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THE EARLIEST ENCRINURID TRILOBITES FROM THE EAST BALTIC AND THEIR TAXONOMIC INTEREST

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Abstract: The earliest known representative of the subfamily Encrinurinae, *Encrinuroides regularis* sp. nov., is described from the glauconitic sandstone of the Mäeküla Member, Billingen Stage (Arenig), from localities in the Baltic-Ladoga Clint area. *Cybele* (subfamily Cybelinae) has its earliest appearance at about the same level, but at different localities, probably indicating their facies dependence. The predominant developing area of the pygidial axis and the general array of spines on the exoskeleton serve to distinguish the Encrinurinae and Cybelinae, but resolve the Staurocephalidae and Dindymeninae within the Encrinuridae. A reassessment of *Encrinuroides* and the genera recently excluded from it (*Frencrinuroides*, *Physemataspis* and *Walencrinuroides*) sustains the utility of an *Encrinuroides sensu lato* grouping and endorses Strusz's evolutionary lineages. *Encrinuroides uncatus* Evitt and Tripp, *E. neuter* Evitt and Tripp and probably *Encrinuroides lapworthi* Tripp belong in *Erratencrinurus* Krueger.

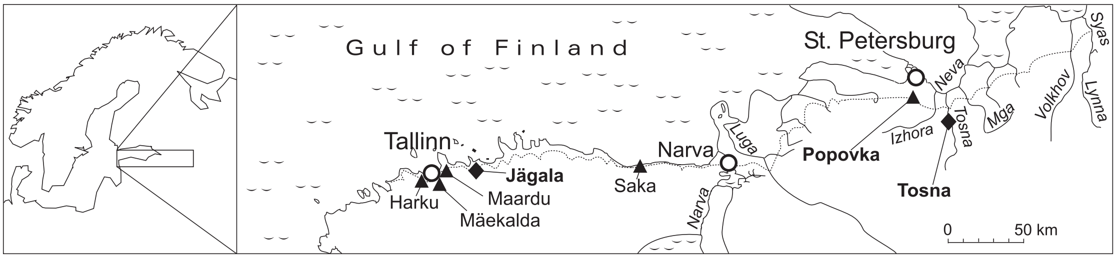
Key words: trilobite, Encrinuridae, *Encrinuroides*, *Cybele*, Ordovician, Arenig, Baltoscandia.

ENCRINURID trilobites are very rare at the beginning of their radiation in the Ordovician of Baltoscandia. The first to appear were the cybelines, which inhabited deep water environments of the Baltoscandian palaeobasin. They occur in the *Megistaspis* (*Paramegistaspis*) *planilimbata* trilobite Zone (Tjernvik and Johansson 1980, p. 184) of the Hunneberg Stage (early Arenig or late Tremadoc: see Maletz *et al.* 1996, figs 4–5; Pärnaste 2002, 2003, text-fig. 2; 2004) in Sweden. Their later expansion into onshore environments occurred simultaneously with the appearance of the first encrinurine (Mägi *et al.* 1989, p. 66; Aru 1990, p. 72) in the *Megistaspis* (*P.*) aff. *estonica* trilobite Zone (= *Prioniodus elegans* conodont Zone) (Pushkin and Popov 1999, p. 172; Pärnaste 2003, 2004), the lowest part of the Billingen Stage (Lower Arenig). Thus, the Baltic encrinurine species is much older than the oldest previously described, *Encrinuroides hornei* Dean, 1974, from the Upper Arenig or Lower Llanvirn Summerford Group of north-eastern Newfoundland (Dean 1974). The new data are significant for understanding the phylogenetic and palaeogeographical origin of the subfamily Encrinurinae.

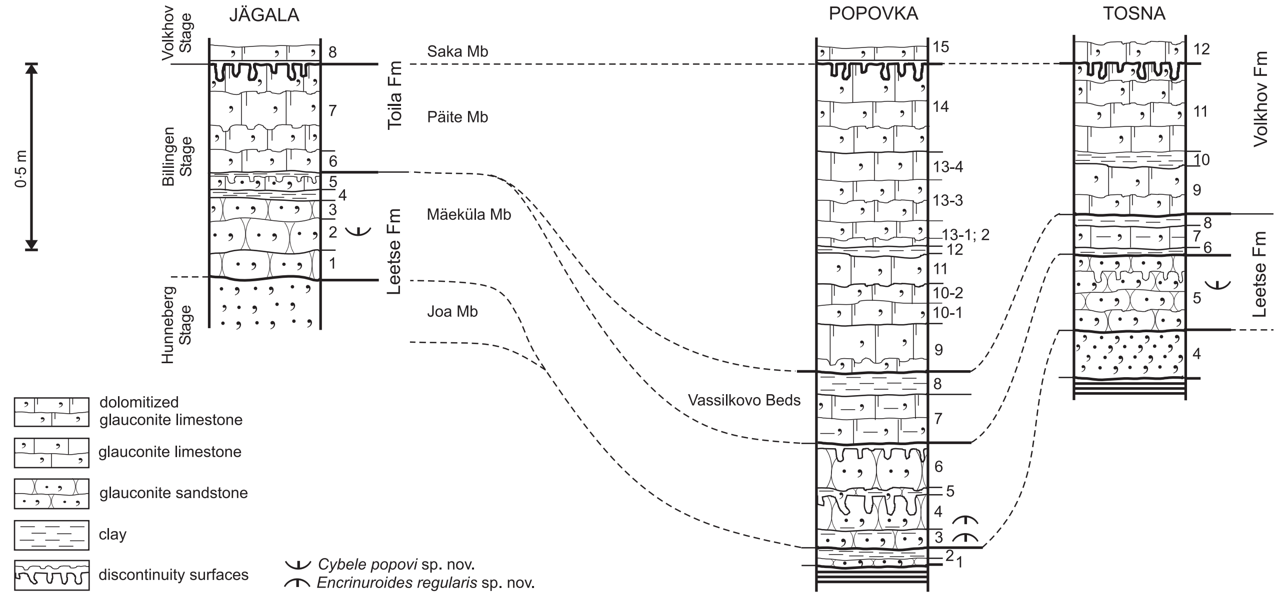
STRATIGRAPHY, LOCALITIES AND SAMPLING

The earliest encrinurines, here assigned to *Encrinuroides* Reed, 1931, are known only from a few localities in eastern Baltoscandia (Text-fig. 1) in the lowest part of the Mäeküla Member of the Leetse Formation (Text-fig. 2). The cybeline *Cybele* Loven, 1845 also occurs at this level but at different localities (Text-fig. 1), which may indicate slightly different ecological requirements or age. The Mäeküla Member consists of variably dolomitized alternating glauconitic sandstones, calcareous sandstones and glauconitic sandy limestones, with clay films or layers commonly covering discontinuity surfaces. Correlation of this member within the Baltoscandian biozones and the local chrono- and lithostratigraphic units was recently discussed in detail by Pärnaste (2002, 2003, 2004).

Slabs of sandstone covered by clay films were brushed clean under running water to expose the fauna on top, and samples of soft clay layers were washed through a 1-mm-mesh sieve to remove clay. Most of the encrinurid exoskeletons originate from such surfaces (not from the interior of the beds), and are unique to the lowest part of the Mäeküla Member. One particular layer of soft clay in the Popovka district (Text-fig. 2, Popovka, layer 3) contains a particularly diverse fauna of trilobites, brachiopods, ostracodes, bryozoans (Pushkin and Popov 1999, pp. 172, 185) and echinoderms. Different parts of the exoskeleton of *Encrinuroides*, including juvenile specimens, occur in this layer together with *Evropeites lamanskii* Balashova, 1966 (Pärnaste 2002), *Ptychometopus schmidti* Balashova, 1966 and *Krattaspis viridatus* Öpik, 1937 (Pärnaste 2003).



TEXT-FIG. 1. Locality map of sections in north Estonian and St. Petersburg regions showing the occurrences of *Encrinuroides regularis* sp. nov. (triangles) and *Cybele* sp. A (rhombs). The names of the sections shown as logs in Text-figure 2 are in bold. Dotted line shows the Baltic-Ladoga Clint (escarpment).



TEXT-FIG. 2. Lithological columns of Billingen Stage sections of the Leetse and Toila/Volkhov formations studied bed by bed where encrinurids have been found. For detailed discussion, see Pärnaste (2003, 2004).

The clay layer on top of the Mäeküla Member at the Jägala waterfall (Text-fig. 2, Jägala, top of layer 5) also contains a rich fauna including ostracodes, echinoderms, brachiopods and a few trilobites. The conodont fauna contains *Acodus deltatus* Lindström, 1955, *Drepanoistodus* cf. *D. forceps* (Lindström, 1955), *Oistodus lanceolatus* Pander, 1856, *Prioniodus elegans* Pander, 1856 (a zonal indicator), and *Scolopodus striatus* Pander, 1856 (determined by A. Löfgren, 2003), indicating either the topmost part of the *P. elegans* Zone or the lowest *O. evae* Zone.

