TWO NEW POLYCHAETE FAMILIES FROM THE UPPER ORDOVICIAN OF ESTONIA

by OLLE HINTS

ABSTRACT. Study of three upper Ordovician borehole sections from Estonia has revealed abundant and well-preserved scolecodonts representing more than 50 species of jaw-bearing eunicid polychaetes. In this paper, two monotypic families, Conjungaspidae and Tretoprionidae, are introduced, based on two new species (*Conjungaspis minutus* gen. et sp. nov. and *Tretoprion astae* gen. et sp. nov.). The most distinctive features of conjungaspids are the small, distally rounded and long-horned carriers, merged with large basal and laeobasal plates, and symmetrical jaw apparatus. Conjungaspids are supposedly a primitive group displaying common features with some placognaths and labidognaths. Tretoprionids are characterized by sub-transversely prolonged and strongly elevated scraper-like denticles in the anterior part of the posterior maxillae, unusual anterior maxillae composed of several weakly fused teeth, and occurrence of a hole or large incision in the outer face of the left posterior maxilla.

EUNICID polychaetes have proboscides armed with jaw apparatuses which, unlike other parts of these soft-bodied worms, are frequently found as fossils. The complex jaw apparatuses are usually found disarticulated into individual denticulated plates and teeth, the scolecodonts. In spite of the fact that the taxonomy of Recent polychaetes is mainly based on the features of the soft body and chetae, applicability of the jaws has also been recognized (Wolf 1980; George and Hartmann-Schröder 1985). Numerous studies of fossil scolecodonts have confirmed their utility in the classification of eunicids (e.g. Kielan-Jaworowska 1966; Edgar 1984; Bergman 1989; Szaniawski and Imaijma 1996; Eriksson 1997; Eriksson and Bergman 1998).

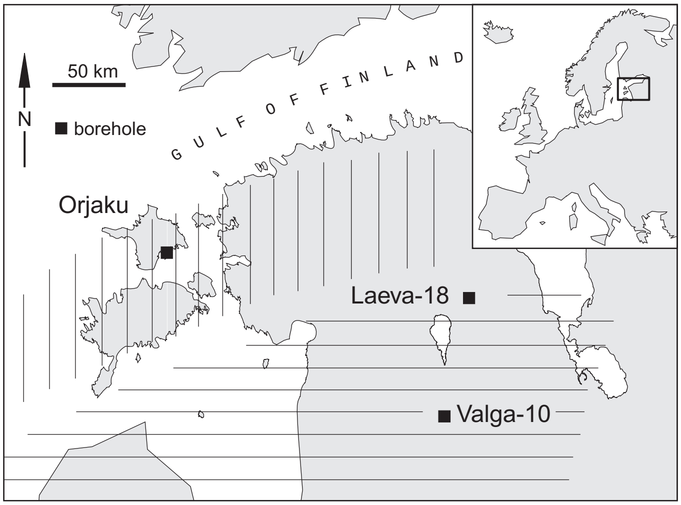
The first finds of polychaete jaws from the upper Ordovician date from the 1870s when Grinnell (1877) and Hinde (1879) erected more than 30 species based on detached jaws from the Cincinnatian of North America. Subsequently, several papers have been devoted partly or entirely to upper Ordovician material (e.g. Eller 1942, 1969; Kielan-Jaworowska 1961, 1962, 1966; Szaniawski 1970; Eisenack 1975).

Study of organic-walled microfossils of three Harjuan (upper Ordovician) borehole sections in Estonia, located in different belts of an onshore–offshore transect (see Text-figs 1–2), has revealed many well-preserved isolated polychaete jaws and some articulated jaw apparatuses. Preliminary results are presented in Hints (1998*b*). The Harjuan fauna probably comprises more than 50 eunicid species. Several new species have been encountered, but as a rule, most of them are represented by material insufficient for appropriate description and naming of new taxa according to the apparatus-based classification concept.

Two exceptions are *Conjungaspis minutus* gen. et sp. nov. and *Tretoprion astae* gen. et sp. nov., both characterized by articulated jaw apparatuses, the architectures of which imply family level status. The intention of the present paper is to describe these two species and to introduce corresponding new genera and families. *C. minutus* and *T. astae* are of particular interest as contributing to a better understanding of the diversity pattern and evolution of Palaeozoic eunicids. In addition, these new species are rather common and may be of some stratigraphical value when their distribution is studied further.

The scolecodonts were extracted from 0·5–1·0 kg samples using the palynological technique described in detail by Kielan-Jaworowska (1966). The number of scolecodonts per 1 kg of rock ranged mostly between 100 and 600, but exceeded 1000 in a few samples. To avoid destruction of fused jaw apparatuses, the sample residues were kept wet and the fossils were stored in glycerine. The descriptive terminology used mainly follows Jansonius and Craig (1971) and Kielan-Jaworowska (1966). The first (posterior) maxillae are abbreviated as 'MI', the second maxillae as 'MII'. The term 'shank' is used for the posteriormost parts (from posterior termination to maximum longitudinal extension of bight) of the MI.

