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Ordovician polychaeturid polychaetes: Taxonomy, distribution and palaeoecology

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The fossil polychaete family Polychaeturidae is considered as monogeneric and comprises four species of the genus *Pteropelta*. *Pteropelta*, originally established on isolated scolecodonts (the carriers), is revised and the apparatus-based *Polychaetura* is shown to be a junior synonym of *Pteropelta*. In addition to *Pteropelta gladiata* and *Pteropelta kielanae*, *Pteropelta huberti* sp. nov., and *Pteropelta* sp. A are herein described from the Upper Ordovician of Estonia and Sweden. Polychaeturids include some of the most common and characteristic scolecodont-bearing polychaetes in the Ordovician of Baltoscandia. They first appeared in the early Darriwilian (Mid Ordovician), flourished in the Late Ordovician and disappeared in the early Silurian. The distribution patterns of individual polychaeturid species infer regional biostratigraphical potential. Polychaeturids were geographically widespread during the Ordovician and have been recorded from at least three palaeocontinents.

Key words: Annelida, Polychaeta, scolecodonts, polychaete jaws, taxonomy, distribution, Ordovician, Baltica.

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Introduction

The fossil record of polychaetes comprises the extremely rare soft-body imprints, calcified dwelling tubes and trace fossils, which are usually problematic to relate to particular species, and scolecodonts, the elements of polychaete jaw apparatuses. In terms of abundance and diversity, scolecodonts represent the vast majority of the fossil record of polychaetes in the Palaeozoic and reveal the ecological importance of this group already in Ordovician times.

Despite 150 years of study, scolecodonts have often been overlooked by palaeontologists, partly due to an unnecessarily complicated taxonomy, which up until the 1960s was almost exclusively single-element-based, without much reference to the architecture of the complex, multi-element jaw apparatuses of eunicidan polychaetes. Obviously such form classification is of little use for understanding the evolution, palaeoecology, and distribution of extinct polychaetes and more or less excludes the utility of scolecodonts in biostratigraphy and palaeogeography.

Following the finds of large numbers of articulated jaw apparatuses in the 1940–1960s an apparatus-based classification concept evolved (Lange 1947, 1949; Kozłowski 1956; Kielan-Jaworowska 1961, 1962, 1966; Szaniawski 1968). Due to the belief that isolated jaws were not diagnostic at the species level little attention was paid to earlier studies, which eventually resulted in the existence of a dual classification system of fossil jaw-bearing polychaetes (e.g., Bergman 1989; Eriksson and Bergman 1998).

Beginning from the 1980s, new large scolecodont collections have been obtained and described, particularly from the Ordovician and Silurian of the Baltic region and North America (for references see Hints and Eriksson 2007a, b). Although some polychaete jaw apparatuses were reconstructed from isolated scolecodonts already by e.g., Kielan-Jaworowska (1966), Szaniawski (1968), and Zawidzka (1971), such reconstructions have become standard practice in scolecodontology ever since Bergman's (1989) monograph on Silurian paulinitids. Fused apparatuses generally are rare in the fossil record in the order of one per hundreds or thousands of isolated jaws, which are abundant and diverse in many types of rocks. The findings of scolecodonts in such great numbers facilitate further studies and open many new perspectives in fossil polychaete research.

As a consequence of the progressing taxonomy, several historical, single-element-based names could be incorporated into the apparatus-based hierarchy combining these two nomenclatures into a single, integrated and biologically meaningful multi-element-based classification (e.g., Bergman 1989, 1995; Eriksson 1997, 1999; Eriksson and Bergman 1998). This also means that, in several cases, more recently erected apparatus-based names may turn out to merely represent junior synonyms.

The aim of this paper is to amend the taxonomic disarray pertaining to the element-based genus *Pteropelta* Eisenack,

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1939, and the apparatus-based *Polychaetura* Kozłowski, 1956, and, to describe two new species from the Ordovician of Baltoscandia. The systematic position of the Polychaeturidae, to which these species belong, is discussed in the light of contrasting opinions by Kielan-Jaworowska (1966), Kozur (1970), Edgar (1984), and Orensanz (1990). Stratigraphically well-constrained collections from several outcrops and boreholes of the Baltic countries, northwestern Russia, midwestern USA and southeast Sweden, enabled also discussions on the stratigraphical and geographical distribution and the palaeoecology of polychaeturids.

The scolecodont collections used for this study were obtained through acid digestion methods described in detail elsewhere (e.g., Hints 1998; Eriksson 2001). In the systematic section, scolecodont descriptive terminology mainly follows that of Kielan-Jaworowska (1966) and Jansonius and Craig (1971).

Institutional abbreviations.—GIT, Institute of Geology at Tallinn University of Technology, Tallinn, Estonia; LO, GeoBiosphere Science Centre, Lund University, Sweden; ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—L, length; L/W, length/width; M, maxilla (followed by a roman numeral indicating its position in the jaw apparatus).

Systematic palaeontology

Class Polychaeta Grube, 1850

Order Eunicida Lamarck, 1809

Family Polychaeturidae Kielan-Jaworowska, 1966

Type genus: *Polychaetura* Kozłowski, 1956, younger synonym of *Pteropelta* Eisenack, 1939.

Discussion.—The family-level classification of Palaeozoic eunicidans was delineated by Kielan-Jaworowska (1966). The monotypic family Polychaeturidae was established particularly on the basis of the distinct carriers, left MI, the basal plate and anterior maxillae (Kielan-Jaworowska 1966: 102). The general labidognath apparatus architecture of polychaeturids is nevertheless similar to that of polychaetaspids and ramphoprionids. Therefore, Kozur (1970) regarded Polychaeturidae as a synonym of Polychaetaspidae, and placed *Pteropelta* as a genus of the latter family. Edgar (1984) emended the diagnosis of the Polychaetaspidae to incorporate four genera (from three families sensu Kielan-Jaworowska 1966); *Ramphoprion*, *Oenonites* (= *Polychaetaspis*), *Kozlowskiprion*, and *Pteropelta* (= *Polychaetura*). Later Orensanz (1990) also supported that idea and used Polychaetaspidae sensu lato in his jaw-based phylogenetic analysis of extant and fossil eunicemorph polychaetes.

In our opinion polychaetaspids and ramphoprionids represent well-constrained phylogenetical groupings, each possessing distinct morphological characteristics. Moreover, since Kielan-Jaworowska's (1966) monograph and the amendments subsequently suggested by Kozur (1970), Edgar (1984), and Orensanz (1990), additional genera have been described and assigned to both the Ramphoprionidae: "*Pararamphoprion*" Männil and Zaslavskaya, 1985, *Protarabellites* Stauffer, 1933, and *Megaramphoprion* Eriksson, 2001; and the Polychaetaspidae: *Dubichaetaspis* Eriksson, 1998 and *Incisiprion* Hints, 1998. If we now follow the amendments proposed by Kozur (1970), Edgar (1984), and Orensanz (1990) and lump all these genera—including *Pteropelta*—into Polychaetaspidae sensu lato, we would loose natural groupings of polychaetaspids and ramphoprionids and a useful rank in the classification hierarchy of fossil polychaetes would also become lost. A possible solution to the problem would be the application of an additional taxonomic rank, either subgenus or subfamily. Subgenera of fossil eunicidans have already been used by Bergman (1989) for paulinitids. His subgenus concept was, however, much narrower than would be in case of e.g., *Dubichaetaspis, Incisiprion*, or *Megaramphoprion*. Introduction of a subfamilial level (i.e., Polychaetaspinae, Ramphoprioninae, Polychaeturinae) could be more suitable. However, only a fraction of the early Palaeozoic jaw-bearing polychaetes is currently described and although Ordovician and Silurian faunas of Baltica and Laurentia are relatively well studied, those of other terranes are poorly known (see details in Hints and Eriksson 2007a). Therefore, many new genera and probably also families will be identified and described in the future. This may, in turn, considerably alter our view on the higher-level classification of early Palaeozoic jaw-bearing polychaetes. For these reasons we consider changing the classification of Kielan-Jaworowska (1966) premature and prefer, for the time being, to retain using Polychaeturidae at the family level.

