

ENTOMOZOACEAN OSTRACODS FROM THE LOWER CARBONIFEROUS OF SOUTH-WESTERN ENGLAND

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ABSTRACT. The Entomozoacea ('entomozoids') are an important group of Palaeozoic ostracods which flourished in the upper Devonian and lower Carboniferous. Although they have traditionally been regarded as planktonic, the carapace morphology of the entomozoaceans provides no clear evidence for either a planktonic or benthic existence and it is concluded that both these modes of life may have been represented within the group. This paper is the first significant published account of these ostracods in the British Carboniferous. Sixteen species from the Tournaisian of Devon, south-western England, are described and illustrated. Six are assigned to known species, one (*Maternella (M.) whitewayensis* sp. nov.) is new and the remainder are dealt with under open nomenclature. The British assemblages, particularly those from excavations made near Whiteway Barton, closely resemble faunas from the lower and middle *latior* Zone of entomozoacean chronology (broadly equivalent to the *Gattendorfia ammonoid Stufe*) reported by Groos-Uffenorde (1974) from the Rheinische Schiefergebirge.

THE ostracods described in this paper belong to the families Entomozoidae Přibyl, 1949 and Rhomboentomozoidae Gründel, 1962 which are regarded herein as constituting the superfamily Entomozoacea Přibyl, 1949. The entomozoaceans (often called 'entomozoids'—a term avoided here because it is ambiguous) are a peculiar Palaeozoic group in which the carapace is weakly calcified and usually bears a characteristic ribbed ornamentation, giving rise to their colloquial name 'fingerprint ostracods'. They are often considered to have been planktonic and have long been known to occur abundantly in upper Devonian deep-water slates, particularly in Germany where they have proved to be of considerable stratigraphic value (Rabien 1954, 1956). It has become apparent more recently that entomozoaceans are also important in lower Carboniferous (Tournaisian and Viséan) rocks of similar facies (Bless 1973; Becker and Bless 1974; Gründel 1962; Tschigova 1970, 1975; Sanchez de Posada 1977; Groos-Uffenorde in press). Species have been described, or at least illustrated, from the lower Carboniferous of Germany (Kummerow 1939; Rabien 1960; Gründel 1961, 1963, 1979; Koch 1970; Groos-Uffenorde 1974, in press; Sanchez de Posada and Bless 1974), Spain (Jordan and Bless 1970), Poland (Błaszyk and Natusiewicz 1973), U.S.S.R. (Posner 1958; Tschigova 1977), China (Wang 1978), and Canada (Green 1963) as well as from the upper Carboniferous (Namurian A) of Spain (Becker 1975, 1976). However, apart from a few obscure species of '*Entomis*' (Jones 1873, p. 416) and three species which have been briefly mentioned recently (Selwood *et al.* 1982, table 1), no Carboniferous entomozoaceans have yet been documented in the British literature.

The main purpose of the present paper is to describe a small but important collection of these ostracods from the Tournaisian of Devon, south-western England. Much of the material was obtained during the remapping of I.G.S. 1:50,000 sheet 339 (Newton Abbot) under an Institute of Geological Sciences-Exeter University contract. It is all in the form of internal and external moulds in slates and shales and for the most part is well preserved. The literature on entomozoaceans is principally German, the major publication being the monograph of Rabien (1954), and they remain unfamiliar to many English-speaking ostracod specialists. In order to provide some introduction to the group, a brief, general account of the preservation, shell structure, and carapace morphology of upper Devonian and lower Carboniferous species is given here together with a consideration of their palaeoecology in the light of morphological features. A review of the stratigraphic distribution of Carboniferous entomozoaceans follows the systematic section.

PRESERVATION, SHELL STRUCTURE, AND CARAPACE
MORPHOLOGY OF THE ENTOMOZOACEA

Preservation. Unlike those of most fossil ostracods, entomozocean shells very rarely survive as calcareous objects which can be extracted from the rock matrix. They occur most commonly as internal and external moulds in slates and shales (Rabien 1954, p. 21), the cavity between the moulds sometimes partly occupied by reddish-brown material, presumably some form of iron-oxide. In this mode of preservation the valves are almost always disarticulated (Rabien 1954, p. 14) and, as fully discussed by Rabien (1954, pp. 22-25), they are frequently subject to tectonic deformation. According to its orientation with respect to the tectonic 'stretching direction', a specimen may be extended or compressed parallel to its long axis or deformed obliquely into an asymmetric shape (Gooday 1973, fig. 3.5). Deformation can therefore modify taxonomic characters such as valve outline, length/height ratio, and rib spacing and must be taken into account when describing or identifying species.

Entomozoaceans are sometimes preserved in limestones, where they may occur as complete articulated carapaces (Rabien 1954, pp. 13-14). Several such specimens of *Entomozoe* (*Nehdentomis*) *nehdensis* Matern from upper Devonian limestones were examined in section and by scanning electron microscopy by Langer (1973, p. 25). Building on the preliminary observation of Rabien (1954, p. 14), Langer demonstrated that the shell was represented by a thin outer layer (3-5 μm thick) which formed the ornamentation, and an underlying crypto- or microcrystalline layer (15-25 μm thick). He believed that the crystalline structures observed were secondary, the original, weakly calcified shell having been completely replaced by calcite.

Other types of preservation have occasionally been reported. Silicified valves were obtained from limestones by Blumenstengel (1965) and Becker (1977) while Gooday (1973, p. 19) recorded the occurrence of articulated carapaces in the form of external moulds in decalcified 'gingerbread' nodules. Pyritized internal moulds are occasionally found in slates and limestones (Gooday 1973, p. 18; Lethiers 1974, p. 64).

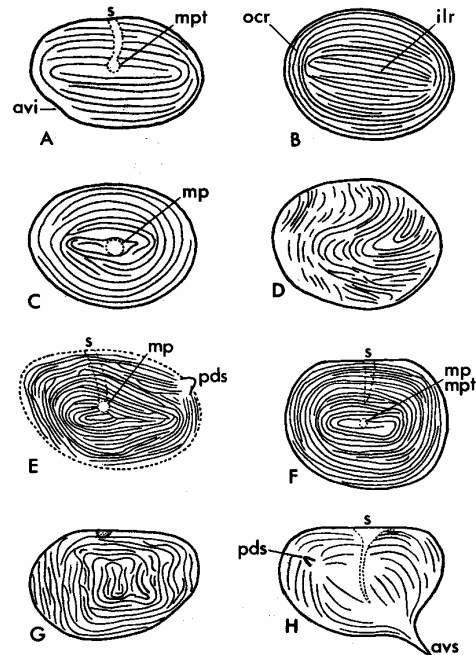
Shell structure. The entomozocean carapace was probably weakly calcified like that of Recent members of the family Halocyprididae (Kummerow 1939, pp. 81, 85; Triebel 1941, p. 327; Rabien 1954, pp. 14, 17; Langer 1973, p. 25; Becker 1976, p. 215; 1977, p. 472). The ribs, however, may have been rather more strongly calcified than the rest of the shell. Langer (1973, p. 25) speculated that, as in recent myodocopids (a group which includes the halocypridids), the carapace wall contained embedded particles of amorphous calcium carbonate as well as oil droplets to aid bouyancy. The shell also seems to have been thin ('sehr dünnchalige': Rabien 1954, p. 14; Becker 1976, p. 216) although Langer (1973, p. 25) believed that this was not true in the case of *E. (N.) nehdensis*. Entomozocean valves are occasionally dislocated in a manner suggesting that they were torn prior to preservation (text-fig. 3; Gooday 1973, p. 20; see also Triebel 1941, p. 327). These observations clearly support the notion of a thin and rather flimsy shell. According to Becker (1977, p. 472) there was also an internal chitinous layer which was 'very thick and . . . formed the interior sculpture'. This seems to echo Groos-Uffenorde's (1974, pp. 78-79) suggestion that the two different types of rib present on external moulds of *Maternella schindewolfi* (Kummerow) were derived from different shell layers.

A rather different view of the nature of the carapace wall was put forward by Blumenstengel (1965, 1973). He argued that because valves may sometimes be silicified, they must have originally been heavily calcified, the calcite having been replaced by silica. This opinion was strongly challenged by Becker (1977, p. 472). However, Becker (1976, p. 216) himself drew attention to a rare species of *Entomoprimitia* from the Frasnian of Belgium which undoubtedly possessed a thick, heavily calcified shell.

Carapace morphology. Carapace terminology is summarized in text-figs. 1 and 2.