[Palaeontology, Vol. 42, Part 5, 1999, pp. 897–906]



TEXT-FIG. 1. Locality map. Horizontal hatching denotes relatively deeper-water facies, and vertical hatching, shallower depositional environments. For detailed reviews of the development and configuration of the Ordovician epicontinental basin of Baltoscandia see, e.g. Männil (1966) and Jaanusson (1976, 1995).

The specimens are housed at the Institute of Geology at Tallinn Technical University (abbreviated GIT).

SYSTEMATIC PALAEONTOLOGY

Class POLYCHAETA Grube, 1850
Order EUNICIDA Dales, 1963
Subdivision uncertain
Family CONJUNGASPIDAE fam. nov.

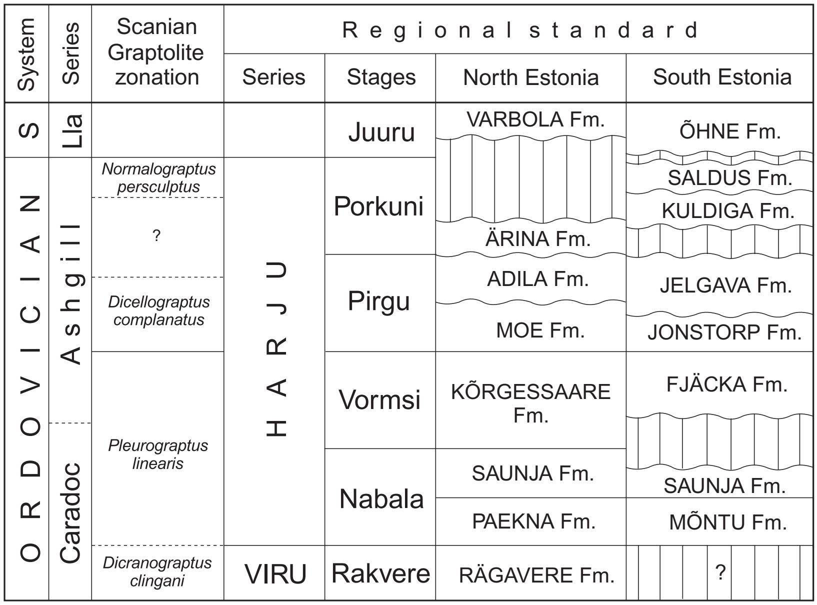
Diagnosis. Jaw apparatus nearly symmetrical, composed of left and right MI, basal and laeobasal plates, intercalary and laeointercalary teeth, lateral teeth and carriers; MI with long shanks, indistinct rami, very high inner faces and small anteriormost denticles in comparison with those in the middle of the ridge; carriers with small distally rounded shafts, and very long and wide horns attached to outer margins of basal and laeobasal plates; basal and laeobasal plates large, sub-triangular, with numerous fairly tightly packed denticles; posteriormost lateral teeth fit to antero-lateral margin of MI, their postero-lateral termination forms ramus-like structures for MI.

Genera included. *Conjungaspis* gen. nov.

Stratigraphical and geographical range. Ordovician of Estonia.

Remarks. The jaw apparatus of conjungaspids differs greatly from those of all other Palaeozoic polychaetes known. It cannot even be assigned to any of the five widely recognized subdivisions of jaw apparatus architectures (for review of polychaete jaw apparatuses see Kielan-Jaworowska 1966; Mierzejewski and Mierzejewska 1975; Szaniawski 1996).

In some respects, jaws of conjungaspids resemble those of some xanioprionids (see Hints 1998*a*), belonging to a placognath apparatus type. Their common features include nearly symmetrical construction of apparatus, elongated MI with long shanks, and occurrence of long basal and laeobasal plates. Xanioprionids apparently lack the carriers, but the outer slopes of their basal and laeobasal plates



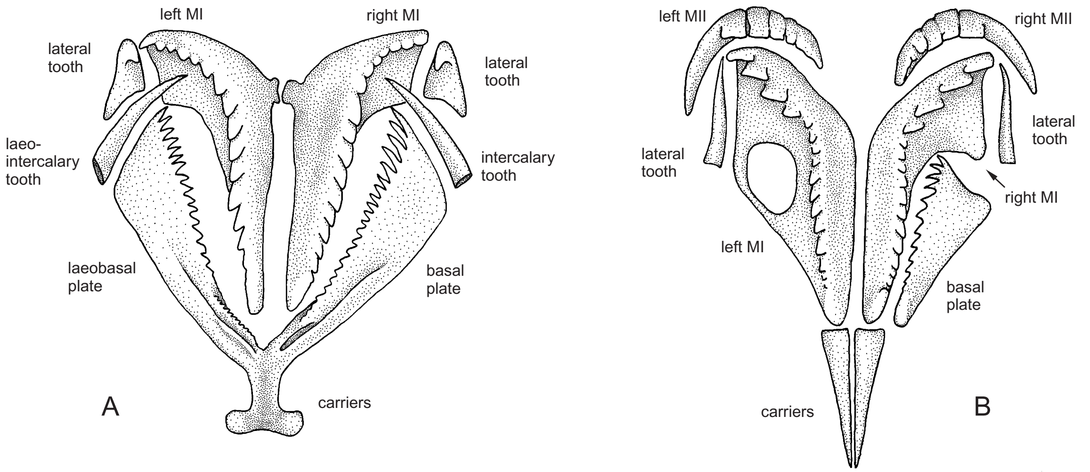
TEXT-FIG. 2. Upper Ordovician stratigraphy of Estonia (after Nõlvak 1997). S, Silurian, Lla, Llandovery.

sometimes have thin, posteriorly extending appendages (see Kielan-Jaworowska 1962; Szaniawski and Wrona 1973), which may be interpreted as homological to the antero-lateral processes, the horns, of the carriers of conjungaspids.