Genus *Pteropelta* Eisenack, 1939

Type species: *Pteropelta gladiata* Eisenack, 1939; Ordovician, Baltic region.

Discussion.—The genus *Pteropelta* was erected by Eisenack (1939) for isolated carriers of bifurcate morphology (the carriers comprise the posteriormost elements of the maxillary apparatuses; for a review of the general architecture of polychaete jaw apparatuses see, e.g., Kielan-Jaworowska 1966; Szaniawski 1996). Eisenack (1939) diagnosed *Pteropelta* as carriers with short median peaks (Medianhöcker in German), situated in the proximal part, and lateral spines (Lateralstacheln in German) with two posteriorly directed wing-like excrescences on the sides. In that same paper he described three new species: *Pteropelta gladiata*, *P. thomsoni*, and *P. glossa*, of which the first was designated as type species.

In 1956, Kozłowski described an articulated jaw apparatus, possessing carriers morphologically identical to those of *Pteropelta*, and named it *Polychaetura gracilis*. Kozłowski noted that with regard to the species of *Pteropelta* distinguished by Eisenack (1939), *Pteropelta thompsoni* seems to correspond to the carriers of *Polychaetura gracilis*. Thus Kozłowski (1956) apparently did not fail to notice the great similarity between *Pteropelta* and his new genus *Polychaetura*. He did, however, share the belief of Lange (1947, 1949) that the isolated elements (scolecodonts) are of little taxonomical value and that a different set of names had to be applied for articulated apparatuses.

Subsequently Kielan-Jaworowska (1966) obtained additional jaw apparatuses and numerous isolated elements belonging to *Polychaetura*, and erected a monogeneric family Polychaeturidae, which included two species; *Polychaetura gracilis* and *Polychaetura* sp. a (the latter has subsequently been described as *Pteropelta kielanae*, see below). She also noted the similarity between the carriers of *Polychaetura* and the scolecodonts described as *Pteropelta* by Eisenack (1939). Nonetheless, for the same reasons as Kozłowski (1956) she did not consider them as congeneric (discussed in closer detail by Kielan-Jaworowska 1968).

Tasch and Stude (1965), referring to the rules of the International Code of Zoological Nomenclature (ICZN), regarded eight apparatus-based generic names, *Polychaetura* included, as junior synonyms to *Eunicites* Ehlers, 1868. The latter amendment was erroneous and strongly criticised by Kielan-Jaworowska (1968). Moreover, Jansonius and Craig (1971) suggested abstaining from assigning fossil polychaete jaws under the generic name *Eunicites* because of the very poor preservation of the type specimen of its type species.

Kozur (1970) was first to regard *Polychaetura* as a junior synonym to *Pteropelta*. For the emended diagnosis of *Pteropelta*, he proposed to use those provided by Kozłowski (1956) and Kielan-Jaworowska (1966) for *Polychaetura*. The question of the type material was, however, left open and Kozłowski's (1956) species *P. gracilis* was kept separate from those described by Eisenack (1939). Perhaps due to the strong criticism on Kozur's (1970) work (e.g., Jansonius and Craig 1971; Szaniawski and Wrona 1973), several authors were reluctant to use *Pteropelta* as opposed to *Polychaetura*. Edgar (1984) provided a cursory discussion on the element-based versus apparatus-based classification with regards to polychaeturids. He did not consider those two generic names as synonymous, but preferred to maintain both classification systems. Hints (1998) also used *Polychaetura* instead of *Pteropelta* but noted that some of the names employed may turn out to be junior synonyms. More recently, Hints (2000), Hints and Eriksson (2007a), and Eriksson and Hints (2009) have illustrated a few polychaeturid jaws (MI, basal plate and carriers) under the generic name *Pteropelta*.

Eisenack's (1939) collection, including the type material of *Pteropelta*, was obtained in the 1930s but became lost during World War II. Neotypes have subsequently been designated for several species of chitinozoans, foraminiferans, and acritarchs (e.g., Eisenack 1959), but not for scolecodonts. With respect to the diagnostics and applicability of a genus, the validity of the type species and its corresponding type specimen are of particular significance. Thus designation of a neotype for *Pteropelta gladiata* is a prerequisite for solving the above described synonymy problem.

The International Code for Zoological Nomenclature recommends that neotypes should derive from a horizon and locality as close as possible to that of the holotype (ICZN; Article 75). In the case of *Pteropelta* this is complicated because Eisenack's (1939) material came from erratic boulders found in Germany, but with a Baltic provenance. The precise age of these boulders are not known, but most likely they are of Ordovician age. Eisenack's (1939) type specimen of *Pteropelta gladiata* is morphologically identical to the carriers of the type specimen of *Polychaetura gracilis* (a well preserved apparatus illustrated by Kozłowski 1956: fig. 17), except being larger. Like Eisenack's (1939) material, Kozłowski's (1956) type specimen was derived from an erratic boulder, the specific age of which is ambiguous. However, the entire apparatus, complemented with isolated jaws recovered from the same boulder, provides much better basis for taxonomy than the single carriers. Considerable variation in size of the jaws of *P. gracilis* was noted by Kielan-Jaworowska (1966: 105) and confirmed by the present authors to be regarded as intraspecific variability. We therefore believe that *Pteropelta gladiata* and *Polychaetura gracilis* represent one and the same species and designate the holotype of *Polychaetura gracilis* as neotype for *Pteropelta gladiata*, thus also making the former name a junior synonym of the latter.

Concerning the two other species of *Pteropelta* described by Eisenack (1939), the single specimen of *Pteropelta glossa* is regarded to be conspecific with *Pteropelta gladiata*. The main difference between the two is the shape of the shaft, which is narrower in *P. gladiata*. The shaft is, however, very thin along the longitudinal axis and its shape thus depends largely on the state of preservation.

We agree with the opinion of Kozłowski (1956: 197) and Kielan-Jaworowska (1966: 102), that *Pteropelta thompsoni* is conspecific with *P. gladiata*. However, one of the specimens assigned to *P. thompsoni* by Eisenack (1939: pl. B: 2, specimen No. 3), has an anterior margin that is nearly straight or slightly convex as opposed to being distinctly concave in those of *P. gladiata*. Similar carriers are found in *P. huberti* described below. The carriers of *P. kielanae* (Hints, 1998) and *Pteropelta* sp. A herein are hitherto unknown, but their left MI share similar, straight posterior margins. Accordingly the anterior margins of the carriers (which fit with the posterior terminations of the MI) of all three species are also expected to be similar. Two of the *P. thomsoni* specimens (including No. 3) were not recovered from an erratic boulder but from an outcrop in Rakvere town (formerly Wesenberg) of northern Estonia. Eisenack (1939: 165) noted that they were derived from "Stufe D_{II}", which corresponds to the Keila Regional Stage. This age determination nevertheless remains ambiguous since most of Rakvere town is actually confined to the outcrop area for strata belonging to the Rakvere Stage. This uncertainty interval, from the Keila to Rakvere stages, overlaps with the known ranges of the three above mentioned species and therefore specimen No. 3 of Eisenack (1939) could belong to any of these.