Many entomozoaceans apparently have valves of equal size (Rabien 1954, p. 14) although Langer (1973, p. 25) found that in *E. (N.) nehdensis*, the right valve projects beyond the left valve along the dorsal margin. There is no evidence for any kind of hinge structure and the valves were therefore

TEXT-FIG. 1. Carapace outlines and rib patterns of typical upper Devonian and Carboniferous entomozoaceans. A-E, family Entomozoidae, subfamily Entomozoinae; F, G, subfamily Entomoprimitiinae; H, family Rhomboentomozoidae. A, generalized *Entomozoe* (*Nehdentomis*). B, generalized *Richterina* (*Richterina*). C, *Maternella* (*Maternella*) *dichotoma* Paeckelman (based on Rabien 1954, pl. 1, figs. 8, 9). D, *Kuzminaella venusta* Tschigova (based on Tschigova 1977, pl. xiii, fig. 6). E, *Truyulsina tuyulsina* Becker (based on Becker 1976, text-fig. 3). F, *Entomoprimitia* (*Entomoprimitia*) *kayseri* Waldschmidt (based on Rabien 1954, pl. 2, fig. 13). G, *Bertilionella* (*Rabienella*) *kegeli* (Matern) (based on Rabien and Rabitz 1958, text-fig. 5). H, *Ungerella* cf. *mempeli* Kummerow (based on Groos-Uffenorde 1974, text-figs. 7, 12). Abbreviations: avi, antero-ventral indentation of margin; avs, antero-ventral spine; ilr, inner longitudinal rib; mp, muscle patch; mpt, muscle pit; ocr, outer concentric rib; pds, postero-dorsal spine; s, sulcus. Except for *Ungerella*, the anterior end points left. Drawn at various scales.

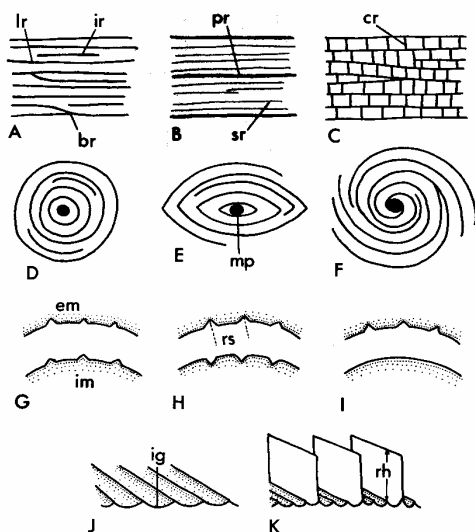


presumably joined in life by an organic, or perhaps chitinous membrane as in the halocypridids. To explain the disarticulated occurrence of valves in deep-water slates, it must be assumed that any such connecting structure decayed rather rapidly after death. Eye tubercles are not developed (Triebel 1941, p. 330; Becker 1976, p. 216). Sexual dimorphism of the carapace has not been reliably documented.

The lateral outline varies considerably within the superfamily but rounded, circular to more or less oval shapes tend to predominate (text-fig. 1). The family Rhomboentomozoidae is characterized by a triangular to subrectangular outline in which the dorsal margin is long and straight; members of the family Entomozoidae, subfamily Entomoprimitiinae are asymmetrically oval and have a shorter straight dorsal margin, while in the subfamily Entomozoinae, the outline is more or less oval with a curved dorsal margin. A slight antero-ventral concavity of the margin is present in some species of *Maternella*, *Entomozoe*, and *Entomoprimitia* (Rabien 1954, p. 94; Gooday 1973, pp. 60-61).

The rhomboentomozoids have a single prominent sulcus (also called a nuchal furrow) arising from near the middle of the dorsal margin and curving downwards so that the concave side faces anteriorly. A sulcus is strongly developed, weakly developed, or absent in most members of the Entomozoidae. However, the subfamily Bouciinae, a poorly known Silurian group which is atypical of the entomozoaceans on a whole, has two sulci, one originating from the dorsal and one from the ventral margin. Two variably developed carapace swellings are present in certain species of the subgenus *E.* (*Entomoprimitia*), the larger one situated antero-ventrally with a smaller inflation behind the sulcus. Antero-ventral and postero-dorsal spines arise from the valve surface in *Ungerella* while *Rhomboentomozoe* bears a single ventral spine and *Truyulsina* has a postero-dorsal spine. Terminal spines are developed at the ends of the valves in two species of *R.* (*Richterina*).

The area of adductor muscle attachment is expressed on the surface of the valve by a pit or a smooth, oval, or circular patch. The pit is either a ventral expansion of the sulcus or an isolated depression. Numerous tiny, circular muscle scars were observed to occur within the muscle pit of *Richterina* (*Fossirichterina*) *semen* (Jones) by Gooday (1973, p. 107). The subgenus *Richterina*



TEXT-FIG. 2. A-K, ribbing terminology. A, longitudinal ribs (lr) with short, intercalated ribs (ir) and bifurcating ribs (br). B, longitudinal ribs differentiated into primary ribs (pr) and secondary ribs (sr). C, longitudinal ribs joined by cross-ribs (cr). D, circular concentric ribs. E, lenticular, concentric ribs. F, spiral ribs around central muscle patch (mp). G, internal mould (im) and external mould (em) with similar ornamentation and H, with reversed ornamentation (rs, rib spacing). I, ornamented external mould with smooth internal mould. J, normal ribs separated by intercostal grooves (ig). K, flange-like ribs (rh, rib height), each pair separated by two normal ribs.

(*Volkina*) has a characteristic small, elongate depression near the dorsal margin of each valve. This may be homologous with the dorsal muscle scar area of some other ostracods (Rabien 1954, p. 15) within which originate muscles connected to various limbs and body parts (Andersson 1974, fig. 10).

In almost all upper Devonian and Carboniferous entomozoaceans the exterior surface of the valve bears ribs separated by intercostal grooves (text-figs. 1 and 2). These are often of uniform strength but in some species are differentiated into stronger primary and weaker secondary ribs. Short cross-ribs may be developed and these subdivide the intercostal grooves into rows of pits. Occasionally, for example in *Bertillonella* (*Rabienella*) *cicatricosa* (Matern), the ribs are replaced by a series of spines arranged in rows. Ribs which extend out from the valve surface as wide flanges have recently been documented (Goody 1973, p. 61; Becker 1977, p. 469). These structures, referred to herein as 'flange-like ribs' are known to occur in the genera *Richterina*, *Maternella*, and *Ungerella*.

Entomozoacean ribs usually follow a more or less regular course, their arrangement and spacing being characteristic for particular species. Elongate carapaces, such as those of *Richterina* and *Entomozoe*, tend to have basically longitudinal ribbing, although in most cases a variable number of outer ribs run concentrically, parallel to the valve margin. In forms with a more rounded outline, the ribs are arranged in a spiral or concentric pattern around a central point (usually the muscle patch) and parallel to the margin. This kind of pattern is found in *Entomoprimitia*, *Truyulsina*, and particularly *Maternella*. Some species have, in addition, a number of more longitudinal, free ending inner ribs. A basically spiral or concentric type of ornamentation is also developed in *Bertillonella*, although here the ribs often follow a somewhat irregular, subtriangular, or subquadrate course. The recently described genus *Kuzminaella* has an unusually irregular, swirling pattern of ribs.

The ornamentation of the original inner surface of the valve, as recorded by internal moulds, usually consists either of ribs or grooves corresponding to the ribs on the outer surface (text-fig. 2G-I). However, the inner surface is occasionally smooth and does not reflect the external ornament.

PALAEOECOLOGY OF THE ENTOMOZOACEA

It has been suggested that entomozoaceans, traditionally regarded as planktonic organisms, were in fact wholly, or in part benthic. In this section these alternative modes of life are scrutinized in the light of certain aspects of the functional morphology and ecology of some Recent ostracods.

Entomozoaceans as planktonic ostracods. Following Kummerow (1939, pp. 80–81), most authors have maintained that entomozoaceans were probably members of the open ocean plankton or micronekton (Triebel 1941, p. 327; Gründel 1962, p. 1196; Becker 1976, p. 215). The morphological evidence includes: (i) the thin, weakly calcified, often streamlined carapace, (ii) the convex ventral margin, and (iii) the tendency for the carapace to become rounded with a high surface-volume ratio (Triebel 1941, p. 327; Gründel 1962, p. 1196; 1965, pp. 599, 606; Becker 1976, p. 215). In addition, the recently documented flange-like ribs of some species increase the surface area of the shell and hence would have retarded its sinking velocity, an obvious advantage for a planktonic animal. The worldwide distribution of entomozoaceans, together with their abundance in facies which are often virtually devoid of other fossils (Franke and Paul 1980, p. 238), also argues for a planktonic existence (Becker 1976, p. 215).

Particular ecological parallels have been drawn between entomozoaceans and the Halocyprididae, a group which includes most of the living, truly oceanic planktonic ostracods. Halocypridids generally occur throughout the water column, but are most abundant at depths of between 100 and 300 m. They are powerful swimmers, propelling their light, generally weakly calcified, boat-like carapaces through the water with surprising speed 'in a zig-zag series of darts' (Lochhead 1968, p. 456) by means of the exopodites of the second antennae. These structures, which bear long swimming setae, emerge through the rostral incisure and strike outwards, backwards, and slightly downwards in a motion resembling the breast stroke (Skogsberg 1920, p. 119; Iles 1961, pp. 304, 323). This powerful swimming stroke is facilitated by the presence of a horizontally orientated rostral incisure and a hollowing of the carapace surface behind the incisure, features which allow a free backwards swing of the exopodite. The swimming musculature is contained in the very large triangular basal segment (protopodite) of the second antenna. The posterior margin of the protopodite is indicated on the carapace surface by a sulcus and, in some species, this segment is accommodated in an antero-dorsal 'shoulder vault' (Müller 1906, p. 6).