The occurrence of carriers is typical of labidognaths and prionognaths; these subdivisions are closely related to each other, as indicated by some intermediate forms (kalloprionids); however, the carriers of prionognaths are arrow-like, without horns. Some labidognaths, in contrast, do have horned carriers, although of a rather different morphology from those of conjungaspids. The labidognath type apparatus may also be nearly symmetrical, as in the case of symmetroprionids (see Bergman 1995). The lateral teeth, fitting tightly to the antero-lateral margins of the maxillae, similarly to conjungaspids, are documented in some polychaetaspid labidognaths, for instance *Oenonites inconstans* (Kielan-Jaworowska, 1966).

Study of both fossil and Recent polychaete jaws enabled Kielan-Jaworowska (1966) to make a distinction between ‘primitive’ and ‘advanced’ characters. According to this, the occurrence of intercalary and laeointercalary teeth and the laeobasal plate, the relatively large size of basal and laeobasal plates, the almost gaping myocoele openings and the posteriorly tapering MI, indicate that conjungaspids constitute a rather primitive group. As discussed above, they display some characteristics common to placognaths and labidognaths, and in some respects, may be considered as intermediate between those. However, the phylogenetic relationships of conjungaspids cannot yet be fully resolved, although probably this family represents a separate lineage which originated in the early part of the Ordovician, surviving among more advanced taxa at least to the end of the Ordovician.

R. Wrona (pers. comm. 1997) has drawn my attention to the possibility that the jaws described here may represent a juvenile ontogenetic dimorphic stage rather than a new higher-rank taxon. Some examples of ontogenetic dimorphism have been discovered both among fossil and Recent eunicids (e.g. Åkesson 1973; Tzetlin 1980; Szaniawski and Wrona 1987; Bergman 1989). However, despite the relatively small size of jaws in *Conjungaspis*, this is unlikely. If *Conjungaspis* represented an ontogenetic stage, then jaws of other stage(s) should be expected to co-occur with it. Yet other scolecodonts found in the samples in which *Conjungaspis* is abundant, are also common in beds where *Conjungaspis* is not recorded. Since there is no palaeontological or sedimentological evidence of sorting, concentration or selective preservation, ontogenetic dimorphism is improbable.



TEXT-FIG. 3. Reconstruction of jaw apparatus of *Conjungaspis* gen. nov. (A), and *Tretoprion* gen. nov. (B). The reconstructions are based on several isolated specimens and some incomplete jaw apparatuses.

Genus CONJUNGASPIS gen. nov.

Derivation of name. From the Latin *conjungo* (=join), referring to the basal and laeobasal plates, which are joined together by the carriers.

Type species. *Conjungaspis minutus* sp. nov.

Species included. *Conjungaspis minutus* sp. nov.; *Conjungaspis* sp., two undescribed specimens from the middle Ordovician of North Estonia.

Stratigraphical and geographical range. Llanvirn to Ashgill, Ordovician of Estonia.

Diagnosis. As for family.

Remarks. Two minute jaw apparatuses belonging to this genus have been collected from the Uhaku Regional Stage (Llanvirn) of northern Estonia. They are not described here since the whole jawed polychaete fauna including the mentioned specimens will be described and discussed elsewhere. It should be noted, however, that one of these apparatuses has few small, arcuate and high jaws with denticulated ridges fused to the anterior part of the apparatus. Their number and arrangement is unclear; nevertheless, they can be regarded as homologous to the anterior maxillae of labidognaths.

