THE SILURIAN TRILOBITE *ENCRINURUS VARIOLARIS* AND ALLIED SPECIES, WITH NOTES ON *FRAMMIA*

by R. P. TRIPP, J. T. TEMPLE, *and* K. C. GASS

ABSTRACT. *Encrinurus variolaris* (Brongniart) from the Wenlock of the Welsh Borderland is redescribed and related species discussed. Of these, *E. diabolus* from the Llandovery of Shropshire and *E. rosensteinae* from the Ludlow of the Welsh Borderland are new. The genus *Frammia* is restricted to *F. arctica* (Salter) and *F. rossica* (Maksimova).

REED (1928, p. 66) subdivided the genus *Encrinurus* into several species-groups, one of which was characterized by *E. variolaris* (Brongniart). Preliminary results of a numerical taxonomic study of encrinurines (currently in progress by Temple and Tripp) reveal no clear-cut species-groups among Silurian species of *Encrinurus*. A *variolaris* species-group is therefore not recognized in the present paper.

Terminology. Miller (1976, pp. 341–343) has distinguished domes (in which the cuticle thickness is reduced towards the apex of the bulge), tubercles (small discrete structures with the appearance of pustular organelles embedded in the cuticle), and pseudotubercles (pustular structures which lack this discrete appearance). Many, but not all, of the raised features of encrinurines are domes (Miller 1976, text-fig. 2*g*). In this paper the term tubercle is used in its conventional general sense. The notation for glabellar tubercles is that proposed by Tripp (1957, 1962), except that the abaxial tubercles in rows II and III are referred to as 2L and 3L (see p. 848). The area underlying the tips of the pleural ribs of the encrinurine pygidium is here, following Whittington and Campbell (1967, p. 471) and Temple (1970, p. 67), referred to as the border; the pygidial doublure is reflexed dorsally and is normally not seen in ventral view. Proportions of various parts of the exoskeleton refer to specimens at least 5 mm long, and are quoted as percentages rounded to the nearest 5%. Except where stated to the contrary, the orientations of isolated parts of the exoskeleton in the photographs are those proposed as standard at Oslo (see Temple 1975), i.e. at right angles to horizontal planes defined by the sagittal lengths of cranidium, hypostome, and pygidium.

A list of localities and registered specimen numbers has been deposited with, and may be purchased from, the British Library, Boston Spa, Yorkshire LS23 7BQ, Great Britain, as Supplementary Publication No. SUP 14008 (7 pages).

TUBERCULATION

Glabella. The glabellar tuberculation of the species described is characterized by four main features:

1. The common presence of tubercle pair I-1. The presence of pair I-1 is a major point of difference from many of the species related to *E. punctatus* (Wahlenberg), in which the most posterior glabellar tubercles are either the pair II-1 or the single small tubercle I-0 (Tripp 1962, text-fig. 1).

2. The forward position of tubercle pairs I-1 and II-1. In *E.* cf. *mullochensis* of Temple (1970, p. 66, pl. 19, figs. 1–2) from the early Llandovery and *E. schmidti* Männil (1968, p. 273, pls. 1–2) from the upper Llandovery, tubercle pair II-1 lies on

[Palaeontology, Vol. 20, Part 4, 1977, pp. 847–867, pls. 113–115.]

or close to the shortest arc joining 2L across the glabella, and tubercle pair I-1 lies far behind this arc. In the species described here both the I-1 and II-1 pairs are situated further forwards, so that pair I-1 often lies closer to the arc joining 2L than does pair II-1.

3. Development of glabellar lobes 2L and 3L. These form nodular tubercles which are usually large in diameter and low in profile compared with the adaxial glabellar tubercles. This feature, which is difficult to objectify, is another distinction from *E. punctatus* and its allies, in which 2L and 3L are more like the adaxial glabellar tubercles in diameter and profile (and thus possibly in function too).

4. The tendency of tubercles III-2 (when present) to lie close to 3L. III-2 and 3L often share a common base, especially in *E. rosensteinae* (Pl. 115, figs. 4, 5). This feature is probably related to the less tubercle-like nature of 2L and 3L compared with *E. punctatus* and its allies, for in the latter III-2 does not usually encroach on to 3L.

The number of tubercles on the posterior part of the glabella of a sample of BM specimens of *E. variolaris* (Table 1) increases during growth, declining again, possibly significantly, in the largest specimens ($0{\cdot}01 < p < 0{\cdot}02$ for two-sided t-test of significance of the quadratic regression coefficient).

TABLE 1. Mean numbers of tubercles on the posterior part of the glabella (series I, II, ii, III, iii inclusive) in Dudley *E. variolaris* at different glabellar lengths.

Length (mm)	Sample size	Mean
3·0–4·9	18	13·67
5·0–6·9	16	14·38
7·0–8·9	6	16·33
9·0–10·9	4	17·25
11·0–13·9	4	15·25

Pygidium. Sagittal tubercles are developed on certain pygidial rachial rings in the species described here, and the distribution of these tubercles is a major distinguishing feature between *E. variolaris*, *E. diabolus*, and *E. rosensteinae*.

Comparison of the three species on this feature is most conveniently made on the basis of Table 2 which shows the frequency of occurrence of tubercles on numbered rachial rings. For each species certain rings bear tubercles more frequently than their neighbours: for *diabolus*, rings 1, 4, 7, 10; for *variolaris*, rings 1, 3, 5, 7; for *rosensteinae*, rings 1, 4, 6, 8. It will be seen that *diabolus* and *rosensteinae* agree in the spacing of the first two maxima (rings 1 and 4) whereas in *variolaris* they are on rings 1 and 3. On

TABLE 2. The numbers of specimens of *diabolus*, *variolaris*, and *rosensteinae* in which tubercles occur on the stated pygidial rachial rings; modal values are shown in bold type. Collections for Tables 2–4 are as follows: *diabolus* from various Salop localities (n = 43); *variolaris* from Dudley (n = 75), *rosensteinae* from various localities (n = 48).

Ring number	1	2	3	4	5	6	7	8	9	10	11	12	13
diabolus	**15**	6	16	**22**	7	14	**17**	12	10	**11**	8	6	1
variolaris	**32**	9	**61**	18	**61**	23	**44**	20	12	5	0	0	0
rosensteinae	**16**	13	14	**32**	16	**31**	20	**25**	12	11	5	0	0

the placing of the more posterior tubercles, however, *rosensteinae* agrees with *variolaris* in having maxima on alternate rings (albeit out of step in the two species), while *diabolus* has maxima on every third ring. Furthermore, the mean number of blanks in the intervals between successive tubercles irrespective of which rings they occur on (Table 3) decreases posteriorly in *variolaris* and *rosensteinae* but increases in *diabolus* (although less significantly, $0{\cdot}01 < p < 0{\cdot}02$ for two-sided test of correlation coefficient). The 'zero' interval (in front of the first tubercle) is analysed in more detail in Table 4. In all three species the first tubercle is developed more commonly on rings 1 or 3 than on 2, discrimination against ring 2 being stronger in *variolaris* than in the other two species where also the onset may be delayed to ring 4 or even further. In summary, there are significant differences in distribution of rachial tubercles between the three species, and these differences do not form a gradually changing sequence corresponding to stratigraphical horizon.

TABLE 3. The mean numbers of blank pygidial rachial rings in successive intervals between tubercles (interval 0 in front of first tubercle) for *diabolus*, *variolaris*, and *rosensteinae*.

Interval	0	1	2	3	4
diabolus	1·54	1·91	1·83	2·20	2·00
variolaris	1·05	1·05	0·91	0·74	0·27
rosensteinae	1·31	1·28	1·00	0·57	0·44

TABLE 4. The numbers of specimens of *diabolus*, *variolaris*, and *rosensteinae* in which the first tubercle occurs on the stated pygidial rachial ring (∞ indicates that no tubercles are developed).

Ring number	1	2	3	4	5+	∞
diabolus	15	5	12	9	2	0
variolaris	32	7	36	0	0	0
rosensteinae	16	10	11	9	1	1

The available collections of *E. variolaris* from Dudley are large enough for further analysis of the pattern of sagittal tubercle development in this species. From the frequencies of tubercles on rings (Table 2) can be derived the expected frequencies of various combinations (pairs, triplets, etc.) of tubercles on particular rings. When this is done there are found to be systematic deviations from the expected values, indicating that there are interactions between the rings which inhibit the development of tubercles on adjacent rings and favour their development on alternate rings. The regularity of spacing of tubercles on alternate rings is thus greater than it would be if the occurrence of tubercles was determined entirely by their absolute probabilities of development. Ring 1 appears to be exceptional in not interacting with other rings, although the presence or absence of a tubercle on ring 1 appears to modify the interactions of the other rings, these being mostly weaker in its presence. It is tempting to regard the tubercle on ring 1 of *variolaris* as having some function or significance (e.g. dimorphic) other than that of the more posterior tubercles.

