." (Pander 1856: 26, original translation of Fåhræus 1982: 20). The element of *S. semicostatus* illustrated by Pander (Fig. 5B) bears little resemblance to any available *Scolopodus* elements, although it is generally similar to some rare varieties of paltodiform or compressed paltodiform elements (Fig. 6C). The latter elements, however, are usually characterised by additional tiny costae on the outer side. Fåhræus (1982) did not recognise this species in Swedish collections.

Scolopodus aequilateralis **Pander, 1856**.—*S. aequilateralis* was originally described as follows: "The cross-section is elongated rectangular. The convex margin of the tooth is formed by a parallel-sided smooth outward arched surface, the concave (margin) by a prominent costa. Two similar costae run on the lateral surfaces from the base to the tip." (Pander 1856: 26, original translation of Fåhræus 1982: 20). *S. aequilateralis* (Fig. 5F) is similar in general shape to the subrounded *Scolopodus* elements (Fig. 8H, I) as well as to the long-based varieties of compressed paltodiform elements (Figs. 6E, 7D). However, the basal rim that characterises the elements figured by Pander is lacking. A small number of costae is typical for the juvenile forms of the subrounded elements (Fig. $8H_1$, H_3), but the cross-section of subrounded elements is triangular (Fig. $8H_2$, I_2), whereas the elements of the compressed paltodifom type have a more or less elongated rectangular cross-section (Fig. $7D_2$, F_2, I_2). Nevertheless, Fåhræus (1982) identified this species with subrounded elements and designated them as symmetrical elements in the *S. sublaevis* apparatus.

Scolopodus quadratus **Pander, 1856**.—The original description of *S. quadratus* is as follows: "The cross-section is square. The convex margin is formed by a broad, smooth and somewhat arched surface. The concave margin is formed by three prominent costae, one median and two lateral. On the lateral surfaces, closer to the convex margin, rises a prominent costa which runs from the base to the tip." (Pander 1856: 26, original translation of Fåhræus 1982: 20). Fåhræus (1982) mentioned this species as the most easily recognizsable among three formal species composing the *S. striatus* apparatus (Fåhræus 1982). He identified *S. quadratus* with the acontiodiform element and designated it as the symmetrical element in the apparatus of *S. quadratus* that was proposed to be a senior synonym of *S. rex*.

As mentioned before, the main difference between *S. quadratus,* as well as the other three *Scolopodus* species of Pander (1856) with available elements, is the absence of smooth basal rims on elements figured by Pander (Fig. 5D). Other morphological characters of *S. quadratus,* such as square cross-section, costate lateral sides and relatively low base, are characteristic of the acontiodiform elements. However, they are not similar to *S. quadratus* in general shape. The elements of *S. costatus* illustrated by Pander do not show any extension of the base whereas acontiodiform elements are characterised by a low base slightly expanded in anterior and posterior directions. Thus, a precise understanding of *S. quadratus* is presently impossible, thereby preventing its recognition as a senior synonym of *S. rex.*

Systematic palaeontology

The generic concept of *Scolopodus* is based on the *S. sublaevis* Pander, 1856 s.f. that was not identified in the collections studied. However, the only one of the sections where Pander collected conodonts was examined. The forthcoming studies of the other Pander's localities will show if the *S. sublaevis* s.f. exist or this species have to be considered as a *nomen dubium*. In the latter case a new type species *S. striatus* Pander, 1856 will be proposed for the genus *Scolopodus*. There is no doubt that the other species of *Scolopodus* described by Pander (1856) are the elements of the *Scolopodus* species that was later described as *Scolopodus rex* Lindström, 1955. The *S. striatus* s.f. is the most easily recognizable from Pander's drawings and is here designated as the name-bearing type for the *S. striatus* Pander.

Family Scolopodontidae Bergström, 1981

Genus *Scolopodus* Pander, 1856

Type species: *Scolopodus sublaevis* Pander, 1856.

