

A revision of the upper Ordovician trilobite genus *Erratencrinurus* with a description of a new species from Hadeland

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Two subgenera are recognized in *Erratencrinurus*: *E. (Erratencrinurus)* and *E. (Celtencrinurus)* each containing two species groups. A third group of taxa here termed *E. (sensu lato)* comprises a mid-Caradoc to late Ashgill stock which retains many of the characters of the oldest known species of *Erratencrinurus*, *E. (s.l.) spicatus* (Tripp). This species is also closest to the probably ancestral *Encrinuroides torulatus*–*Encrinuroides uncatus* lineage. *Erratencrinurus (Erratencrinurus) inopinatus* sp. nov. is described from a newly discovered, unusually diverse fauna in the upper Ashgill (probably Rawtheyan) Kalvsjø Fm. in the Hadeland district of the Oslo Region.

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The upper Ordovician (?Rawtheyan) Kalvsjø Fm. in Hadeland is largely a limestone unit and has hitherto yielded few trilobites. This is in marked contrast to the underlying, more argillaceous, Kjørrven Fm. which contains at least 26 trilobite species (Owen 1978; 1981 Table 1). However, road widening excavations north of Sverigetjern [NM80908620] in 1988 exposed several metres of fossiliferous shales, siltstones and impure limestones containing species of the trilobites *Brachyaspis*, *Stygina*, *Prionocheilus*, *Toxochasmops*, an indeterminate lichid and *Erratencrinurus*. Other elements of the fauna comprise at least nine brachiopod species, streptelasmaid corals, crinoids and stick bryozoans. Most of the genera in this fauna are also known from the underlying Kjørrven Fm. suggesting a localized, brief, return to similar environmental conditions. Whilst the other trilobites are too incompletely known for specific identification, it is clear that the *Erratencrinurus* species is new and is not *E. (E.) brutoni* which occurs abundantly in the underlying formation.

Erratencrinurus is known from the mid-Caradoc to late Ashgill of Laurentia, Baltica and the Anglo-Welsh area. Specific differentiation is relatively easy as it is largely based on semi-quantitative criteria such as cephalic tuberculation and pygidial segmentation. However, analysis of the Kalvsjø Fm. material has highlighted problems of

the recognition of species groups and subgenera within *Erratencrinurus*. This paper addresses these problems and is undertaken in conjunction with Owen's revision of the Encrinuridae for the Treatise on Invertebrate Paleontology and Heath's study of the latest Ordovician–early Silurian stratigraphy and sedimentology in Hadeland.

Systematic palaeontology

The encrinurine terminology used herein is essentially that of Evitt & Tripp (1977) but the glabellar tubercle notation is largely that of Strusz (1980, pp. 3–5) with the minor modifications suggested by Owen (1981, pp. 47–48). Thus rows of tubercles are numbered 0, 1, 2, 3 etc. away from the sagittal line. Each row of tubercles on the posterior part of the glabella is related to the pair of lobes or furrows which it links. Longitudinally paired tubercles are indicated by a pair of asterisks, e.g. 2L–0*. As noted by Edgecombe & Chatterton (1987, p. 344) this tubercle terminology is descriptive, not necessarily based on precise homologies, and is essentially based on the condition in adult specimens. It is accepted, however, that a degree of variation, including ontogenetic migration of tubercle position may be present in a species. The specimens from Hade-

land are housed in the Paleontologisk Museum, Oslo (PMO).

Family ENCRINURIDAE Angelin, 1854.

Subfamily ENCRINURINAE Angelin, 1854

Genus *Erratencrinurus* Krueger, 1971

Type species. – Subsequently designated Krueger (1972), *Erratencrinurus capricornu* Krueger, 1971, pp. 1147–1149, pl. 6, figs. 1, 2; pl. 7, figs. 1–3; text-figs. 1, 3G, 13, 14, from glacial erratics of the Rakvere Stage (F) (upper Caradoc, approximately Marshbrookian–Actonian) near Binz (Rostock district), East Germany.

Historical background. – The genus *Erratencrinurus* was established by Krueger (1971) for a group of species bearing glabellar spines occurring in Pleistocene erratics of mid to late Caradoc age in the Baltic area. With the exception of *E. seebachi* (Schmidt) these species were also new, namely *E. capricornu*, *E. kauschi*, *E. nebeni*, *E. ceras*, *E. kummerowi* and *E. paetzensis*. Krueger also described three Ashgill species from erratics which he ascribed to *Encrinurus*: *E. melzenensis* Krueger, *E. moe* Männil and *E. striatus* (Angelin). The latter two had previously been described from *in situ* in Estonia and Sweden, respectively.