SYSTEMATIC PALAEONTOLOGY

Terminology. Terminology applied to encrinurine exoskeletal morphology mainly follows the revised Treatise on Invertebrate Palaeontology, Part O (Whittington 1997) and Evitt and Tripp (1977). The lateral extent of the glabella as well as the (true) axial furrow of the cephalon has been variously interpreted in cybelines, especially in those with adaxially deeply incised glabellar furrows. The adaxial deepening of the lateral glabellar furrows is a common cybeline plesiomorphy associated in many cases with the effacement of its abaxial ends. It is seen for instance in *Miracybele* sp. 1 of Ross (1972, pl. 17, fig. 26), '*Cybellela*' *dentata* (Esmark, 1833) (see Nikolaisen 1961, pl. 3, fig. 1), *Cybeloides* (*Paracybeloides*) Hupé, 1955 (see Whittington 1965, pl. 32, fig. 14), *Bevanopsis ulrichi* Cooper (1953, pl. 13, fig. 21) and *Cybeloides anna* Ludvigsen (1979, pl. 20, fig. 28). In several cases the incision of furrows that curve gently rearwards adaxially is deep enough to produce a continuous (exsag.) groove, which can also be more depressed than the (true) axial furrow. Evitt and Tripp argued (1977, p. 113) on the basis of the cybeline *Cybeloides virginiensis* Evitt and Tripp, 1977 that the lateral termination of the glabella is marked by this adaxial furrow, and suggested homology of that furrow in the adults with the single axial furrow of protaspides and in comparable stages of other genera. However, I concur with the abaxial one being the true axial furrow, considering effacement to be a secondary feature. This is also supported by the distinction of the non-pitted glabellar lobe from the pitted fixigenal lobe as shown in the taxa mentioned.

The terms 'major row' and 'interrow' glabellar tubercles are adopted from Edgecombe and Chatterton (1987). The position 1 tubercle pairs of the major rows I, II and III of cybelines are situated opposite the corresponding lateral lobes, or are positioned slightly forwards or rearwards, depending on the course of the corresponding glabellar furrows. The IV-1 tubercle pair is in between bifurcated S3 furrows, and the V-1 lies somewhat anteriorly. Similar allometry occurs in encrinurines, except for the appearance of an additional so-called major row on the anterior lobe. Absence of that row in phylogenetically and ontogenetically early encrinurines (see Edgecombe and Chatterton 1987 for discussion of glabellar tubercle development), and in ancestral cybelines, indicates an analogy with the interrow tubercles, which appear simultaneously during ontogeny with the enlargement and inflation of the glabella (cf. Evitt and Tripp 1977, p. 129, text-fig. 8A–B). Consequently, the core of the encrinurine tubercular notation of Strusz (1980) and Owen and Heath (1989) based on position relative to lateral lobes is used, but with two exceptions (Text-fig. 3A). Firstly, the major rows on the frontal lobe are marked by subscripts as $4L_1$ and $4L_2$, corresponding to F4 and F6 of Strusz (1980). As the interrow tubercles represent the lobe area rather than furrows, the second exception presents an intermediate system for the interrow notation using l (lower case) instead of S (Owen 1981) or i (a small roman numeral of Tripp 1957), though the number in subscript counts the interrows. However, the major row tubercles may also be longitudinally paired (as for the lateral glabellar lobe tubercles, the adaxial fixigenal tubercles and the anterior border tubercles); then Owen's use of asterisks (1981, p. 48) is applied.

Ramsköld (1986, p. 529, text-fig. 2) described a 'row of circumocular tubercles', labelling four major ones on the fixigena from CT1 to CT4. A similarly distinct tubercle on the eye-ridge, fitting within the same ring, is named here CT0 (Text-fig. 3A). Another prominent tubercle, situated near the posterior edge of the fixigenal field, is called here a fulcral tubercle, FT (Text-fig. 3A). It marks the beginning of the doublure with a slight curvature on the ventral side, not clearly discernible in dorsal view. The position of the FT coincides with the point of flexure of the gena at the fulcral line. Homologies of that tubercle arise in early ontogenetic stages of the group (see Evitt and Tripp 1977, pl. 6, fig. 2; pl. 14, fig. 19; pl. 17, fig. 1; Chatterton 1980, pl. 14, figs 2, 8–10; pl. 15, figs 1, 12, 15, 20, 30). It is probably equivalent to the postocular tubercle (pt) of Evitt and Tripp (1977, p. 114, figs 1, 6–10, 12–14, 16–18). Ramsköld (1986, p. 529) considered CT2 to be homologous with the postocular tubercle, a view endorsed by Edgecombe and Chatterton (1987, pp. 340–341, text-fig. 5) and Edgecombe *et al.* (1988, p. 780, text-fig. 2). However, the appearance of the additional tubercle behind the 'main ring' of circumocular tubercles in the newly described encrinurine throws doubt on that presumed homology.

The number of adaxial tubercles on the fixigenae (see Temple and Tripp 1979, p. 225, fig. 1) is a characteristic feature of individual encrinurid species (Temple and Tripp 1979, p. 227; Edgecombe and Chatterton 1987, p. 344; 1990, p. 822, table 1). These could analogously be recognized as longitudinally paired or single tubercles opposite the corresponding glabellar tubercles (Text-fig. 3A). The adaxial tubercles may be shifted slightly rearwards together with the shift of the posteroadaxial corner of the fixigena (depending on convexity of the glabella and fixigena). The new species suggests that there is a greater degree of positive allometry than had been recognized earlier (see Edgecombe and Chatterton 1987, p. 344), which could be used in cladistic analysis of encrinurine phylogeny.

The axial furrow of the pygidium (Text-fig. 3B–C) is recognized here as delimiting the axial rings abaxially (see discussion by Temple and Tripp 1979, p. 228), leaving an intermediate area between the rings and the hindmost interpleural furrows. The area terminates sagittally in a variably developed postaxial termination, and is interpreted as a homology of the pleural rib(s) on encrinurines (Temple and Tripp 1979; Ramsköld 1986, p. 530) (Text-fig. 3B), and a non-homology of that of cybelines (Owen and Tripp 1988, p. 280). I agree with Owen and Tripp, who rejected the homology of that intermediate area with anterior bands of the pleurae, despite the similarities of the surface textures of these two areas [see *Miracybele mira* (Billings, 1865) and *Cybelurus occidentalis* Dean, 1973]. That area of the cybeline pygidium is called the basal lobe of the terminal piece herein (Text-fig. 3C).

The term 'continuity of pygidial pleurae and axial rings' is preferred to 'number of congruent pygidial segments' (see Temple and Tripp 1979, p. 229). Although the first is difficult to assess, the latter also depends on width-length-height relations to the number of pleurae and the angle between the pleural and axial furrows. It is therefore a graphical by-product rather than the appearance of homology. Unfortunately, the system of describing the pleural rib-axial ring relations as employed here is often impossible to use owing to the imperfect preservation.

The area underlying the tips of the pleural ribs of the pygidium is referred to here as the border, following Whittington and Campbell (1967) and Tripp *et al.* (1977), but the pygidial doublure is not seen in dorsal or side views. The pygidial border of encrinurids usually bears a variably well-developed groove, the vincular furrow. An analogous coaptative structure appears on some pliomerid and phacopid pygidia, as well as on encrinurine cephala (cf. Whittington and Campbell 1967, pl. 11–13).

Abbreviations. LP, the precranidial lobe on the librigena; LA, the anterior lobe of the glabella; and LM, the middle lobe of the glabella, following Pärnaste (2003). The abbreviations describing the preservation of sclerites of trilobites are: c, corroded; is, internal/ventral surface of exoskeleton; pet, partly eroded exoskeleton; t, exoskeleton intact. Except where otherwise stated (sag., exsag., tr.), all dimensions in the sagittal or exsagittal directions refer to length, and all dimensions in the transverse direction refers to width. Measurements are made along the surface of the exoskeleton (see Pärnaste 2003, p. 244, text-fig. 4).

Repository. The type and figured specimens are housed in the Institute of Geology at Tallinn University of Technology (GIT Collection No. 389). The specimens were coated with ammonium chloride before being photographed.

Order PHACOPIDA Salter, 1864
Suborder CHEIRURINA Harrington and Leanza, 1957
Family ENCRINURIDAE Angelin, 1854

Notes on subfamilial differentiation. Many characters considered as diagnostic for the subfamilies Encrinurinae Angelin, 1854 and Cybelinae Holliday, 1942 by Evitt and Tripp (1977) and Strusz (1980) are plesiomorphic within the family Encrinuridae Angelin, 1854 (for discussion, see Edgecombe *et al.* 1988, p. 796), and most of the other apomorphic characters have exceptions within each subfamily. Comparison of the new encrinurid material with other representatives of the family reveals some additional characters that enable the two families to be distinguished. Moreover, I suggest that the characters described below also indicate the probable ancestors among the Tremadoc paraphyletic Pliomeridae Raymond, 1913 and Pilekiidae Sdzuy, 1955, of which some genera share characters with encrinurines and some with cybelines.