Diagnosis.—Hyaline and partly albid, finely costate coniform conodonts with rounded cross-section and not greatly expanded base. Apparatuses consist of 3–6 morphotypes of symmetrical as well as asymmetrical elements.

Remarks.—The genus *Scolopodus* was originally used by Pander (1856) to include simple cones with lateral and posterior grooves or costae. He defined *Scolopodus* as "Slender, differently shaped teeth with the front and hind margins rounded off and the convex surfaces more or less ribbed. They are distinguished at first sight from the genera described above by their harder substance, white colour and

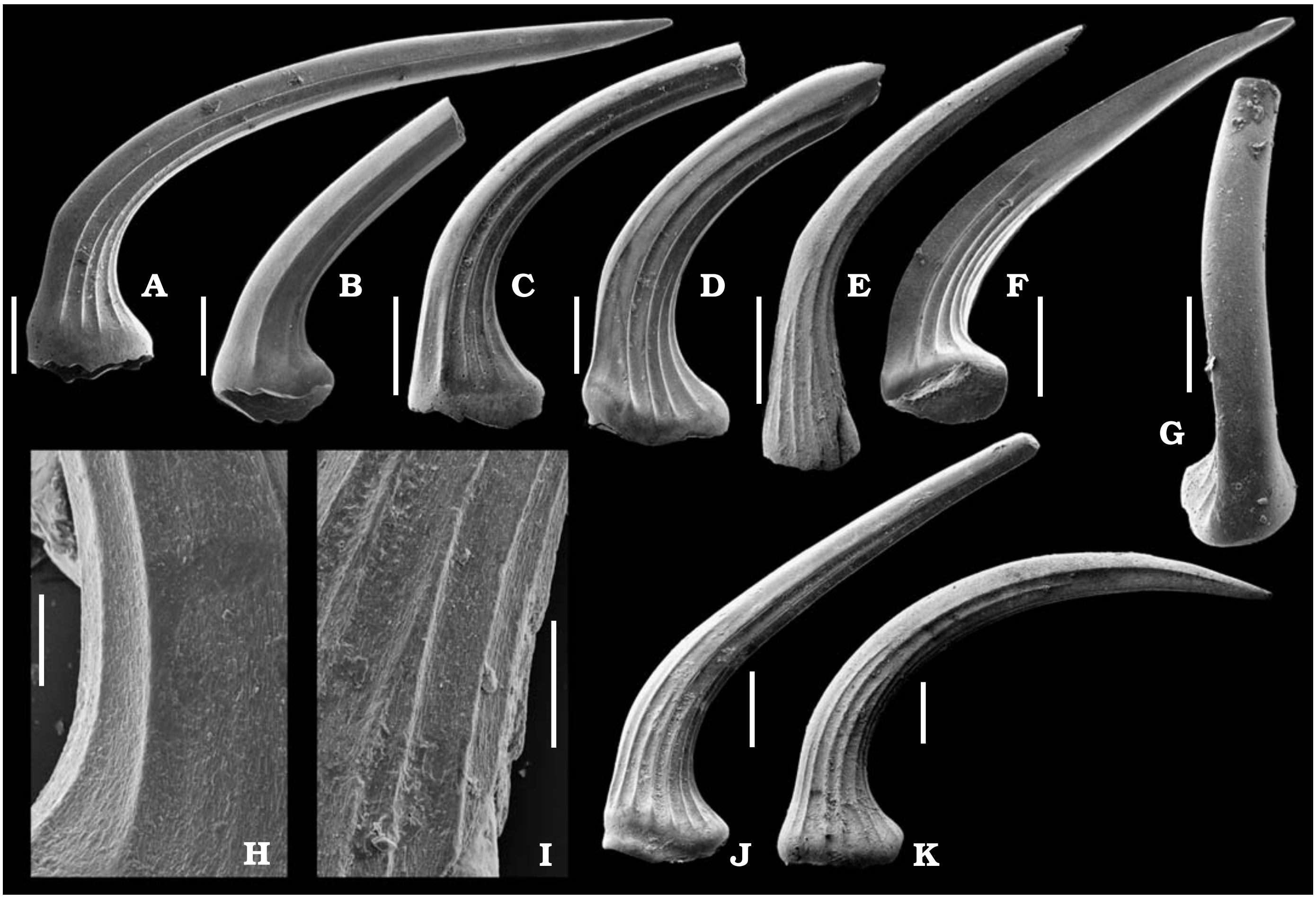

Fig. 6. **A**–**I**. *Scolopodus striatus* Pander, 1856 from the Popowka River locality, St. Petersburg region, Russia. All elements are from the uppermost *Prioniodus elegans* Zone (Early Ordovician). **A**. Compressed paltodiform element (S), short-based variant, neotype specimen PMU In 1030. **B**. Acontiodiform element (P), PMU In 1007. **C**. Compressed paltodiform element (S), short-based variant, PMU In 1003. **D**. Paltodiform element (S), inner view, PMU In 1006. **E**. Compressed paltodiform element (S), long-based variant, PMU In 1008. **F**. Scandodiform elements (M), inner view, PMU In 1004. **G**. Scandodiform elements (M), anterior view, PMU In 1005. **H**. Acontiodiform element (P), detail of the cusp, PMU In 1001. **I**. Compressed paltodiform element (S), detail of the cusp, PMU In 1002. **J**, **K**. *Scolopodus striatus* Pander, 1856 from the presumably Pander's collection of conodonts from the Mining Institute, St. Petersburg region, Russia. **J**. Compressed paltodiform element (S), short-based variant, paratype specimen PMU In 1028. **K**. Compressed paltodiform element (S), short-based variant, PMU In 1029. Scale bars 200 μm, except H, I for which are 50 μm.