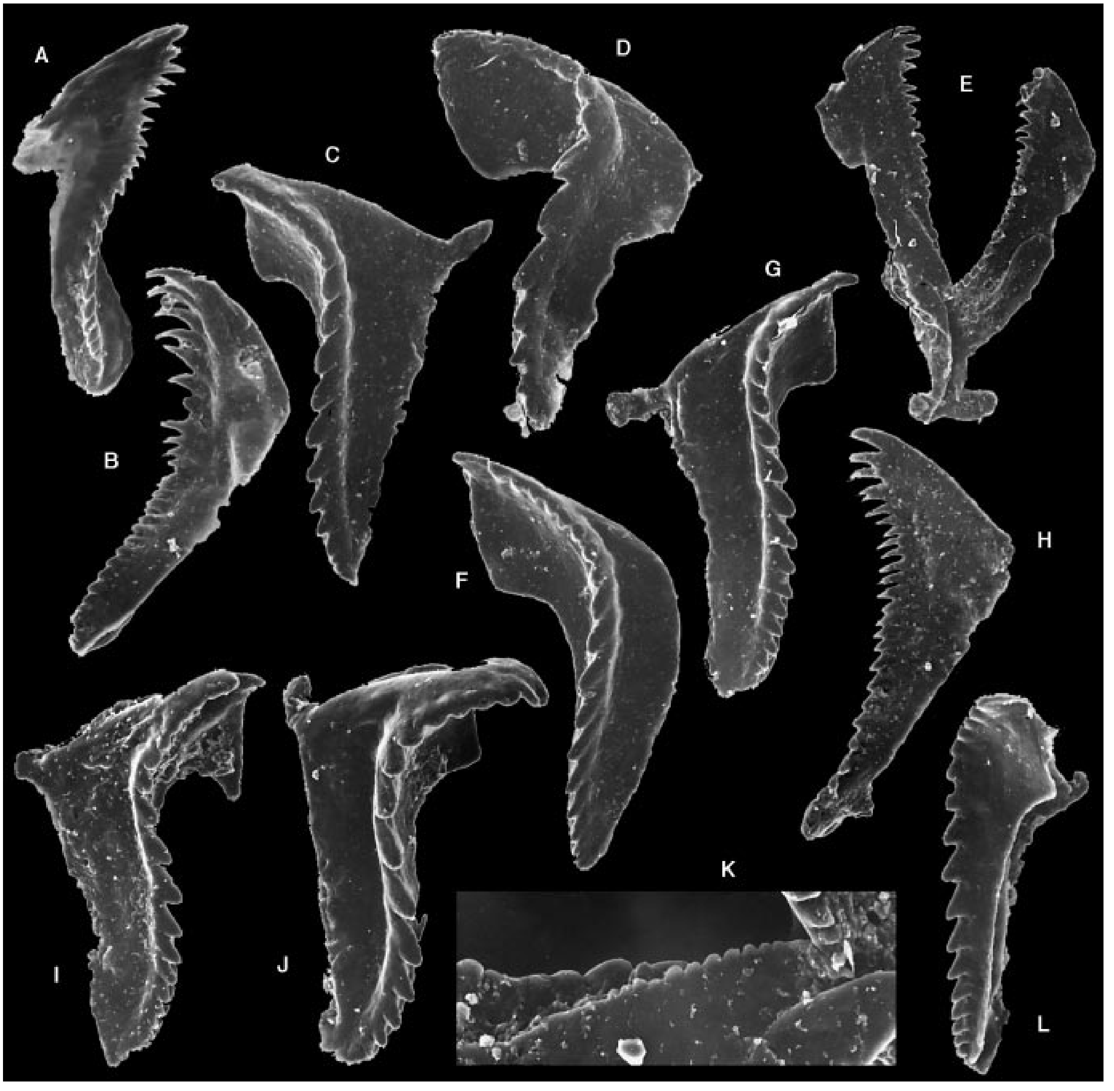
Conjungaspis minutus sp. nov.

Text-figures 3A, 4

Derivation of name. From the Latin *minutus* (=small), referring to the size of jaws of this species.

Holotype. Carriers fused with basal and laeobasal plates, GIT Sc 105, Text-figure 4E, K.

Type horizon and locality. Kuldiga Formation, Porkuni Regional Stage (top Ashgill); Valga-10 borehole, depth 321·9 m.



TEXT-FIG. 4. *Conjungaspis minutus* gen. et sp. nov.; Valga-10 borehole, depth 321·9 m, Porkuni Regional Stage. A, GIT Sc 101; laeobasal plate in dorsal view; × 200. B, GIT Sc 102; basal plate in dorsal view; × 180. C, GIT Sc 103; left MI in dorsal view; × 175. D, GIT Sc 104; left MI in dorsal view; × 180. E, GIT Sc 105 (holotype); carriers fused with basal and laeobasal plates in dorsal view; × 120. F, GIT Sc 106; left MI in dorsal view; × 175. G, GIT Sc 107; right MI in dorsal view; × 150. H, GIT Sc 108; basal plate in dorsal view; × 180. I, GIT Sc 110; right MI fused with lateral tooth in dorsal view; × 240. J, GIT Sc 109; right MI in dorsal view; × 200. K, detail from posterior part of the laeobasal plate of the holotype (GIT Sc 105), tilted 90° compared with E; × 400. L, GIT Sc 111; right MI in right lateral view; × 240.

Material. One incomplete apparatus, 76 right MI, 60 left MI, 54 basal and laeobasal plates some joined with the carriers, some isolated carriers. Valga-10 borehole, depth 316·4–321·9 m; Orjaku borehole, depth 76·65–92·4 m.

Distribution. Vormsi, Pirgu and Porkuni regional stages (Ashgill) of Estonia.

Diagnosis. Dentary in MI differentiated, denticles in the anterior third of jaw length (including the anteriormost one) smaller than those in the middle of the ridge; MI more or less curved; basal and laeobasal plates triangular, elongated, with numerous tightly packed denticles.

Description. Right MI: Length 0·2–0·4 mm, length/width ratio 1·5–3·3. Anterior 0·2–0·4 of the jaw is in most specimens strongly curved distally, forming approximately a 45° angle with the posterior part of the jaw. Sometimes, however, the jaw may be nearly straight. Minute triangular ramus reaches to 0·2–0·3 of jaw length, there is no distinct bight. Inner slope is considerably higher than the outer and thus the jaw is inclined distally. There is a small irregular extension in the inner margin at about anterior 0·3 of jaw length. The dentary consists of 15–21 denticles. In the anterior part of the jaw the denticles are usually smaller than those located in the middle of the ridge, being sometimes developed as poorly distinguishable protuberances. There is no distinct cusp or fang. The myocoele is almost gaping; ligament rim is indistinguishable. Denticle pits are better visible in the posteriormost part of the jaw.