SYSTEMATIC PALAEONTOLOGY

Family ENCRINURIDAE Angelin, 1854
Genus ENCRINURUS Emmrich, 1844
Encrinurus variolaris (Brongniart, 1822)

Plate 113; text-figs. 1, 2, 3B, 4A

1822 *Calymene variolaris* Brongniart, p. 14 (name only).
v. 1839 *Calymene variolaris* Brongn. (var.?); Murchison, p. 655, pl. 14, fig. 1.
1850 *Cybele variolaris* Brongniart, sp.; Fletcher, pp. 404–405, pl. 32, figs. 6–10.
1853 *Encrinurus variolaris* Brongn. sp.; Salter, p. 7, pl. 4, figs. 13, 14.
1871 *Encrinurus variolaris* Brongniart, sp.; Baily, pp. 67–68, pl. 23, fig. 3.
1878 *Cryptonymus variolaris* Brongniart; Vogdes, p. 21, pl. 1, figs. 6–10; pl. 3, figs. 13, 14 [cop. Salter 1853].
v. 1884 *Encrinurus variolaris*; La Touche, pl. 10, fig. 253.
1907 *Cryptonymus variolaris* Brongn.; Vogdes, p. 74, pl. 3, figs. 1–9, *non* fig. 10 [figs. 1–4, 7–9 cop. Fletcher 1850, figs. 5–6 cop. Salter 1853].
1917 *Cryptonymus variolaris*; Vogdes, pl. 3, figs. 1–9 [cop. Vogdes 1907].
v.*1925 *Encrinurus magnituberculatus* Reed, pp. 72–73, pl. 2, fig. 3, 3*a*.
v. 1954 *Encrinurus variolaris* (Brongniart); Temple, pp. 315–318, text-figs. 1, 2.
v. 1962 *Encrinurus variolaris* (Brongniart); Tripp, pl. 65, figs. 17–20.
1972 *Encrinurus* (*Frammia*) *variolaris* (Brongniart); Schrank, pl. 13, fig. 8.
v. 1973 *Encrinurus variolaris* (Brongniart); Clarkson and Henry, pp. 123–125, figs. 12–16.

Diagnosis. Glabella strongly convex, standing well above cheek; 2L and 3L represented by large nodular tubercles; tubercles I-1 forwardly placed, II-1, III-1 distinct. Fixigenal spine small or absent. Rostral plate wedge-shaped. Pygidium non-mucronate, composed of nine to eleven rings and seven or eight pleural ribs. Four or more sagittal tubercles. Sagittal groove present.

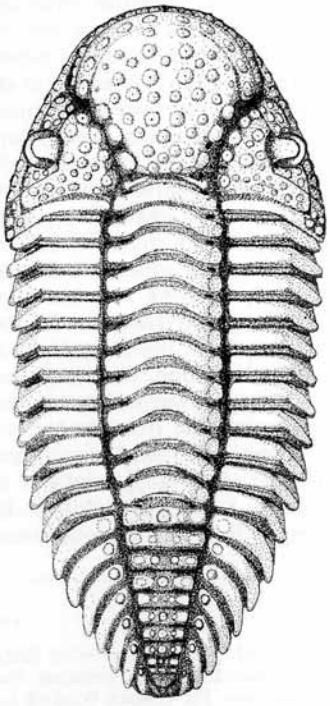
Proposed neotype. BU 55 (dorsal exoskeleton). Murchison 1839, pl. 14, fig. 1. Much Wenlock Limestone Formation, Dudley, West Midlands. Figured herein as Plate 113, figs. 1–2. For discussion of the nomenclatural problems surrounding this species, and reasons for proposing a neotype, see Tripp, Temple, and Gass 1977.

Dimensions (in mm) of neotype. Sagittal length of cranidium (normal projection) 12·6; sagittal length of thorax 19·3; sagittal length of pygidium (normal projection, excluding half ring) 14·4; width of glabella across lateral tubercles on frontal lobe 9·2; width of glabella across 2L 5·9; width of occipital ring 8·2; maximum width of thoracic rachis 7·9; maximum width of pygidium 13·8.

Occurrence. Wenlock Series: Wenlock Shale; rare. Much Wenlock Limestone Formation; common at Dudley (over 100 specimens including many enrolled dorsal shields), rare at other localities in the Dudley, Walsall, Much Wenlock, and Woolhope outcrops of the Welsh Borderland. Ludlow Series: Lower Ludlow, Dudley; Lower Elton Beds; rare.

Description. Sagittal length of cephalon varies from 45% to 55% width. Glabella about as wide as long, width across 2L 60% width across frontal lobe, strongly rounded in outline anteriorly, strongly convex longitudinally and transversely, sagittal profile descends more steeply in some specimens than in others. Glabella rises well above cheek at back. Frontal lobe 55% length of glabella. 2L and 3L represented by nodular tubercles, subequal in size and larger than other cranidial tubercles, granulate and imperforate on some specimens. 2L, 3L, and abaxial tubercles of frontal lobe and of anterior border of cranidium overhang rachial

furrow. 1L a low, sunken ridge, which is directed towards, but dies out before reaching, tubercle I-1. 3S and 2S short but deep depressions between lobes; 1S short and shallow, merging with broad occipital furrow adaxially. Occipital ring longest sagittally, wider and higher than 1L, bowed forwards, moderately convex in both directions. Rachial furrow deep and narrow, deepening opposite preglabellar furrow, continuing on to free cheek, continuous with border furrow; fossula immediately posterior to anterior branch of facial suture; apodemes directed forwards and inwards at junctions with 2S, 1S, and occipital furrow. Preglabellar furrow broad, shallowing, and dying out mesially. Anterior border of cranidium short (sag.), weakly convex, with slight sagittal depression. Fixed cheek strongly convex, sloping steeply outwards. Palpebral lobe elevated, height varies from equal to double length (exs.) of lobe; anterior extremities from 150% to 160% anterior width of glabella apart, midlength opposite 2S. Palpebral furrow broad, more strongly developed on some specimens than on others. Eye ridge absent. Posterior border shorter than occipital ring adaxially, widening (exsag.) strongly abaxially, transverse or backwardly directed, convexity strong adaxially, weak abaxially. Posterior border furrow narrow, uniting with lateral border furrow. Fixigenal spine typically absent, genal angle roundedly rectangular; short, thorn-like fixigenal spine present on 12% of cranidia up to 6 mm in sagittal length, occasionally present on larger specimens (Pl. 113, fig. 3). Anterior branch of facial suture runs obliquely inwards and forwards to fossula, where it plunges downwards then rises upwards, and curves forwards and inwards to midline. Posterior branch of facial suture curves outwards across cheek, curving backwards across lateral border, cutting lateral margin just anterior to genal angle.



TEXT-FIG. 1. Reconstruction of *Encrinurus variolaris* (Brongniart). ×2·5.

Eye lobe rounded, moderately large and tall, constricted at base, not marked off from field; lens surface occupies upper half of lobe. Free cheek large, sloping steeply outwards. Field wide, weakly convex. Precranidial lobe long (exs.), convex. Lateral border as wide as field, narrowest (tr.) near midlength, more strongly convex in outline posteriorly than anteriorly, flattened. Anterior border narrows strongly anteriorly. Lateral border furrow broad and shallow throughout; anterior furrow dies out adaxially. Doublure of cephalon extends from immediately inside genal angle forward, underlying cheek border, widest posteriorly; shallow vincular depression extends from opposite fossula and dies out posteriorly.

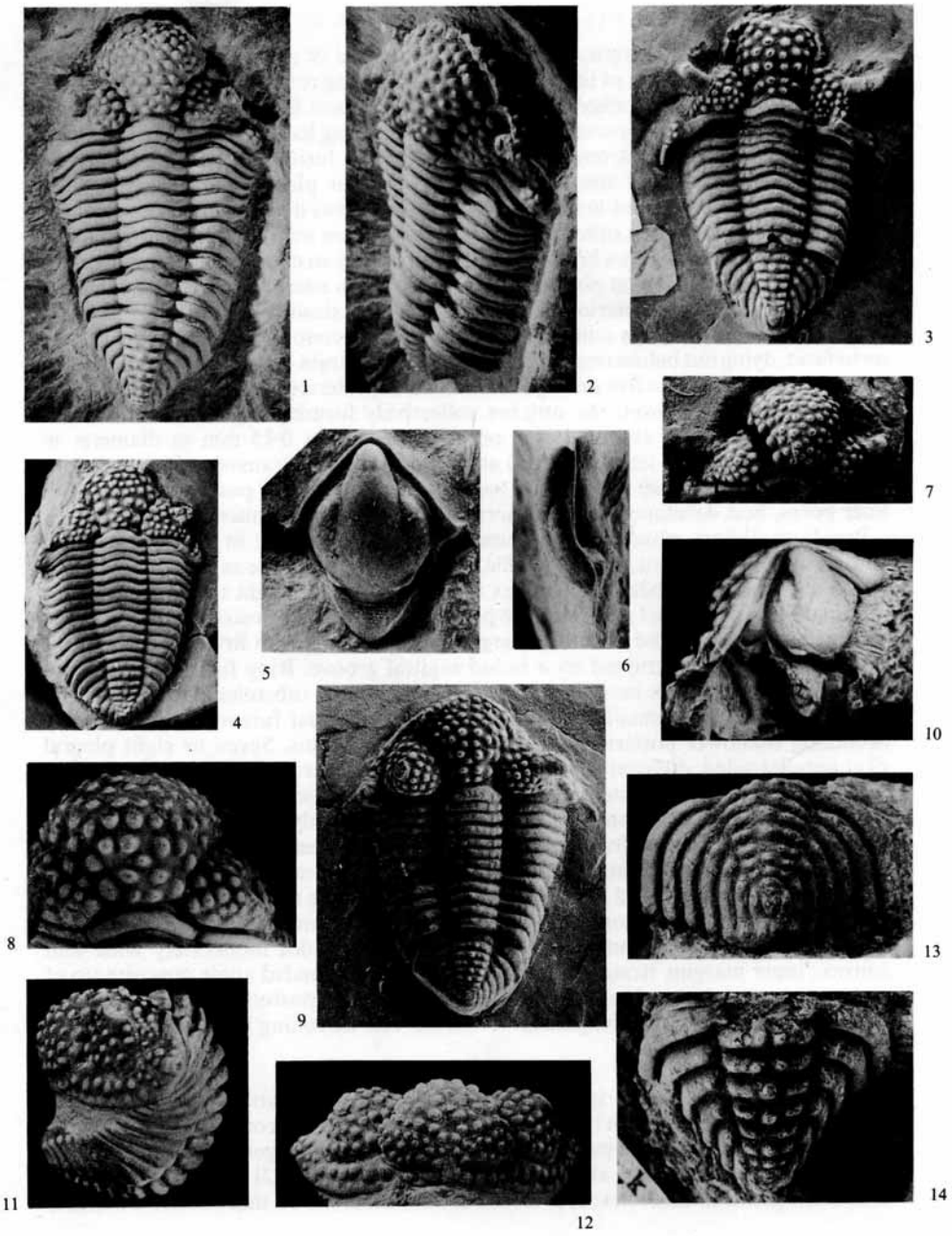
Rostral plate narrow, wedge-shaped, truncated by rostral suture or narrowing to a point; low sagittal tubercle on some specimens.