In conclusion, studies of appropriate type material as well as new scolecodont collections have supported the taxonomic amendment originally proposed by Kozur (1970). The

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Fig. 1. Elements of jaw apparatuses of Ordovician polychaeturid polychaete *Pteropelta gladiata* Eisenack, 1939. **A**–**I**. Left MI, all in dorsal view. **A**. GIT 592-34, sample OM97-5, Väike-Pakri Cliff, Estonia, Kunda Stage, Darriwilian. **B**. GIT 592-35, sample OM97-20, Väike-Pakri Cliff, Estonia, Uhaku Stage, Darriwilian. **C**. GIT 592-36, sample OM03-51, Viru Mine, Estonia, Kukruse Stage, Sandbian. **D**. GIT 433-24, sample OM03-51, Viru Mine, Estonia, Kukruse Stage, Sandbian. **E**. GIT 592-37, sample OM97-116, Väike-Pakri Island, Estonia, Kukruse Stage, Sandbian. **F**. GIT 592-38, sample OM-205, Vaemla F-364 borehole, 140 m, Estonia, Keila Stage, Sandbian. **G**. GIT 592-39, sample M96-81, Orjaku borehole, 112.5 m, Estonia, Rakvere Stage, Katian. **H**. GIT 592-40, sample M96-1, Laeva 18 borehole, 187.45 m, Estonia, Pirgu Stage, Katian. **I**. LO 10476, sample 04E1-3, Stormyr-2 borehole, 213.65 m, Sweden, Pirgu Stage, Katian. **J**–**Q**. Right MI, all in dorsal view. **J**. GIT 433-25, sample OM03-51, Viru Mine, Estonia, Kukruse Stage, Sandbian, magnified (J_1) and reduced to the same scale as O, to show size variation (J_2). **K**. GIT 592-41, sample OM03-51, Viru Mine, Estonia, Kukruse Stage, Sandbian. **L**. GIT 592-42, sample OM-205, Vaemla F-364 borehole, 140 m, Estonia, Keila Stage, Sandbian. **M**. GIT 592-43, sample M96-49, Orjaku borehole, 47.62 m, Estonia, Pirgu Stage, Katian. **N**. GIT 592-44, sample M96-49, Orjaku borehole, 47.62 m, Estonia, Pirgu Stage, Katian. **O**. GIT 592-45, sample D-102/22, Lelle D-102 borehole, 141.42 m, Estonia, Pirgu Stage, Katian. **P**. GIT 592-46, sample D-102/49, Lelle D-102 borehole, 146.18 m, Estonia, Vormsi Stage, Katian. **Q**. LO 10477, sample 04E1-3, Stormyr-2 borehole, 213.65 m, Sweden, Pirgu Stage, Katian. **R**. Left MI, ventral view, GIT 592-47, sample OM97-5, Väike-Pakri Cliff, Estonia, Kunda Stage, Darriwilian. **S**. Left MI, left lateral view, GIT 592-48, sample M96-81, Orjaku borehole, 112.5 m, Estonia, Rakvere Stage, Katian. **T**. Right MI, right lateral view, GIT 592-49, sample M96-81, Orjaku borehole, 112.5 m, Estonia, Rakvere Stage, Katian. **U**. Apparatus, GIT 592-50, sample M-4711, Suhkrumägi outcrop, Estonia, Kunda Stage, Darriwilian. **V**. Apparatus, GIT 592-51, sample M-4430, Orjaku borehole, 135.6 m, Estonia, Keila Stage, Sandbian/Katian. **W**. Basal plate, GIT 592-52, sample M-4711, Suhkrumägi outcrop, Estonia, Kunda Stage, Darriwilian. **X**. Carriers, GIT 315-34, sample M96-77, Orjaku borehole, 63.8 m, Estonia, Pirgu Stage, Katian. **Y**. Carriers, GIT 592-53, sample M96-49, Orjaku borehole, 47.62 m, Estonia, Pirgu Stage, Katian. SEM micrographs, scale bars 100 µm.

name *Polychaetura* Kozłowski, 1956 is regarded as a junior synonym of *Pteropelta* Eisenack, 1939, and *Polychaetura gracilis* Kozłowski, 1956 as a junior synonym of *Pteropelta gladiata* Eisenack, 1939.

Pteropelta gladiata Eisenack, 1939

Fig. 1.

1939 *Pteropelta gladiata* sp. nov.; Eisenack 1939: 164, pl. C: 2.
1939 *Pteropelta glossa* sp. nov.; Eisenack 1939: 164, pls. B: 1, C: 2–3.
1939 *Pteropelta thompsoni* sp. nov.; Eisenack 1939: 165, pl. B: 3.
1956 *Polychaetura gracilis* sp. nov.; Kozłowski 1956: 192–195, figs. 17–18.
1956 *Polychaetura* sp. a; Kozłowski 1956: fig. 19.
1966 *Polychaetura gracilis* Kozłowski; Kielan-Jaworowska 1966: 103–105, pls. 22, 23: 3–7, text-fig. 8L.
1982 "Zusammengesetzte Maxille links"; Schallreuter 1982: pl. 2: 5.
1996 *Polychaetura gracilis* Kozłowski; Szaniawski 1996: pl. 2: 6.
1998 *Polychaetura gracilis* Kozłowski; Hints 1998: 496, fig. 12A–D.
2000 *Pteropelta gladiata* Eisenack; Hints 2000: pl. 2: 3–4.
2007 *Pteropelta gladiata* Eisenack; Hints and Eriksson 2007a: fig. 4F–G.
2009 *Pteropelta gladiata* Eisenack; Eriksson and Hints 2009: fig. 5k–l.

Type material: Holotype: carriers figured by Eisenack 1939: pl. C: 2 (specimen lost), neotype: apparatus (ZPAL Sc 0/1/1) figured by Kozłowski 1956: fig. 17 .

Type locality and horizon: Erratic boulder No. 0.116 of Baltic origin, Upper(?) Ordovician age, collected from Wyszogród, Poland.

Remarks.—This species has been described in detail by Kozłowski (1956) and subsequently also by Kielan-Jaworowska (1966). In one of the articulated apparatuses recovered (Fig. 1U) we discovered anterior maxillae with an unusual morphology. At least the right MII, but possibly also the MIV and the left MII appear to be composed by lamella-like plates, each one terminating dorsally into a denticle. Similarly, Kielan-Jaworowska (1966: 104–105) noted in the description of *Polychaetura gracilis* that the boundaries between the denticles of the anterior maxillae are prolonged along the entire width of the jaw and (for the left MIII) that the jaw becomes separated into individual denticles. Such type of anterior maxillae is characteristic of *Tretoprion astae* Hints, 1999 and may suggest a relationship between the Polychaeturidae and Tretoprionidae (see also discussion of *Pteropelta kielanae* below).

Based on the extensive collections from Estonia *Pteropelta gladiata* is the only polychaeturid species, which has incised posterior margin in left MI and concave (incised) anterior margins of carriers.

The variability of *P. gladiata* is relatively wide concerning both size (cf. Fig. 1O and J_1) and general morphology of the posterior maxillae (see for example specimens in Fig. 1C and D which are from the same sample). In addition, there is a notable morphological trend within the lineage. In the left MI this concerns the inner wing, which is relatively wider in Darriwilian to early Katian specimens (Fig. 1A–G) compared to younger material (Fig. 1H, I). Generally, the right MI becomes more elongated with a longer shank and reduced ramus (cf. Fig. 1L and P). Like Kielan-Jaworowska (1966) we consider these differences to fall within the intraspecific variability. It should be added that the proposed neotype represents the older morphotype of the species.