1. The developmental changes in segmentation concern different regions in different subfamilies (and families). Encrinurines commonly change during ontogeny and phylogeny in the number of pygidial pleurae and axial rings, and in their conjoinment with each other. As ontogeny shows, the appearance of additional rings can arise anywhere on the axis (e.g. *Encrinuroides tholus* Evitt and Tripp 1977, pl. 4, fig. 4 vs. fig. 6: = 1./1, 2./1, 3./2, 4./2, etc. vs. 1./1, 2./1, 3./1, 4./1, etc.), not only at its posterior portion (e.g. *Physemataspis coopi* Evitt and Tripp 1977, pl. 14). In contrast, cybeline pygidia generally possess a constant number of pleurae continuous with the axial rings, and the new rings on holaspids appear only on the terminal piece, or a new segment embodies conjoined pleural and axial parts when (dis)appearing. It should be noted that the continuity and conjoinment of the axial rings with pleural ribs is more clearly discernible on the ventral side of well-preserved specimens showing the muscular attachment pattern (paper in prep.). The development of the cybelines mostly includes changes to the size of the anterior pleural bands (plus the size of the axis and the number of axial rings on the terminal piece). Besides, a decrease in the number of the continuous pygidial segments is an evolutionary trend in the Cybelinae during the Ordovician (from five, e.g. *Cybele*, to four, e.g. *Cybellela* Reed, 1928 and *Atractopyge* Hawle and Corda, 1847, to two, e.g. *Dindymene* Hawle and Corda, 1847). However, the number of pleurae and axial rings on adults is quite constant within individual genera of both subfamilies. In other Cheirurina an analogous pattern of reduction of the pygidial axial rings in some evolutionary circumstances is suggested by the evolutionary lineage *Sphaerocoryphe* Angelin, 1854 – *Deiphon* Barrande, 1850 during the late Ordovician or early Silurian. The reappearance of additional pygidial axial rings is seen in a lineage involving *Sphaerocoryphe* Angelin, 1854 – *Onycopyge* Woodward, 1880 (see Holloway and Campbell 1974, p. 412), across the Ordovician/Silurian boundary.

2. The development of spines in particular areas differs between encrinurid subfamilies. In the cybelines spines appear on the periphery of the exoskeleton, where they are developed on the pleural tips of the posterior half of the thorax, commonly with an appearance of the macropleura on the anteriormost of those segments. They may also be developed on the border areas of the cephalon: the anterior cranidial border, librigenal border, rostral plate and the occipital ring. In some instances, long spines appear on the tips of the pygidial pleurae. In contrast, the encrinurines only developed spinosity on the axial area: on some thoracic rings, the pygidial axis (considering the mucro as such), or on the glabella. Differentiation on the arrangement of spines indicates certain types of enrolment, moulting and mode of life of these two groups.

Subfamily ENCRINURINAE Angelin, 1854

Genus ENCRINUROIDES Reed, 1931

Type species. Cybele sexcostata Salter, 1848, p. 343, pl. 8, fig. 10. Neotype selected and redescribed by Whittington (1950); Sholeshook Limestone, Sholeshook near Haverfordwest, Pembrokeshire, south-west Wales; middle Ashgill.

Diagnosis. See Strusz (1980, p. 8).

Remarks. Strusz (1980) provided a diagnosis of *Encrinuroides* and included 19 species within it. Edgecombe and Chatterton's cladistic analyses (1990, p. 823) resulted in their restriction of *Encrinuroides sensu stricto* to *E. autochthon* Tripp, 1962, *E. polypleura* Tripp, 1967, *E. sexcostatus* (Salter, 1848), *E. stincharensis* (Reed, 1928), *E. sublanceolatus* (Reed, 1935), *E. tuberculosis* (Collie, 1903) and *E. waigatschensis* Burskiy, 1966, with most of the rest being ascribed to *Encrinuroides sensu lato.*

The concept of the genus *Encrinuroides* and its paraphyly was discussed in detail by Edgecombe and Chatterton (1990), Lespérance and Desbiens (1995) and Edgecombe *et al.* (1998). They used cladistic parsimony analysis and the characters were chosen for the investigation by the numerical taxonomic methods of Temple and Tripp (1979) (Edgecombe and Chatterton 1990) or somewhat different attributes (Lespérance and Desbiens 1995; Edgecombe *et al.* 1998). They revealed several ambiguous aspects of the phylogeny of *Encrinuroides* and the encrinurids generally.

However, the choice of characters using PAUP is discriminative and somewhat subjective, especially with respect to the Lespérance and Desbiens analyses, but those by Edgecombe and others (see above) were more rigorous. Reet Männil (1986, p. 106, fig. 3) showed that in Baltoscandian encrinurines, the width-length relations of the cephala and pygidia and their axial parts are facies-dependent. Such highly variable characters do not describe phylogenetic relations at generic level. Unfortunately, the primary generic concepts of the new genera *Walencrinuroides* and *Frencrinuroides* established by Lespérance and Desbiens (1995) (based on species previously placed in *Encrinuroides*) are based on characters that are facies-dependent or plesiomorphic within the group (cf. Lespérance and Desbiens 1995, p. 4, fig. 1). Another important reason for ambiguity in the cladistic analyses is that the phylogenetic trees have been hitherto rooted on the very small, probably immature, or progenetic *E. hornei* Dean, 1974. This was, until now, the oldest known encrinurine but it differs in many respects from the new earliest representative of the subfamily described herein (see below). The new data help to clarify the phylogeny of the early encrinurines and to identify diagnostic criteria for species previously described as *Encrinuroides*.

Discussion of genera excluded from Encrinuroides s. l.

Physemataspis Evitt and Tripp, 1977 was erected as a monotypic genus based on *P. coopi* Evitt and Tripp, 1977 from the uppermost Llanvirn Botetourt Formation, Virginia, claimed as being closely related to *Encrinuroides insularis* Shaw, 1968 (Evitt and Tripp 1977, p. 138; Strusz 1980, pp. 9, 43). Edgecombe and Chatterton (1990) assigned the latter to this genus and Tripp (1980*a*) added his newly described *P. mirabilis*. Lespérance and Desbiens (1995) included *E. neuter* Evitt and Tripp, 1977 and *E. uncatus* Evitt and Tripp, 1977 in *Physemataspis* on the basis of their semicircular glabellae. The 'apomorphies' of the last two mentioned species, the unpaired sagittal tubercles on the pygidium and spines on the thorax, were used to establish a new subgenus, *Physemataspis* (*Prophysemataspis*) Lespérance and Desbiens, 1995. However, these characters are shared with *Erratencrinurus* Krueger, 1971 and *Encrinuroides lapworthi* Tripp, 1980*a*. A similar array of several groups of tubercles on *E. neuter* and *E. uncatus*, and also on representatives of *Erratencrinurus*, includes the following: 1L–4L -1 position tubercles symmetrically arranged, and several l -0 tubercles in between them; nine tubercles on the cranidial anterior border including one in the medial depression (or eight with no medial tubercle); the prominent tubercles opposing them on LP; a row of tubercles along the inner edge of the librigenal border; plus some large tubercles on the base of the genal spine. Additionally shared is a relatively long cranidial anterior border sloping anteriorly down at a similar angle to that of the anterior lobe of the glabella. In conclusion, I suggest that *E. neuter* and *E. uncatus* are better assigned to *Erratencrinurus*, as should probably the poorly preserved *E. lapworthi*, and thus the subgenus *P.* (*Prophysemataspis*) becomes its junior synonym.

The Argentinian Lower Caradoc encrinurine *Lasaguaditas oweni* Edgecombe *et al.*, 1998 shares the above-mentioned similarities to *Erratencrinurus*. In addition, *L. oweni* possesses reduced S3 apodemes similar to those of *Erratencrinurus seebachi* (Schmidt, 1881) (see Öpik 1937, text-fig. 33, p. 119) from Rakvere Stage (Upper Caradoc) of Estonia, and a few genal field tubercles similar to those of *Erratencrinurus capricornu* Krueger, 1971 (see Krueger 1971, pl. 6) from slightly younger Rakvere rocks. Specific characters of the Argentinian encrinurine comprise the shortness of the cephalon (especially of LA) and the pygidium, which is relatively less segmented; and the tuberculation is diminutive and sparse in both areas. The first character is homoplasic with Laurentian Middle and Upper Ordovician cheirurids (cf. Laurentian acanthoparyphines vs. Baltic *Nieszkowskia* Schmidt, 1881, and *Holia* Bradley, 1930 vs. *Ainoa* Männil, 1958, *in* Adrain 1998). The appearance of the same neotenic pattern in different families probably indicates an environmental or climatic influence. The unpaired sagittal tubercles shared with the above-mentioned taxa are also known on the pygidium of an undetermined Upper Ordovician encrinurid from Tasmania (Edgecombe *et al.* 1999, p. 246, text-fig. 7F), which shows the ancestral condition of continuity of segmentation between the axial and lateral lobes (more pleurae are continuous with the corresponding axial ring). Thus, *Lasaguaditas* Edgecombe *et al.*, 1998 may be the ancestor of the last, as well as the entire, group of above-mentioned taxa.