Left MI: L = 0·18–0·35 mm, L/W = 1·3–4·8. The jaw is an almost mirror reflection of the right MI. Its dentary consists of 14–18 denticles similar to those in the right jaw.

Basal plate is long and sub-triangular, approximately three times longer than wide and slightly shorter than right MI. Its dentary has about 25 denticles, those in the anterior 0·2–0·5 of jaw length are long, very slender and sharp and relatively widely spaced. Posterior denticles are triangular, rather small and often poorly distinguishable. Right horn of the carriers is merged with the outer margin, slightly posterior from the mid-length of the jaw. If the carriers are separated from the basal plate, the joining area is marked by an irregular incision.

Laeobasal plate is similar to basal plate but its dentary usually has less denticles, anteriormost of which are relatively smaller. In addition, the denticulated ridge on it is twisted to a more or less vertical position posteriorly, and the incision for the left horn of carriers is more distinct and longer than in basal plate. In the type specimen, there is a small additional ridge with about ten minute denticles in the posterior part of the jaw, to the left of the main ridge.

Carriers are somewhat shorter than basal and laeobasal plates. They are V-shaped with a relatively small shaft and long and wide horns attaching to outer margins of the basal and laeobasal plates. Posteriormost part of carriers has rounded extensions on the distal sides.

Posteriormost lateral teeth are triangular and fit tightly to the outer-lateral margin of left and right MI, forming a ramus-like supplement for MI. Their myocoeles are continuations of those of the posterior maxillae.

Intercalary and laeointercalary teeth are long and comparatively strong, approximately as long as the antero-lateral margins of the basal plates.

Variability. The greatest variability has been observed in the number and size of denticles in the posterior maxillae and in the basal and laeobasal plates, and in the shape of the inner margins of posterior maxillae which may, or may not have irregular appendages and curvature of the posterior jaws.

Remarks. *C. minutus* differs from the middle Ordovician specimens mentioned above in having more curved ridges and more clearly differentiated dentary in MI, and relatively more slender basal and laeobasal plates. In addition, the size of jaws of *C. minutus* is about twice of that of the undescribed specimens.

Subdivision EUNICEA LABIDOGNATHA Ehlers, 1864
Family TRETOPRIONIDAE fam. nov.

Diagnosis. The maxillary apparatus consists of sub-symmetrical MI, anterior maxillae, triangular basal plate, lateral teeth and carriers. Carriers sub-triangular, 2·5 times longer than wide. Three to five anteriormost denticles in MI very high, sub-transversely prolonged into scraper-like structures; outer face of left MI with a large rounded or oval perforation; MII composed of weakly fused, scraper-like denticles, the first of which is provided with a slender posteriorly directed ramus.

Genera included. *Tretoprion* gen. nov.

Stratigraphical and geographical range. Ordovician of Estonia.

Remarks. The jaw apparatus of tretoprionids corresponds to that of a typical labidognathid; that is, it has sub-symmetrical MI without hooks, several pairs of anterior maxillae, basal plate, lateral teeth and carriers. The general form of the posterior part of the tretoprionid jaw apparatus is perhaps most similar to that of polychaetaspids and polychaeturids. In detail, however, there are several notable differences. The type of denticulation characteristic of tretoprionids has not been observed in any other scolecodonts. Although sub-transversally prolonged denticles occur in the jaws of *Rhytiprion* Kielan-Jaworowska, 1966, in that case they are relatively longer (transversely) and less elevated from the ridge than in tretoprionids.

The form of the second, and probably of the other anterior maxillae is restricted to most labidognaths known, except for some polychaeturids. In the latter family, however, left and right MI, basal plate and the carriers are differently shaped. This jaw architecture resembles somewhat also that of some xanioprionids, which have the middle part of the posterior maxillae composed of weakly fused teeth. However, the shape of these loose denticles is different and the entire apparatus of tretoprionids has little in common with xanioprionid placognaths.

The carriers are usually considered to express broader evolutionary relationships (Wolf 1980; Edgar 1984). The carriers most similar to those of tretoprionids occur in paulinitids. However, in the latter family they are usually wider and with a pronounced head. Elongate carriers are also present in leptoprionids and some ramphoprionids, but in these families they are rectangular rather than triangular as in tretoprionids. The shape and arrangement of other jaws in tretoprionids are unlike those of paulinitids, leptoprionids and ramphoprionids, hence probably excluding close relationship between tretoprionids and the mentioned families.

In consequence, the genus *Tretoprion* cannot be assigned to any known family. Several characteristic features like the distinct type of denticulation, and the shape of the carriers, basal plates and MI justifies the erection of the new family Tretoprionidae.

Genus TRETOPRION gen. nov.

Derivation of name. From the Greek *treto*, with a hole, and *prion*, a saw, referring to the perforated shape of the outer face of the left MI.

Type species. *Tretoprion astae* sp. nov.

Species included. *Tretoprion astae* sp. nov.