Triebel (1941, pp. 327–328), Rabien (1954, p. 15), and Becker (1976, p. 216) have argued that entomozoaceans also possessed a strongly developed second antenna protopodite because they often have a similar sulcus and, in a few species, an antero-ventral swelling which is comparable to the halocypridid shoulder vault. From the supposed presence of a large protopodite, it is inferred that they were sufficiently adept swimmers to maintain themselves in the plankton. However, it seems unlikely that the entomozoaceans swam like halocypridids because they have no rostral incisure. Rabien (1954, p. 94) has proposed that the swimming exopodites ('Ruder-Antennae') may have emerged at the antero-ventral marginal indentation which is present in a few species (see above). If this were the case, these species, at least, must have swum at best rather weakly since the swimming stroke would have included a significant downward component tending to rotate the carapace rather than drive it swiftly and horizontally forwards.

On the other hand, the absence of an incisure does not necessarily preclude a planktonic mode of life. In *Thaumatoocypris echinata* Müller, a very rare ostracod which has been caught only twice, this structure is absent. *T. echinata* is nevertheless planktonic (Kornicker and Sohn 1976b, p. 21) and apparently swims with downward and backward movements of the first and second antenna endopodites and exopodites (Skogsberg 1920, p. 119; Iles 1961, p. 322). It is also significant that *Polycope*, which resembles many entomozoaceans in having an approximately circular outline and no rostral incisure, has a 'comparatively swift and rather tenacious method of swimming involving the first antennae, second antennae exopodites as well as the maxillae' (Skogsberg 1920, p. 119 footnote). However, members of this genus spend most of their time on the bottom and are not truly planktonic.

Entomozoaceans as benthic ostracods. This alternative hypothesis was first proposed by Blumenstengel (1965, 1973) because he believed that the entomozoacean carapace was more strongly calcified than had hitherto been suspected (see above). Kozur (1972a, pp. 642–643) also thought that entomozoaceans were benthic. He considered them to be typical, deep-water psychrosphaeric ostracods, mainly because they are absent, or very rare in upper Devonian cephalopod limestones. In

Kozur's view, the weakly calcified carapace and the widespread distribution and faunal uniformity of entomozoaceans are characteristic of benthic psychrosphaeric ostracods, as well as free-swimming forms, while their greater than average size and high surface to volume ratio he believed to be positive indicators of a deep-water, benthic existence. Becker (1977, p. 472), on the other hand, did not accept that entomozoaceans in general had heavily calcified carapaces and opposed the views of Blumenstengel and Kozur as being too far-reaching (Becker 1976, p. 216). However, he did accept (Becker 1976, p. 215) that the heavily calcified species of *Entomoprimitia* mentioned above was probably benthic.

There is no convincing morphological basis for rejecting the hypothesis that at least some entomozoaceans were benthic. In certain respects (weak calcification, lack of rostral incisure, rounded outline) genera such as *Bertillonella*, *Maternella*, and *Kuzminaella* resemble living representatives of the deep-sea family Thaumatoocyprididae which are mainly benthic or nektobenthic (Kornicker and Sohn 1976b, p. 21). Like some of the Entomozoacea, many thaumatoocypridids possess an antero-ventral concavity of the margin (see particularly *Thaumatoconcha hessleri* Kornicker and Sohn 1976b, fig. 47). The concavity bears no obvious relationship to either the first or second antennae (Kornicker and Sohn, 1976b, p. 20), thus casting doubt on Rabien's (1954, p. 94) suggestion that the marginal indentation of entomozoaceans is a rudimentary rostral incisure.

Conclusion. No single conclusion regarding the palaeoecology of these ostracods can be derived from a consideration of their morphology. The evidence is ambiguous: the weak carapace calcification, flange-like ribs, and inferred presence of a large second antenna protopodite in some species all suggest a planktonic existence while the similarities between some entomozoaceans and the Recent, mainly bottom-dwelling thaumatoocypridids indicate that a benthic mode of life should not be ruled out for some species.

It is quite possible that a variety of ecologies are represented among upper Devonian and Carboniferous Entomozoacea. Some groups, perhaps those in which the sulcus and shoulder vault are weakly developed or absent, may have been benthic or nektobenthic, like *Polycope* and most thaumatoocypridids. Rare, heavily calcified forms were almost certainly benthic (Becker 1976). Others may have been sufficiently strong swimmers to maintain themselves as permanent members of the plankton. Becker (1977, p. 472) also concluded that 'different modes of life are quite possible' for entomozoaceans. This view is supported by the fact that the halocypridids, sometimes regarded as ecological analogues of the entomozoaceans, are themselves not exclusively planktonic. Species of the important genus *Bathyconchoecia* Deevy are members of the deep-water benthos or, in the case of a species recently discovered in Bermuda, cavernicolous (Angel, pers. comm.).

MATERIAL

Geological Setting. In the area covered by the I.G.S. 1:50,000 Newton Abbot map, Devonian and Carboniferous rocks occupy six thrust-bounded successions which are characterized by distinct facies, particularly in the upper Devonian. The successions are summarized on Sheet 339 and in the Newton Abbot Memoir (in press). Lower Carboniferous entomozoids have been obtained from two of these sequences.

(i) The Teign Valley Succession. Entomozoaceans occur sparsely in the Hyner Shale, a formation comprising dark bluish-grey shales which span the Devonian-Carboniferous boundary, and also in the overlying grey and green shales of the Trusham Shale. This succession is structurally autochthonous and is characterized by an upright fold style.

(ii) The Ugbrooke-East Ogwell Succession. A well-preserved entomozoid fauna occurs in the Whiteway Slate. This formation consists of purple, grey and green slates and, like the Hyner Shale, it includes the Devonian-Carboniferous boundary. The Ugbrooke-East Ogwell Succession is allochthonous and characterized by recumbent, north-facing folds.

Full information on the structure and stratigraphy of the area will be published in the Newton Abbot Memoir.

Localities. The ostracods were obtained from the localities listed below. In the systematic section these are identified by abbreviations (WS1, etc.). The Newton Abbot Memoir includes an illustration (fig. 11) showing the position of the trenches and exposures at Whiteway Barton. Except where indicated, the specimens were collected by Drs. E. B. Selwood and R. A. Waters.

Whiteway Slate locality 1 (WS1): SX 8844 7525; exposure behind barn and cutting alongside it; north end of Whiteway Barton farmyard.

Whiteway Slate locality 2 (WS2): SX 8860 7545-8857 7754; loose debris collected from north-eastern side of ploughed field just north of Whiteway Barton.

Whiteway Slate locality 3 (WS3): SX 8857 7553; from trench trending 146° parallel to north-eastern edge of field between SW 8857 7533 and 8856 7555, beginning 24.6 m from north-western edge of field and running south-eastward for 30.4 m at distance of 3.6 m from north-eastern edge of field. Specimens collected from south-eastern end of trench to 5.2 m along it in north-westerly direction.

Whiteway Slate locality 4 (WS4): SX 8857 7553; specimens collected between 5.2 and 10.6 m from south-eastern end of same trench.

Whiteway Slate locality 5 (WS5): SX 8857 7554; specimens collected between 10.6 and 13.7 m from south-eastern end of same trench.

Trusham Shale locality 1 (TS1): SX 8426 8113; exposure on eastern side of track just north of Leigh Farm.

Trusham Shale locality 2 (TS2): SX 8428 8138; exposure produced by ploughing in field east and south of Emmett Copse.

Hyner Shale locality 1 (HS1): SX 8424 8123; exposure in same field, about 18.2 m south of locality TS2.

Bampton Limestone Formation locality 1 (BLF1): SS 9722 2385; exposure on western side of road, opposite Higher Hukely, north-east of Bampton. Collected by Dr. J. M. Thomas.

Techniques. Latex casts of external moulds were prepared according to the technique described by Rigby and Clark (1965). These casts precisely reproduce the external ornamentation of the shell and also produce better photographic results than the original specimens. All photographs were obtained on Kodak Panatomic × 35 mm film using the Leica Aristophot system with micro-mirror reflex attachment and bellows. The text-figures were drawn with the aid of a Wild M5 'Zeichentubus'.

SYSTEMATIC PALAEOLOGY

Following German practice, more than half of the sixteen species are described under open nomenclature (Matthews 1973). The suprageneric classification adopted in this paper is that of Gründel (1962, p. 1203). All specimens are deposited in the Institute of Geological Sciences in London (registration numbers AD2537-2551, 2676-2817) and Leeds (AD3686-3706, 3719-3759, ZO4386-4394).

Order MYODOCOPIDA Sars, 1866 Superfamily ENTOMOZOACEA Přibyl, 1949

Diagnosis. Large ostracods, usually > 1 mm, with weakly calcified carapace which lacks rostrum and rostral incisure. Sulcus well developed, weakly developed, or absent. Surface often with longitudinal, concentric, or spiral ribs. (Modified after Sylvester-Bradley 1961, p. 388).

Discussion. Following Gründel (1969, p. 30), this superfamily is limited to the families Entomozoidae and Rhomboentomozoidae. It is not considered to include the enigmatic Bolbozoidae. However, Gründel's (1969) combination of the Entomozoacea with the Entomoconchacea, another group of unusual Palaeozoic ostracods, to form the suborder Entomozocopina of the order Myodocopida has been refuted (Kozur 1972a, p. 7) and there is probably no close relationship between these two superfamilies. Indeed, Kornicker and Sohn (1976a) have argued that the Entomoconchacea probably belong to the Halocypridina (a suborder including the Thaumatoocypridacea and Halocypridacea) and may have been ancestral to the living thaumatoocypridaceans.