lack of keels" (Pander 1856: 25, original translation of Lindström 1955: 594). Lindström (1955) emended the definition of *Scolopodus* to include "hyaline, drepanodiform elements with rounded cross-section and symmetrical as well as asymmetrical elements. The sides of the elements may be finely costate. The base is not greatly expanded" (Lindström 1971). Van Wamel (1974) expanded the definition of *Scolopodus* to include both hyaline and partly albid conodonts, based on the assumption of general similarity with North American *Scolopodus*-like species. Almost all available *Scolopodus* elements from the green sands of the Popowka River locality are hyaline. Nevertheless, the finds of partly albid elements in the clays of the Hunneberg Stage underlying the green sands permit the *sensu lato* generic definition of *Scolopodus* emended by van Wamel (1974).

The current generic concept of *Scolopodus* is based on *S. sublaevis* Pander, 1856 s.f. until it invalidity will be proved by future studies.

Scolopodus striatus Pander, 1856

Figs. 5A, B, D, ?E, F, 6, 7, 8.

1856 *Scolopodus striatus* sp. nov.; Pander 1856: 26, pl. 2: 8a–d, pl. A: 5f.

1856 ?*Scolopodus costatus* sp. nov.; Pander 1856: 26, pl. 2: 7a–d, pl. A: 5e.

1856 *Scolopodus semicostatus* sp. nov.; Pander 1856: 26, pl. 2: 4a–b, pl. A: 5e.

1856 *Scolopodus aequilateralis* sp. nov.; Pander 1856: 26, pl. 2: 5a–c, pl. A: 5e.

1856 *Scolopodus quadratus* sp. nov.; Pander 1856: 26, pl. 2: 6 a–d, pl. A: 5d.

1955 *Scolopodus rex* sp. nov.; Lindström 1955: 595, 596, pl. 3: 32.

1955 *Scolopodus rex* sp. nov. var. *paltodiformis* nov.; Lindström 1955: 596, pl. 3: 33, 34.