Evitt & Tripp (1977, p. 120) considered that *Erratencrinurus* was derived from the North American *Encrinuroides torulatus*–*Encrinuroides uncatus* lineage as was another new genus, *Celtencrinurus*. This genus was essentially the *Encrinurus punctatus* group of species from the upper Caradoc and Ashgill of Scotland, Northern Ireland and E. Canada (Tripp 1957). Added to this was *Encrinurus cornutus* Ingham, 1974, from the mid-Ashgill of Northern England. *Celtencrinurus* was thus defined as comprising *C. multisegmentatus* (Portlock) (the type species), *C. trispinosus* (Reed), *C. laurentinus* (Twenhofel), *C. lamonti* (Tripp), *C. praecursor* (Tripp) and *C. cornutus* (Ingham).

The multivariate analysis of the Encrinurinae undertaken by Temple & Tripp (1979) showed the two groups of species previously assigned to *Erratencrinurus* and *Celtencrinurus* were clearly separated from other members of the subfamily on the second eigenvector of the Principal Component Analysis. The two groups showed some separation from each other on the third eigen-

vector. Temple & Tripp (1979, p. 244) suggested that this might best be expressed at subgeneric level; a view supported in principle by Strusz (1980, p. 9) who none the less maintained separate genera. Owen (1981, p. 48) formally recognized the two groups as subgenera and described three new species from the Ashgill of the Oslo Region: *E. (E.) imperfectus*, *E. (E.) brutoni* and *E. (C.) kiaeri*. Lespérance & Tripp (1985) also adopted this taxonomic position but restricted the concept of *Erratencrinurus* (*Celtencrinurus*) to exclude (*inter alia*) *E. praecursor* and *E. kiaeri*. These were reassigned to *Erratencrinurus* (s.l.).

The use of a weakly constrained *sensu lato* grouping is clearly undesirable but there are some instances in trilobite taxonomy where it has been a necessary, pragmatic approach. The late Ordovician species of *Calymene* (see Ingham 1977, p. 98) and some species of *Harpidella* (see Owen & Bruton 1980, p. 19) are notable examples. The problem in *Erratencrinurus* is emphasized by the lack of consensus in the placement of some species even before Lespérance & Tripp's restricted diagnosis of *E. (Celtencrinurus)*. Thus, for example, '*Encrinurus*' *cornutus* was ascribed to *Celtencrinurus* by Evitt & Tripp (1977) and Strusz (1980), *Erratencrinurus* (*Erratencrinurus*) by Owen (1981) and plotted with other members of the latter group in Temple & Tripp's (1979) analysis. '*Encrinurus*' *kingi* Dean was assigned to *Erratencrinurus* by McNamara (1979) and *E. (Erratencrinurus)* by Owen (1981) but to *Celtencrinurus* by Strusz (1980).

The new species from Hadeland apparently lacks glabellar spines which hitherto have been considered diagnostic of *Erratencrinurus* (*Erratencrinurus*) by several authors. However, it has a tubercle pattern which is much closer to members of that group than to species of *Erratencrinurus* (*Celtencrinurus*). It highlights the fact that there are no individual diagnostic criteria distinguishing groups within *Erratencrinurus*. The recognition of subgenera and species groups must rest on combinations of characters. An appreciation of possible phylogenies also helps greatly.

Groupings within Erratencrinurus. – Fig. 1 shows features of the cranidium and pygidium shared by groups of species within *Erratencrinurus*. Characters common to all species (such as tuberculiform glabellar lobes L2 and L3 and the presence of 3L–1 tubercles) are not included. Most of the features have been used in earlier diagnoses of *Erra-*