It has usually been considered that the Entomozoacea were related in some way to the myodocopids. Thus Sylvester-Bradley (1961, p. 388) placed them, with a question mark, in the suborder Myodocopina together with the extant superfamilies Thaumatoocypridacea, Cypridinacea, and Halocypridacea and the fossil Entomoconchacea. Polenova and Zanina (1960), however, classified the family Entomozoidae (= Entomozoacea) with the living Polycopidae (*Polycope* and *Polycopsis*) in the suborder Cladocopa of the order Myodocopida. These two groups have in common the absence of a rostral incisure and, in some cases, an oval or circular lateral outline. The case for a

relationship between the entomozoaceans and polycopids has been argued by Kozur (1972a, p. 641; 1972b, p. 8). Analysis of evolutionary trends led him to the conclusion that an advanced entomozoacean, perhaps *Bertillonella*, was ancestral to the Carboniferous to Triassic genus *Discoidella*, which in turn evolved into *Polycope* and *Polycopsis*. Kozur (1972a, p. 641) found *Discoidella* very difficult to separate from polycopids in material from Triassic deep-water sediments. These opinions have been incorporated into two recent and authoritative classifications (Pokorný 1978, p. 130; Maddocks 1982, table 1) in both of which the entomozoaceans and polycopids are combined together within the suborder Cladocopa, order Myodopida.

The claim that polycopids are descended from entomozoaceans is difficult to assess because the classification of myodocopids is based largely on their soft-part anatomy (Kornicker and Sohn 1976b, pp. 4–6). However, several points argue against such a direct relationship. First, there is no immediately obvious similarity in the carapace shape of the two groups as there is between the Palaeozoic entomoconchaceans and their probable living descendants, the thaumatocypridaceans (Kornicker and Sohn 1976a, pls. 2, 3). The absence of a rostral incisure in both groups may be of no significance since this is a primitive condition and hence not evidence for a phylogenetic relationship (Kornicker and Sohn 1976b, p. 5). Secondly, some entomozoaceans have what appear to be thirty to fifty tiny, round adductor muscle scars (Gooday, 1973; 1978, pl. 1, fig. 9). There are only three such scars in polycopids. Thirdly, *Polycope* is known from the Carboniferous (Pokorný 1978, p. 132) and may occur as early as the middle Devonian (Whidborne 1890; Přibyl 1953), well before the first occurrence of *Discoidella*, or indeed *Bertillonella*. For these reasons I prefer at present to regard the Entomozoacea as a distinct Palaeozoic group of myodocopids of which the precise affinities are unclear (see also Kornicker and Sohn 1976b, p. 6).

Family ENTOMOZOIDAE Přibyl, 1949

Type genus. Entomozoe (Jones, 1861) *sensu* Přibyl, 1949.

Diagnosis. Valves of equal or slightly differing sizes. Lateral outline bean-shaped, egg-shaped, asymmetrically or symmetrically oval. Straight section of dorsal margin short, never corresponding to greatest carapace length and sometimes replaced by curved dorsal margin; dorsal angles rounded where present. Sulcus strongly developed, weakly developed, or absent; where present it is straight or concave towards anterior end. Secondly, postero-ventral sulcus developed in one subfamily (Bouciinae). Muscle attachment area either absent or represented by smooth patch or pit. Spines or protuberances occasionally developed. Ornamentation usually present and in most genera comprises ribs of equal or unequal strength. Ribs are arranged transversely (Bouciinae), longitudinally, spirally, or concentrically, but are occasionally irregular or broken into minute spines. (Slightly modified after Rabien 1954, p. 44; Gründel 1962, p. 1158.)

Discussion. The Entomozoidae comprises three subfamilies: the Entomozoinae, Entomoprimitiinae, and the Bouciinae, the latter including only the unusual Silurian genus *Boucia* Agnew.

Subfamily ENTOMOZOINAE Přibyl, 1949

Diagnosis. Lateral outline bean-shaped, egg-shaped, or symmetrically oval. Straight dorsal margin never clearly developed, sometimes absent. Ornamentation in earlier forms basically longitudinal with concentric ribs at end; in later forms concentric or spiral. (After Gründel 1962, p. 1203.)

Discussion. The Entomozoinae includes the following genera and subgenera: *Entomozoe* (*Entomozoe*) Přibyl, 1949; *E. (Richterina)* Jones, 1874; *E. (Nehdentomis)* Matern, 1929; *Kuzminaella* Tschigova, 1977; *Maternella (Maternella)* Rabien, 1954; *M. (Steinachella)* Gründel, 1979; *Rabienites* Tschigova, 1977; *Richterina (Richterina)* Gürich, 1896; *R. (Fossirichterina)* Matern, 1929; *R. (Volkina)* Rabien, 1954; *Truyulsina* Becker, 1975.

Genus RICHTERINA Gürich, 1896

Type species. Cytherina costata Rh. Richter, 1869.

Diagnosis. Lateral outline symmetrical, in form of elongate to broad oval with equally curved dorsal and ventral margins and equally rounded ends. Sulcus not developed. Central muscle pit or patch may be developed. Indentation of carapace near dorsal margin developed in one subgenus. Ornamentation comprises (i) longitudinal ribs of equal strength, inner ones ending free before ends of valve but outer ones continuing concentrically parallel to margin, or (ii) longitudinal primary ribs and weaker secondary ribs with cross-ribs sometimes also present. Terminal spines occasionally developed.

Subgenus RICHTERINA (RICHTERINA) Gürich, 1896

Diagnosis. Simple muscle pit not developed but muscle patch may be present. Dorsal indentation of carapace absent. Ribs typically of equal strength, inner ones ending free, outer ones running concentrically, but in one species of unequal strength. Terminal spines developed in two species.

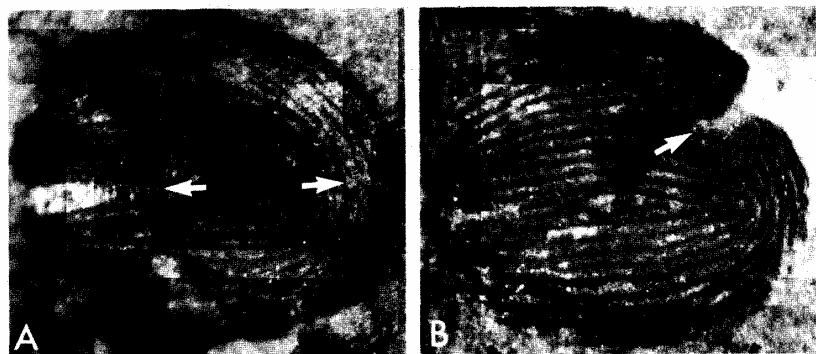
Discussion. The difficulties created by Matern's (1929) designation of *R. (R.) costata* as the type species of *Richterina* are dealt with by Gründel (1962, p. 1201).

Richterina (Richterina) latior Rabien, 1960

Plate 74, fig. 1; text-figs. 3, 4A-F

- (?) 1879 *Entomis gyrata* (Rh. Richter, 1856); Jones, p. 186, pl. xi, fig. 4.
- (?) 1890 *Entomis richteri* Jones, pp. 321-322, pl. xi, fig. 3.
- v* 1960 *Richterina (Richterina) latior* Rabien, pp. 69-74, pl. 1, figs. 1-4; pl. 2, figs. 6, 7.
- v. 1961 *Richterina (Richterina) latior* Rabien; Gründel, pp. 123-125, pl. 11, fig. 6; text-figs. 13-16.
- v. 1974 *Richterina (Richterina) latior* Rabien; Groos-Uffenorde, pp. 80-81, pl. 4, fig. 5.
- v. 1974 *Richterina (Richterina) latior* Rabien; Alberti, Groos-Uffenorde, Streel, Uffenorde and Walliser, p. 270.
- (?) 1977 *Richterina (Richterina) latior* Rabien; Tschigova, pp. 105-107, pl. xiv, fig. 3.
- (?) 1978 *Richterina (Richterina) latior* Rabien; Wang, p. 4, pl. 2, figs. 17, 18.

Diagnosis. Species of *Richterina* having broadly oval and symmetrical lateral outline with mean length/height ratio of 1.4-1.6. Surface bears twenty-five to thirty-five longitudinal ribs of equal



TEXT-FIG. 3. *Richterina (Richterina) latior* Rabien, 1960. Two external moulds photographed under glycerol. Note tear-like features (arrowed). A, AD2696, maximum dimension 1.70 mm. B, AD2696, maximum dimension 2 mm.

strength, following straight course with few bifurcations; at least four, usually six to twelve ribs are concentric at ends of valve, most of remainder terminate before ends. Rib spacing regular and relatively wide, averaging about 0.04 mm. Circular muscle patch interrupts several central ribs. (Modified after Rabien 1960, p. 69.)

Material studied. About ninety specimens: localities WS1 (AD2539, 2540, 2543, 2547, 2551); WS2 (AD2676, 2678, 2679, 2685-2688, 2691, 2692, 2692A, 2695, 2695B, 2696, 2697B, 2698A, 2698B); WS4 (AD2786); WS5 (AD2806); TS1 (AD3720, 3726, 3728, 3731, 3733, 3737, 3738, 3741); TS2 (AD3744, 3745, 3748, 3753-3756, 3758); HS1 (AD3686-3689, 3693, 3696, 3698-3670, 3702, 3704-3706).