1964 *Scolopodus rex* Lindström; Lindström 1964: 37, figs. 10H, 47h.

1972 non *Scolopodus rex* Lindström; Bergström et al. 1972: pl. 1: b.

1974 *Scolopodus rex* Lindström; Viira 1974: pl. 3: 22, 23.

1974 *Paltodus scolopodiformis* sp. nov.; Sergeeva 1974: pl. 1: 10, 11.

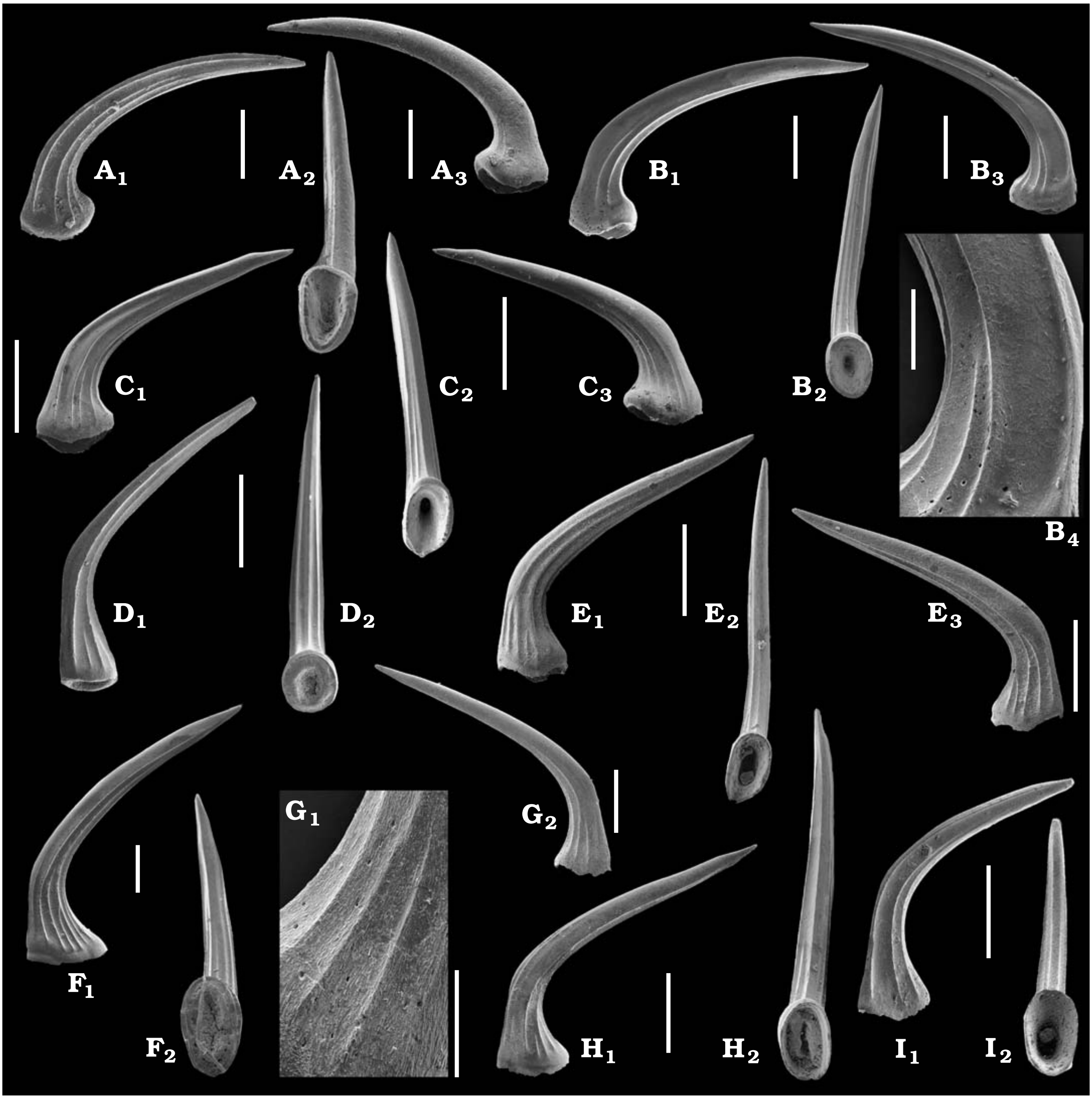

Fig. 7. *Scolopodus striatus* Pander, 1856 from the Harku section, Estonia. All elements are from the sample H-5, the lower part of the *Baltoniodus navis* Zone (Early Ordovician). **A**–**C**. Paltodiform elements (S). **A**. Short-based variant, PMU In 1009 in inner (A_1) and posterior (A_2), and outer (A_3) views. **B**. Medium-based variant, PMU In 1011 in inner (B_1), posterior (B_2), and outer (B_3) views; detail of the cusp (B_4). **C**. Medium-based variant, PMU In 1012 in inner (C_1), posterior (C_2), and outer (C_3) views. **D**, **E**. Compressed paltodiform elements (S). **D**. Long-based variant, PMU In 1013 in lateral (D_1) and posterior (D_2) views. **E**. Short-based variant, PMU