Stratigraphic and geographic range.—Volkhov to Juuru regional stages (Darriwilian to basal Llandovery) of Baltoscandia (Estonia, NW Russia, Sweden, Poland), Baltic erratic boulders, upper Richmondian (Katian) of Ohio, USA; possibly Ordovician(?) of Kazakhstan.

Pteropelta kielanae (Hints, 1998) comb. nov.

Fig. 2A–C.

1966 "*Polychaetura*" sp. a; Kielan-Jaworowska 1966: 105–106, pl. 23: 1, 2.
1998 *Polychaetura kielanae* sp. nov.; Hints 1998: 497–498, figs. 12H–L.
2000 *Pteropelta kielanae* (Hints); Hints 2000: pl. 2: 8.

Emended diagnosis.—Hints (1998: 498) diagnosed this species as differing from *Polychaetura gracilis* in having wider posterior maxillae (MI), a left MI with straight instead of incurved posterior margin and a longer inner wing. It differs from *P. gracilis*, *P. huberti*, and *Pteropelta* sp. A in having a right MI with sub-rectangular instead of triangular outline of the shank.

Remarks.—Hints (1998: fig. 12H) illustrated a fused right MII and MIV from this species in which the same feature as discussed above for *Polychaetura gracilis* can be observed, i.e., that the individual denticles of these anterior maxillae are weakly fused and their boundaries continue through the element providing a lamella-like appearance. Whether or not *P. huberti* and *Pteropelta* sp. A also have similar anterior maxillae is presently not known. If this proves to be a feature typical for all polychaeturids their supposedly close relationship to polychaetaspids and ramphoprionids (Kielan-Jaworowska 1966) may need reconsideration.

Stratigraphic and geographic range.—*Pteropelta kielanae* is most common in the Haljala and Keila stages (Sandbian to basal Katian) of Estonia and NW Russia. Questionable finds derive from the Uhaku Stage (upper Darriwilian) of Estonia and Kukruse Stage (basal Sandbian) of south-eastern Sweden (MEE, unpublished data).

Pteropelta huberti sp. nov.

Fig. 2J–AI.

1998 *Polychaetura* sp. A; Hints 1998: 498–499, figs. 12E–G.
2000 *Pteropelta* sp. A; Hints 2000: pl. 2: 1, 2.

Etymology: Named in honour of Hubert Szaniawski in recognition of his work on fossil scolecodont-bearing polychaetes.

Type material: Holotype: left MI, GIT 592-1, Fig. 2X; paratypes: GIT 592-2 to 592-26.

Type locality: Lelle D-102 borehole, central Estonia.

Type horizon: Vormsi Regional Stage (Katian).

Material.—Several hundred right and left MI, ca 50 basal plates, and seven pairs of carriers from Laeva 18, Lelle D-102, Rapla and Orjaku drill cores and Viru mine section.

Diagnosis.—Posterior maxillae of *Pteropelta huberti* are most

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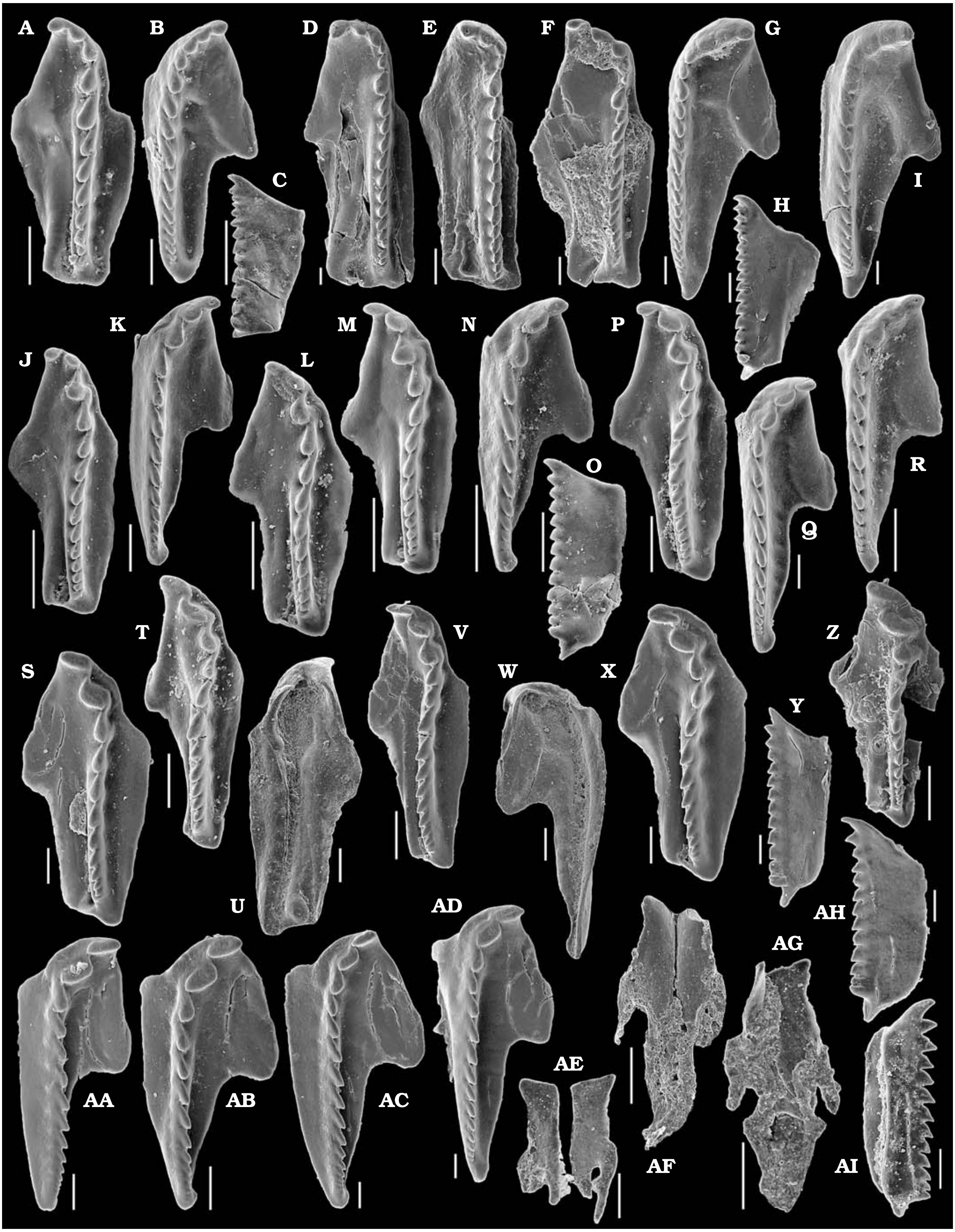
similar to those of *P. kielanae*. The main differences concern (i) outline of the shank, which is sub-triangular in *P. huberti*, but sub-rectangular in *P. kielanae*; (ii) inner wing in left MI, which is longer in *P. huberti* and with more slanting anterior margin; (iii) dentary in left MI, where the largest denticle is the second or third in *P. huberti* instead of fourth or fifth as in *P. kielanae*. *Pteropelta huberti* differs from *P. gracilis* in having almost straight posterior margin in left MI and straight or slightly convex anterior margin in carriers. *P. huberti* commonly differs from other species of *Pteropelta* also in having two anteriormost denticles in both MI transversally extended.