Cephalon coarsely tuberculate; tubercles usually hemispherical and perforate. Glabellar tubercle formula I-1; (ii-0); II-1; (iii-0); III-1, (2); IV-1, V-1, VI-1 usually distinguishable on frontal lobe. Tubercle I-1 (pair may be partially or completely fused) almost as large as II-1, forwardly placed. Tubercle II-1 forwardly placed. III-1 large. Abaxial tubercles on frontal lobe enlarged and overhanging rachial furrow. Anterior border of cranidium with nine to fourteen tubercles, irregular in size and arrangement; sagittal tubercle absent; abaxial tubercles not enlarged. Five large tubercles on fixed cheek alongside rachial furrow; four of them interspaced with lateral glabellar tubercles; fifth tubercle, opposite anterior border, smaller; three tubercles between palpebral lobe and rachial furrow. Field of free cheek with up to fourteen scattered tubercles of various sizes. Tubercles three deep on precranidial lobe. Border of free cheek with an adaxial row of large tubercles and a faint outer row, sometimes continued on to anterior border. Large tubercles at fixigenal angle and on lateral border adjacent. Abaxial part of border and tubercles granulate, margin finely perforate on well-preserved specimens. Fields of fixed and free cheeks finely and sparsely pitted. Occipital ring and posterior border usually without tubercles; perforations (as on thoracic segments) may be present.

Hypostome rhombic, 85% as wide as long, anterior margin narrowly rounded. Middle body inflated, subcircular in posterior outline. Longitudinal median lobe large, projecting anterior to middle body but not overhanging anterior border, widening and dying out backwards. Maculae large and swollen, smooth. Anterior border short, flexed ventrally downwards. Anterior border furrow shallow in front of median lobe, widening and deepening abaxially. Anterior wing large, sloping obliquely upwards, backwards, and outwards, placed at about 40% sagittal length of hypostome from front; rounded wing-process near extremity. Lateral border extremely narrow. Lateral border furrow deep, undercutting middle body. Posterior tongue about 20% length of hypostome, slightly recurved dorsally. Doublure not known. Surface of middle body coarsely granulate, of tongue more finely granulate; longitudinal median lobe smooth.

EXPLANATION OF PLATE 113

Figs. 1–13. *Encrinurus variolaris* (Brongniart). All specimens testiferous. Figs. 1–3, 5, 6, 10–12, Much Wenlock Limestone Formation, Dudley, West Midlands. Figs. 4, 9, 'Lower Ludlow', Dudley, West Midlands. Fig 7, Much Wenlock Limestone Formation, west side of Wrens Nest Hill, Dudley, West Midlands. Fig. 8, Much Wenlock Limestone Formation, Woolhope, Hereford-and-Worcester. Figs. 13, 14, Much Wenlock Limestone Formation, Buckenhill Wood, 1 mile SSW. Woolhope, Hereford-and-Worcester. 1, 2, dorsal exoskeleton (proposed neotype, BU 55, figured Murchison 1839, pl. 14, fig. 1). Dorsal and oblique right anterolateral views. Note deformity on right side. ×1·5. 3, dorsal exoskeleton, BU 181. ×1·5. 4, dorsal exoskeleton, BM 59036. Note adaxial position of tubercle on 3L. ×1. 5, 6, hypostome, BM In. 59340. Ventral (anterior of standard) and right lateral views. ×3·5. 7, densely tuberculate cranidium, NMW 71. 6G. 252. Posterior of standard view. ×3. 8, broad cranidium, IGS GSM 33098. Posterior of standard view. ×3. 9, small dorsal shield, BM 59035, illuminated to show right fixigenal spine and sagittal tubercles on thorax. ×2·5. 10, cephalon and hypostome, SM A28444 (figured Temple 1954, text-figs. 1, 2). Oblique left posterior ventral view, showing articulation, apodemes, and part of vincular furrow on doublure of free cheek. ×2·75. 11, 12, enrolled dorsal exoskeleton, BU 580. Left lateral and anterior views. ×2·5. 13, 14, pygidium, SM A16538 (holotype of *E. magnituberculatus* Reed). Posterior and anterior of standard views. ×3·5.



TRIPP, TEMPLE and GASS, *Encrinurus variolaris*

Thorax about 150% length of cranidium, composed of eleven thoracic segments. Rachis exceeds 35% width of thorax anteriorly, widening to sixth segment, narrowing posteriorly, moderately arched transversely, rings bowed forwards mesially: lateral nodes faintly developed on some specimens. Articulating half ring and furrow broad, apodeme near abaxial extremity of furrow. Rachial furrow shallow and narrow. Anterior pleurae directed straight outwards, posterior pleurae curve gently backwards. Inner part of pleura horizontal, outer part curves downwards more strongly in some specimens than in others. Adaxial part of pleura composed of a broad (exs.) swollen band, separated by a broad pleural furrow from an extremely narrow anterior band. Articulating flange at posterior margin of pleura narrows out before fulcrum. Abaxially to fulcrum posterior band narrows (exs.) steadily and a large bevelled articulating facet develops anteriorly. Pleural furrow continues almost transversely on to facet, dying out before reaching lateral margin. Margin of facet oblique, posterior bands not produced into free points. Abaxial end of posterior band separated by notch from abaxial end of facet, the notches collectively forming a granulated vincular groove. Dorsal spines absent. Large pores (up to about 0·15 mm in diameter in specimens of cranidial length 10 mm) arranged in roughly transverse line on rachis (where up to nine pores) and abaxial parts of pleurae. Tips of posterior bands with finer pores, best developed on posteriormost three or four segments.

Pygidium almost equal to cranidium in length, triangular in outline, strongly convex in both directions, high in profile, approximately as wide as long. Rachis 40% width of pygidium, moderately convex in both directions; eight to ten rings and a terminal piece; postaxial ridge may be present, not reaching posterior margin. First ring strongly demarcated but not enlarged or continuous with first rib, subsequent rings increasingly interrupted by a broad sagittal groove. Ring furrows broad and deep, shallower towards back. Four or more large sagittal tubercles placed in sagittal groove; two or three smaller tubercles abaxially. Rachial furrow deep anteriorly becoming shallower posteriorly, extending to tip of rachis. Seven or eight pleural ribs, parallel-sided, directed increasingly strongly backwards, curving downwards at fulcrum. One tubercle at adaxial extremity, larger on successive ribs; a few weak tubercles abaxially on strongly tuberculate specimens only. Tips of ribs projecting bluntly, granulate and perforate on well-preserved specimens. Rib furrows deep and broad, extending to margin, except for hindmost which may join behind postaxial ridge. Articulating ring and furrow well formed, apodeme near extremity of furrow. Articulating facet as on thoracic pleurae, but larger; pleural furrow runs parallel to anterior margin, dying out before lateral margin. Border moderately wide and convex; inner margins straight, meeting at an acutely rounded angle opposite tip of rachis, accommodating longitudinal median lobe of hypostome upon enrolment. Doublure reflexed roundedly, parallel to border, and extending for almost full width of border.

Variation. *E. variolaris*, as interpreted here, is a very variable species. A dorsal exoskeleton 36 mm in length (Pl. 113, fig. 3) differs from the neotype in the following important features: 1, taller palpebral lobes; 2, presence of fixigenal spines; 3, sparser glabellar tuberculation and absence of tubercles ii-0, iii-0; 4, 2L and 3L little larger than other glabellar tubercles; 5, presence of faint tubercles on thorax. These features

occur commonly in small dorsal exoskeletons up to 20 mm in length; the specimen figured is exceptional in retaining them to a large size. Additionally, sagittal tubercles on the seventh, ninth, and eleventh thoracic rings are frequently conspicuous on small specimens (Pl. 113, fig. 9).

Other variable features include:

1. Relative width and convexity of the glabella (compare Pl. 113, figs. 3, 4, and 8). Variation in convexity of the glabella has been commented on by both Fletcher (1850, p. 405) and Vogdes (1878, p. 21).