In 1014 in lateral (E_1), posterior (E_2), and lateral (E_3) views. **F**. Short-based variant, PMU In 1015 in lateral (F_1) and posterior (F_2) views. **G**. Long-based variant, PMU In 1016 in lateral (G_2) view; detail of the cusp (G_1). **H**. Short-based variant, PMU In 1017 in lateral (H_1) and posterior (H_2) views. **I**. Short-based variant, PMU In 1018 1017 in lateral (I_1) and posterior (I_2) views. Scale bars 200 µm, except A_4 and G_1 for which are 50 µm.

1974 *Scolopodus rex* Lindström; van Wamel 1974: 94, pl. 5: 18.
1974 non "*Scolopodus rex*" Lindström; Serpagli 1974: 86–87, pl. 17: 1a–3b, pl. 28: 10.
1976 *Scolopodus rex* Lindström; Dzik 1976: fig. 17h, ?k,n, l, ?m, non i.
1976 non *Scolopodus rex* Lindström; Landing 1976: 640, pl. 4: 14.
1978 *Scolopodus rex* Lindström; Löfgren 1978: 109, 110, pl. 1: 38, 39.
1982 Scolopodus *quadratus* Pander; Fåhræus 1982: 21, pl. 2: 1–14, pl. 3: 1–8, 15.
1981 non aff. *Scolopodus rex* Lindström; Ethington and Clark 1981: 104, 105, pl. 12: 1, 2.