Lespérance and Desbiens (1995) established two new genera: *Frencrinuroides* based on *Encrinuroides capitonis* Frederickson, 1964, *E. gibber* Dean, 1979, *E. tholus* Evitt and Tripp, 1977 and *E. torulatus* Evitt and Tripp, 1977; and *Walencrinuroides*, comprising *E. autochthon* Tripp, 1962, *Walencrinuroides gelaisi* Lespérance and Desbiens, 1995, *E. lapworthi* Tripp, 1980*b*, *E. polypleura* Tripp, 1967, *E. rarus* (Walcott, 1877) and *E. stincharensis* (Reed, 1928). Each genus was based on a single autapomorphy uniting its contained species. That supposedly diagnostic of *Walencrinuroides*, the shape of the pygidium (as wide as long) can be facies dependent (see above), as can the shape of the cranidium, claimed to be diagnostic of *Frencrinuroides*. Moreover, the last and other supposedly diagnostic characters of *Frencrinuroides* (see Lespérance and Desbiens 1995, p. 11) are shared with representatives of *Walencrinuroides* and *Encrinuroides s.s*. The monophyly of the two genera established by Lespérance and Desbiens requires additional character support, as was earlier discussed in detail by Edgecombe *et al.* (1998). They included three new characters in the original Lespérance and Desbiens' matrix, which failed to confirm the monophyly and composition of these two genera, but assisted in delimiting *Erratencrinurus*. However, their character no. 19 (sculpture of the lateral border), in combination with some other characters, clusters the Ordovician encrinurines into several groups (see below). Based on the available data, the absence of an inner row of tubercles on the lateral border was thought to be the ancestral state by Edgecombe *et al.* (1998). It is, but for Cheirurina as a whole. The lateral border tubercles first appear in a Tremadocian pilekiid *Victorispina holmesorumi* Jell, 1985 (cf. Jell 1985, pl. 29), and a few small tubercles are faintly developed on the earliest known encrinurine species *E. regularis* sp. nov. (see below). Two conditions of border tubercles were suggested by Edgecombe *et al.* (1998, p. 689) to be non-homologous with each other: one, showing numerous smaller tubercles, and the other with fewer larger tubercles. Some additional synapomorphies (see below) show that the multistate coding of this character supports restriction of *Encrinuroides s.s.*

1. Irregularly spaced, moderate-sized tubercles on the lateral border co-occur with tubercles (in several rows?) sparsely spaced over the librigenal field. Other synapomorphies follow: eyes situated on low (short) rounded eyesocle restricted from the librigenal field by the deep eyesocle furrow; low (short) LP defined by shallow anterior border furrow; librigenal field narrow (tr.) with the anterior branch of the facial suture slightly shorter than the posterior branch. The pygidial characters co-occurring with such cephalic characters are: a convex (tr., sag.) axis that consists of numerous rings with increasing density rearwards (in relation to pleural ribs, e.g. 1./1, 2./1, 3./2, 4./2–3, 5./3–5, 6./3–5+, etc.), and bears paired sagittal tubercles that are more pronounced posteriorly; pleurae end in a short blunt spine, with no facet anterolaterally; the terminal rib pair is parallel-sided, in some instances with a ridge (= N^1, in Ramsköld 1986, p. 530) between them (e.g. *E. sexcostatus* in Whittington 1950, pl. 68, fig. 9). These conditions are present in *E. autochthon, E. stincharensis* and *E. polypleura* from the upper Llanvirn and lowest Caradoc of Girvan, Scotland, *E. sexcostatus* (with diminished tubercles) from the Ashgill of Wales, and probably (judging by the pygidial characters) also *E. septemcostatus* Kolobova, 1983 and *E. waigatschensis* Burskiy, 1966 from the Caradoc of Kazakhstan and Vaigach, respectively, supporting the concept of the *Encrinuroides s.s.* group (cf. Strusz 1980, p. 45, fig. 9; Edgecombe and Chatterton 1990). More doubtfully the Trentonian *E. tuberculosis* (Collie, 1903) is considered to belong to this group. It also closely resembles *E. gibber*, but the vague figure of Collie (1903, pl. 59, fig. 3) does not allow exact comparison. Unfortunately *E. hornei* Dean, 1974 from the Upper Arenig or Lower Llanvirn Summerford Group of north-eastern Newfoundland is too poorly known and lacks preserved librigenae, but it is similar in size to, and resembles, *E. autochton* in its tubercle array on the small genae, glabella, occipital ring and posterior borders, as well as in its low eyes. It probably belongs in *Encrinuroides s.s.* However, its palpebral lobe is delimited by a distinct palpebral furrow curving towards the anterior suture at the base of the eye, an apomorphy shared with *Cromus* (cf. Webby 1980, pl. 32, figs 7, 10). Yet the pygidial sagittal tubercles are paired or multiplied unlike the condition in the latter genus (cf. Edgecombe and Chatterton 1992, figs 7–8).

2. The appearance of the lateral border tubercles as a row close to the border furrow is accompanied by librigenal tubercles, some arranged (as a row) along the anterior suture and others as a circum-ocular row. Along with this: the eyes are situated on a tuberculate (or granulose) eye-socle of a variably tall cylindrical eyestalk (and usually also bears tubercles or granules on the palpebral lobe); the LP is variable in height with one or several rows of tubercles; the anterior branch of the suture found alongside the librigenal field is usually longer than the posterior; and the pygidial axis bears single sagittal tubercles. These conditions characterize *Erratencrinurus* (e.g. *E. neuter*, *E. uncatus*) and *Lasaguaditas oweni*, and are common in many Silurian encrinurines.

3. The adaxial librigenal border tubercles are absent from *Encrinuroides capitonis*, *E*? *insularis*, *E. obesus*, *E. periops*, *E. rarus*, *E. torulatus*, *Frencrinuroides edseli*, *Walencrinuroides gelaisi*, *W.* sp. A of Edgecombe *et al.*, 1998 and *Physemataspis coopi*. The last of these has the most tubercles and several apomorphies distinguishing it at generic level, so it is excluded from the following discussion, as a separate group. However, its close relationship with *Encrinuroides s.l.*, especially with *E*? *insularis*, has been pointed out repeatedly (Evitt and Tripp 1977; Strusz 1980; Edgecombe and Chatterton 1990; Lespérance and Desbiens 1995). The absence of librigenal border tubercles in the other taxa co-occurs with eyes on a tall eyestalk declined slightly rearwards, two comparatively large tubercles on a relatively wide (tr.) field, and a few tubercles that may appear along the anterior suture (e.g. in *E. torulatus*). LP is defined by a distinct furrow on the latest Llanvirn *E*? *insularis* and juvenile *E. torulatus*, and on the early Caradoc *E. rarus*, *F. edseli*, *W. gelaisi* and *W.* sp. A. These species also have a shorter (tr.) librigena with equal anterior and posterior branches of the facial suture in smaller specimens, but have an anterior branch somewhat longer in larger specimens, as well as a relatively larger torulus in juvenile stages (common also on *E. tholus*, for which there are no librigenal data). The other species, *E. capitonis*, *E. obesus* and *E. periops*, differ in having the LP with no independent inflation defined by shallow anterior furrow, and the eyestalk is somewhat narrower. However, the extremely shallow, hardly discernible, anterior furrow appears in the earliest representative, *E. regularis*, and is also relatively less developed as in other earlier encrinurids, such as *E. autochtoni*, *E. polypleura* and *E. stincharensis*, and also in juvenile *F. edseli.* The pygidial characters of this third group emerge as: axis with numerous rings abruptly increasing in density at the rearmost pleurae, of which the last pair ends in a ‘loop’ termination of variable size, not reaching the border; axial rings with paired tubercles along the entire sagittal extent

(juvenile status) or more pronounced only anteriorly. Those with a long genal spine also have a relatively longer anteriormost pleural spine with the appearance of a concave facet anteriorly (*E. capitonis*, *E*? *insularis*, *E. rarus*, *E. tholus*, *F. edseli*). In conclusion, the features described above do not support the recognition of *Walencrinuroides* and *Frencrinuroides*, but sustain the usefulness of an *Encrinuroides s.l.* grouping.

Encrinuroides regularis sp. nov.

Text-figures 3A–B, 5A–T, 6A–R

1966 *Krattaspis viridatus* Öpik; Balashova, p. 20, pl. 1, fig. 7 [*non* fig. 9, ?11, 12 (= *K. viridatus*); *non* fig. 10 (= indet.)].
1989 *Encrinuroides* Reed; Mägi, Viira and Aru, p. 66.
1990 *Encrinuroides* sp. nov.; Aru, p. 72.