2. Glabellar tuberculation (text-fig. 2). In densely tuberculated specimens II-1 and III-1 are no larger than other glabellar tubercles and cannot readily be distinguished (Pl. 113, fig. 7). Tubercle pair I-1 is usually forwardly placed, partly opposite 2L (Pl. 113, figs. 1, 7, 8, 9), but is occasionally placed further back and clearly associated with the 1L ridges (Pl. 113, figs. 3, 4). Tubercles III-2 may be absent, distinct from III-1 and 3L, or partly fused with 3L.

3. Outline and tuberculation of the rostral plate. In many specimens the rostral plate narrows to a point at the rostral suture and bears no clear tubercles (Pl. 113, fig. 12; text-fig. 4A); in others (BM In. 31370 from the Much Wenlock Limestone Formation, Woolhope), the rostral plate is truncated by a short rostral suture, and may bear up to three tubercles longitudinally placed.

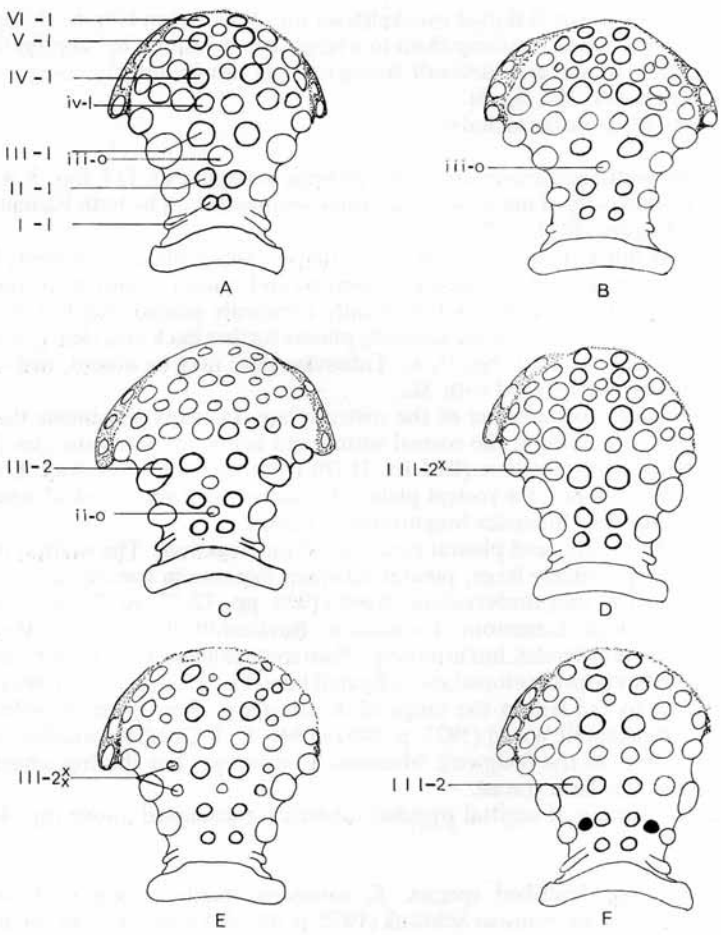
4. Size of the sagittal and pleural tubercles of the pygidium. The sagittal tubercles are always comparatively large; pleural tubercles increase in size on successive ribs. The holotype of *E. magnituberculatus* Reed (1925, pp. 72–73, pl. 2, fig. 3, 3*a*) from the Much Wenlock Limestone Formation, Buckenhill Wood, near Woolhope, certainly has large tubercles, but little larger than some other specimens of *E. variolaris*. The specimen has been developed and is figured here (Pl. 113, figs. 13–14). We consider this pygidium to fall within the range of *E. variolaris*. Reed later recorded a free cheek from Buckenhill Wood (1927, p. 548) in Mr. C. I. Gardiner's collection. This collection is now in the Sedgwick Museum, Cambridge, but the free cheek is not there, and has not been traced.

5. The distribution of sagittal pygidial tubercles is discussed above (pp. 848–849, Tables 2–4).

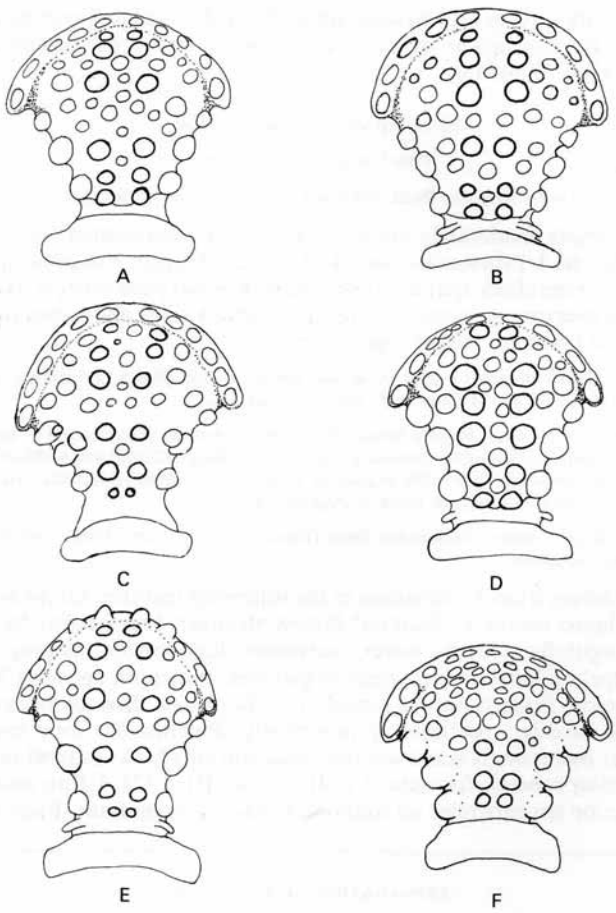
Remarks. Among described species, *E. variolaris* stands closest to *E. erraticus* Schrank [= *E. obtusus erraticus* Schrank (1972, p. 45, pl. 13, figs. 4–7; pl. 14, figs. 1–5) which differs so greatly from *obtusus* that we consider it a distinct species], and to *E. obtusus* (Angelin) (see Schrank 1972, p. 45, pl. 13, fig. 3). *E. variolaris* differs mainly in the smaller number of pygidial ribs (see Table 5). Schrank (1972, pp. 44–47) referred *E. obtusus* (including *E. erraticus*) and *E. variolaris* to *Frammia* Holtedahl, 1914, which he regarded as a subgenus of *Encrinurus*, following Bolton (1965). *Frammia* is discussed further below.

Whittington and Campbell (1967, p. 468) have discussed the resemblances between *E. variolaris* and their genus *Fragiscutum*. We agree with them, both as to the over-all similarity and also in considering the ten thoracic segments of *Fragiscutum* to be an important distinguishing feature.

Shergold and Bassett (1970, p. 113) have recorded a major shelly faunal change at



TEXT-FIG. 2. Arrangement of glabellar tubercles in *Encrinurus variolaris* (Brongniart). Tubercles I–II–III–IV–V–VI-1 emphasized. A, BU 723. Much Wenlock Limestone Formation, Dudley, West Midlands. Figured Tripp 1962, pl. 65, fig. 17. Tubercles I-1 on a common base. B, T 716. Much Wenlock Limestone Formation, Dudley, West Midlands. Figured Schrank 1972, pl. 13, fig. 8. C, BM 59036. 'Lower Ludlow', Dudley, West Midlands. Plate 113, fig. 4. Tubercle ii-0 present; 3L transversely enlarged with tubercle III-2 close. D, OUM C372. Wenlock Shale, Malvern, Hereford-and-Worcester. Figured Tripp 1962, pl. 65, fig. 18. Tubercle III-2* present. E, BU 724. Much Wenlock Limestone Formation, Dudley, West Midlands. Figured Tripp 1962, pl. 65, fig. 19. Tubercles III-2⁂ present. F, BU 181. Much Wenlock Limestone Formation, Dudley, West Midlands. Plate 113, fig. 3. Tubercle iii-0 absent, III-2 and tubercles (black) between 2L and II-1 present.



TEXT-FIG. 3. Arrangement of tubercles in *Encrinurus*, *Frammia*, and *Fragiscutum*. Tubercles I–II–III–IV–V–VI-1 emphasized. A, *E. diabolus* sp. nov., Purple Shales, Devil's Dingle, Buildwas, Salop. Holotype, BM It. 14096. B, *E. variolaris* (Brongniart), Much Wenlock Limestone Formation, Dudley, West Midlands. Proposed neotype, BU 55. C, *E. rosensteinae* sp. nov., Lower Bringewood Beds, south of Whitbach Farm, Salop. BM It. 13780. D, *E. erraticus* Schrank, Encrinurus-Kalk erratic (Ludlow Series), Neubrandenburg, East Germany. Holotype, figured Schrank 1972, pl. 13, fig. 7. E, *Fragiscutum rhytium* Whittington and Campbell, Hardwood Mountain Formation, Maine, U.S.A. USNM 154275, figured Whittington and Campbell 1967, pl. 12, figs. 1–2. F, *Frammia arctica* (Salter), Read Bay Formation, Garnier Bay, Somerset Island, Canadian Arctic. GSC 25064 (and the lectotype, BM 59681, Cornwallis Island).

the junction of the Lower and Middle Elton Beds. *E. variolaris* occurs rarely in the Lower Elton; *E. rosensteinae* sp. nov. is not known below the Lower Bringewood Beds, in which it is abundant.

Encrinurus diabolus sp. nov.