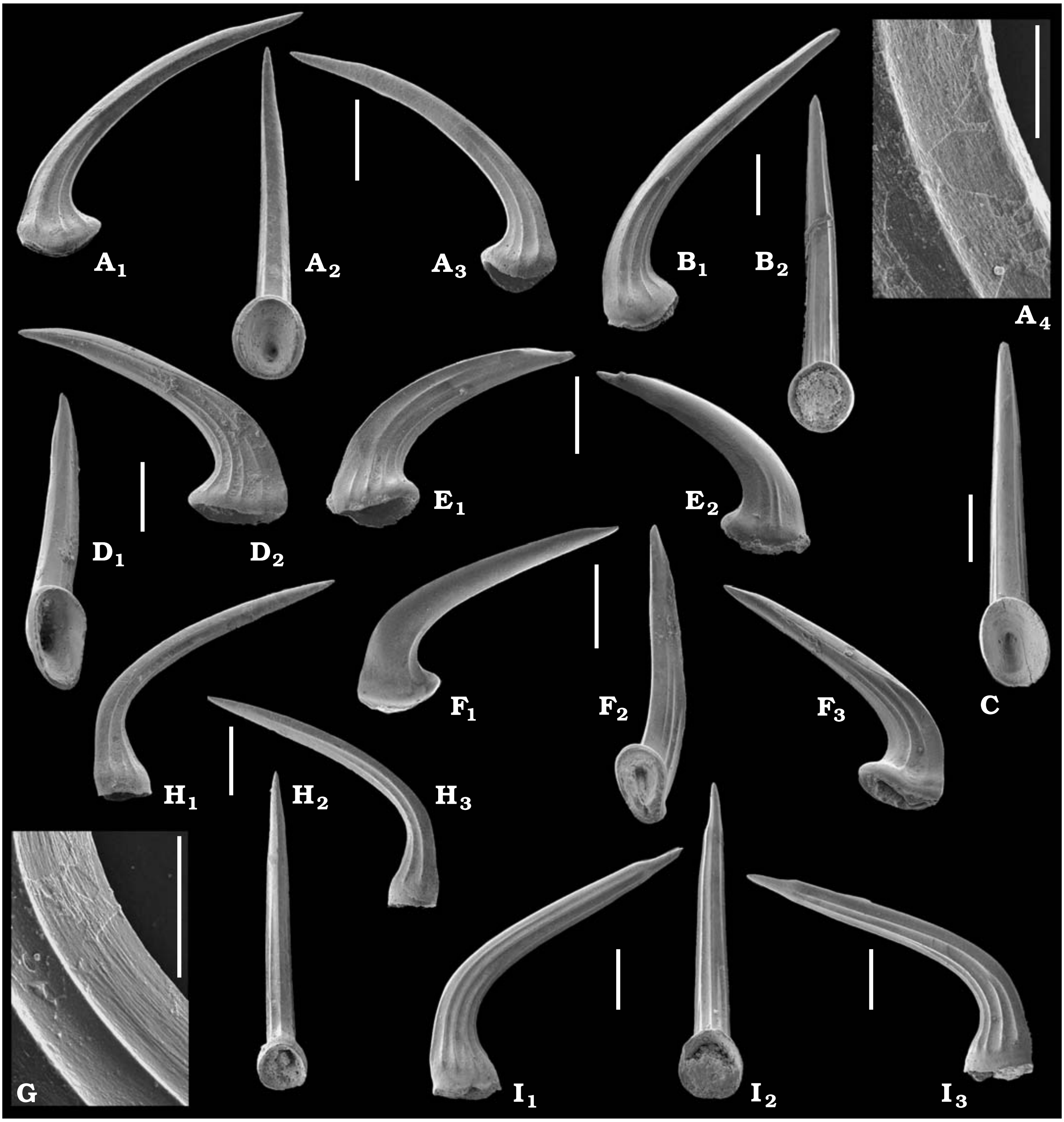

Fig. 8. *Scolopodus striatus* Pander, 1856 from the Harku section, Estonia. All elements are from the sample H-5, the lower part of the *Baltoniodus navis* Zone (Early Ordovician). **A**–**C**. Acontiodiform elements (Sa). **A**. PMU In 1019 in inner (A_1), posterior (A_2), and outer (A_3) views; detail of the cusp (A_4), note the absence of striation. **B**. PMU In 1020 in inner (B_1) and posterior (B_2) views. **C**. PMU In 1021 in posterior view. **D**–**F**. Scandodiform elements (M). **D**. PMU In 1022 in posterior (D_1) and inner (D_2) views. **E**. PMU In 1023 in inner (E_1) and outer (E_2) views. **F**. PMU In 1024 in outer (F_1), posterior (F_2), and inner (F_3) views. **G**. Detail of the cusp, PMU In 1025, note the striation. **H**, **I**. Subrounded elements (Sa). **H**. PMU In 1026 in lateral (H_1), posterior (H_2), and lateral (H_3) views. **I**. PMU In 1027 in lateral (I_1), posterior (I_2), and lateral (I_3) views. Scale bars 200 μm, except A_4 and G for which are 50 μm.