Stratigraphical and geographical range. Caradoc? and Ashgill of Estonia.

Diagnosis. As for family.

Tretoprion astae sp. nov.

Text-figures 3B, 5

Derivation of name. In honour of Dr Asta Oraspõld, who has been working on the sedimentology of the beds that yield abundant jaws of this species.

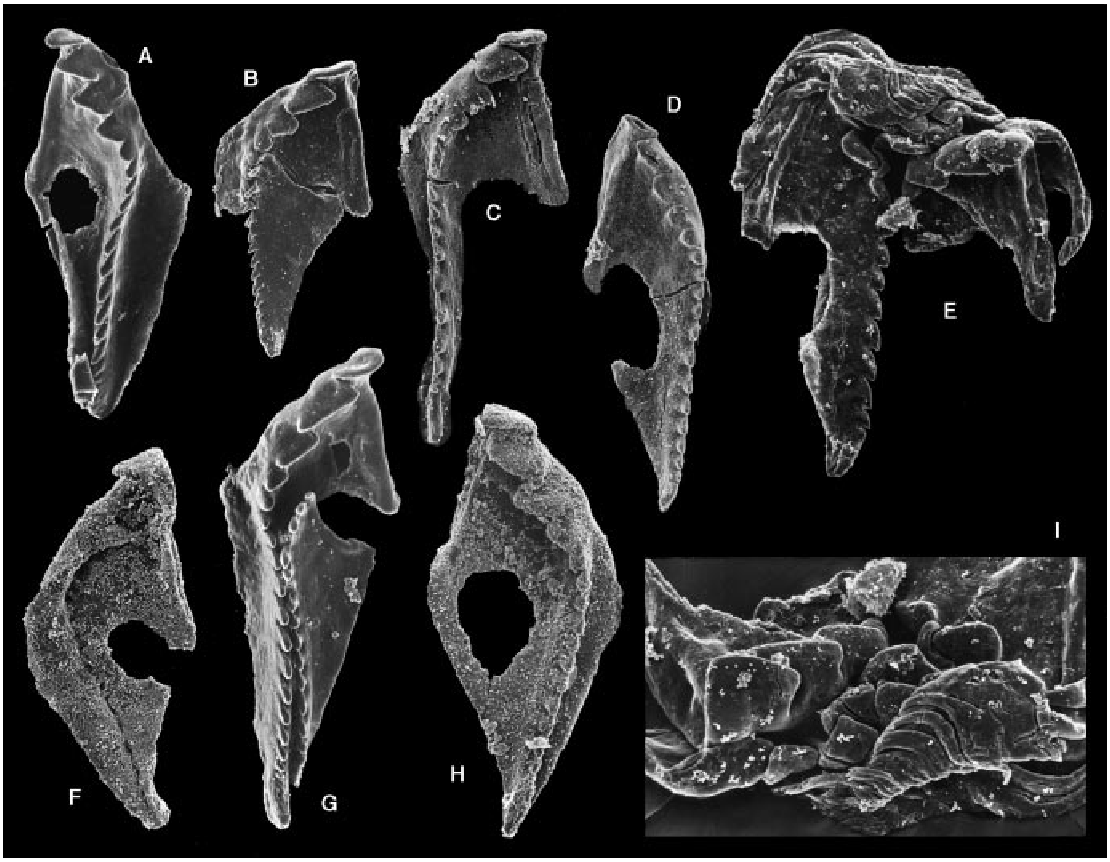
Holotype. Left MI with an unpaired carrier fused on it, GIT Sc 112, Text-figure 5A.

Type horizon and locality. Moe Formation, Pirgu Regional Stage (Ashgill); Orjaku borehole, depth 58·57 m.

Material. In addition to the type specimen: two incompletely preserved apparatuses, two right MI fused with basal plate, one right MI fused with right MII, 35 right and 25 left MI, some broken MII, one basal plate. Laeva-18 borehole, depth 222·4 m; Orjaku borehole, depth 54·0–92·4 m.

Distribution. Vormsi and Pirgu regional stages (Ashgill) of Estonia.

Diagnosis. As for genus.



TEXT-FIG. 5. *Tretoprion astae* gen. et sp. nov. A, G from the Orjaku borehole, depth 58·57 m, Pirgu Regional Stage; B–F and H–I from the Laeva-18 borehole, depth 222·4 m, Vormsi Regional Stage. A, GIT Sc 112 (holotype); left MI with unpaired carrier preserved on it in dorsal view; × 125. B, GIT Sc 113; broken right MI fused with basal plate in dorsal view; × 120. C, GIT Sc 114; right MI in dorsal view; × 160. D, GIT Sc 115; left MI in dorsal view; × 120. E, GIT Sc 116; incomplete apparatus in dorsal view; × 150. F, GIT Sc 117; left MI in ventral view; × 180. G, GIT Sc 118; right MI fused with basal plate in dorsal view; × 145. H, GIT Sc 119; left MI in dorsal view; × 160. I, detail of GIT Sc 116 from anterior side; × 300.