Taxa		1L-1 or 1S-1	1L-0	2L-0	3L-0	L1-S2 penta- gon	Glabella tuber- cles	spines	Border tubercles		Pygidium	
									Ant.	Post	axial rings	pleural ribs
E. (<i>Erratencrinurus</i>) <i>nebeni</i> group	<i>inopinatus</i> nov.						45-50		?10		>30	8
	<i>cornutus</i>			some 2S-0		open	~35		8		25-30	9-11
	<i>seebachi</i>						35-40		9		32-36	9-11
	<i>kummerowi</i>						35-40		9		36	11
	<i>nebeni</i>						40-45		9		30-32	9-11
	<i>kauschi</i>						~50		9		25	8-10
	<i>vigilans</i>						45		9		28	10
E. (<i>Erratencrinurus</i>) <i>capricornu</i> group	<i>ceras</i>						—		—		—	—
	<i>paetzensis</i>						—		—		—	—
	<i>capricornu</i>						35-40		8		—	8
	<i>imperfectus</i>						—		8		≥ 28	10
	<i>brutoni</i>						~32		10		29-30	11-13
E. (<i>Erratencrinurus</i>) <i>Celtencrinurus</i> <i>multisegmentatus</i> group	<i>trispinosus</i>						40		8		31	12
	<i>laurentinus</i>						29		8		40	15
	<i>perceensis</i>						23		8		~30	11
	<i>multi- segmentatus</i>						25		8		30-32	12-13
	<i>lamonti</i>						25		8		32	12-14
	<i>kiaeri</i>						32		10		26-29	10-13
	<i>moe</i>						~35		10		31	12
E. (<i>Erratencrinurus</i>) <i>kiaeri</i> group	<i>praecursor</i>						20-25		8		32	11
	<i>spicatus</i>	P	A	A	A	A	23-26	A	8	P	21	6
E. (<i>Erratencrinurus</i>) (sensu lato)	sp. A			2S-0		open	41		8	—	21	8
	sp. B						30-35		8		—	—
	<i>melzensis</i>						—		—		—	—
	<i>kingi</i>						34		—		25	11
	<i>striatus</i>						~30		9/10	—	26	11-12

Fig. 1. The distribution of selected cranial and pygidial characters in species of *Erratencrinurus*. Horizontal shading indicates the presence of a character, dots its absence. E. (s.l.) sp. A and E. (s.l.) sp. B are the indeterminate species described by Tripp (1974) and Lespérance & Tripp (1985) respectively. Approximate temporal succession within each lineage indicated by arrows.

tencrinurus and *Celtencrinurus* (at generic or subgeneric level) and the terms are largely self-evident. The exception is the 'L1-S2 pentagon', which refers to the arrangement of tubercles on the posteromesial part of the glabella of some species. Tubercles 1L-1 (or 1S-1), 2L-1 and a sagittally arranged 2L-0 pair mark the corners and, in the case of the posterior 2L-0 tubercle, the centre of the pentagon. In one instance, *E. (E.) cornutus*, there are no 2L-0 tubercles, but a

single 3S-0 tubercle is present in some specimens, thus marking the anterior corner of an 'open' pentagon. Some morphological features such as the degree of asymmetry in glabellar tuberculation, the shape of L1 and S1 and the presence of weak tubercles on the pygidial axis have been used as diagnostic criteria by earlier workers but do not vary in any consistent way and have been excluded from Fig. 1.

'*Encrinurus*' *spicatus* Tripp, 1974 from the mid-

Caradoc of Wisconsin, provided the link between both *E. (Erratencrinurus)* and *E. (Celtencrinurus)* and the other encrinurines on Temple & Tripp's (1979) PCA ordination of species. It was assigned to *Celtencrinurus* by Strusz (1980) and *E. (Erratencrinurus)* by Owen (1981) thus emphasizing similarities to both groups as it is both a morphological and temporal intermediate between them and the probably ancestral *Encrinuroides torulatus-Encrinuroides uncatus* lineage. It and several other species are here considered to belong in *Erratencrinurus* but represent a stock or stocks (*E. (sensu lato)*) which may have given rise to the two named subgenera in the mid-Caradoc. *E. (s.l.)* sp. A (= *Encrinurus* sp. of Tripp 1974) from the same gross unit (the Galena Fm.) as *E. (s.l.) spicatus* has a 2S-0 tubercle and thus approaches the L1-S2 pentagonal arrangements of tubercles of *E. (E.) nebeni* and its allies. It may therefore be a link with that group of species.

The features of *Erratencrinurus (s.l.) spicatus* could be viewed as representing the primitive condition for the genus but some 'derived' states

may have occurred independently in different groups and reversals to the 'primitive' condition are evident in the later histories of some lineages. In view of this, the lack of ontogenetic information, the incomplete knowledge of some species and the stratigraphical uncertainties inherent in several species being known only from glacial erratics, a rigorous cladistic or stratophenetic analysis of *Erratencrinurus* is not undertaken. None the less, a possible phylogenetic scheme is shown on Fig. 2.