Dimensions.

<i>Adults</i>			
	Number of specimens	Range	Mean
Length (mm)	31	0.95-2.30	1.53
Height (mm)	31	0.60-1.75	1.05
L/H ratio	31	1.21-1.75	1.43
<i>Juveniles</i>			
	Number of specimens	Range	Mean
Length (mm)	8	0.50-0.90	0.76
Height (mm)	8	0.40-0.70	0.57
L/H ratio	8	1.23-1.42	1.33

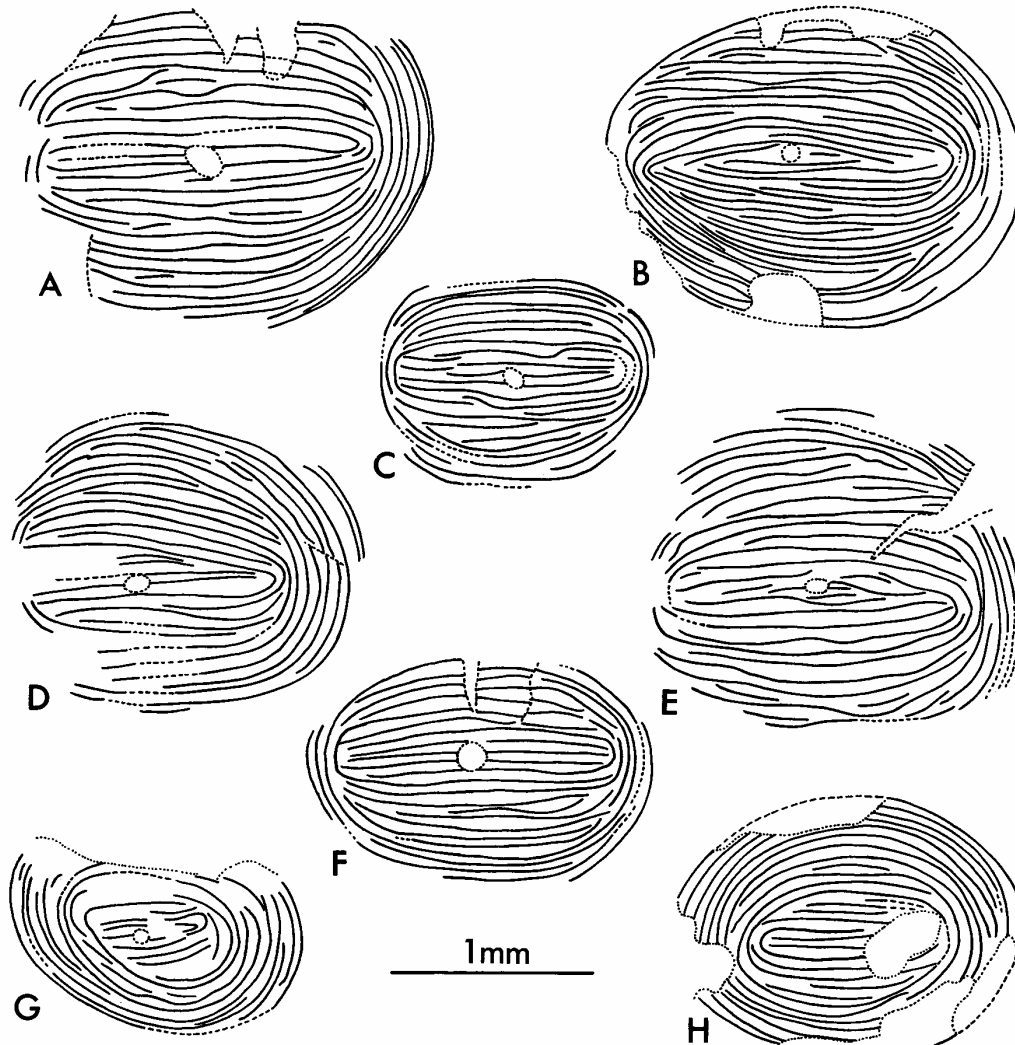
Description of British material

Adults. The lateral outline is broadly and symmetrically oval, with gently curved dorsal and ventral margins and broadly and equally rounded ends. The surface bears twenty-five to thirty-four narrow longitudinal ribs separated by broader intercostal grooves; five to eight outer ribs run concentrically, parallel to the ends of the valve. In one atypical specimen (text-fig. 4b) some of the ribs follow a rather more narrowly rounded course at one end of the valve. Ribs which are intercalated between the main ribs occur fairly frequently. The rib spacing varies from 0.032 to 0.070 mm (mean 0.045 mm) near the centre of the valve, decreasing slightly towards the margin. At the centre of most valves there is a smooth, circular, sometimes rather indistinct muscle patch, 0.075-0.15 mm in diameter, which cuts across one or two ribs.

Juveniles. The valves have a rather more elongate outline than the adults and bear twenty to twenty-seven ribs with a spacing of 0.023-0.032 mm.

Discussion. *R. (R.) latior* has been regarded as a typical richterinid which, according to Gründel (1962, pp. 1188-1190, fig. 5), evolved directly from *R. (R.) striatula* (Rh. Richter, 1848). Rabien (1960, p. 73) notes that these two species can be distinguished only by their length/height ratios, the number of concentric ribs and the rib spacing and remarks that between '*R. striatula* und der neuen Art bestehen also keine prinzipiellen, sondern nur graduelle Merkmalsunterschiede'. A closer scrutiny, however, reveals further differences. i. The adductor muscle attachment area is represented in *R. (R.) latior* by a circular patch which interrupts several ribs, but in *R. (R.) striatula* by a broadening of two adjacent intercostal grooves near the centre of the valve (Gooday 1978, pl. 1, fig. 3). Rabien (1960, p. 69) records an 'undeutlicher kleiner Fleck' near the centre of the valve, but a muscle patch is clearly visible in some of the British specimens. In view of the importance attached to the muscle attachment area in ostracod taxonomy, this difference between the two species may be of some significance. ii. Cross-ribs are sometimes present at the ends of the valve in *R. (R.) striatula* (Gooday 1978, pl. 1, figs. 2, 3) but are never developed in *R. (R.) latior*. iii. The ribbing pattern of *R. (R.) latior* is less regular, usually with more numerous intercalated ribs than in *R. (R.) striatula*, and always with some inner longitudinal ribs which curve around at the ends of the valve. iv. Internal moulds are clearly ornamented in *R. (R.) latior* but smooth in *R. (R.) striatula*. For these reasons it is concluded that the two species may not be particularly closely related.

It is interesting to note that the ribbing patterns of *R. (R.) latior* and *Maternella (M.) dichotoma* may be rather strikingly similar (compare particularly the somewhat unusual specimen illustrated in text-fig. 4b with Gooday, 1978, pl. 3, fig. 4). However, since the lateral outlines of these two species are



TEXT-FIG. 4. A-F, *Richterina (Richterina) latior* Rabien, 1960. A, AD2697B, internal mould. B, AD2698A, internal mould. C-F, AD2696, external moulds. G, H, *Richterina (Richterina)* sp. 1, internal moulds (G, AD2698B; H, AD2696).

different and conform clearly with the diagnosis of their respective genera (symmetrical in *R. (R.) latior*, asymmetrical in *M. (M.) dichotoma*), it seems likely that this resemblance is the result of convergent evolution.

Jones (1879, pl. xi, fig. 4) illustrated as *Entomis gyrata* a German oyster which had a ribbing pattern similar to that of *R. (R.) latior*. The only apparent difference is that Jones's figure indicates the presence of spines on the ribs. In a later paper, Jones (1890) described a new species, *Entomis richteri*, from a single specimen collected at Whiteway Farm (near localities WS1-5). This specimen, which is apparently now lost, measured 2×1.4 mm and had about fifteen ribs, only one of which

seems to be concentric in Jones's (1890, pl. xi, fig. 3) figure. The identity of *E. richteri* is unclear but it may have been based on an incomplete specimen of *R. (R.) latior*.

The Chinese specimens illustrated by Wang (1978) as *R. (R.) latior* have rather more numerous and less regularly arranged ribs than in typical European material. In these respects they are somewhat similar to *R. (R.) aff. latior* of Jordan and Bless (1970) and Gründel (1963).

Distribution. South-western England, Rheinische Schiefergebirge, Thüringia, European part of U.S.S.R. and possibly Kwangsi Province, China.

Richterina (Richterina) sp. 1

Text-figs. 4G, H

Material Studied. Two internal moulds: locality WS2 (AD2696, 2698B).

Dimensions.

Length (mm)	Height (mm)	L/H ratio
1.72	1.25	1.38
> 1.62	—	—

Description. The lateral outline is incompletely known but apparently broadly oval with equally rounded ends. The surface of the most complete specimen bears about thirty ribs across the greatest height. Approximately ten central ribs run parallel to the long axis and either end free or curve around at the ends of the valve. The remaining ribs run concentrically, parallel to the margin. There are some short, intercalated ribs. The rib spacing varies from 0.04 to 0.05 mm. One specimen has a small central muscle patch, interrupting a single rib. Internal moulds are ornamented by broad ribs separated by narrow grooves.