Description.—Right MI: L = 0.3–1.2 mm, L/W ratio = 2.0–3.0. Anterior half of jaw considerably wider than posterior half. Outer-lateral margin is almost straight or with a small incurvature in the middle. Sub-rounded, more or less club-shaped ramus extends to 0.43–0.55 of jaw length from anterior. Bight more or less anteriorly concave; in smaller specimen it may be almost transverse and perpendicular to length axis. Outer margin along the shank is directed posteriorly in the first half of the shank, then it bends continuously and is directed towards the end of the dentary. Posteriormost termination generally developed into a small tubercle. Dentary comprises 11–17 sub-conical denticles, first three (particularly first two) of which may be prolonged transversally into short ridges. Denticles rather tightly packed and decrease gently in size particularly posterior of midlength where they are also more slanted. Posteriormost part of dentary commonly slightly dextrally bent. Inner margin sub-parallel to dentary and inner face is steep. Anteriorly inner face widens slightly, forming a more or less distinct inner wing that extends for approximately 0.9 of jaw length. Anteriormost termination of inner wing forms a more or less well-developed cove, anterior of which the inner face is very narrow in dorsal view. In ventral view the myocoele is almost gaping with a cover extending for 0.05–0.07 of jaw length.

Left MI: L = 0.33–1.1 mm, L/W ratio = 2.0–3.1. Sub-rectangular jaw with its widest part usually just anterior of midlength. Outer margin runs most often postero-laterally for 0.4–0.5 of jaw length, where it bends and continues towards the denticulated ridge, and then continues sub-parallel to dentary until it meets the posterior margin. Sometimes a small bight, similar in extension to that in right MI, can be seen. Below the ramus the edge of the outer face is thinner and less sclerotised which sometimes gives the outer margin a ragged, semi-translucent appearance. Such specimens in particular resemble the morphology of the ramus and bight of the right MI. Long, almost rectangular inner wing reaching to 0.70–0.75 of jaw length from posterior with an inner margin sub-parallel to dentary. Relatively wide, almost straight and transverse posterior margin forms 0.35–0.50 of jaw width. Dentary consists of 10–15 denticles, three first ones may be prolonged transversally like in right MI. If not prolonged, the first two are smaller than the third denticle. Dentary particularly elevated on a ridge in posterior half of jaw. In ventral view, myocoele is almost gaping, cover extends to approximately 0.05 of jaw length. Small denticle pits visible in the narrow furrow that corresponds to the dentary and which widens anteriorly.

Basal plate: Sub-trapezoidal element approximately half as long as right MI. L = 0.35–0.8 mm, L/W ratio varies from 2.0 to 3.3. Inner margin is longer than outer margin. In dorsal view, posteriormost termination usually has posteriorly-directed, narrow and blunt extension. Dentary houses 10–18

Fig. 2. Elements of jaw apparatuses of Ordovician polychaeturid polychaete *Pteropelta kielanae* (Hints, 1998), *Pteropelta* sp. A and *Pteropelta huberti* sp. nov. → All in dorsal view except U, W and AI which are in ventral view. **A**–**C**. *Pteropelta kielanae* (Hints, 1998) **A**. Left MI, GIT 592-27, sample OM-169, Metsküla F-198 borehole, 35.12 m, Estonia, Haljala Stage, Sandbian. **B**. Right MI, GIT 592-28, sample OM-176, Metsküla F-198 borehole, 24.13 m, Estonia, Keila Stage, Sandbian. **C**. Basal plate, GIT 159-41, sample OM-135, Apraksin Bor borehole, 144.25 m, St. Petersburg Region, Russia, Haljala Stage, Sandbian. **D**–**I**. *Pteropelta* sp. A. **D**. Left MI, GIT 592-29, sample M-4416, Vasalemma 758 borehole, 8.65 m, Estonia, Keila Stage, Katian. **E**. Left MI, LO 10478, sample 04E1-3, Stormyr-2 borehole, 213.65 m, Estonia, Pirgu Stage, Katian. **F**. Left MI, GIT 592-30, Båticke-3 borehole, 313.6 m, Sweden, Pirgu Stage, Katian. **G**. Right MI, GIT 592-31, Båticke-3 borehole, 313.6 m, Sweden, Pirgu Stage, Katian. **H**. Basal plate, GIT 592-32, Båticke-3 borehole, 313.6 m, Sweden, Pirgu Stage, Katian. **I**. Right MI, GIT 592-33, sample OM98-43, Saku quarry, Estonia, Oandu Stage, Katian. **J**–**AI**. *Pteropelta huberti* sp. nov. **J**. Left MI, GIT 592-2, sample OM03-44, Viru mine, Estonia, Uhaku Stage, Darriwilian. **K**. Right MI, GIT 592-3, sample OM03-44, Viru mine, Estonia, Uhaku Stage, Darriwilian. **L**. Left MI, GIT 592-4, sample OM03-49, Viru mine, Estonia, Uhaku Stage, Darriwilian. **M**. Left MI, GIT 592-5, sample OM03-49, Viru mine, Estonia, Uhaku Stage, Darriwilian. **N**. Right MI, GIT 592-6, sample OM03-43, Viru mine, Estonia, Uhaku Stage, Darriwilian. **O**. Basal plate, GIT 592-7, sample OM03-43, Viru mine, Estonia, Uhaku Stage, Darriwilian. **P**. Left MI, GIT 592-8, sample M96-78, Orjaku borehole, 107.4 m, Estonia, Rakvere or Nabala Stage, Katian. **Q**. Right MI, GIT 592-9, sample M96-78, Orjaku borehole, 107.4 m, Estonia, Rakvere or Nabala Stage, Katian. **R**. Right MI, GIT 592-10, sample M96-40, Laeva 18 borehole, 228.08 m, Estonia, Nabala Stage, Katian. **S**. Left MI, GIT 592-11, sample D-102/49, Lelle D-102 borehole, 146.18 m, Estonia, Vormsi Stage, Katian. **T**. Left MI, GIT 592-12, sample M96-34, Laeva 18 borehole, 221.35 m, Estonia, Vormsi Stage, Katian. **U**. Left MI, GIT 592-13, sample M96-35, Laeva 18 borehole, 223.4 m, Estonia, Vormsi Stage, Katian. **V**. Left MI, GIT 592-14, sample D-102/49, Lelle D-102 borehole, 146.18 m, Estonia, Vormsi Stage, Katian. **W**. Right MI, GIT 592-15, sample M96-35, Laeva 18 borehole, 223.4 m, Estonia, Vormsi Stage, Katian. **X**. Left MI, holotype, GIT 592-1, sample D-102/49, Lelle D-102 borehole, 146.18 m, Estonia, Vormsi Stage, Katian. **Y**. Basal plate, GIT 592-16, sample D-102/49, Lelle D-102 borehole, 146.18 m, Estonia, Vormsi Stage, Katian. **Z**. Left MI, GIT 592-17, Båticke-3 borehole, 315.0 m, Sweden, Pirgu Stage, Katian. **AA**. Right MI, GIT 592-18, sample D-102/49, Lelle D-102 borehole, 146.18 m, Estonia, Vormsi Stage, Katian. **AB**. Right MI, GIT 592-19, sample D-102/49, Lelle D-102 borehole, 146.18 m, Estonia, Vormsi Stage, Katian. **AC**. Right MI, GIT 592-20, sample D-102/49, Lelle D-102 borehole, 146.18 m, Estonia, Vormsi Stage, Katian. **AD**. Right MI, GIT 592-21, sample D-102/49, Lelle D-102 borehole, 146.18 m, Estonia, Vormsi Stage, Katian. **AE**. Carriers, GIT 592-22, sample OM97-209, Laeva 18 borehole, 222.4 m, Estonia, Vormsi Stage, Katian. **AF**. Carriers, GIT 592-23, sample OM97-209, Laeva 18 borehole, 222.4 m, Estonia, Vormsi Stage, Katian. **AG**. Carriers, GIT 592-24, sample OM97-209, Laeva 18 borehole, 222.4 m, Estonia, Vormsi Stage, Katian. **AH**. Basal plate, GIT 592-25, sample D-102/49, Lelle D-102 borehole, 146.18 m, Estonia, Vormsi Stage, Katian. **AI**. Basal plate, GIT 592-26, sample M96-35, Laeva 18 borehole, 223.4 m, Estonia, Vormsi Stage, Katian. SEM micrographs, scale bars 100 µm.