In order to avoid a formal taxonomy which is too divisive and yet conserve established names, *Erratencrinurus (Erratencrinurus)* and *E. (Celtencrinurus)* are here defined and each considered to contain two species groups. A revised diagnosis of the genus as a whole is not given here as it must await the revision of the other encrinurine genera. Subgeneric diagnoses are restricted to characters distinguishing the subgenera from each other and from the species included in *E. (s.l.)*. the nominate subgenus is considered last as it precedes the description of the new species from Hadeland.

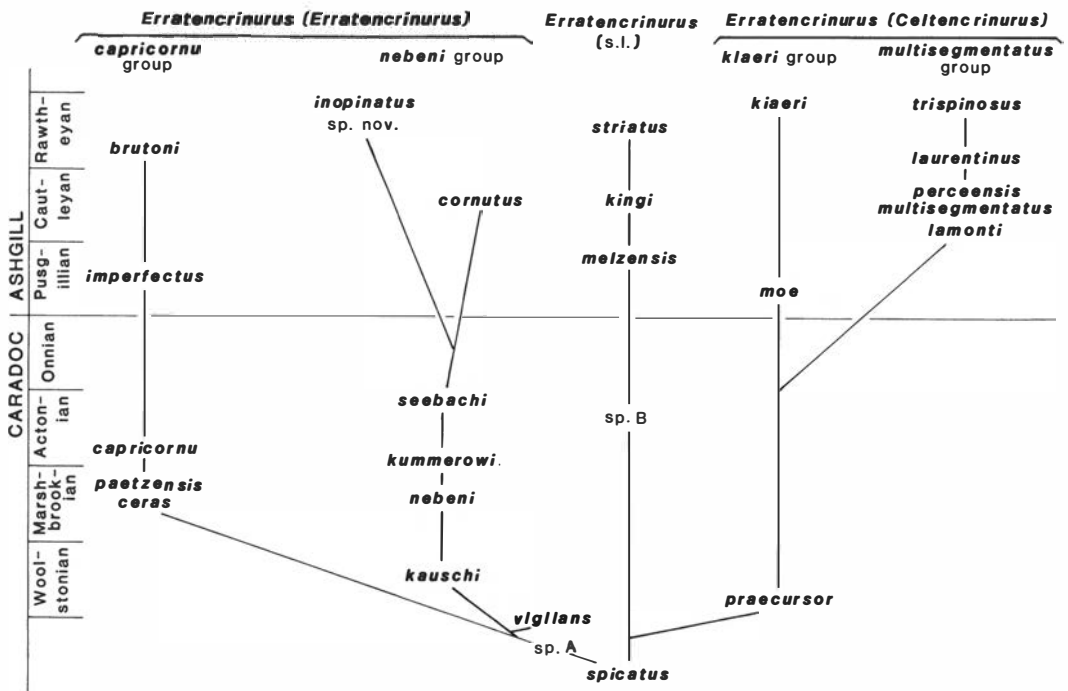


Fig. 2. Suggested phylogeny of species of *Erratencrinurus* showing the groupings recognized herein. Precise mid-Caradoc age of *E. (s.l.) spicatus* not known nor are the relative positions of Caradoc species of *E. (Erratencrinurus)*. *E. (s.l.)* sp. A (= *Encrinurus* sp. of Tripp 1974) may belong to the main lineage of that group or (as shown here) to a side branch possibly leading to *E. (Erratencrinurus)*. *E. (s.l.)* sp. B is *E. (s.l.)* sp. of Lespérance & Tripp 1985.

Subgenus *Erratencrinurus* (*Celtencrinurus*) Evitt & Tripp, 1974.

Type species. – Original designation, *Calymene multisegmentatus* Portlock, 1837, p. 6, pl. 2, Fig. 7, from the Killy Bridge Fm. (Cautleyan), Pomeroy, Co. Tyrone, Northern Ireland (see Tunnicliff 1978).

Included species. – *E. (C) multisegmentatus* (Portlock), *E. (C) lamonti* (Tripp), *E. (C) perceensis* (Cooper), *E. (C) laurentinus* (Twenhofel), *E. (C) trispinosus* (Tripp), *E. (C) praecursor* (Tripp), *E. (C) moe* (Männil), *E. (C) kiaeri* Owen.