Plate 114, figs. 1–7; text-fig. 3A

v. 1938 *Encrinurus mullochensis* Reed; Whittard, pp. 122–124, pl. 5, figs. 1–5.

Diagnosis. Glabella moderately convex. 2L and 3L represented by large nodular tubercles; tubercles I-1 forwardly placed, II-1, III-1 distinct. Fixigenal spine diminutive, thorn-like. Free cheek sparsely tuberculate. Rostral plate narrow, parallel-sided. Pygidium non-mucronate, composed of up to fifteen rings and seven pleurae. Four or more sagittal tubercles. Sagittal groove present.

Holotype. BM It. 14096 (internal mould of dorsal shield). Purple Shales (Telychian), Devil's Dingle, Buildwas, Salop (see Cocks and Walton 1968). Plate 114, figs. 1–2.

Dimensions of holotype (*in mm*). Sagittal length of cranidium (normal projection) 4·6; sagittal length of thorax 6·5; sagittal length of pygidium (normal projection excluding half ring) 4·6; width of glabella across lateral tubercles on frontal lobe 3·4; width of glabella across 2L 2·3; width of occipital ring 2·9; maximum width of thoracic rachis 3·2; maximum width of pygidium 6·7.

Occurrence. Llandovery Series: *Pentamerus* Beds (Fronian), Salop; rare. Purple (or Hughley) Shales (Telychian), Salop; common.

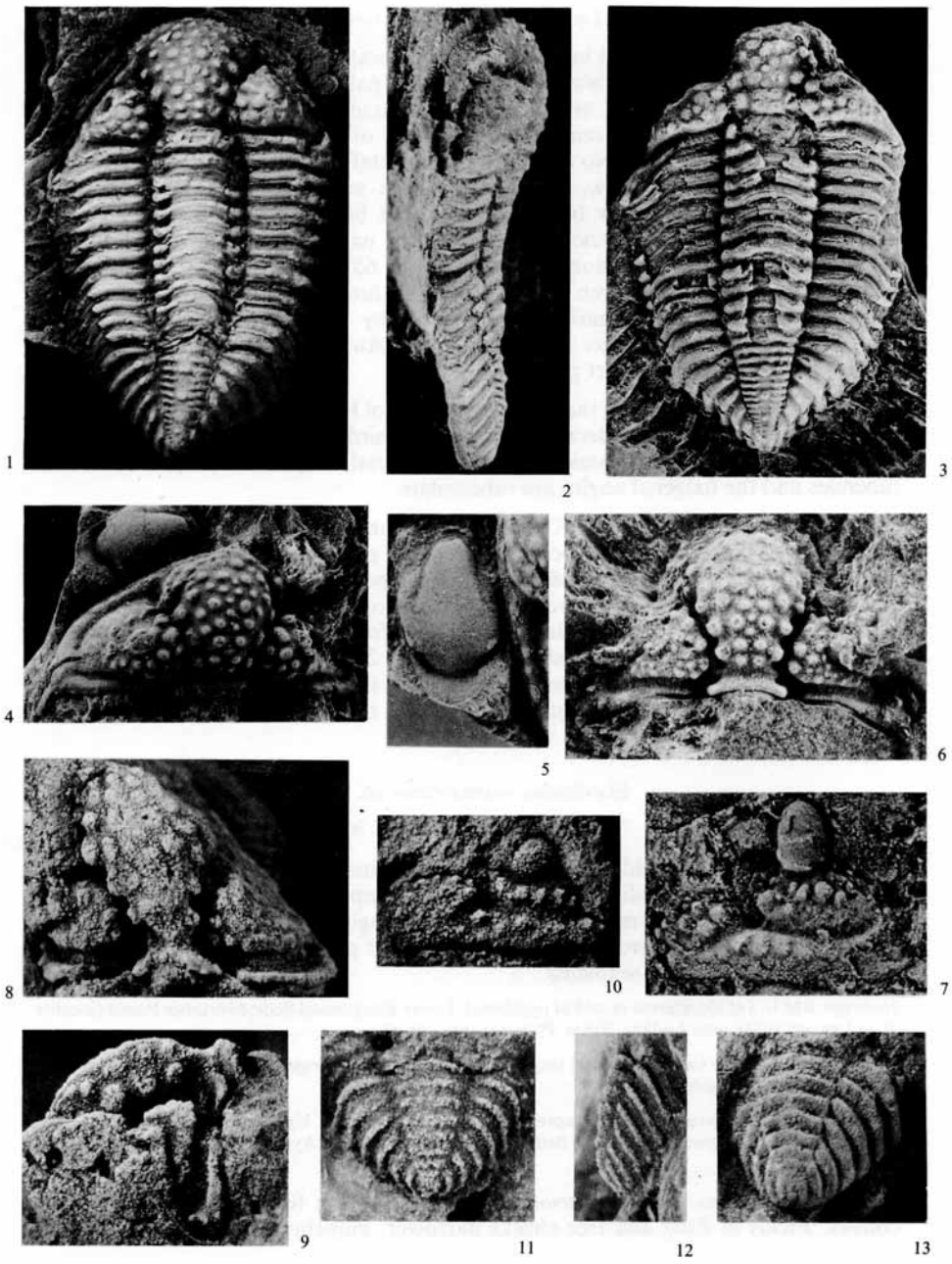
Description. Differs from *E. variolaris* in the following features. Glabella moderately convex. 1L almost obsolete. Occipital furrow stronger. Preglabellar furrow deeper, continuous sagittally. Cheeks lower, narrower, less convex, sloping less steeply sideways. Palpebral lobes placed closer to glabella, midlength opposite 3L. Posterior border transverse. Fixigenal spine diminutive, thorn-like, directed backwards. Field of free cheek broader, particularly posteriorly. Precranidial lobe much shorter. Lateral border increasingly narrower than field towards back. Lateral border furrow deeper. Glabellar tubercle formula: I-1; II-1; iii-0; III-1, (2); I-1 on swollen neck of glabella. Nine or ten tubercles on anterior border of cranidium. Four tubercles on

---

EXPLANATION OF PLATE 114

Figs. 1–7. *Encrinurus diabolus* sp. nov. Figs. 1–5, 7, Purple Shales (Telychian), Devil's Dingle, Buildwas, Salop. Fig. 6, *Pentamerus* Beds (Fronian), Hurst Coppice, Buildwas, Salop. All specimens except Fig. 6 partly testiferous. 1, 2, internal mould of dorsal shield, holotype, BM It. 14096. Dorsal and left lateral views. ×4·5. 3, dorsal exoskeleton, BM It. 14097. ×3·5. 4, cephalon and hypostome, IGS DEX 4786. Dorsal (posterior of standard) view. ×3·75. 5, the same. Hypostome. Anterior of standard view. ×5·5. 6, cranidium, IGS DEX 5979. Posterior of standard view. Internal mould. ×4·5. 7, left free cheek, SM A 97364. ×9.

Figs. 8–13. *Encrinurus* sp. Racine Dolomite? inter-reef, Wisconsin, U.S.A. Internal moulds except fig. 13, which is a latex cast from an external mould. 8, 9, cranidium, MPM 26515, erratic block, Brookfield, Waukesha County. Dorsal (posterior of standard) and left lateral views. ×6·5. 10, left free cheek, MPM 26522, erratic block, Wauwatosa, Milwaukee County. ×6. 11, 12, pygidium, MPM 26242. Milwaukee City Quarry, Wauwatosa, Milwaukee County. Dorsal (anterior of standard) and right lateral views. ×9. 13, pygidium, MPM 26516, erratic block, Brookfield, Waukesha County. Anterior of standard view. ×5.



TRIPP, TEMPLE and GASS, *Encrinurus*

adaxial margin of fixed cheek interspaced with lateral glabellar tubercles; third from back transversely enlarged. Two tubercles between palpebral lobe and rachial furrow. Field of free cheek with six or seven tubercles, mainly adaxially; strongly pitted. Tubercles two deep on precranidial lobe. Border of free cheek with five tubercles adjacent to border furrow. No tubercles on occipital ring, borders of cranidium, or thorax. Rostral plate narrow, parallel-sided, not wedge-shaped. Middle body of hypostome longer, posterior tongue shorter and broader; hypostome finely and uniformly granulate. Thoracic rachis relatively narrow, outer parts of pleurae strongly downturned. Pygidium broader, length 65% width, rachis 35% anterior width. Up to fifteen rings, seven pleural ribs. First three rings continuous, subsequent rings strong abaxially, increasingly interrupted by sagittal groove. Three to five sagittal tubercles much longer (sag.) than rings. Anterior ribs curve gently downwards. Tips of ribs form short points.

Variation. Two cranidia from the *Pentamerus Beds* of Hurst Coppice differ from topotype material only in minor details: the enlarged third tubercle from the back on the adaxial margin of the fixed cheek of topotype material is replaced by a pair of smaller tubercles and the fixigenal angles are tuberculate.

Remarks. Distinctive features of *E. diabolus* are summarized in Table 5. The specimens referred by Whittard to *E. mullochensis* Reed and placed in the synonymy are well-preserved dorsal shields of *E. diabolus*. The new species differs from *E. mullochensis* Reed (1931, p. 19) and from the related *E.* cf. *mullochensis* (Temple 1970, pp. 66–68, pl. 19, figs. 1–10) from the early Llandovery of Meifod, Montgomeryshire, as follows: 1, the tuberculation of the cranidium is coarser; 2, 1L is less strongly developed; 3, tubercles I-1 and II-1 are forwardly placed; 4, there are fewer rachial rings and fewer pleural ribs in the pygidium; 5, tubercles on the pygidial rachis are more strongly developed.