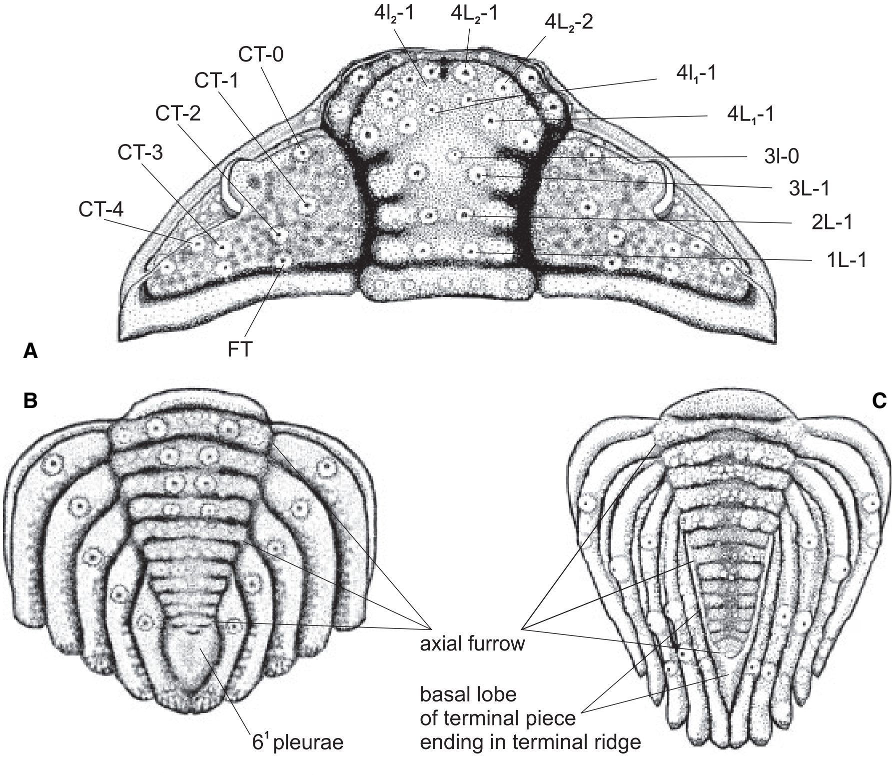
Derivation of name. Latin, *regularis*, with reference to the regular glabellar tuberculation.

Holotype. GIT 389- 7 (t), an incomplete cranidium (Text-fig. 5A–D), from the Mäeküla Sandstone, layer 3 (Text-fig. 2), Billingen, Popovka River section, St. Petersburg Region, Russia.

Other material. Six fragmentary juvenile cranidia, GIT 389- 8, 14–15, 28 (t), -9–10 (pet); six fragments of cranidia, 389- 2, 11–13, 16–17 (t); four more or less fragmentary librigenae, 389- 18–20 (t), -23 (cpet); seven pygidia, 389- 1, 3, 6, 26–27 (t), -4–5 (cpet); two fragments of pygidia 389- 21–22 (t).

Stratigraphic range. Mäeküla Member, Billingen Stage, Popovka, St. Petersburg Region, Russia; Harku, Maardu and Mäekalda in the vicinity of Tallinn, and Saka, north-east Estonia.

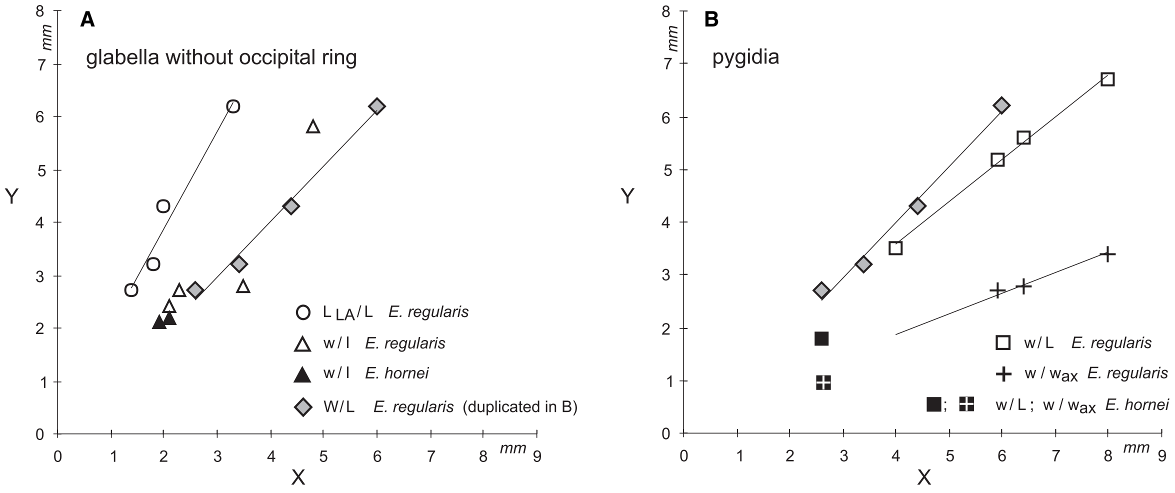
Diagnosis. Exoskeleton with comparatively flat middle lobe, and low palpebral fixigena; anterior portion of cephalon and genal area abaxial from the eyes curve steeply downwards. Glabella with equal L1 and L2, and symmetrically developed glabellar tubercles: 1L–2L–3L–$4L_1$ -1, $4L_2$ -2 and the second anterior border tubercle lie in one curved line. Anterior cranidial border deeply inclined medially, bearing six symmetrically distributed tubercles. Librigenal border straight, with no inflation, bearing a few very low tubercles at the axial furrow; the very shallow anterior border furrow hardly distinguishes it from the prematurely short LP with low inflation and a few tubercles, developed on the broadest area, i.e. laterally. Rostral suture concave. Prominent fixigenal circumocular tubercles in regular ring around eye. Pygidium with five pairs of pleurae



TEXT-FIG. 3. A, reconstruction of the cephalon of *Encrinuroides regularis* sp. nov. with indications on terminology of fixigenal tuberculation as follows: CT0–CT4, circumocular tubercles; FT, fulcral tubercle. 'Major row' and 'inner-row' tubercles are indicated accordingly: 1L-1, 2L-1, 3L-1, $4L_1$-1, $4L_2$-1, $4L_2$-2, and 3l-0, $4l_1$–1, $4l_2$–1. B, pygidium of *E. regularis* showing the axis ending ahead of the loop-like 6^1 pleurae. C, pygidium of *Cybele* sp. A where the basal lobe of the terminal piece is indicated.

extending to the posterior border and united sixth pair appears as a convex 'loop' behind the axial lobe. The axis shows 12 rings with paired small tubercles anteriorly and a low, lens-shaped ridge breaking the rearmost rings sagittally.

Description. Cephalon is relatively flat both sagittally and transversely except in juvenile specimens, which are rather convex with a hemispherical anterior glabellar lobe (in frontal view) and highly vaulted genal lobes. Glabella excluding occipital ring is about as long as wide at the deeply incised fossula if measured along surface of exoskeleton, although slightly elongated in dorsal view (Table 1, Text-fig. 4A); narrowest at L2. Occipital ring is as wide as the frontal glabellar lobe in dorsal view, 1·5 times as long as the L1, staying constant transversely, also slightly bowed forwards medially, bearing several tubercles. Length of L1 and L2 subequal, L3 slightly longer. Short (tr.) but wide (exsag.) glabellar furrows, which are longer (tr.) in juveniles, resulting in a relatively wide middle lobe (LM). S0 and S1 apodemes large, S2 slightly smaller and S3 small and low. Length of the frontal lobe about half that of the glabella (excluding occipital ring). The prominent longitudinal anteromedian glabellar furrow rises up from the deeply incised pit in the anterior furrow extending beyond the anteriormost row of tubercles. Symmetrically arranged, glabellar major row, first position tubercles 1L–2L–3L–4L$_1$ -1 and a 4L$_2$ -2 tubercle lie in a curving row parallel to the axial furrow to meet the second tubercle of the anterior border of the cranidium; the tubercles adaxial to those 3l$_1$ -0, 4l$_1$ -1, 4L$_2$ -1, lie along a similar line, meeting the adaxial first tubercle of the anterior border. Consequently, the anteriormost major row tubercles situated just behind the anterior border match the tubercles on the anterior



TEXT-FIG. 4. Scatter plots (*x/y*) of length-width relations of different dimensions (cf. abbreviations in Table 1) of *Encrinuroides regularis* sp. nov. (empty and grey markers) and *Encrinuroides hornei* (black markers) measured by Dean (1974, p. 12). Lines mark the linear trendlines. A, preoccipital glabella; note variation between the glabellar length-width relations in plan view (triangles) and those measured along the surface (rhombs). B, pygidia; the trendlines depict the growth difference of particular skeletal parts.

TABLE 1. Length-width relations of *Encrinuroides regularis* sp. nov. (GIT 389- 1–15) and *Encrinuroides hornei* (GSC 32743–32746) (Dean 1974, p. 12); A, cranidia; B, pygidia (cf. graphically Text-fig. 4). Measurements made along the surface of exoskeleton are indicated by capitalized words; lower case is used to mark those measured in plan view; values in per cent are in bold. L_{LA}, length of anterior lobe; w_{axis}, maximum width of pygidial axis.