Occurrence and range. – Upper Caradoc to upper Ashgill (Rawtheyan) of the Scoto-Appalachian area (Scotland, N. Ireland, E. Canada) lower Ashgill of Estonia, Rawtheyan of Norway.

Diagnosis. – Glabella narrow posteriorly, expanding in front of S2, bearing 20–40 large symmetrically arranged tubercles but not spines. Tubercles 1L–0 and immediately adjacent 1L–1 invariably present as are 2L–0 and 3L–0 in all but the oldest part of the Scoto-Appalachian lineage. Posterior cranial border tuberculate in some species. Pygidium bearing about 26–40 axial rings and 10–15 pleural ribs.

Discussion. – *Erratencrinurus* (*Celtencrinurus*) comprises two species groups (Figs. 1 & 2). The more primitive of these is the upper Caradoc to upper Ashgill lineage leading from *E. (C) praecursor* from Scotland through the Estonian *E. (C) moe* to *E. (C) kiaeri* from Norway. Like *E. (s.l.) spicatus* and its allies, members of this species group lack 2L–0 and 3L–0 tubercles and have a tuberculate posterior cranial border. These features contrast with those of the probable derivative of this primitive group, the Ashgill Scoto-Appalachian species which constituted Lespérance & Tripp's (1985) more restricted concept of *E. (Celtencrinurus)*. This latter group also consistently has eight tubercles on the anterior cranial border as does *E. (C.) praecursor* but not *E. (C.) moe* and *E. (C.) kiaeri* which have ten. Only *E. (C.) laurentinus* and *E. (C.) trispinosus* have axial tubercles on the pygidium.

Erratencrinurus (sensu lato)

Included species. – *E. (s.l.) spicatus* (Tripp), *E.*

(*s.l.*) *kingi* (Dean), *E. (s.l.) melzensis* (Krueger), *E. (s.l.) striatus* Angelin, *E. (s.l.)* sp. A (= *Encrinurus* sp. of Tripp 1974), and *E. (s.l.)* sp. B (= *Erratencrinurus* (*s.l.*) sp. of Lespérance & Tripp 1985).

Occurrence and range. – Middle and upper Caradoc of North America, middle Ashgill (Cautleyan) of N. England, Ashgill (precise level not known) of Sweden and the Baltic area.

Discussion. – These species have the glabella parallel-sided or expanding anteriorly, bearing about 23–35 large tubercles most of which are symmetrically arranged. L1 is ridge-like. A 1L–1 tubercle close to sagittal line invariably present but median tubercles are very uncommon opposite L1–L3. The pygidium has only about 21–26 axial rings and 6–12 pleural ribs.

Although geographically dispersed, the members of this group retain most of the 'primitive' characters of its oldest member *E. (s.l.) spicatus*. The only species with a median tubercle on the posterior part of the glabella are *E. (s.l.)* sp. A from the Galena Fm. in Iowa which has a 2S–0 tubercle and *E. (s.l.) spicatus* from the Boda Limestone of Siljan, Sweden where 1L–0 is present. The posterior border of the cranidium is tuberculate in the Caradoc species *E. (s.l.) spicatus* and *E. (s.l.)* sp. B and (distally only) in *E. (s.l.) melzensis*, the precise Ashgill age of which is not known. The posterior border of the Cautleyan *E. (s.l.) kingi* is smooth. Although some species are incompletely known, the upper Caradoc and Ashgill species have a greater number of glabellar tubercles, pygidial axial rings and pygidial pleural ribs than does *E. (s.l.) spicatus*. There are a few axial tubercles on the pygidium of *E. (s.l.) spicatus* and *E. (s.l.)* sp. A but not on those of *E. (s.l.) kingi* and *E. (s.l.) striatus*. Pygidia of the other species have not been recorded.

Subgenus *Erratencrinurus* (*Erratencrinurus*) Krueger, 1971.

Type species. – As for genus.

Included species. – *E. (E.) capricornu* Krueger, *E. (E.) ceras* Krueger, *E. (E.) imperfectus* Owen, *E. (E.) brutoni* Owen, *E. (E.) kauschi*, Krueger, *E. (E.) nebeni* Krueger, *E. (E.) kummerowi* Krueger, *E. (E.) seebachi* (Schmidt), *E. (E.) cornutus* (Ingham), *E. (E.) inopinatus* sp. nov. and *E. (E.?) vigilans* (Hall).