Discussion. The ribbing pattern of this form resembles that of *R. (R.) latior* but there are fewer inner longitudinal ribs and proportionally more outer concentric ribs. The various ostracods described under the name *R. (R.) aff. latior* either have fewer ribs (Sanchez de Posada and Bless, 1974) or more ribs (Gründel 1963; Jordan and Bless 1970) than *R. (R.) sp. 1*. Their ribbing is also less regular with fairly numerous intercalation and bifurcations. A specimen of *Maternella steinachensis* Gründel 1961 from the *Pericyclus* Stufe, illustrated by Gründel (1963, pl. 2, fig. 7), is rather similar to *R. (R.) sp. 1*.

Genus MATERNELLA Rabien, 1954

Type species. *Richterina(?) costata* var. nov. *dichotoma* Paeckelman, 1913.

Diagnosis. Lateral outline slightly asymmetrical and somewhat egg-shaped. Ventral margin more strongly curved than dorsal margin, posterior end more broadly rounded than anterior end. Maximum length just over half carapace height, maximum height and breadth somewhat behind mid-point. Sulcus not developed. More or less well-developed muscle patch lies at centre of sculpture. Strong, narrow ribs run concentrically or spirally, parallel to margin; in central part of valve ribs may run parallel to long axis. Weak cross-ribs or pits may be developed in intercostal grooves. Spines absent. (Modified after Rabien 1954, p. 134).

Discussion. The essential difference between *Maternella* and *Richterina* lies in the shape of the lateral outline which is symmetrical about the dorsal-ventral and anterior-posterior axes in *Richterina* but asymmetrical about these axes in *Maternella*.

A first step towards subdividing this unwieldy genus was taken by Gründel (1979) who established a new subgenus *Steinachella* for maternellids in which the ribs are not usually drawn out parallel to the long axis of the valve, but are arranged spirally or concentrically around the sculpture centre. An additional point is that all species of *M. (S.)* (with the possible exception, discussed below, of the problematical *M. pfaffenbergensis*) have simple, low ribs, whereas in several species of *M. (M.)* the ribs are flange-like.

The nominate subgenus still includes a rather heterogenous array of species and it may ultimately be necessary to split the genus further.

Subgenus MATERNELLA (MATERNELLA) Rabien, 1954

Diagnosis. In central part of valve ribs are arranged more or less longitudinally or rhomboidally; variable number of ribs are concentric at ends of valve. Flange-like ribs may be developed. (Modified after Gründel 1979, p. 756.)

Discussion. As Gründel (1979, p. 757) pointed out, the ribbing patterns in the subgenera *Richterina* (*Richterina*) and *Maternella* (*Maternella*) show convergent trends which, in lower Carboniferous material, make them difficult to distinguish if the lateral outline is incomplete. It is also worth noting that in some lower Carboniferous species of *M.* (*M.*) the lateral outline, while showing more or less obvious anterior-posterior asymmetry (anterior end more narrowly rounded than posterior), appears, at least in British material, to have dorsal and ventral margins of approximately equal curvature, thereby deviating from the generic diagnosis. Lateral outlines of this kind have been observed in *M.* (*M.*) aff. *arcuata* (Pl. 74, figs. 3, 4), *M.* (*M.*) *clathrata* (Pl. 74, fig. 2; although Groos-Uffenorde 1974, p. 76 mentions an antero-ventral indentation of the margin), and *M.* (*M.*) *whitewayensis* sp. n. (see below). This point deserves further scrutiny.

Maternella (*Maternella*) aff. *arcuata* Gründel, 1961

Plate 74, figs. 3-4

v. 1974 *Maternella* cf. *arcuata* Gründel, 1961; Groos-Uffenorde, p. 74, pl. 2, fig. 5.

Material studied. Fourteen specimens: locality WS3 (AD2732, 2732A, 2765, 2766, 2768A, 2769, 2770).

Dimensions.

Length (mm)	Height (mm)	L/H ratio
2.10	1.55	1.35
1.60	1.15	1.43
1.45	1.10	1.32
1.10	0.80	1.38
1.10	0.80	1.38
1.00	0.75	1.33
0.85	0.65	1.31

Description of British material

Adults. The lateral outline is broadly oval, the dorsal and ventral margins are gently curved, and the ends broadly rounded and apparently symmetrical. The surface bears fifty to sixty fine concentric ribs separated by rather narrower grooves. In the outer part of the valve, the ribs are arranged parallel to the margin. Towards the interior they become more nearly longitudinal and follow an elongate, lenticular course which is sharply pointed at either end. A number of shorter ribs are intercalated between these inner and outer regions. The rib spacing varies from 0.022 to 0.032 mm. Fine cross-ribs with a spacing of 0.025-0.040 mm are clearly, although rather variably developed. At the centre of the ornamentation is a small, poorly defined muscle patch, about 0.10 mm diameter. Internal moulds have a well-developed ornamentation, similar to that on the outer surface.

Juveniles. Four specimens are probably juveniles. They are 0.85-1.10 mm long and have thirty-one to thirty-five ribs with a spacing of 0.022-0.025 mm.

Discussion. Unlike the species described by Gründel (1961, p. 133), this form has clearly developed cross-ribs and an apparently more symmetrical outline. The British material is identical to that described by Groos-Uffenorde (1974).

Some of the specimens illustrated by Jordan and Bless (1970, figs. 14-20) as *R.* (*R.*) aff. *latior* are reminiscent of *M.* (*M.*) aff. *arcuata* but the ribbing is less regular and is not arranged in a clearly lenticular pattern in the central part of the valve.

Distribution. South-western England, Rheinische Schiefergebirge.

Maternella (Maternella) cf. circumcostata Rabien, 1960

Material studied. Three poorly preserved and incomplete internal moulds: localities WS2 (AD2696), TS1 (AD3724, 3726; strongly deformed).

Dimensions. Approximate lengths: 1.60 mm (specimen lying parallel to tectonic stretching direction), 1.15 mm, 0.80 mm.

Description. The internal moulds have broad ribs separated by narrow grooves. There are twenty to thirty mostly spiral ribs across the height of the valve. In the central part of the valve, the ribs are lenticular, following a narrowly rounded or angular course at either end. The rib spacing is 0.05–0.06 mm.

Discussion. The three specimens are similar to *M. circumcostata*, as described by Rabien (1960, pp. 78–82) and Groos-Uffendorde (1974, p. 74), but are not well enough preserved to be positively identified.

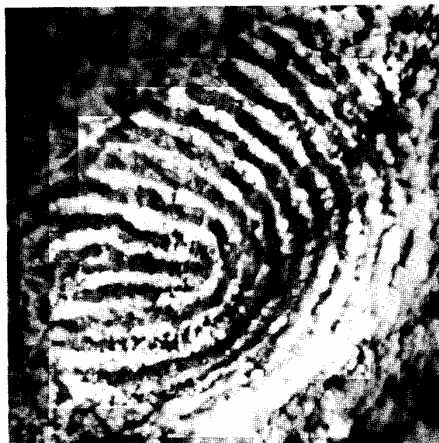
Maternella (Maternella) sp., aff. *M. circumcostata* Rabien, 1960 *sensu* Groos-Uffendorde (1974)

Text-fig. 5

v. 1974 *Maternella (Maternella) sp.*, aff. *M. circumcostata* Rabien, 1960; *sensu* Groos-Uffendorde, pp. 74–75, pl. 5, figs. 4, 7; text-fig. 5.4–7.

Material studied. One incomplete external mould: locality TS1 (AD3719).

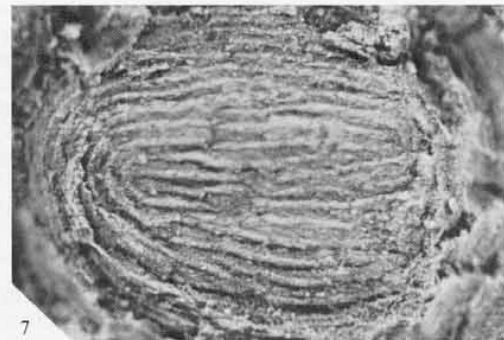
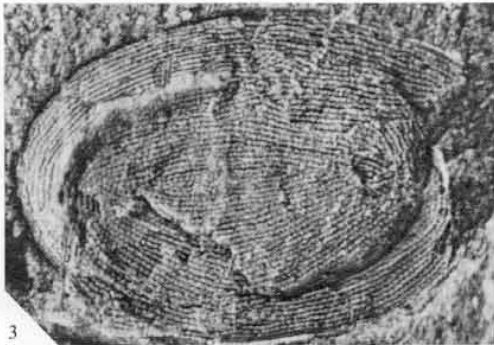
Dimension. Approximately 1.40 mm.



TEXT-FIG. 5. External mould of *Maternella (Maternella) sp.*, aff. *circumcostata* Rabien, 1960, *sensu* Groos-Uffendorde (1974), maximum dimension 1.40 mm, AD3719.