Description. Right MI: Length 0·23–0·78 mm, length/width ratio 2·2–3·0. Outer-lateral margin is nearly straight, ramus extends to 0·32–0·4 of jaw length, its tip is narrow. Shank is long and very slender, ligament scar is rather indistinct. The denticulated ridge is curved distally at first 0·3 of jaw. The dentary consists of 12–21 denticles, the first three of which (especially the first one) are rather high and prolonged transversally into short ridges. The following denticles are small and laterally triangular increasing towards the posterior third of the ridge. The cover reaches to approximately 0·15 of jaw length; ligament rim is indistinct; denticle furrow is rather narrow.

Left MI: Length 0·25–0·45 mm, length/width ratio 1·7–3·3. Jaw is mostly rhomboidal in outline, inner margin and the ridge are curved distally at about the mid-length of the jaw. Outer face has its maximum lateral extension slightly before the mid-length of the jaw, posterior from that the outer face is rather fragile and often broken. Outer face has a large perforation in its central portion. The dentary is very similar to that in right MI, although the number of denticles is slightly smaller (13–16). The cover extends to 0·15–0·25 of jaw length, ligament rim is indistinct, denticle furrow is narrow and the denticle pits are usually invisible in the posterior part.

Basal plate: Triangular jaw, approximately twice as long as wide, has two-thirds of length of the right MI. Its inner margin is 1·25 times longer than the outer margin. Anterior margin is almost straight, slightly curved anteriorly in the distal end. Dentary consists of *c.* 14 posteriorly decreasing denticles, those in the anterior half of the jaw are somewhat more slender. The cover extends to one-third of jaw width.

Right MII is an arcuate jaw composed of about four sub-transversely prolonged denticles which are loosely fused to each other in the distal part. The first denticle is the largest, its long postero-laterally directed termination forms a ramus. Such 'rami' are found separately from the other part of the jaw. The proximal portion of the jaw, the shank, is a sub-triangular plate without distinct denticles.

Left MII has been not found well-preserved, but some loose 'rami' display great similarity to those in the right MII.

MIII, MIV, MV. At least part of them is present, but they cannot be studied in detail because they are hidden by other jaws in the apparatus. Probably similar to MII.

Anterior jaw (?) is a small comb-like jaw, composed of at least seven curved and very slender teeth in the anterior part of the apparatus.

Posteriormost lateral teeth are conical, relatively slender teeth, approximately as long as the outer-lateral margins of MI.

Carriers are relatively long triangular plates, approximately half as long as MI, in fused form 2·5 times longer than wide. Head is almost straight and perpendicular to the inner margin.

Variability. The variability of the posterior maxillae of *Tretoprion astae* mainly concerns the outline of the left MI, which due to a fragile jaw wall may have a rather different shape. In addition, the degree of curvature of jaws, length/width ratio, and length of the shank in right MI, may vary quite markedly. The arrangement of the dentary, except for the total number of denticles, is relatively constant in all specimens studied.

Remarks. A unique and intriguing characteristic of *Tretoprion astae* is the hole in the middle part of the outer face of the left MI. Such perforation is present in all specimens, even the smallest ones. If the narrow strip of the jaw wall to the left of the hole is broken, or perhaps never formed in some specimens, then the outer face has a large incision, and the anterior half of the jaw is a mirror image of the anterior part of the right MI (see Text-fig. 5D). The possibility that the hole was developed to fit some as yet unknown jaw element, which might have been sited on the outer face of the left MI seems to be unlikely. For the time being, the special function of this structure, if there was any, remains unclear.

Acknowledgements. This study was carried out at the Institute of Geology at the Tallinn Technical University. Part of the SEM study was performed at the Institute of Paleobiology PAN, Warsaw. I am most grateful to Prof. D. Kaljo, Dr R. Riding, Dr S. H. Williams and M. Eriksson for their help and many invaluable suggestions concerning the manuscript. My sincere thanks are also due to Dr C. Culicki for his assistance in SEM work, and to G. Baranov for making the photographs.

This study is a contribution to IGCP Project No. 410 and was supported by grants Nos 3516 and 3751 from the Estonian Science Foundation.

REFERENCES

ÅKESSON, B. 1973. Morphology and life history of *Ophryotrocha maculata* sp. n. (Polychaeta, Dorvilleidae). *Zooloogica scripta*, **2**, 141–144.

BERGMAN, C. F. 1989. Silurian paulinitid polychaetes from Gotland. *Fossils and Strata*, **25**, 1–127.

—— 1995. *Symmetroprion spatiosus* (Hinde), a jawed polychaete showing preference for reef environments in the Silurian of Gotland. *GFF*, **117**, 143–150.

DALES, R. P. 1963. *Annelids*. Hutchinson University Library, London, 200 pp.

EDGAR, D. R. 1984. Polychaetes of the Lower and Middle Paleozoic: a multi-element analysis and phylogenetic outline. *Review of Palaeobotany and Palynology*, **43**, 225–285.

EHLERS, E. 1864–68. *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt*. Wilhelm Engelmann, Leipzig, 748 pp.

EISENACK, A. 1975. Beiträge zur Anneliden–Forschung, I. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **150**, 227–252.

ELLER, E. R. 1942. Scolecodonts from the Erindale, Upper Ordovician, at Streetsville, Ontario. *Annals of the Carnegie Museum*, **29**, 241–270.