A, cranidia									B, pygidia					
no.	Length (L)	L_{LA}	Width (W)	L/W (%)	L_{LA}/L (%)	length (l)	width (w)	l/w (%)	no.	Length (L)	width (w)	L/w (%)	w_{axis}	w_{ax}/w (%)
389-7	7·1	3·3	6	**118**	**46**	6·1	4·8	**127**	389-5	7·5				
389-15	4·8	2	4·4	**109**	**42**	3·7	3·6	**103**	389-4	6·7	8	**84**	3·4	**43**
389-14	3·7	1·8	3·4	**109**	**49**	3·1	2·3	**135**	389-3	5·6	6·4	**88**	2·8	**44**
389-9	3·1	1·4	2·6	**123**	**44**	2·8	2·1	**133**	389-6	5·2	5·9	**88**	2·7	**46**
32743						2·2	2·1	**105**	389-1	3·5	4	**88**	1·8	**45**
32744						2·1	1·9	**111**	32746	1·8	2·6	**69**	1	**38**

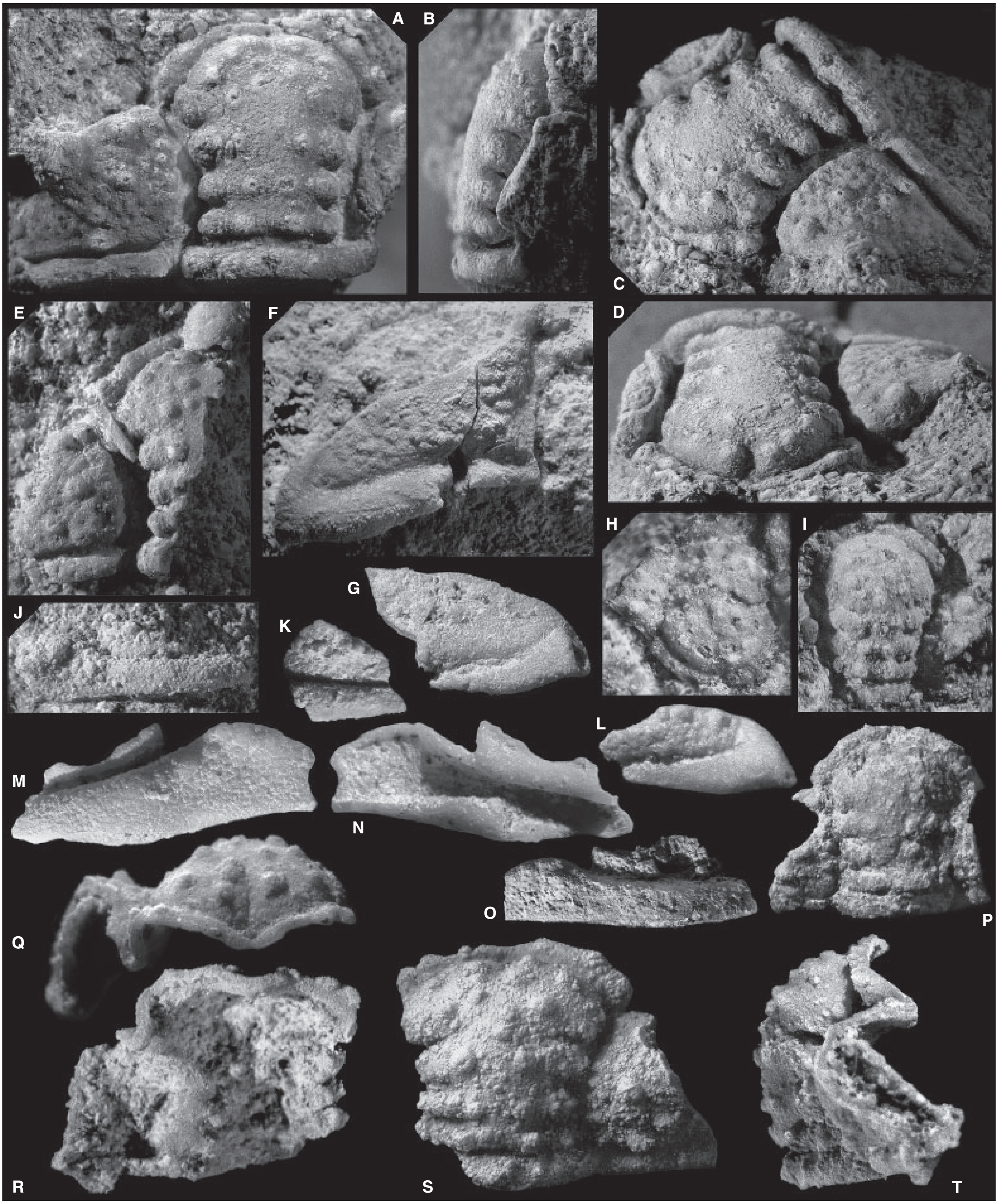
border. Anterior fossula is rather deeply incised. Axial furrow is broad and deep throughout, posterior border furrow and occipital furrow slightly less so, but the preglabellar furrow is narrower, although well incised. Anterior cranidial border bowed strongly downwards medially, bearing six symmetrically distributed tubercles, three on each side, increasing in size abaxially, in which direction they also become more closely spaced. Length of the anterior border increases slightly abaxially in larger specimens, but is a constant length in smaller, less vaulted specimens (Text-fig. 5H–I, P). Posterior border narrow (exsag.), approximately two-thirds the length (exsag.) of the occipital ring, broadening (exsag.) a little and curving down evenly at the genal angle, which is pointed but without a spine or tubercles at the base. The genal angle of the mature specimen is less sharply pointed than that of the immature. Posterior branch of facial suture cuts the cephalic margin a short distance in front of the genal angle (Text-fig. 5F–G, L). Eyes positioned far from the glabella opposite L3. Palpebral lobe is comparatively large, raised, but not strongly elevated; palpebral furrow shallow and wide. Eye-ridge relatively low and broad, flanked by very weakly incised furrows. Position of the circumocular tubercles is: CT0 on the mid-extent of the eye-ridge, CT1 on the midline of palpebral and posterior fixigena, CT2 on the mid-length of the posterior fixigena slightly adaxial from the eye and FT just behind it at the posterior edge of the fixed cheek or slightly adaxial in more vaulted juvenile specimens, and CT4 close to the posterior suture (Text-fig. 3A). Another exsagittal pair of tubercles is situated abaxial from the CT2-FT on a juvenile specimen (Text-fig. 5L), but is reduced on a more mature specimen (Text-fig. 5F). All of these tubercles are equal in size, comparable to that of the major row tubercles of the glabella. Genal field is also moderately deeply pitted and sparsely covered by granules, some close to the axial furrow arranged more or less regularly in pairs opposing each lateral glabellar lobe. This array of adaxial fixigenal tubercles represents the ancestral state for the encrinurines (see also discussion in Edgecombe and Chatterton 1987, p. 345). One peculiar, relatively large specimen (Text-fig. 5F) is unusual in showing less symmetry on the tubercle array of the fixigenal field, being sparsely covered with coarse tubercles. It is not known whether this simply reflects the normal range of variation within the species or is an aberrant specimen.

Free cheek with almost straight border delimited by a deep lateral border furrow from the pitted field area. The librigenal field is not known entirely, but a fragmentary free cheek (Text-fig. 5K) shows a wider (tr.) librigenal field than the lateral border (at least posteriorly), a row of small tubercles on the pitted area, some gathered at the posterior branch of the facial suture probably opposite CT4 of the fixigena, and some more anterior to them, following the circumocular ring. The relatively stout (raised) lateral border is angular in cross-section, showing a shallow vincular furrow ventrally, dying out anteriorly ahead of the axial furrow concurrently with the flattening of the border itself. Short precranidial lobe is equal in size to the cranidial anterior border and almost flat but slightly inflated close to the axial furrow. A row of a few low tubercles lies on LP, the largest probably opposite the lateralmost tubercle of the anterior border of the cranidium. A weak anterior furrow is visible only at its lateral end but gradually shallows adaxially where the precranidial lobe can be differentiated from the anterior border mostly by a difference in sculpture. The border area is densely granulated with one low tubercle opposite the fossula. Rostral suture slightly concave.

Rostral plate, hypostome and thorax unknown.