Occurrence and range. – Mid/upper Caradoc (approximately Woolstonian to Actonian) of the Baltic area, Ashgill (Pusgillian to Rawtheyan) of Norway, mid Ashgill (Cautleyan) of N. England, ?Mid Caradoc of Eastern North America.

Diagnosis. – Glabella expanding forwards bearing 30–50 large glabellar tubercles, most symmetrically arranged and one or more extended as spines (? except in the youngest species unequivocally ascribed to the subgenus, *E. (E.) inopinatus* sp. nov). Tubercle 1L–1 present in one species group and 2L–0 (rarely 2S–0) in the other group. The latter also has a pentagonal arrangement of tubercles on the posterior part of the glabella whereas the former has only a very sparse tuberculation here. Posterior border of cranium smooth. Pygidium bearing about 25–36 axial rings and 8–13 pleural ribs. *Erratencrinurus (E.?) vigilans* Hall – see Ludvigsen 1979, Fig. 27) from the Trenton Group of New York and Ontario (mid Caradoc) lacks glabella spines and may best be viewed as closed to the ancestor of the subgenus.

Discussion. – There are two distinct species groups within *E. (Erratencrinurus)* centred on *E. (E.) capricornu* and *E. (E.) nebeni*. They may eventually be best separated at subgeneric level but important gaps in knowledge of species in the *E. (E.) capricornu* group (Fig. 1) preclude this being done satisfactorily at the moment. The two species groups recognized here are not the same as those of Krueger (1971) whose criteria were either difficult to discern accurately or related to features not preserved in some species (see also Owen 1981, p. 48). The scheme used here does, however, correspond to the grouping of Baltic species on Krueger's text-figs. 2 and 3.

The *E. (E.) capricornu* group

This group comprises the Baltic upper Caradoc species *E. (E.) ceras*, *E. (E.) paetzensis* and *E. (E.) capricornu* together with *E. (E.) imperfectus* and *E. (E.) brutoni* from the Pusgillian and Rawtheyan respectively of the Oslo Region. It is characterized by the very sparse tuberculation of the posteromesial part of the glabella – 1L–1 and 1L–0 are invariably absent, 2L–0 is only present in *E. (E.) paetzensis* and 3L–0 in the Norwegian species. In all species, S1 is transversely directed

but only extends across the glabella in *E. (E.) paetzensis*. The anterior part of the cranium and the pygidium are unknown or very poorly known in *E. (E.) ceras* and *E. (E.) paetzensis*, thus preventing generalization being made on the morphology of these areas. *E. (E.) capricornu* and *E. (E.) imperfectus* have eight tubercles on the anterior cranial border (the 'primitive' state for the genus) but the youngest species, *E. (E.) brutoni*, has ten. The pygidia of these three species lack axial tubercles and show a progressive increase in the number of pleural ribs.

The *E. (E.) nebeni* group

This group includes the mid-upper Caradoc Baltic species *E. (E.) kauschi*, *E. (E.) nebeni*, *E. (E.) kummerowi* and *E. (E.) seebachi* and probably gave rise to *E. (E.) cornutus* from the Cautleyan of N. England and (separately) *E. (E.) inopinatus* sp. nov. from the Rawtheyan of Hadeland. The last of these differs from the other members of the subgenus in probably lacking glabellar spines – a reversal to the 'primitive' condition for the genus.

The *E. (E.) nebeni* group is typified by the pentagonal arrangement of tubercles/spines at 1L–1 (or 1S–1) and 2L–1–0*. *E. (E.) cornutus* lacks the longitudinally paired 2L–0 tubercles but some specimens to have a tubercle at 2S–0, constituting the apex of the pentagon. This pentagonal arrangement of tubercles was considered by Strusz (1980, p. 9) to be a diagnostic feature of *Erratencrinurus* (excluding '*Celtenocrinurus*'), but it is confined to the *E. (E.) nebeni* group. It is not, however, unique to this one group of encrinurines and was evolved independently in other lineages such as the '*Encrinurus variolaris plexus*' of Strusz (1980, see also Edgecombe & Chatterton 1987) and *Balizoma* Holloway (see Ramsköld 1986). The number of glabellar tubercles is consistently large (35–40) and there are commonly nine tubercles on the anterior border of the cranium although this is less certain in *E. (E.) inopinatus* sp. nov. and *E. (E.) cornutus* has eight. S1 either circumscribes L1 or is directed transversely without being continuous across the glabella. The pygidium bears 8–11 pleural ribs and has a few tubercles on the axis in *E. (E.) kauschi* and *E. (E.) seebachi* but not in the other species.