EXPLANATION OF PLATE 74

- Fig. 1. *Richteria (Richteria) latior* Rabien, 1960. AD2697B, internal mould, maximum dimension 2 mm.
 Fig. 2. *Maternella (Maternella) clathrata* (Kummerow, 1939), form 1. AD2770, internal mould, maximum dimension 2 mm.
 Figs. 3, 4. *Maternella (Maternella) aff. arcuata* Gründel, 1961. 3, AD2770, internal mould, maximum dimension 2.10 mm. 4, AD2732, latex cast of external mould, maximum dimension 1.60 mm.
 Fig. 5. *Maternella (Maternella) sp. 5 sensu* Groos-Uffendorde (1974). AD2692, external mould, width of upper part 1.75 mm.
 Figs. 6, 7. *Maternella (Maternella) whitewayensis* sp. nov. 6, Holotype, AD2767, latex cast of external mould, maximum dimension 2.43 mm. 7, AD2729A, internal mould, maximum dimension 2.16 mm.



GOODAY, Carboniferous entomozoacean ostracods

Description of British specimen. The external mould has broad ribs separated by intercostal grooves of similar width. There are eleven to twelve ribs between the centre and outer margin with a spacing of about 0.05 mm. They follow a spiral course which is approximately oval and more narrowly rounded at the anterior end. There are few intercalated ribs.

Discussion. The single specimen compares well with Groos-Uffenorde (1974) species. It is distinguished from *M. cf. circumcostata* by the broad ribs and the oval rather than lenticular course of the ribbing.

Distribution. South-western England, Rheinische Schiefergebirge.

Maternella (Maternella) clathrata (Kummerow, 1939)

Plate 74, fig. 2; text-fig. 6A-J

- (?) 1879 *Entomis gyrata* (Rh. Richter, 1859); Jones, pl. xi, figs. 8a, b, 18a, b.
 v* 1939 *Richterina (Richterina) clathrata* Kummerow, pp. 59-60, pl. 7, fig. 4.
 (?) 1961 *Maternella gyrata* (Rh. Richter, 1859); Gründel, pp. 132-133, pl. 12, fig. 6.
 v. 1974 *Maternella clathrata* (Kummerow, 1939); Groos-Uffenorde, p. 76, pl. 3, figs. 1, 2, 6; pl. 6; text-fig. 6.1-8.

Diagnosis. Relatively large species of *Maternella (Maternella)* with broadly oval lateral outline. Surface bears twenty to thirty-two (occasionally more) narrow ribs across height of valve, most of them following concentric, oval course, parallel to margin, with fairly numerous intercalated ribs towards centre. Variable number of ribs in outer part of valve often deflected outwards sigmoidally. Main ribs may be joined by weaker cross-ribs. Rib spacing: 0.035-0.083 mm. Central muscle patch interrupts several ribs.

Material studied. Form 1, about thirty-five specimens: localities WS2 (AD2695, 2695A, 2696, 2698A, 2698B), WS3 (AD2716, 2717, 2727, 2729B, 2729C, 2729D, 2730B, 2737-2739, 2753, 2754A, 2754B, 2759, 2766-2770, 2772, 2773). Form 2, three specimens: localities WS2 (AD2695, 2698A, 2698B), WS3 (AD2772B).

Dimensions.

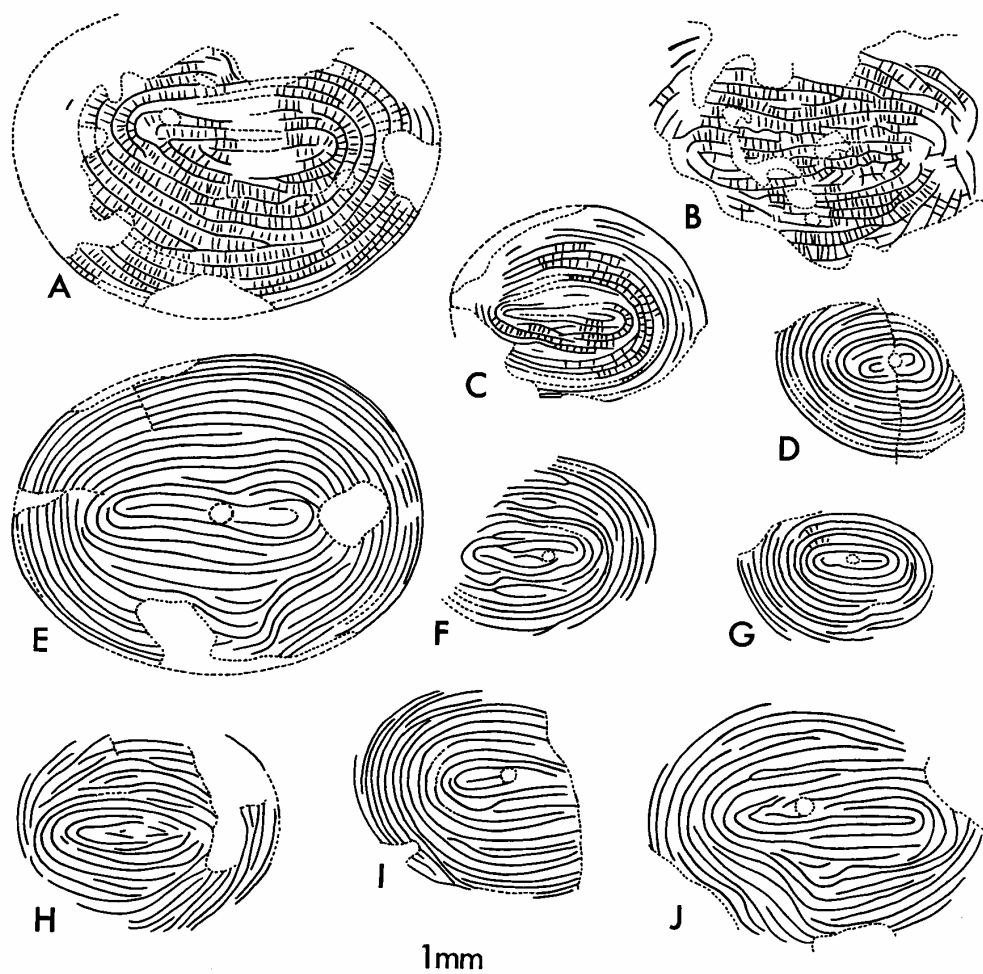
		Number of specimens	Range	Mean
Form 1	Length (mm)	10	0.80-2.00	1.30
	Height (mm)	10	0.75-1.20	1.05
	L/H ratio	10	1.23-1.40	1.36
Form 2	Length (mm)		Height (mm)	
	{ 2.15 1.67		{ > 1.17 —	

Description of British material

There are two rather distinct forms.

Form 1. (Pl. 74, fig. 2; text-fig. 6D-J.) The lateral outline is broadly oval, the dorsal and ventral margins are gently curved, and the posterior end is more broadly rounded than the anterior end. The surface bears twenty to thirty-two narrow, mainly concentric ribs separated by broader intercostal grooves. In the outer part of the valve the ribs run parallel to the margin while towards the interior they are more nearly longitudinal, occasionally with a slight tendency to bend inwards on either side of the muscle patch. Near the end of the valve a variable number of ribs are often deflected outwards in an approximately sigmoidal pattern towards the margin but there is no evidence for a corresponding flexure of the margin. In the best-preserved specimen (text-fig. 6E) this deflection occurs near the posterior end. The rib spacing varies from 0.035 to 0.054 mm centrally, decreasing somewhat towards outside. Branched and intercalated ribs occur, particularly near the centre. Cross-ribs are not developed, or only weakly developed. A small central muscle patch is usually present. It is 0.075-0.150 mm in diameter and interrupts one to two ribs. Internal moulds bear broad ribs separated by intercostal grooves of similar width.

Form 2. (Text-figs. 6A-C.) This form is characterized by the presence of well-developed cross-ribs and a tendency for several pairs of inner ribs to meet anteriorly at an acute angle. The rib spacing of the best-preserved specimen is broader (0.05-0.083 mm) than in form 1.



TEXT-FIG. 6. *Maternella (Maternella) clathrata* (Kummerow, 1939). A-C, form 2: A, AD2695, internal mould; B, AD2698A, external mould; C, AD2772B, internal mould. D-J, form 1, all external moulds except where stated otherwise: D, AD2769; E, AD2770, internal mould; F, AD2696; G, AD2754A; H, AD2698B; I, AD2729C; J, AD2696.

Discussion. Kummerow's (1939) holotype of *M. (M.) clathrata* has been examined and is closely similar to form 2 while many of the specimens assigned by Groos-Uffenorde (1974) to this species are certainly conspecific with form 1. In the British material these two varieties seem distinct but Groos-Uffenorde's (1974, text-fig. 6) specimens clearly demonstrate their intergradation.

R. (M.) gyrata of Gründel (1961), and some of the specimens described by Jones (1879) as *Entomis gyrata* are close to *M. (M.) clathrata* in lateral outline and ribbing pattern although the synonymies cannot be confirmed. *R. (R.) kiliginae* Posner, 1958, *M. n. sp. 3* of Groos-Uffenorde (1974), and *M. (M.) n. sp.* of Gründel (1979) all have more ribs than *M. (M.) clathrata*.

Distribution. South-western England, Rheinische Schiefergebirge and possibly Thüringia.