Pygidium (Text-figs 3B, 6) subpentagonal in outline, low in profile, slightly inclined downwards at the distal ends of the pleurae and more sharply behind the end of the axis. Pygidial length is 84–88 per cent of width (Table 1, Text-fig. 4B). Axis gently convex (tr.), occupying about two-fifths of the maximum pygidial width anteriorly, narrowing to a third of its anterior width towards the fifth interpleural furrow; profile almost flat or slightly convex upwards. Axis has 12 rings, becoming gradually narrower (sag., exsag.) rearwards along the axis; the first two rings are continuous with the corresponding pleural segment (Text-fig. 6R), then two couples followed by two trebles of rings join the following pleurae (Text-figs 3B, 6P–R). The relationship between the pleurae and axial rings can be described numerically as 1./1, 2./1, 3./2, 4./2, 5./3, 6./3. Anterior articulating half-ring narrow (sag., exsag.), tapering only distally and defined posteriorly by a deep articulating furrow with relatively shallow apodemal pits. Inter-ring furrows narrow and well-incised laterally, shallowing medially, especially over the posterior half of axis where there is a slightly convex medial band. Axial furrow is wide and deep, shallowing at the fifth pair of pleurae and then dying out shortly behind the fifth interpleural furrow, indicated by inter-ring apodemes at the sixth pleurae. Five swollen pleurae terminating in short blunt spines overhang the pygidial border progressively, less markedly rearwards, forming a posteriorly shallowing vincular groove below them on the ventral side; and a sixth pair also swollen, but not divided adaxially, forms a 'loop' (for this term, see Strusz 1980, p. 51; Edgecombe and Ramsköld 1996, p. 217) that does not reach the posterior border (Text-fig. 6A, P). The posterior border shortens evenly medially in posterior view (while the pleural tips are orientated horizontally in a straight line; see Text-fig. 6K), with doublure elongating medially (on the ventral side) (Text-fig. 6R) showing a shallow, rounded posteromedian embayment [which presumably reflects a relatively low and rounded (tr.) rhynchos of the hypostome]. Deep, parallel interpleural furrows separate ribs; the latter curve evenly at about three-fifths of their extent to become parallel to the axis, although the tips of the posteriormost pleurae are slightly recurved. Anterior bands of pleurae not developed, except on the first pleura where the band is ridge-like and short; articulating groove on the anterior edge (Text-fig. 6N–O) (cf. Whittington and Campbell 1967, pl. 12, fig. 13; Evitt and Tripp 1977, pl. 11, fig. 1c; Bruton and Haas 1997, p. 18, text-fig. 10a (arg), pl. 9, fig. 8a) is short (tr.), reaching about one-fifth of pleural lateral extent as far as the tubercle of the first pleura. The posterior pleural bands are rounded evenly in cross-section to their abaxial end with no facet, but a small ridge encircles the blunt free points. All pleurae bear a tubercle of moderate size positioned close to the axis but at a different distance in each pleural pair (see Text-figs 3B, 6B, G), or they may be subdued (Text-fig. 6P). Pairs of axial tubercles of similar size are present medially on the first four rings; all rings are finely granulose. A row of coarse granules lies along the posterior margin of the pleurae and the entire dorsal surface of exoskeleton is finely granulose.

Discussion. Comparison of *Encrinuroides regularis* with the next earliest encrinurine *E. hornei* Dean, 1974 (pp. 10–13, pl. 3, figs 4, 7–13) from the late Arenig of



north-east Newfoundland is complicated as the specimens of the latter are poorly preserved and much smaller (Text-fig. 4; Table 1). It is obvious that some juvenile characters are present on *E. hornei*; thus, the pygidium is proportionally broader with more pleurae conjoining the axial rings by one to one anteriorly, and the pleurae ending in longer free spines. However, the cephala are similar in their long glabellar furrows and deeply pitted fixigenal fields with small similarly positioned adaxial tubercles (cf. Dean 1974, pl. 3, fig. 4). The new species differs from *E. hornei* in missing -0 tubercles (1L -0, l1 -0, etc.) on the glabella, and by having a much shallower palpebral furrow effacing at the eye-ridge, a larger genal region ending in a pointed tip at the genal angle, and a cranidium with a regularly tuberculate anterior border.

The features of *Encrinuroides regularis* show that it could have been an ancestor of several groups that diverged by different heterochronic patterns. It shares several *Encrinuroides s.s.* characters (see Edgecombe and Chatterton 1990, p. 823) with the type species *E. sexcostatus* from the Ashgill of Wales, including a narrow-based glabella and blunt pleural tips that are not significantly turned out. It differs in its librigenal characters, its hardly discernible anterior border furrow, the presence of fewer tubercles on the lateral border, and in features of the anterior border of the cranidium. The anterior border of the type species (see Whittington 1950, 1965; Price 1974), and that of the other British species (*E. autochton*, *E. obesus*, *E. periops*, *E. polypleura*, *E. stincharensis*) from various upper Llanvirn–Caradoc units in the Girvan district (Reed 1935; Tripp 1962, 1965, 1967, 1980*a*, *b*) is only slightly convex in the horizontal plane and very short (sag., exsag.) without any prominent tubercles. The new species has a deeply sloping down, medially relatively long (sag., exsag.), anterior border with three tubercles on each side. Unfortunately, the above-mentioned species are represented only by internal moulds, which may explain the relative narrowness of the anterior border and the absence of these tubercles.

The only other species with a medially flat glabella is the late Whiterockian *E. rarus* (Walcott, 1877), from the Esbataottine Formation in the Mackenzie Mountains, Canada, which shares similarly sparse and symmetrically arranged glabellar tubercles, shown especially well by a juvenile specimen figured by Ludvigsen (1975, pl. 3, fig. 22). The appearance of these characters of the adult *E. regularis* in the juvenile stage of *E. rarus* indicates the peramorphic state of those in *E. rarus*. However, *E. regularis* bears fewer tubercles on an L4 that is also much narrower than that of *E. rarus*. The anterior border furrow of the cephalon is insignificantly defined, the cranidial border is wider (sag., exsag.) with a deep swelling into the anterior pit, and the arrangement of prominent tubercles on the fixed cheeks is different. The pygidium of *E. regularis* has one fewer pair of pleurae than *E. rarus* with a flatter (sag., tr.) axis, possessing fewer axial rings in its posterior part.

The minimal glabellar width occurs across L2 in *E. regularis* whereas it is at the L1 lobes on most other *Encrinuroides s.l.* However, the first condition is present in early life stages of several species within the group, such as in *E. hornei* (see Dean 1974, pl. 3, fig. 13), *E. rarus* (see Chatterton 1980, pl. 14, figs 2, 7–10), *E. tholus* (Evitt and Tripp 1977, pl. 4, fig. 3), *E. torulatus* (Evitt and Tripp 1977, pl. 2, fig. 2), *E. uncatus* (Evitt and Tripp 1977, pl. 6, fig. 1) and *Walencrinuroides*? sp. nov. of Edgecombe *et al.* (1998, pl. 12). It also occurs in several Silurian encrinurines (see Strusz 1980, text-figs 11–16). Hence, this character seems to be a plesiomorphic or a juvenile character appearing in early stages of the different groups descended from *E. regularis*. However, it can be reduced by the counteracting broadening of the glabella from the occipital furrow caused by the progressive inflation of the glabella from that location.

A similar array of fixigenal circumocular tubercles CT0–CT4, and FT on the fixed cheeks is traced on juvenile *E. uncatus* Evitt and Tripp, 1977 from the lower Caradoc Oranda Formation in Virginia (see Evitt and Tripp 1977, pl. 6, fig. 2), which bears additionally a torulus opposite S2. It also has prominent tubercles on the occipital ring and five pairs of symmetrical glabellar tubercles; otherwise, it shares several apomorphies with *Erratencrinurus* (see above), suggesting at least a shared ancestry with that genus.

TEXT-FIG. 5. A–T, *Encrinuroides regularis* sp. nov. A–D, GIT 389- 7; dorsal, lateral, oblique anterolateral and frontal views of holotype fragmentary cranidium (t); ×7. E, GIT 389- 8; dorsal view of fragmentary cranidium (t); ×7. F–G, GIT 389- 2; dorsal and ventral views of posterior fixigena (t); ×7. H–I, GIT 389- 9; anterodorsal and dorsal views of poorly preserved juvenile cranidium (pet); ×10. A–I from Bed 3, Popovka, St. Petersburg Region, Russia. J, GIT 389- 23; dorsal view of corroded fragmentary librigena (cpet), Maardu, Estonia; ×7. K, GIT 389- 18; dorsal view of fragmentary librigena (t); ×7. L, GIT 389- 16; dorsal view of posterior fixigena (t); ×10. M–N, GIT 389- 20; dorsal and ventral views of fragmentary librigena (t); ×7. O, GIT 389- 19; dorsal view of fragmentary librigena (t) that may be the anterior part of K; ×7. P, GIT 389- 14; dorsal view of juvenile cranidium (t); ×10. Q–T, GIT 389- 15; anterior, ventral, dorsal and lateral views of juvenile cranidium (t); ×10. K–T from a clayey film in bed 3 (Text-fig. 2), Popovka, St. Petersburg Region, Russia. All specimens from the Mäeküla Member.

TEXT-FIG. 6. A–R, *Encrinuroides regularis* sp. nov. A–E, GIT 389- 3; A–D, posterior, dorsal, lateral, and anterior views of pygidium (t); × 10; E, a fragment of posterior part, before breakage of the sixth pleura; ×5. F–G, GIT 389- 1; lateral and dorsal views of the smallest pygidium (t); × 10; A–G from Popovka, St. Petersburg Region, Russia. H, GIT 389- 5; dorsal view of fragmentary pygidium (cpet); Mäekalda, Tallinn, Estonia; ×5. I–J, GIT 389- 4; dorsal and posterior views of corroded fragmentary pygidium (cpet); Maardu, Estonia; ×5. K–R, GIT 389- 6; posterior views (adaxial pleural field horizontal or pleural tips horizontal), and lateral, anterior, dorsal, oblique and ventral views of pygidium (t), and a fragment of anterior edge showing the articulating groove; K–L, ×5; M–N, P–R, ×10; O, ×20; all from the Mäeküla Member; GIT 389- 6, from clayey film in bed 3, Popovka.