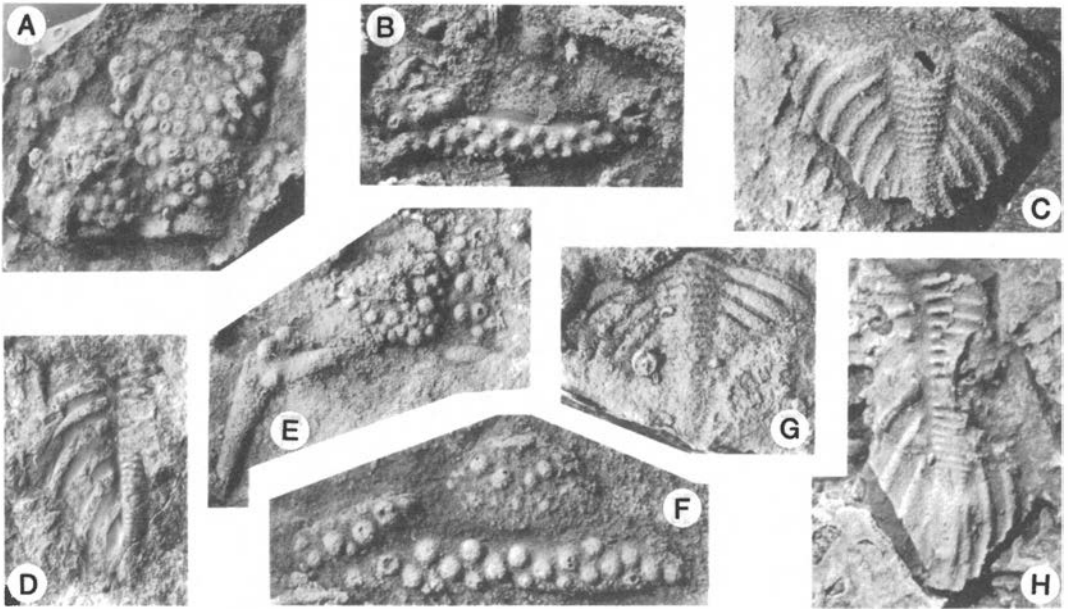


Fig. 3. *Erratencrinurus (Erratencrinurus) inopinatus* sp. nov. from the upper Kalvsjø Fm. (?high Rawtheyan) of Hadeland. All except D from Lunner-Sløvika road, 50 m N of Sverigetjern. A, latex cast of holotype cephalon, dorsal view. PMO 118.555, $\times 2\frac{1}{2}$. B. Latex cast of paratype free cheek, lateral view. PMO 118.556, $\times 3\frac{1}{2}$. C. Internal mould of pygidium, dorsal view. PMO 118.568, $\times 2\frac{1}{2}$, Bjertnestangen shore section. E. Latex cast of incomplete cranium, dorsal view. PMO 118.559, $\times 2$. F. Latex cast of free cheek, lateral view. PMO 118.560, $\times 3$. G. Latex cast of paratype pygidium, dorsal view. PMO 118.561, $\times 2\frac{1}{2}$. H. Internal mould of pygidium, dorsal view. PMO 118.562, $\times 3$.

Erratencrinurus (Erratencrinurus) inopinatus sp. nov.

Fig. 3A–H.

Holotype. – A cephalon (PMO 118.555, Fig. 3A) from the upper part of the Kalvsjø Fm. (probably late Rawtheyan) on the Lunner-Sløvika road 50 m N of Sverigetjern, Hadeland [NM 80908620].

Paratypes. – A free cheek (PMO 118.556, Fig. 3B) and two pygidia (PMO 118.561 and 118.562, Fig. 3G, H respectively) from the type locality and horizon.

Other material. – An incomplete cranium, a fixed cheek fragment, a free cheek, two pygidia (all topotypes) and a pygidium from the uppermost Kalvsjø Fm. on the shore section at Bjertnestangen [NM 76158720]. A topotype partial cranium and a free cheek were destroyed during preparation but latex casts are illustrated here (Fig. 3E, F) as they add morphological information not preserved in the other material.