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subtriangular denticles of which the anteriormost generally is the largest one. In ventral view, cover comprises 0.5–0.7 of jaw width.

Carriers: Fused carriers are about 2.2 times longer than wide. The shaft of a single carrier has two posteriorly directed branches, the proximal one being 3 times longer than the distal one. Anterior margin of carriers are nearly straight.

Variability.—The outline, especially the length/width ratio varies considerably in the first maxillae. The anteriormost denticles of these elements, moreover, may be developed into short transverse ridges. In the basal plate, two types of denticulation occur: (i) all denticles are relatively large and of nearly equal size and shape, and (ii) anteriormost denticles are smaller and/or more slender than the remaining ones.

Remarks.—The development of the anteriormost denticles in the MI into transverse ridges is unique for *Pteropelta huberti* among the polychaeturids, but similar denticles are not uncommon for Ordovician scolecodonts. Two examples, where such ridges are developed in extreme form are seen in the jaws of *Rhytiprion magnus* Kielan-Jaworowska, 1966 (cf. Bergman et al. 2003) and *Kaljoprion laevaensis* Hints, 2008. Moreover, the long-ranging *Tretoprion astae* Hints, 1999 and a species of *Pistoprion* (Kielan-Jaworowska 1966: pl. 7: 1; Hints 2000: pl. 1: 2) possess similar ridges in their maxillae. Thus taxa having different types of jaw apparatuses (placognath and labidognath) could develop such denticles. Only in the case of *P. huberti*, however, the lack or presence of this feature can be considered as falling within the range of the intraspecific variability. It is noteworthy that the ridges in *P. huberti* are well developed only in specimens occurring in the uppermost part of its stratigraphical range (Vormsi and Pirgu stages, upper Katian), where it co-occurs with *R. magnus*, *K. laevaensis*, and *T. astae.* It is therefore likely that the development of such denticles in *P. huberti* had functional advantage, perhaps for certain types of diet or burrowing.

Stratigraphic and geographic range.—*Pteropelta huberti* ranges from the Uhaku to Pirgu regional stages (Darriwilian to Katian) in Baltoscandia and Poland, being most characteristic of the Nabala and Vormsi stages (middle Katian).

Pteropelta sp. A

Fig. 2D–I.

2009 *Pteropelta* sp.; Eriksson and Hints 2009: fig. 5m, o (n tentatively).

Material.—Three right MI, three left MI, two Bp from the Saku quarry and the Vasalemma 758 borehole of Estonia and the Stormyr-2 and Båticke-3 boreholes of Sweden.

Description.—Right MI: L = 1.0–1.2 mm, L/W ratio = 2.3–2.5. Outer margin runs straight postero-dextrally and just above mid-length bends, enclosing a sub-rounded ramus extending to approximately 0.5 of jaw length from anterior; bight, vaguely concave anteriorly. Posterior of ramus outer face comparably wide, tapering gently and evenly. Posteriormost termination of jaw bluntly subtriangular and dorso-ventrally compressed compared to the elevated denticles. Dentary houses 18–19 tightly packed denticles that decrease evenly in size posteriorly. Fourth and sixth denticles may be slightly smaller than surrounding ones. Anterior part of dentary arranged sub-transversally to length-axis. Elevation of the dentary more pronounced in anterior half of jaw. Inner face is narrow and steep, very narrow inner wing representing c. 0.85 of jaw length may be visible. In ventral view cover comprises 0.1 of jaw length.

Left MI: L = 0.75–1.6 mm, L/W ratio = 2.2–2.9. Sub-rectangular sturdy jaw with wide, nearly straight transverse posterior margin. Outer margin runs straight postero-sinistrally and bends at approximately 1/3 to half of jaw length, sometimes enclosing a relatively narrow ramus-like feature, and continuing postero-dextrally and sub-parallel to dentary in posterior half of jaw. Dentary houses 16–18 sub-triangular, relatively tightly packed denticles. First three denticles arranged sub-transversally to length axis and decrease evenly in size, following one or two are considerably smaller whereas the next one is as big as the first denticle. Posterior of this, denticles decrease evenly and gently in size. Denticulated ridge particularly elevated and well-developed in posterior half of jaw. Long, sub-rectangular inner wing extending for 0.65–0.77 of jaw length. Its inner margin is straight and parallel to dentary. Anterior of inner wing, inner face is not visible in dorsal view. In ventral view cover comprises approximately 0.1 of jaw length.

Basal plate: Sub-trapezoidal element. L= 0.36–0.58 mm, L/W = c. 2.2. Inner margin is longer than outer margin. Anterior margin wider than posterior one. Posteriormost termination usually has posteriorly-directed, narrow and blunt extension. Dentary houses 12–14 sub-triangular denticles which are slightly bigger in posterior half of jaw.

Remarks.—Although this species is distinctive and differs from all other polychaeturids, it is here kept under open nomenclature because of the limited amount of material available. The jaws of *Pteropelta* sp. A are most similar to those of *P. kielanae*. The main difference in the right MI is the shape of the posteriormost termination; the undenticulated ridge is longer and somewhat pointed in *Pteropelta* sp. A, as a posterior continuation of the outer face. The few jaws hitherto recovered of *Pteropelta* sp. A are, moreover, bigger and have an over-all sturdier appearance than to those of *P. kielanae*. The MI dentary of *Pteropelta* sp. A is more differentiated (especially in the left MI where small, intermediate denticles occur) and has more denticles than that of *P. kielanae*. By contrast to the other polychaeturids that have a left MI most reminiscent of those of the polychaetaspid genus *Oenonites*, the left MI of *Pteropelta* sp. A has a general morphology superficially resembling those of certain ramphoprionids (*Protarabellites*) or even kalloprionids (see, e.g., Eriksson 2001, 2006). See also discussion by Kielan-Jaworowska (1966: 102–103).

Stratigraphic and geographic range.—*Pteropelta* sp. A is recorded from the Keila and Oandu stages (lowermost Katian) of northern Estonia and from the Pirgu Stage (upper Katian) of Gotland, Sweden.