Subfamily CYBELINAE Holliday, 1942

Genus CYBELE Loven, 1845

Type species. Calymene bellatula Dalman, 1827, p. 228, pl. 1, fig. 4a–c. Lectotype (RM Ar.6049) selected and redescribed by Owen and Tripp (1988); Husbyfjöl (Västana), Östergötland, Sweden, lower Kunda Stage (upper Arenig – lower Llanvirn); by subsequent designation of Vogdes (1890).

Diagnosis. Cybeline with the cranidial anterior border elongating adaxially to a slightly elevated bulge or a short spine delimited posteriorly by deeply incised preglabellar furrow. The preglabellar furrow narrows and shallows remarkably abaxially and an isolated anteromedian pit of the glabella is positioned close to it. Pygidium with five pairs of pleurae.

Remarks. Owen and Tripp (1988) gave a detailed redescription of the type and comparative specimens of *Cybele bellatula* and identified its typical features, including the appearance of the anteromesial depressed area with the median pit at its apex on the cranidium. They described the differentiation of that character within cybelines, showing its importance in generic classification of the group. An additional character that shows apomorphic states valuable for generic classification of cybelines is the development of the tubercles on the cranidial anterior border, and their distribution between two areas: at the anterolateral corners and on the medial part.

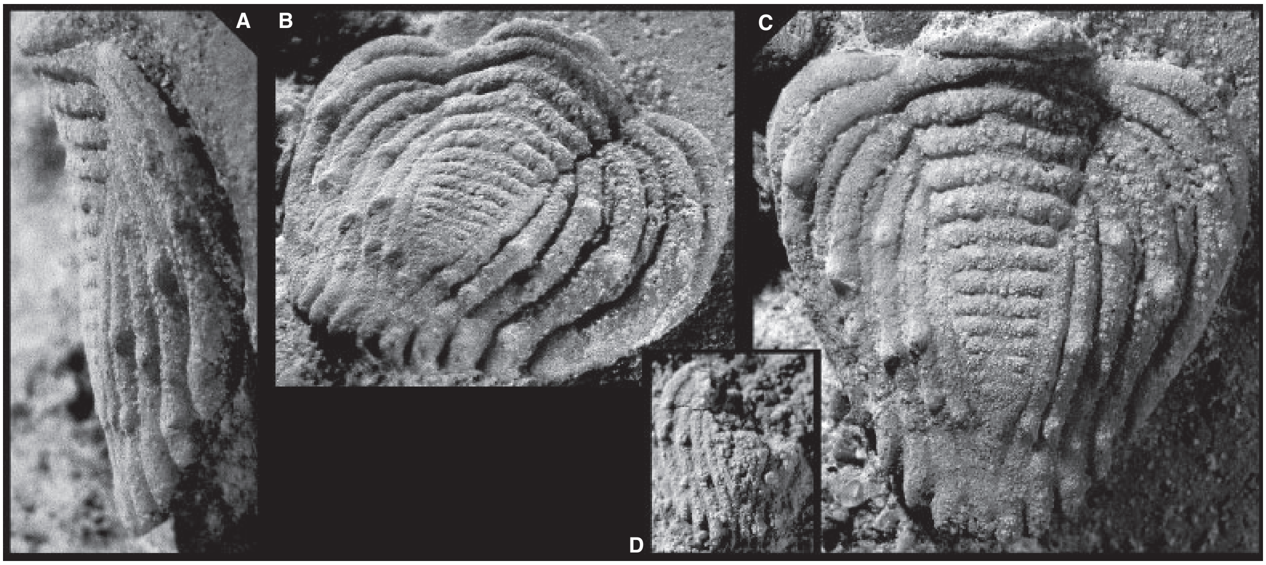
Cybele sp. A
Text-figures 3C, 7A–D

1989 *Cybele* Loven; Mägi, Viira and Aru, p. 66.
1990 *Cybele*? sp. nov.; Aru, p. 72 (North-Estonian Confacies Belt).
1997 *Cybele* sp.; Dronov, Popov and Tolmacheva, p. 21, text-fig. 22 (Tosna L-784, 6816).

Material. GIT 389- 24 (t), almost complete test of pygidium (Text-fig. 7A–C), from the Mäeküla Sandstone, layer 5 (Text-fig. 2) at Tosna River section (=Tosna L-784, 6816 in Dronov *et al.* 1997), St. Petersburg Region, Russia. A pygidium GIT 389-25 (cpet), with incompletely preserved and slightly corroded test (Text-fig. 7D), from the Mäeküla Sandstone, layer 2 (Text-fig. 2) at Jägala section, North Estonia (Text-fig. 1).

Stratigraphical range. Mäeküla Member, Billingen Stage, Tosna, St. Petersburg Region, Russia, and Jägala, Estonia.

Description. Pygidium rounded-triangular in outline, rather flat in the pleural region, slightly concave above the doublure. Pygidial length is 105–120 per cent of its maximum width (at the fifth axial ring), and axis anteriorly occupies 45–55 per cent of that. Generally the axis is almost flat (sag., tr.) except anteriorly, where it curves gently upwards. It has 15 rings; the first five are continuous with corresponding pleurae and occupy sagittally (without considering the articulating half-ring) 34 per cent of pygidial length; the 10 following rings attributed to the terminal piece occupy 38 per cent of the pygidial length (of the holotype). A prominent articulating half-ring is elongate medially



TEXT-FIG. 7. A–C, *Cybele* sp. A, GIT 389- 24; lateral, oblique posterolateral, and dorsal views of pygidium; Mäeküla Member, Bed 5, Tosna, St. Petersburg Region, Russia; ×9. D, *Cybele* cf. sp. A, GIT 389- 25; dorsal view of corroded fragmentary small pygidium; Mäeküla Member, Bed 2, Jägala, Estonia; ×4.

where there is a shortening of the first axial ring. The next four rings are arched gently forwards and separated by non-functional half-rings that are progressively smaller rearwards along the axis. Consequently, the apodemes of the first five rings are directed slightly anteriorly and faintly incised adaxially, and the sixth is slightly so. The following seventh to twelfth apodemes are transverse and the thirteenth and fourteenth are directed slightly anteriorly again. All corresponding inter-ring furrows become weaker and narrower rearwards, until a very weakly incised last furrow marks the end of the axial segmentation. In addition, the inter-ring furrows shallow adaxially in front of the very gently concave (tr.) sagittal band. The terminal piece, distinguished from the pleural region by the fifth interpleural furrow, shows a narrow intermediate area between the pleural ribs and slightly inflated axial rings. This area, together with the relatively short, laterally narrow, slightly concave, postaxial ridge provide a basal lobe of the terminal piece (= 'post-pleural region' of Owen and Tripp 1988, p. 280), which is low in this species. Axial furrow weak and shallow at the first segment but slightly more distinct at the next four, then shallows again. Five pleurae, separated by sharp, narrow interpleural furrows, curve strongly rearward first, then slightly inward above the doublure, and finally gently outward. Exceptionally, the anteriormost pair is nearly straight at its posterior end. A deep, narrow, pleural furrow divides the pleurae into convex (sag., exsag.) anterior and posterior bands. The anterior band of the first pleura is almost equal in length to the posterior band anterolaterally, curving ventrally down posterolaterally. Those of the following pleurae gradually diminish rearwards to become obscure at the fifth pleura. The parallel-sided posterior bands widen beyond the margin, and end in free spines spaced close together in an almost horizontal arc of 20 per cent of pygidial length. Pleural tips are short but truncate with multiple openings at the tip preserved such as on *E. uncatus* (see Evitt and Tripp 1977, p. 118, pl. 7, fig. 13b), and slightly out-curving. The horizontal placement of pleural tips predicts the less transversely convex anterior of the cephalon. Surface of pygidium finely granulated, bears a few tubercles on every pleura and paired low ones on the second and fifth axial rings.

Discussion. *C.* sp. A is known only from its pygidium, which differs from that of slightly younger Kunda-type species by its flatter axial and pleural regions, somewhat longer and lower terminal piece with a narrower basal lobe, and narrower and shorter terminal spine.

A cranidium, termed *Miracybele* sp. nov. by Tjernvik and Johansson (1980, p. 184) is found in slightly older beds of the *M.* (*P.*) *planilimbata* Zone, and a few more cranidia and pygidia probably of the same genus have been reported from somewhat younger beds of the *M.* (*P.*) *estonica* Zone (ibid. p. 188) of Sweden. Unfortunately, this material is unpublished and comparison with *C.* sp. A must await future study.

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