Derivation of name. – Latin *inopinatus* – unexpected; referring to the discovery of a relatively

diverse trilobite fauna including this species in a unit which had previously yielded few trilobites.

Diagnosis. – Glabella moderately swollen, expanding even forward and bearing about 45–50 large, symmetrically arranged tubercles but probably not spines. Tubercle formula: 1L–2–1; 2L–(3)–2–1–0*; 3L–3–2*–1–0; 4L–3–2–1–0. Posteromesial part of glabella bears pentagonally arranged tubercles. L1 tuberculiform. Anterior border of cranium bearing nine or ten tubercles. Fixed cheek with smooth border and heavily tuberculate field. Free cheek field sparsely tuberculate, border strongly so. Pygidium with eight pleural ribs and over 30 axial rings. No tubercles on pygidial axis.

Description. – Glabella expanding gently and evenly forward in front of the occipital ring to 1.7 times its width at L1. Occipital ring about 1.4 times the glabellar width at L1 and occupying about 10% of the sagittal glabellar length. Posterior edge of ring arched gently forwards mesially; anterior edge almost transverse and defined by very narrow (sag., exsag.) shallow

occipital furrow. L1–L3 tuberculiform. Glabella bearing about 45–50 tubercles which are large but apparently not extended as spines. Tubercle formula: 1L–2–1; 2L–(3)–2–1–0*; 3L–3–2*–1–0; 4L–3–2–1–0. Mesial tubercles in 1L and 2L positions form a filled pentagon. Some adventitious mesial tubercles present on anterior part of glabella. Preglabellar furrow shallow but distinct, arched strongly forwards. Anterior border of cranidium bears nine or ten large tubercles but poor preservation in the mesial part of this area makes this difficult to assess. Axial furrow weak but marks breaks in slope of both glabella and the swollen fixed cheek. Posterior border smooth, transversely directed, broadening (exsag.) distally. Genal spine of unknown length directed abaxially at about 20° to the sagittal line; bearing three large tubercles proximally. One of these tubercles is at the angle between posterior border and spine, and the other two are anteriorly placed along the short (exsag.) cranial part of the lateral border. Field of fixed cheek densely covered in large tubercles, some overhanging the shallow posterior border furrow. Base of palpebral stalk well away from glabella opposite L3. Posterior branch of facial suture transverse proximally, directed abaxially rearwards at 30° to the sagittal line over its outer three quarters. Course of anterior branch not known.

Free cheek triangular. Broad, gently swollen border bears about 20 large tubercles. Pre-cranial lobe with an outer row of about four large tubercles and an inner one of about five smaller tubercles. A few small tubercles also present on outer row adjacent to lateral border. Border furrow broad and shallow. Field gently swollen, coarsely pitted and bearing a few scattered tubercles close the steep visual surface.

Hypostoma and thorax not known.

Pygidium triangular in outline; precise proportions not known but probably broader than long. Gently convex (tr.) axis occupying most of the length of the pygidium; tapering rearwards at about 15° and composed of more than 30 rings. No tubercles on axis. Anterior two rings continuous with anterior two of eight pleural ribs. Axial furrows little more than break in slope between axis and flat-lying inner part of pleural lobe. Pleural ribs arched abaxially rearwards; anterior rib directed at about 60° to sagittal line, posterior rib almost parallel to and extending beyond axis. Outer part of pleural lobe gently declined. Ribs end in short free points. Ribs sep-

arated by deep furrows which are narrow on the external surface but very much broader on internal moulds.

Discussion. – The large number of glabellar tubercles and pentagonal arrangement of tubercles on the posteromesial part of the glabella place *E. (E.) inopinatus* in the *nebeni* species group. However, it differs from all other members of the group in apparently lacking glabellar spines, possibly in having ten tubercles on the anterior cranial border, in having a markedly tuberculiform L1 (= tubercle 1L–2) and in having longitudinally paired 3L–0 tubercles. The only other member of the *nebeni* group with a median tubercle opposite L3 is *E. (E.) cornutus* (Ingham) from the Cautleyan of northern England in which a single spine is developed at this position. Both *E. (E.) inopinatus* and *E. (E.) cornutus* were probably late, independent, derivatives from the main, Baltic *nebeni* group lineage. Both show significant deviations from the more homogeneous morphology of the earlier members of the group (Fig. 1) but the scheme introduced herein enables their taxonomic position to be recognized.

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