Encrinurus rosensteinae sp. nov.

Plate 115, figs. 1–13; text-fig. 3c

Diagnosis. Glabella weakly convex. Fixigenal spine absent. Rostral plate small, square, or elongate. Pygidium non-mucronate, composed of up to eleven rings and nine pleural ribs. Four or more sagittal tubercles. Sagittal groove strongly developed. A transverse row of tubercles on occipital ring and posterior cranidial border, and on thoracic and pygidial segments.

Holotype. BM It. 14139 (external mould of pygidium). Lower Bringewood Beds, Mortimer Forest (locality 31 of Lawson 1973), near Ludlow, Salop. Plate 115, figs. 10, 13.

Dimensions of holotype (in mm). Sagittal length of pygidium (normal projection, excluding half ring) 7·3; maximum width of pygidium 7·6.

Occurrence. Ludlow Series: Lower Bringewood Beds; very common. Upper Bringewood Beds. Lower Leintwardine Beds. Upper Leintwardine Beds. 'Lower Ludlow Shales.' 'Aymestry Group.' 'Upper Ludlow Shales.'

Description. Differs from *E. variolaris* in the following features. Glabella weakly convex. Fields of fixed and free cheeks narrower. Palpebral lobes placed closer to

glabella. Fixigenal angle angulate; fixigenal spine absent. Precranidial lobe shorter. Lateral border of free cheek evenly convex, not curving inwards posteriorly. Tubercles I-1 forwardly placed but markedly smaller than II-1, one sometimes absent. Tubercles III-2 often share a common base with 3L. Frontal lobe more sparsely tuberculate. Twelve tubercles on anterior border of cranidium. Five or six smaller tubercles on fixed cheek alongside rachial furrow. Two tubercles between rachial furrow and palpebral lobe. Seven tubercles on field of free cheek. Tubercles two deep on precranidial lobe. Rostral plate small, square or elongate, tuberculate. Hypostome with shorter, almost parallel-sided longitudinal median lobe, granulation uniformly coarse. Thorax shorter; rachis comparatively wider, greatest width near midlength in some specimens. Pygidium comparatively larger, almost as long as thorax. Nine to eleven rings plus a terminal piece and nine pleural ribs. Rachis narrower, raised but flat-ended. Border with a posterior sagittal indentation. Four or more sagittal tubercles. Sagittal groove seen to be more strongly developed on internal than on external mould. A transverse row of tubercles along occipital, thoracic, and pygidial segments; adaxial tubercle on pygidial ribs only slightly larger on successive pleurae.

Variation. One specimen (Pl. 115, fig. 11) has a sagittal tubercle II-0, in place of the usual II-1 (compare Tripp 1962, pl. 66, fig. 8). A cranidium from the Lower Bringewood Beds, Mary Knoll Valley (BM It. 14132) differs conspicuously from other specimens in the shape of the glabella, which is broad-based and tapers slowly to a point anteriorly, instead of being broadly rounded. A dorsal exoskeleton from the steam shaft, Colwall tunnel (BM I. 6197) has a narrower rostral plate.

TABLE 5. Distinctive features of *Encrinurus variolaris* and allied species.

CHARACTER \ SPECIES	*diabolus*	*variolaris*	*rosensteinae*	*obtusus*	*erraticus*	*anticostiensis*
GLABELLA						
Convexity	moderate	strong	weak	moderate	moderate	strong
Tubercle 1-1	large	large	small, inconsistent	small	large	large
Tubercle iii-0	small	fairly large	small	fairly large	large	fairly large
ANTERIOR BORDER OF CRANIDIUM						
Number of tubercles	9 - 10	9 - 14	12	12	10	?10
FIELD OF FIXED CHEEK						
Number of tubercles between palpebral lobe and rachial furrow	2	3	2	2	3	2
Modal number of tubercles alongside rachial furrow	4	5	5 - 6	5	5	4
FIELD OF FREE CHEEK						
Modal number of tubercles	7	14	7	12	6	?
FIXIGENAL SPINE	small	small or absent	absent	absent	absent	?
ROSTRAL PLATE	narrow, parallel sided	narrow, wedge shaped	square or elongate	narrow, trapezoidal	?	?
PYGIDIUM						
Number of rings (excluding terminal piece)	13 - 15	8 - 10	9 - 11	11 - 14	12 - 14	19 - 21
Number of ribs	7	7 - 8	9	10 - 11	11	8
Modal tubercle placing	1,4,7,10	1,3,5,7	1,4,6,8	1,2,4,6,9	4,7,9,11	2,7,10,14,18
Sagittal groove	weak	strong	strong	moderate	moderate	absent
STRATIGRAPHICAL DISTRIBUTION	Llandovery	Wenlock and Ludlow	Ludlow	Ludlow	Ludlow	Llandovery

Encrinurus sp.

Plate 114, figs. 8–13

Occurrence. Middle Wenlock: Racine Dolomite? inter-reef. Erratics, Brookfield, Waukesha County, Wisconsin. Milwaukee City Quarry and Hartung Quarry, Wauwatosa, Milwaukee County, Wisconsin. Erratics, Wauwatosa. Sugar Run Formation. Lehigh Quarry, 35 kilometres west of Kankakee, Kankakee County, Illinois. Wenlock Series: Sugar Run Formation? Grafton Quarry, 1·6 kilometres east of Grafton, Jersey County, Illinois.

Description. Size small for the family. Cranidium known only from internal mould. Glabella longer than wide, strongly convex. Rachial furrows deep. 1L obsolete. Occipital and posterior border furrows strong. Fixigenal spine absent. Eye large, slightly pedunculate. Field of free cheek narrow (tr.). Glabellar tubercles II-1 and III-1 distinct. Two tubercles between palpebral lobe and rachial furrow. Six tubercles on field of free cheek. Anterior border of cranidium, rostral plate, hypostome, and thorax not known. Pygidium non-mucronate, composed of seven to nine rings and seven pleural ribs. Rachis about 35% width. Sagittal tubercles usually on first, third, fifth, seventh, eighth, and ninth rings.

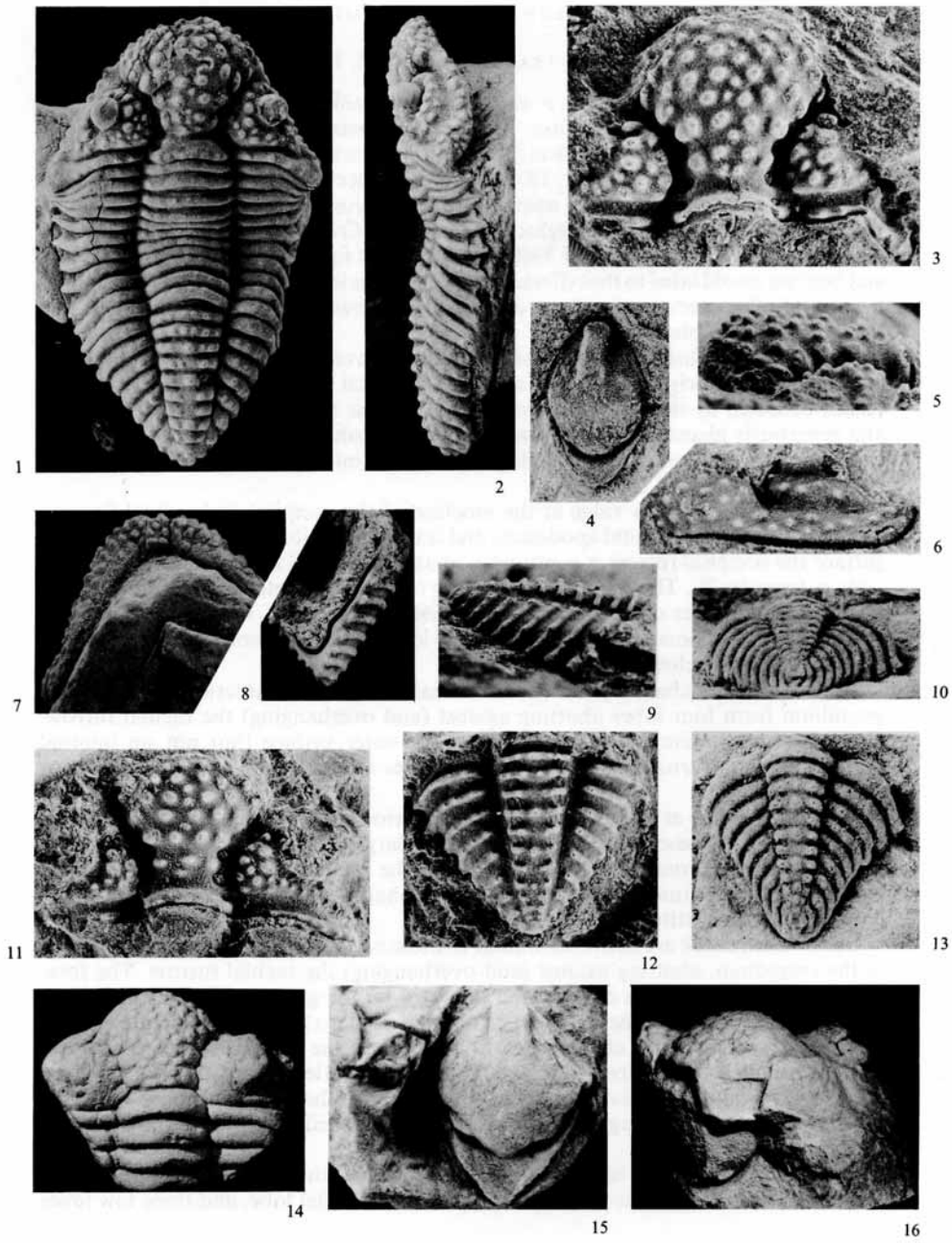
Variation. One pygidium from an erratic at Brookfield differs in its less convergent rachial furrows, and its pleurae curve less strongly backwards.