1982 *Scolopodus sublaevis* Pander; Fåhræus 1982: 21, pl. 1: 1–17, pl. 3: 9–14.

1988 *Scolopodus* spp.; Bergström 1988: pl. 3: 43–45.

1990 *Scolopodus rex* Lindström; Stouge and Bagnoli 1990: 25, pl. 9: 1–6.

1993 non *Scolopodus rex* Lindström; Lehnert 1993: pl. 4: 4.

1994 non *Scolopodus rex* Lindström; Seo et al. 1994: pl. 10: 10–12.
1995 *Scolopodus*? *rex* Lindström; Löfgren 1995: fig. 9as–at.
1998 non *Scolopodus rex* Lindström; Zhang 1998: pl. 17: 5–8.
2000 non *Scolopodus rex* Lindström; Dubinina 2000: pl. 11: 20, 23.
2001 *Scolopodus quadratus* Pander; Rasmussen 2001: pl. 17: 12.
2001 *Scolopodus* sp.; Tolmacheva et al. 2001: fig. 5: 28.

Topotype: Specimen PMU In 1028 (Fig. 6A).

Topotype horizon: The Billingen Regional Stage, *Prioniodus elegans* Zone.

Topotype locality: The Popowka River section, the East Baltic.

Material.—190 acontiodiform elements, 123 scandodiform elements, 44 subrounded elements, 95 paltodiform, and 253 compressed paltodiform elements.

Emended diagnosis.—A species of *Scolopodus* consisting of five element morphotypes: acontiodiform, subrounded, compressed paltodiform, paltodiform and scandodiform. All elements are nongeniculate, finely costate and dominantly hyaline. Acontiodiform elements are symmetrical and nearly symmetrical elements with a low, slightly bloated base; symmetrical subrounded elements are characterised by high base with round to triangular cross-section and almost straight reclined cusp. Compressed paltodiform elements are asymmetrical with variable height of the base. Asymmetrical paltodiform and scandodiform elements have smooth outer sides, costate inner sides and twisted cusps.

Description.—Acontiodiform elements (Figs. 6H, B, 8A–C) are symmetrical and nearly symmetrical with low base and reclined cusp. The base is bloated and slightly expanded posteriorly. The lateral sides of elements are costate and usually carry from 1 to 5 prominent costae. Anterior and posterior sides of the elements are usually smooth but occasionally costate with the costae confined to the basal region. Basal margin is rounded, circular or oval in cross-section: basal cavity is shallow. These elements are considered to be the P elements.

Subrounded elements (Fig. 8H, I) are symmetrical with a high base, a deep basal cavity and a reclined, cusp that is strongly recurved above the base and rounded in cross-section. Most large adult specimens have four or five costae on the lateral sides as well as costae on the posterior side. Anterior side of the elements is usually smooth, or rarely costate. Basal margin is flat with triangular cross-section. These elements are considered to be Sa elements.

Compressed paltodiform elements (Figs. 6A, C, E, J, K, 7D–I) are slightly asymmetrical, laterally compressed elements with reclined cusp and base of variable height. Both lateral and posterior sides bear prominent costae. Anterior is smooth, or rarely costate. Two morphological variants can be recognised: short-based (Figs. 6A, C, 7E, F, H, I) and long-based (Figs. 6E, 7D, G). Short-based elements are more numerous whereas long-based forms are relatively less common in the collections as are elements with short, posteriorly extended base (Fig. 7F). Long-based elements are usually less asymmetrical and smaller than other compressed paltodiform elements. Basal margin is usually flat with oval or rounded cross-section.

Paltodiform elements (Figs. 6D, 7A–C) are asymmetrical with a curved cusp and base of variable height. Inner side is costate whereas the outer side is usually smooth, but occasionally with fine costae. Rare specimens have prominent costae in the posterior part of the outer side. Two variants of paltodiform elements can be recognised: moderate-based with a deep basal cavity and short based with a shallow basal cavity. Base is elongated or suboval in cross-section and slightly bloated posteriorly, forming a broad basal rim. Paltodiform and compressed paltodiform elements are considered to be the transition series of S elements.