—— 1969. Scolecodonts from well cores of the Maquoketa Shale, Upper Ordovician, Ellsworth County, Kansas. *Annals of the Carnegie Museum*, **41**, 1–17.

ERIKSSON, M. 1997. Lower Silurian polychaetaspid polychaetes from Gotland, Sweden. *GFF*, **119**, 213–230.
—— and BERGMAN, C. F. 1998. Scolecodont systematics exemplified by the polychaete *Hadoprion cervicornis* (Hinde, 1879). *Journal of Paleontology*, **72**, 477–485.
GEORGE, J. D. and HARTMAN-SCHRÖDER, G. 1985. *Polychaetes: British Amphinomida, Spintherida and Eunicida*. Synopses of the British Fauna (New Series), 32. The Pitman Press, Bath, 221 pp.
GRINNELL, G. B. 1877. Notice of a new genus of annelids from the Lower Silurian. *American Journal of Science and Arts*, **14**, 229–230.
GRUBE, A. E. 1850. Die Familien der Anneliden. *Archiv für Naturgeschichte, Berlin*, **16**, 249–364.
HINDE, G. J. 1879. On annelid jaws from the Cambro-Silurian, Silurian and Devonian formations in Canada and from Lower Carboniferous in Scotland. *Quarterly Journal of the Geological Society, London*, **35**, 370–389.
HINTS, O. 1998*a*. Late Viruan (Caradoc) polychaete jaws from North Estonia and the St. Petersburg district. *Acta Palaeontologica Polonica*, **43**, 471–516.
HINTS, O. 1998*b*. Harjuan (Late Ordovician) eunicid polychaetes of Estonia. Unpublished M.Sc. thesis, University of Tartu, Estonia.
JAANUSSON, V. 1976. Faunal dynamics in the Middle Ordovician (Viruan) of Baltoscandia. 301–326. *In* BASSETT, M. G. (ed.). *The Ordovician System – proceedings of a Palaeontological Association symposium*. University of Wales Press, Cardiff, 696 pp.
—— 1995. Confacies differentation and upper Middle Ordovician correlation in the Baltoscandian Basin. *Proceedings of the Estonian Academy of Sciences, Geology*, **44**, 73–86.
JANSONIUS, J. and CRAIG, J. H. 1971. Scolecodonts: I – descriptive terminology and revision of systematic nomenclature; II – lectotypes, new names for homonyms, index of species. *Bulletin of Canadian Petroleum Geology*, **19**, 251–302.
KIELAN-JAWOROWSKA, Z. 1961. On two Ordovician polychaete jaw apparatuses. *Acta Palaeontologica Polonica*, **6**, 237–254.
—— 1962. New Ordovician genera of polychaete jaw apparatuses. *Acta Palaeontologica Polonica*, **7**, 291–325.
—— 1966. Polychaete jaw apparatuses from the Ordovician and Silurian of Poland and comparison with modern forms. *Paleontologia Polonica*, **16**, 1–152.
MÄNNIL, R. M. 1966. *Evolution of the Baltic Basin during the Ordovician*. Valgus Publishers, Tallinn, 200 pp. [In Russian, with English summary].
MIERZEJEWSKI, P. and MIERZEJEWSKA, G. 1975. Xenognath type of polychaete jaw apparatuses. *Acta Palaeontologica Polonica*, **20**, 437–444.
NÕLVAK, J. 1997. Sedimentary cover, Ordovician, introduction. 52–55. *In* RAUKAS, A. and TEEDUMÄE, A. (eds). *Geology and mineral resources of Estonia*. Estonian Academy Publishers, Tallinn, 436 pp.
SZANIAWSKI, H. 1970. Jaw apparatuses of the Ordovician and Silurian polychaetes from the Mielnik borehole. *Acta Palaeontologica Polonica*, **15**, 445–472.
—— 1996. Scolecodonts. 337–354. *In* JANSONIUS, J. and McGREGOR, D. C. (eds). *Palynology: principles and applications 1*. American Association of Stratigraphic Palynologists Foundation, 462 pp.
—— and IMAJIMA, M. 1996. Hartmaniellidae – living fossils among polychaetes. *Acta Palaeontologica Polonica*, **41**, 111–125.
—— and WRONA, R. 1973. Polychaete jaw apparatuses and scolecodonts from the Upper Devonian of Poland. *Acta Palaeontologica Polonica*, **18**, 223–267.
—— —— 1987. Polychaete jaws from the Cape Melville Formation (Lower Miocene) of King George Island, west Antarctica. *Palaeontologia Polonica*, **49**, 105–125.
TZETLIN, A, B. 1980. *Ophryotrocha schubravyi* sp. n. and the problem of evolution of the mouth parts in the Eunicemorpha (Polychaeta). *Zoololgitèeskij Žurnal*, **56**, 666–676. [In Russian, with English summary].
WOLF, G. 1980. Morphologische Untersuchungen an den Kieferapparaten einiger rezenter und fossiler Eunicoidea (Polychaeta). *Senckenbergiana Maritima*, **12**, 1–182.

OLLE HINTS

Institute of Geology
at Tallinn Technical University
Estonia pst. 7
10143 Tallinn, Estonia
e-mail olle@gi.ee

Typescript received 7 October 1998
Revised typescript received 5 March 1999