Remarks. This form, although as yet imperfectly known, is related to the three British species described above. Among North American species, it can be compared with *E. anticostiensis* Twenhofel (1928, p. 330, pl. 59, fig. 9 only) from the Jupiter Formation of Anticosti Island, from which it differs in the smaller number of segments in the pygidium.

EXPLANATION OF PLATE 115

Figs. 1–13. *Encrinurus rosensteinae* sp. nov. Ludlow Series. Figs. 1–3, testiferous, 4–11, internal moulds, 12, 13, latex cast. 1, 2, 7, dorsal exoskeleton, BU 171. 'Lower Ludlow', Sedgley, West Midlands. Dorsal, right lateral and anteroventral views. ×2·5. 3, 5, cranidium, BM It. 13780. Lower Bringewood Beds, south of Whitback Farm, Salop. Dorsal and left lateral views. ×4·5. 4, hypostome, BM In. 14017. Lower Bringewood Beds, Mortimer Forest (locality 31 of Lawson 1973), near Ludlow, Salop. Anterior of standard view. ×4·5. 6, left free cheek, BM It. 14100. Lower Bringewood Beds, Mortimer Forest (locality 31 of Lawson 1973), near Ludlow, Salop. ×5·5. 8, pygidium, BU 1919. Probably Aymestry Limestone, View Edge, Craven Arms, Salop. Oblique right posteroventral view, showing posterior sagittal indentation in border. ×3. 9, 12, pygidium, BM It. 13779. Lower Bringewood Beds, south of Whitbach Farm, Salop. Right lateral and dorsal views. ×4·5. 10, 13, pygidium, holotype, BM It. 14139. Latex cast from external mould. Lower Bringewood Beds, Mortimer Forest (locality 31 of Lawson 1973), near Ludlow, Salop. Posterior and dorsal views. ×4·5. 11, cranidium, BM It. 13788. Lower Bringewood Beds, Quarry opposite North Lodge, Millichope Park, Salop. Showing three instead of the usual four tubercles in row II of the glabella. Posterior of standard view. ×3·7.

Figs. 14–16. *Frammia arctica* (Salter). Testiferous specimens. 14, 15, incomplete cephalon, hypostome, and three thoracic segments, lectotype, BM 59681 (?figured Salter 1852, pl. 5, fig. 14*a*). Upper Silurian, Cornwallis Island. 14, dorsal view. ×3. 15, ventral view. ×4·5. 16, cranidium, left free cheek, rostral plate, and hypostome, GSC 47564. Read Bay Formation, Garnier Bay. Anterior view. ×2·75.



TRIPP, TEMPLE and GASS, *Encrinurus*, *Frammia*

Genus FRAMMIA Holtedahl, 1914

The type species of *Frammia* is *F. dissimilis* Holtedahl (1914, p. 35, pl. 8, figs. 17–19) from the Ludlow of the Canadian Arctic, which was considered subsequently by Holtedahl (1924, p. 131) and Bolton (1965, p. 4) to be a synonym of another Canadian Arctic species, *E. arcticus* Salter, 1852. [Note: the species *arcticus* is here ascribed to Salter who first introduced the name, albeit provisionally, in 1852 (p. ccxxi, pl. 5, fig. 14, 14*a*), rather than to Haughton who erected *Cromus arcticus* in 1858 (p. 241, pl. 6, figs. 1–5). A cephalon (BM 59681) possibly that figured by Salter (pl. 5, fig. 14*a*) and bearing an old label to that effect, is here chosen as lectotype of the species, Pl. 115, figs. 14–15. The specimen has been developed; it shows three thoracic segments and the hypostome in place.]

In order to establish the features of *Frammia* we have studied Salter's, Haughton's, and Holtedahl's original material and also material from Garnier Bay and Seal Island collected by the University of Ottawa and the Geological Survey of Canada and generously placed at our disposal by Dr. T. E. Bolton. All the material studied is considered to be conspecific. The following notes are intended to supplement Bolton's (1965) redescription of *arcticus*.

1L is reduced to a low ridge at the junction of the occipital and rachial furrows between the 1S and occipital apodemes, and is thus not visible dorsally. On the dorsal surface the occipital furrow is continuous abaxially with 1S and is followed immediately in front by 2L. The occipital ring is long (sag.) and is notched anterolaterally to form two small lobes of which the anterior one simulates a 1L lobe or occipital lobe and the posterior one corresponds to the acute lobes at the front corners of the thoracic rachial rings (see below).

2L, 3L, and the abaxial parts of the frontal lobe and the anterior border of the cranidium form four lobes abutting against (and overhanging) the rachial furrow. The lobes are circumscribed adaxially on the outer surface (but not on internal moulds) by faint furrows: the two foremost lobes are flat-topped, the two posterior ones less so.

Beneath the lobe at the distal end of the anterior border of the cranidium on the adaxial side of the base of the rachial furrow is a large, deep apodeme-like projection, and obliquely in front of this at the base of the rachial furrow and immediately behind the facial suture is what appears to be a shallow fossula: these two structures may, however, constitute a composite fossula.

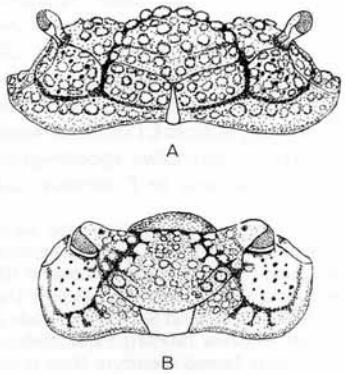
On the fixed cheek are five lobes similar to those on the glabella and anterior border of the cranidium, abutting against (and overhanging) the rachial furrow. The foremost of these cheek lobes opposes the foremost on the glabellar side of the rachial furrow (as may the next one or two back on each side), so that these lobes are square-ended; the two posterior cheek lobes do not oppose the glabellar lobes. The genal angle is rounded. The palpebral lobe continues the gentle upward slope of the fixed cheek away from the rachial furrow so that the tops of the lobes rise above the plane tangent to the occipital ring and frontal lobe of the glabella. Surface of the palpebral lobe bears a pit.

On the free cheek there is a low, flat-topped lobe abutting against the continuation of the rachial furrow at the abaxial end of the precranidial lobe, and three low lobes

abaxially to this on the lateral border beyond the anterior furrow. On the opposite side of the rachial furrow continuation is a low flat-topped lobe opposing the first-mentioned of these lobes. The visual surface of the eye is separated from the cheek by an eye socle of variable height (up to 1·3 mm).

The exoskeleton is very thick, so that, whereas on the outer surface the cranidial furrows are narrow with the two sides almost touching (often actually touching in the case of the lobes flanking the rachial furrow from 3L forwards), on the internal mould the furrows are wide.

The outer surface of the cranidium (excluding the occipital ring and borders) is tuberculate, but the inner surface (as seen on internal moulds) is usually almost smooth. Each tubercle apparently bears a pore (occasionally more than one) represented externally by a depression and internally by a ventrally raised rim. The glabellar tubercle formula (excluding lobes adjoining rachial furrow) is: I-1; II-1; iii-0; III-1, 2* or 2_*.



TEXT-FIG. 4. Reconstructed anterior views of the cephala of *Encrinurus variolaris* (Brongniart) and *Frammia arctica* (Salter), showing differences in the rostral plates; based largely on the following specimens: A, *E. variolaris*, Much Wenlock Limestone Formation, Dudley, West Midlands. BU 580. B, *F. arctica*, Read Bay Formation, Garnier Bay, Somerset Island, Canadian Arctic. GSC 25064. ×1·5.

The rostral plate (text-fig. 4B) is large, trapezoidal, wider (tr.) than long (sag.), narrowest (tr.) at hypostomal suture, posteriorly concave against facial suture; on GSC 47564 (Pl. 115, fig. 16) the rostral plate is 4 mm wide (max., tr.) and the glabella 8 mm wide at ends of preglabellar furrow. Anteriorly the rostral plate bears the raised cephalic margin and in front of this the foremost part of the plate is turned back almost at a right angle as the doublure.

The hypostome, of generalized encrinurine structure, is rather broad and with a strong macula.

Five complete thoraces have been studied, and all are interpreted as showing eleven segments. The anterior corners of the rachial rings are drawn out anterolaterally into acute lobes, thus causing the rachial furrows of each segment to be slightly oblique to the exsagittal line and to be offset abaxially at the front of each segment relative to the rachial furrows of the segment in front. The adaxial ends of the pleurae are abruptly but slightly obliquely truncated at the rachial furrow where they oppose the abaxial ends of the rings across the sharply delimited rachial furrow. The distal end of the posterior pleural band forms a short blunt pleural spine separated by a notch

(the notches collectively forming a vincular groove, presumably for the cheek margin) from the distal end of the articulating facet.