Scandodiform elements (Figs. 6F, G, 8D–F) are strongly asymmetrical with a very low base and a laterally compressed, keeled cusp that is strongly recurved above the base and twisted. The inner side of elements carries prominent costae, whereas the outer side is usually smooth. Some large specimens have fine costae that are confined to the base and lower part of cusp. Base is slightly expanded posteriorly and suboval in cross section. Basal cavity is shallow. Scandodiform elements are considered to be M elements.

The number of costae on elements of all morphotype groups is different and varies from one to six, or even seven, but is not strongly influenced by the overall size of the elements. Small juvenile elements usually have fewer costae. The main and most prominent costae are often associated with short additional costae that are confined to the basal region. The edge of the basal margin of all elements is smooth with a low rim on the basal margin; all costae begin a short distance from the basal margin. The surface of elements of all morphotypes groups is usually smooth but occasionally fine longitudinal striation is present in addition to the costae; juvenile elements are more often striated.

All elements are characterised by the basal cavity tips that are situated close to the anterior margin of the elements (Fig. 3).

Remarks.—Fåhræus (1982) divided *S. striatus* between two Pander species, mainly on the basis of the presence of fine striations on the surface of *S. sublaevis* elements and their absence in *S. quadratus*. Examination of a large number of elements from the Popowka River locality as well as from the Harku section shows the rare occurrence of striations on the surface of all morphotypes of elements. Moreover, elements may be smooth (Fig. 7B$_4$) or striated (Fig. 8G) or with intermediate structures (Fig. 7G$_1$). Juvenile elements are more often striated than adult or gerontic ones. Therefore, it is likely that striations and other surface microstructures were formed, or are preserved, as a result of biological or taphonomic processes and do not represent features of systematic value.

Some symmetrical and slightly asymmetrical elements of *Scolopodus* reported outside Baltoscandia (Dubinina 2000; Lehnert 1993; Ji and Barnes 1994; Zhang 1998) are morphologically very similar to *S. striatus*. The difference between Baltoscandian and North American forms was discussed by Ethington and Clark (1981) and later by Ji and Barnes (1994) who assigned the North American *Scolopodus* to *Scolopodus subrex* Ji and Barnes, 1994 based on the higher number of costae, its greater height and sometimes costate anterior margin of the base. Ethington and Clark (1981) noted that small additional costae are not typical for the North American *Scolopodus rex*-like forms. However, the *S. striatus* elements in the available collections from Baltoscandia demonstrate wide variability in the morphological characters listed above. Some rare varieties of paltodiform and scandodiform elements bear costae on the outer side, and also the anterior side of some large compressed paltodiform elements can be costate. Moreover, the number of costae varies significantly from sample to sample. The earliest representatives of *S. striatus* from the clays of the Hunneberg Stage are characterised by relatively fewer costae whereas the elements from the Billingen Stage (at the Ottenby section, Sweden) bear more numerous and high costae. However, all scandodiform *Scolopodus* elements from Baltoscandia are nongeniculate. *Scolopodus* with geniculate scandodiform elements in the apparatuses like those reported from China by Zhang (1998: pl. 17: 8) seem to belong to another species of *Scolopodus*.

Stratigraphic and geographic range.—From the upper part of the *Paroistodus proteus* Zone up to the *Baltoniodus norrlandicus* Zone in the St. Petersburg district (Pander 1986; Sergeeva 1974; Tolmacheva et al. 2001), Estonia (Viira 1974), Sweden (Lindström 1955, 1964; Fåhræus 1982; van Wamel 1974; Löfgren 1978; Stouge and Bagnoli 1990), Norway (Rasmussen 2001), and Poland (Dzik 1976).

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