Discussion

Stratigraphical distribution.—Kielan-Jaworowska (1966: 102) referred the stratigraphical and geographical distribution of *Polychaetura* (= *Pteropelta*) as the Ordovician of the Baltic region. Without further explanation she extended the stratigraphical range of the family into the Silurian (Kielan-Jaworowska 1966: fig. 7). As revealed from the collections at hand, polychaeturids are found abundantly in Ordovician strata, beginning from the basal Darriwilian (topmost Volkhov Regional Stage). Only a few specimens have been recorded from the Silurian so far; in the basal Llandovery of Estonia (Õhne Formation, Juuru Regional Stage). Neither the extensive scolecodont collection from the Silurian (upper Llandovery through Ludlow) of Gotland, Sweden, nor smaller Silurian collections from Estonia, Great Britain, and the Canadian Arctic, have yielded any polychaeturids (Hints et al. 2000, 2006; Eriksson 2002; Eriksson et al. 2004; Rubel et al. 2007; personal observations by the authors). These facts supplemented with literature data suggest that the family was flourishing in the Mid through Late Ordovician and disappeared relatively early in the Silurian.

Based on the stratigraphical distribution of individual *Pteropelta* species, *P. gladiata* represents the oldest and most long-ranging lineage, likely being ancestral to other polychaeturid taxa (Fig. 3). Among the known polychaeturids it has the smallest and most slender maxillae whereas the younger species developed sturdier jaws and a left MI

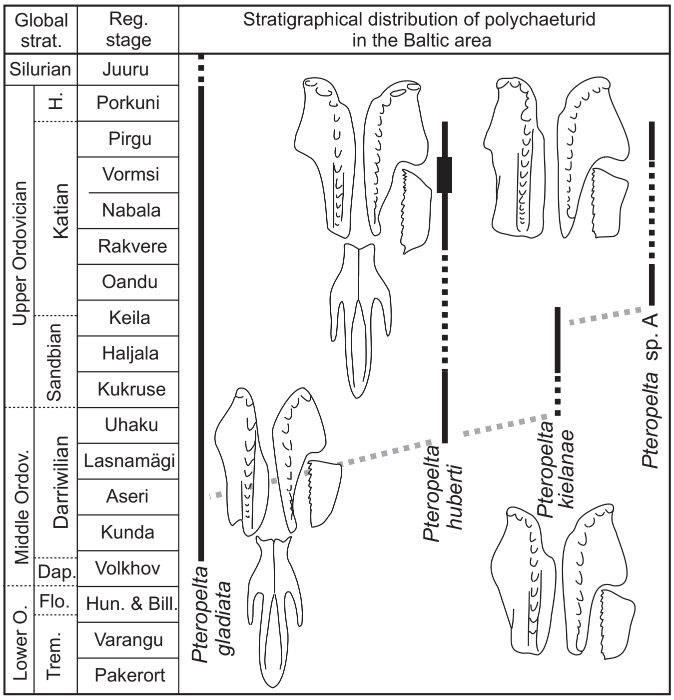

Fig. 3. Stratigraphical distribution of polychaeturids in the Baltic region and also showing the tentative phylogenetic relationship between the different species. The stratigraphical chart is slightly modified from Nõlvak et al. (2006). Abbreviations: Dap., Dapingian; Flo., Floian; H., Hirnantian; Hun. & Bill., Hunneberg and Billingen; Reg., regional; Trem., Tremadocian.

with a posterior termination that is typically wider and almost transversally straight. This can be observed in all other species described herein, with the most extreme variety represented by the rare *Pteropelta* sp. A, which has a left MI reminiscent of those of *Protarabellites* and some species of *Kalloprion*. The *P. gladiata* lineage gradually evolved and the youngest representatives (from Katian and lowermost Llandovery strata) generally exhibit the most slender jaws.

Pteropelta huberti ranges stratigraphically from the Uhaku to Pirgu regional stages (upper Darriwilian to Katian) of Baltoscandia. It is relatively common, although not abundant, in the lower part of its range (Uhaku and Kukruse stages). It has a range gap from the Haljala through Oandu stages (cf. Hints 1998) but reappears as a Lazarus taxon in the beginning of the Rakvere Stage, and has a conspicuous abundance peak in the Vormsi Stage. Its morphological evolution, particularly the development of the anteriormost denticles in the MI into transversally extended ridges, is time-constrained.

P. kielanae is a characteristic species of the Haljala and Keila stages (Hints 1998). Only a single, poorly preserved specimen possibly belonging to *P. kielanae* has been recovered from the Uhaku Stage of Estonia and a few probable specimens were recently recorded from the Kukruse Stage of the Tvären-2 drill core, south-eastern Sweden (Lindström et al. 1994; unpublished collection of MEE). The stratigraphical applicability of this relatively short-ranging species, as inferred by Hints (2000), is confirmed in this study.

The material of *Pteropelta* sp. A is too limited to allow detailed discussion on its distribution. Its occurrence in Estonia, nonetheless, falls between the disappearance of *P. kielanae* and the reappearance of *P. huberti* (Fig. 3).

Based on the distribution pattern of polychaeturid species the following characteristic intervals can be distinguished in the Middle through Upper Ordovician of Baltoscandia; (i) the range of *P. gladiata* with no accompanying polychaeturid species (Volkhov to Lasnamägi stages), (ii) the lower range of *P. huberti* (Uhaku and Kukruse stages), (iii) the range of *P. kielanae* (Haljala and Keila stages), (iv) the upper range of *P. huberti* (Rakvere and Nabala stages), (v) the acme of *P. huberti* and appearance of the transversal ridges in MI of this species, as well appearance of the more slender morphotype of *P. gladiata* (Vormsi Stage). This collectively infers biostratigraphical utility of polychaeturids.

Palaeobiogeography.—Polychaeturids were very common and widespread in the Baltic region, including present-day Estonia, northwestern Russia, Poland, and Sweden (Fig. 4; Eisenack 1939; Szaniawski 1970; Hints 1998, 2000; Hints et al. 2007; Eriksson and Hints 2009; Eriksson unpublished material). Polychaeturids have also been recovered from numerous erratic boulders with a Baltic provenance (Eisenack 1939; Kozłowski 1956; Kielan-Jaworowska 1966; Schallreuter 1982).

Although the historical accounts on North American scolecodonts (e.g., Hinde 1879; Stauffer 1933; Eller 1942, 1945, 1969) do not seem to include polychaeturids, more re-

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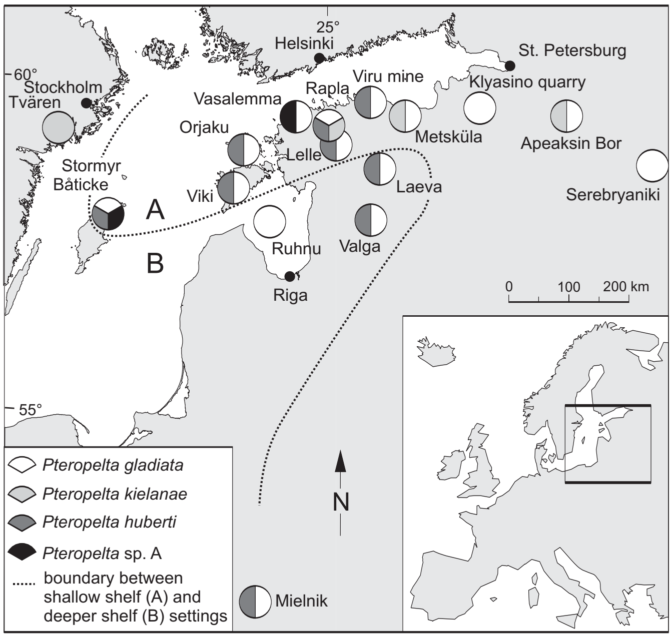