The pygidium is non-mucronate, with twelve to fifteen rachial rings without sagittal groove or tubercles, and ten (rarely eleven) pleurae. Shape of rachial rings, obliquity and offsetting of rachial furrows, as in thoracic segments. The border is ventrally facing, widening markedly forwards, with a slightly raised inner rim diminishing posteriorly, and a posterior sagittal indentation.

E. (*Frammia*) *rossicus* Maksimova (1970, p. 207, pl. 2, figs. 9–15), from the Ludlow of Vaigach Island, Arctic U.S.S.R., is known only from its cranidium, free cheek, and pygidium, but is clearly closely related to *F. arctica*. It differs apparently in its stronger cephalic tuberculation, and in the more direct opposition of the three main glabellar lobes against those on the fixed cheek; the rostral plate of *rossicus* is not known.

Other species, described and undescribed, show a gradation between *F. arctica* and *E. variolaris* and allied species. For instance, the exoskeleton figured by Bolton (1965, pl. 2, fig. 10) differs from *F. arctica* in the presence of 1L, the absence of extremely large lobes on the cheek, and the presence of sagittal tubercles on the pygidium. It resembles *E. variolaris* more closely than it does *F. arctica* and *F. rossica*. If, however, the range of *Frammia* were to be extended to include *E. variolaris*, following Schrank (1972), it would be difficult to draw a line excluding certain species of the *E. punctatus* species-group. At present, therefore, we prefer to restrict the genus *Frammia* to *F. arctica* and *F. rossica*.

Acknowledgements. We thank the authorities of the following Institutions for the loan of specimens (abbreviated prefixes of specimen numbers are given in parentheses): Birmingham University (BU); British Museum (Natural History), London (BM); Institute of Geological Sciences, London (IGS); Sedgwick Museum, Cambridge (SM); Oxford University Museum (OUM); National Museum of Wales, Cardiff (NMW); Geological Survey of Canada (GSC); National Museum of Ireland, Dublin (NMI); Milwaukee Public Museum (MPM); Palaeontological Museum, Oslo. Dr. P. D. Lane and Mr. D. Mikulic have generously loaned specimens from their personal collections. We also thank Dr. A. W. A. Rushton for helpful advice. Tripp thanks the Leverhulme Trust for the award of a Research Fellowship.

REFERENCES

ANGELIN, N. P. 1854. *Palaeontologia Scandinavica.* Part 1. *Crustacea formationis transitionis* Fasc. 2, Lipsiae: T. O. Weigel, pp. 1–9, 21–92, pls. 25–41.

BAILY, W. H. 1871. *Figures of characteristic British fossils* (*Palaeozoic Division*), *with descriptive remarks.* Part 3. London. 62–92, pls. 21–30.

BOLTON, T. E. 1965. Trilobites from Upper Silurian rocks of the Canadian Arctic Archipelago: *Encrinurus* (*Frammia*) and *Hemiarges. Contribution to Canadian palaeontology*, 1. *Bull. geol. Surv. Canada*, **134,** 1–14, pls. 1–3.

BRONGNIART, A. 1822. *Histoire naturelle des Crustacés fossiles . . . Les Trilobites.* Paris, 65 pp., 4 pls.

CLARKSON, E. N. K. and HENRY, J.-L. 1973. Structures coaptatives et enroulement chez quelques trilobites ordoviciens et siluriens. *Lethaia*, **6,** 105–132, figs. 1–16.

COCKS, L. R. M. and WALTON, G. A. 1968. A large temporary exposure in the Lower Silurian of Shropshire. *Geol. Mag.* **105,** 390–397.

EMMRICH, H. F. 1844. *Zur Naturgeschichte der Trilobiten.* Meiningen, 28 pp., 1 pl.

FLETCHER, T. W. 1850. *Observations on* Dudley trilobites. Part 2. *Q. Jl geol. Soc. Lond.* **6,** 402–405, pl. 32.

HAUGHTON, S. 1858. Description of the plates to illustrate the geology of Captain M'Clintock's ice-travels. *J. R. Dublin Soc.* **1,** 239–250.

HOLTEDAHL, O. 1914. On the fossil faunas from Per Schei's Series B in south western Ellesmereland. *Rept 2nd Norwegian Arctic Exp. in the 'Fram' 1898–1902*, No. 32, 1–48.
—— 1924. Report of the scientific results of the Norwegian expedition to Novaya Zemlya 1921, Vol. 2. *Geology*, No. 22, 1–183.
LA TOUCHE, J. D. 1884. *A handbook of the Geology of Shropshire*. London, 91 pp., 22 pls.
LAWSON, J. D. 1973. New exposures in forestry roads near Ludlow. *Geol. J.* **8,** 279–284.
MAKSIMOVA, Z. A. 1970. Silurian trilobites of Vaigach Island. *In* S. V. CHERKESOVA (ed.). *Stratigraphy and fauna of the Silurian of Vaigach*. NIIGA, Leningrad, 195–209, pls. 1–2. [In Russian.]
MÄNNIL, R. 1968. *Encrinurus schmidti* sp. n. (Trilobita) from the Llandoverian of Estonia. *Eesti NSV Teaduste Akadeemia Toimetised* [*Keem. Geol.*], **17,** 273–278, pls. 1–2.
MILLER, J. 1976. The sensory fields and life mode of *Phacops rana* (Green, 1832) (Trilobita). *Trans. R. Soc. Edinb.* **69,** 337–367, pls. 1–4.
MURCHISON, R. I. 1839. *The Silurian System*. London, xxxii + 768 pp., pls. 1–37.
REED, F. R. C. 1925. Some new Silurian trilobites. *Geol. Mag.* **62,** 67–76, pl. 2.
—— 1927. Palaeontological notes on the Silurian Inlier of Woolhope. *Q. Jl geol. Soc. Lond.* **83,** 531–550.
—— 1928. Notes on the Family Encrinuridae. *Geol. Mag.* **65,** 51–77.
—— 1931. The Lower Palaeozoic trilobites of the Girvan District, Ayrshire. *Palaeontogr. Soc.* (*Mongr.*), suppl. 2, 1–30.
SALTER, J. W. 1852. Geology. *In* SUTHERLAND, P. C., *Journal of a Voyage in Baffin's Bay and Barrow Straits, in the years 1850–1851*. Vol. 2. London, App., ccxvii–ccxxxiii, pls. 5–6.
—— 1853. Figures and descriptions illustrative of British organic remains, Decade 7. *Mem. geol. Surv. U.K.* pls. 1–10.
SCHRANK, E. 1972. Proetacea, Encrinuridae und Phacopina (Trilobita) aus silurischen Geschieben. *Geologie*, **21,** Beih. 76, 1–117, pls. 1–21.
SHERGOLD, J. H. and BASSETT, M. G. 1970. Facies and faunas at the Wenlock/Ludlow boundary of Wenlock Edge, Shropshire. *Lethaia*, **3,** 113–142.
TEMPLE, J. T. 1954. The hypostome of *Encrinurus variolaris* and its relation to the cephalon. *Geol. Mag.* **91,** 315–318.
—— 1970. The Lower Llandovery brachiopods and trilobites from Ffridd Mathrafal, near Meifod, Montgomeryshire. *Palaeontogr. Soc.* [*Mongr.*], 1–76, pls. 1–19.
—— 1975. Standardisation of trilobite orientation and measurement. *Fossils and Strata*, **4,** 461–467.
TRIPP, R. P. 1957. The trilobite *Encrinurus multisegmentatus* (Portlock) and allied Middle and Upper Ordovician species. *Palaeontology*, **1,** 60–72, pls. 11–12.
—— 1962. The Silurian trilobite *Encrinurus punctatus* (Wahlenberg) and allied species. Ibid. **5,** 460–477, pls. 65–68.
—— TEMPLE, J. T. and GASS, K. C. 1977. *Calymene variolaris* Brongniart, 1822 (Trilobita): proposed use of the plenary powers to designate a neotype in harmony with current use. *Bull. Zool. Nomencl.* **33,** 250–252.
TWENHOFEL, W. H. 1928. Geology of Anticosti Island. *Mem. geol. Surv. Canada*, **154,** 1–481, pls. 1–60.
VOGDES, A. W. 1878. *A monograph on the genera* Zethus, Cybele, Encrinurus *and* Cryptonymus. Charleston, 35 pp., 4 pls.
—— 1907. The genus *Encrinurus*; its history, its species, its proper division in the family of trilobites. *Trans. San Diego Soc. Nat. Hist.* **1,** 61–83, pls. 1–3.
—— 1917. Palaeozoic Crustacea—the publications and notes on the genera and species during the past twenty years, 1895–1917. Ibid. **3,** 1–141, pls. 1–5.
WHITTARD, W. F. 1938. The Upper Valentian trilobite fauna of Shropshre. *Ann. Mag. nat. Hist.* (11), **1,** 85–140, pls. 2–5.
WHITTINGTON, H. B. and CAMPBELL, K. S. W. 1967. Silicified Silurian trilobites from Maine. *Bull. Mus. comp. Zool. Harv.* **135,** 447–483, pls. 1–19.

R. P. TRIPP
Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

J. T. TEMPLE
Department of Geology
Birkbeck College
Gresse Street
London W1P 1PA

K. C. GASS
5101 N. 21st. St.
Milwaukee
Wisconsin 53209
U.S.A.

Typescript received 21 July 1976
Revised typescript received 25 November 1976