Fig. 4. Sketch map showing selected occurrences of four species of polychaeturid polychaete genus *Pteropelta* in the Baltic Region. Note that the localities may expose strata of different stratigraphical intervals. The boundary between shallow and deeper shelf facies is tentative; it has shifted in time due to basin infilling and sea level changes. Thus, for instance, the occurrence of *P. gladiata* in the Ruhnu and Valga drill cores does not infer its relation to deeper shelf settings. All localities are boreholes, unless stated otherwise. For more information about the localities see the on-line catalogue at http://sarv.gi.ee.

cent studies from the type Cincinnatian region, USA, have revealed their occurrence in the Ordovician of Laurentia (Eriksson and Bergman 2003; Hints and Eriksson 2007a). By contrast to Baltoscandia, however, they are extremely rare and only a handful of specimens of *P. gladiata* out of collections comprising tens of thousands of scolecodonts have been recorded from the upper Richmondian Stage (equivalent to the Baltoscandian Pirgu Stage and, parts of the, Vormsi Stage) Whitewater Formation at Cowan Lake and Caesar Creek Emergency Spillway, south-eastern Ohio (see Eriksson and Bergman 2003 for data on the collections). Note, however, that the specimen referred to as *Pteropelta* sp., by Eriksson and Bergman (2003: fig. 5.18) may in fact not be of polychaeturid affinity.

Despite the relatively poor geographical coverage of Ordovician and Silurian scolecodonts outside Baltica and Laurentia (e.g., Eriksson et al. 2004; Hints and Eriksson 2007a, b) some remarks can be made with regards to other palaeocontinents. A small collection of scolecodonts from the Upper Ordovician of Kazakhstan described by Klenina (1989) possibly includes polychaeturids. Despite its poor preservation and undesirable photographic angle, one of the specimens appears to be a left MI of *Pteropelta* (Klenina 1989: pl. 2:6). It has the characteristic wide inner wing that occupies half the jaw length, an almost gaping myocoele, and a dentary closely similar to that of *P. gladiata* and *P. kielanae*. Klenina (1989) described this specimen as a new species; *Marleneites temporarius*. *Marleneites* Eller, 1945 is a single-element-based genus, erected to include simple placognath jaws. Its type species, *Oenonites marginatus* Eller, 1944, shows some similarities to the MI of *Pistoprion* Kielan-Jaworowska, 1966. Hence, if *Marleneites* is at all a valid genus it is only distantly related to polychaeturids.

An unpublished collection of Palaeozoic scolecodonts from Iran (Ali Kazemi and Mohammad Ghavidel-syooki, personal communications 2001–2004) contains some polychaeturid jaws that are strikingly similar, and possibly conspecific, to those of *Pteropelta* sp. A described herein, showing that polychaeturids occurred also in peri-Gondwanan regions.

Hence, polychaeturids were geographically widespread during the Ordovician, occurring in at least three palaeocontinents. As far as is known now, however, they were most abundant in, and characteristic to, the Baltic realm. This suggests that the origination of polychaeturids may also have occurred in Baltica, as noted already by Eriksson et al. (2004), Hints et al. (2004), and Hints and Eriksson (2007a).

Notes on palaeoecology.—In the Ordovician shallow to mid-shelf settings of Baltica polychaeturids represented the third most common (specimen-rich) polychaete family after polychaetaspids and mochtyellids. Their relative frequency among all scolecodont-bearing polychaetes is commonly 10–20%, but may occasionally exceed 40% (Hints 1998 Hints et al. 2003, 2005; Eriksson and Hints 2009). In most parts of the succession this is on account of *P. gladiata*, with the exception of the Vormsi Stage where *P. huberti* has been recovered in abundance. Both *P. kielanae* and *Pteropelta* sp. A are rare, usually forming only a few per cent of the scolecodonts in a sample.

Pteropelta gladiata commonly co-occurs with other species of the genus. In the Vormsi Stage in several Estonian lo-

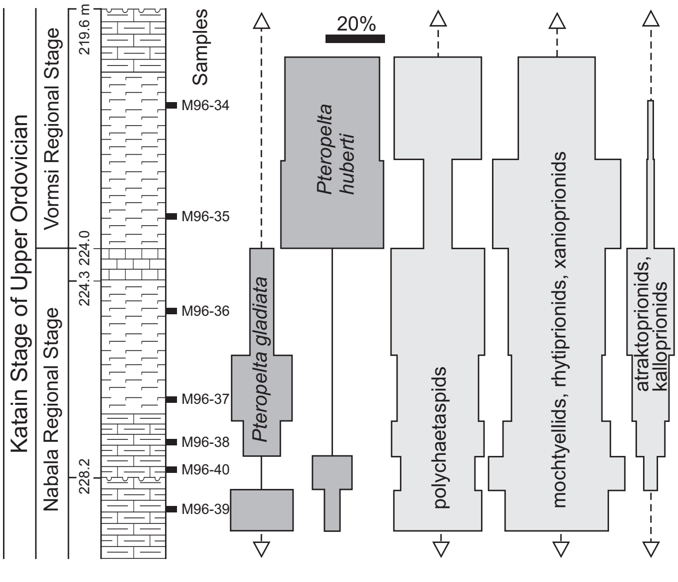

Fig. 5. Pattern of relative abundance (%) of polychaeturid polychaetes *Pteropelta gladiata* and *Pteropelta huberti* in the Laeva 18 drill core, central Estonia. The counts are based on a total of 572 posterior maxillae (MI), of which 147 belong to polychaeturids. Arrow heads indicate that the ranges continue beyond the interval shown.

calities its abundance shows strongly negative correlation with that of *P. huberti* (Fig. 5), which may suggest either niche competition or, more likely, different environmental preferences. Interestingly, *P. huberti* and *P. kielanae* have never been found together despite the obvious overlap in their ranges (Fig. 3). However, this may be due to the fact that none of the species is particularly abundant in pre-Vormsi strata—altogether less than one hundred jaws have been recovered.

Different polychaeturid species seem to have had somewhat different environmental preferences. *P. gladiata* and *P. kielanae* were most common in onshore settings such as those that were present in northern Estonia, being notably less abundant or missing in deeper shelf environments (Hints 2000). By contrast, the frequency maximum of *P. huberti* was restricted to the transitional facies belt between the shallow shelf settings and basinal facies (Estonian Shelf and Livonian Basin, respectively, according to Harris et al. 2004). In addition to the Estonian occurrences and a single find from the northern Gotland subsurface (Fig. 2Z), *P. huberti* was recovered in abundance from the Mielnik IG-1 borehole, NE Poland, some 700 km south of the Estonian localities. The bulk of the scolecodonts from that core were described by Szaniawski (1970), but the specimens assigned here to *P. huberti* were not (collection of Hubert Szaniawski at ZPAL studied in Warsaw by OH). According to Modliński (1973), the Mielnik locality represents similar position on the palaeobasin transect as the Estonian localities. Moreover, Szaniawski's sample, representing the 1120–1126 m interval, that contains *P. huberti*, corresponds stratigraphically to the acme of the species as recorded in Estonia. Hints et al. (2007) reported that *P. huberti* is associated with certain shelly faunas, particularly the *Hulterstadia* brachiopod association, that also have restricted distribution within the palaeobasin.

The few specimens of *Pteropelta* sp. A thus far recovered from northern Estonia were derived from the mud-mound associated facies of the Vasalemma Formation. Similarly, the records from the considerably younger Pirgu Stage of subsurface of Gotland are related to mud-mounds (Eriksson and Hints 2009). The occurrence of *Pteropelta* sp. A thus indicates a preference for mound and reef environments.

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