Maternella (Maternella) sp. 5 sensu Groos-Uffenorde (1974)

Plate 74, fig. 5; text-fig. 8D

vp. 1974 *Maternella sp. 5* Groos-Uffenorde, p. 80, pl. 3, fig. 3 (not pl. 6 = *M. (M.) whitewayensis sp. nov.*).*Material studied.* Two specimens: locality WS2 (AD2695, 2692).*Dimensions.*

	Length (mm)	Height (mm)
AD2695	>2.35	>2.25
AD2692	>1.75	>2.14

Description of British material. The carapace outline is not known. The surface bears fairly narrow ribs separated by broad, flat intercostal spaces. The ribs follow an approximately lenticular course and, in the central part of the valve, several meet anteriorly and posteriorly at an acute angle. In the outer part of the valve, the ribs are more evenly curved and probably run parallel to the margin. Intercalated ribs are fairly numerous. The rib spacing ranges from 0.06 mm to 0.13 mm. At the centre of the ornamentation is a circular muscle patch, about 0.075 mm in diameter, which interrupts at least one rib. Internal moulds have broad ribs separated by narrow grooves.

Discussion. Apart from the more clearly lenticular arrangement of the ribs around the central muscle patch, the two British specimens are similar to the external mould illustrated by Groos-Uffenorde (1974, pl. 3, fig. 3).

Distribution. South-western England, Rheinische Schiefergebirge.

Maternella (Maternella) whitewayensis sp. nov.

Plate 74, figs. 6-7; text-figs. 7A-D

v. 1961 *Richterina (Richterina)? cf. empleura* Kummerow, 1939; Gründel, pp. 126-127, pl. 11, fig. 7.vp. 1974 *Maternella sp. 5* Groos-Uffenorde, p. 80, pl. 6 (not pl. 3, fig. 3).

Derivation of name. From Whiteway Barton, Kingsteignton, Devon.

Holotype. Internal mould (AD2766) and corresponding external mould (AD2767), both incomplete; text-fig. 7A and Pl. 74, fig. 6.

Type locality. WS3: SX88577553; trench trending 146° parallel to north-eastern edge of field between SX88577533 and SX88567555, beginning 24.6 m from north-western edge of field running south-eastward for 30.4 m at distance of 3.6 m from north-eastern edge of field. Material collected from south-eastern end of trench to 5.2 m along it in a north-westerly direction.

Horizon. Middle *Gattendorfia*-Stufe.

Other material studied. Only from the type locality; four corresponding internal and external moulds (AD2701, 2702, 2729A, 2729D, 2769, 2770, 2772, 2773), two external moulds (AD2700, 2761), two internal moulds (AD2754A, 2760).

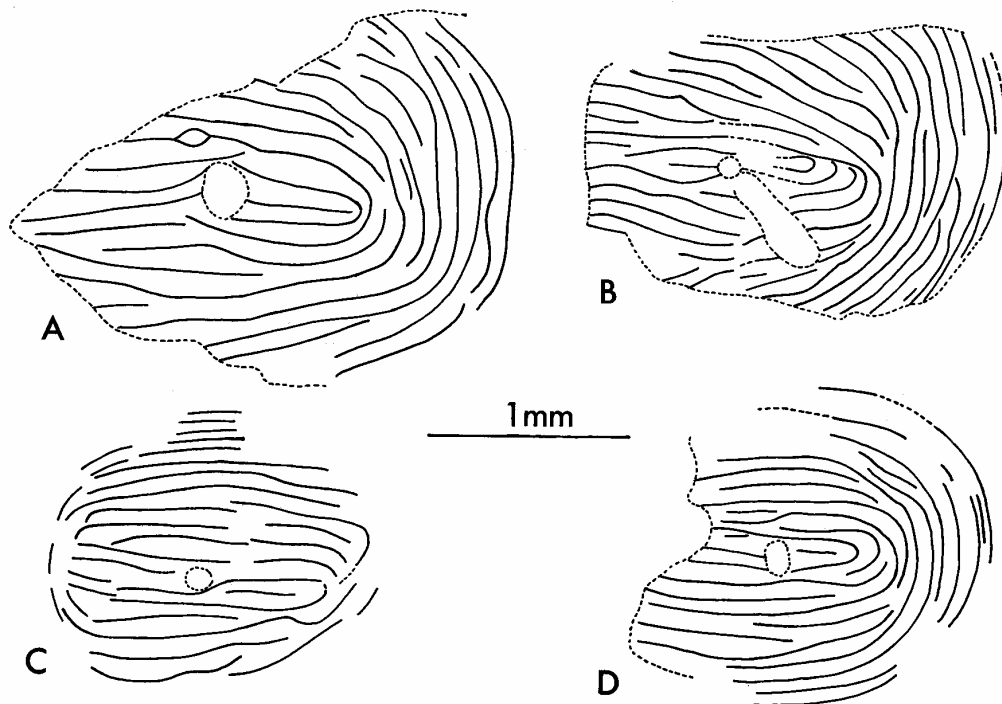
Diagnosis. Large species of *Maternella (Maternella)* (length >2 mm) with fairly elongate lateral outline. Surface bears approximately twenty to thirty-five ribs across height. Inner ribs more or less longitudinal, outer six to seven ribs run concentrically. Rib spacing fairly wide: 0.05-0.10 mm. Central muscle patch relatively large, and slightly depressed. Shallow, sulcus-like structure (?original) may be developed.

Dimensions.

Specimen	Reg. no.	Length (mm)	Height (mm)	L/H ratio
Fairly complete ext. mould	AD2700	2.12	1.51	1.40
Fragmentary ext. mould	AD2701	1.71	1.08	
	AD2702	1.71	1.08	
Fairly complete int. mould	AD2729A	2.16	1.71	1.26

Specimen	Reg. no.	Length (mm)	Height (mm)	L/H ratio
Fragmentary ext. mould	AD2729D	1.79	1.35	
Fragmentary int. mould	AD2754A	1.53	1.35	
Fairly complete int. mould	AD2760	1.97	1.58	1.25
Fairly complete ext. mould	AD2761	2.07	1.44	1.44
Holotype int. mould	AD2766	2.56	2.07	
Holotype ext. mould	AD2767	2.43	1.84	
Fragmentary int. mould	AD2769	2.16	1.71	
Fragmentary ext. mould	AD2770	2.03	1.53	
Complete int. mould	AD2772	2.07	1.53	1.35
Incomplete ext. mould	AD2773	1.80	1.49	

Description. The lateral outline is broadly oval with a mean L/H ratio of 1.37. None of the specimens is complete, but those which are most complete appear to be rather more narrowly rounded at the anterior end. The dorsal and ventral margins seem to be of approximately equal curvature. The surface bears twenty-three to thirty-two narrow ribs which follow a rather irregular course and are separated by broad, shallow intercostal grooves. Six or seven outer ribs run concentrically. Shorter ribs are intercalated, particularly near the centre of the valve. In some specimens, for example the holotype, it can be clearly seen that the ribs extend a short distance from the valve surface as flange-like structures. The rib spacing is wide; in five specimens it averages 0.055 mm, 0.066 mm, 0.070 mm, 0.093 mm, and 0.100 mm. There is a smooth, slightly depressed central muscle patch, 0.15–0.25 mm in diameter, which interrupts two or three ribs. Several specimens have a shallow, sulcus-like structure extending down from the dorsal margin towards the centre of the valve. This may not be an original feature. The ornamentation of internal moulds is similar to that of the outer surface except that the ribs are rather broader.



TEXT-FIG. 7. *Maternella (Maternella) whitewayensis* sp. nov., external moulds. A, Holotype, AD2767. B, AD2770. C, AD2729D. D, AD2773.

Discussion. This species resembles *M. grammica* (Kummerow, 1939) in size, ribbing pattern, the presence of a somewhat depressed muscle patch, and, in some specimens, of a shallow, sulcus-like structure (see Rabien 1960, p. 84). Kummerow's (1939) specimens of *M. grammica*, and its synonym *M. lenticularis* (Kummerow, 1939), have been examined. They differ from *M. whitewayensis* in having a more rounded lateral outline ($L/H = 1.1-1.3$ according to Rabien 1960), somewhat fewer ribs with a correspondingly wider rib spacing, and a triangular or lenticular, rather than longitudinal, arrangement in the central part of the valve. The ribs in *M. grammica* also appear to be more prominently flange-like than those of *M. whitewayensis*. Another similar form, *M. empleura* (Kummerow, 1939) (holotype examined), is smaller (length = 1.44 mm) than the new species and has more regular ribbing.

There are specimens of *M. whitewayensis* in Groos-Uffenorde's (1974) material of '*M. sp. 5*' from the upper *Gattendorfia* Stufe (Stockum samples 924, 930). However, specimens from the base of the middle *Gattendorfia* Stufe (sample 916) belong to a distinct species, described above.

Distribution. South-western England, Rheinische Schiefergebirge, Thüringia.

Subgenus MATERNELLA (STEINACHELLA) Gründel, 1979

Type species. *Richterina (Maternella) steinachensis* Gründel, 1961.

Diagnosis. Ribs arranged spirally or concentrically around sculpture centre and not drawn out parallel to long axis of valve. Ribs never flange-like. (Modified after Gründel 1979, p. 757.)

Discussion. This subgenus includes the following species: *Maternella geniceraensis* Jordan and Bless, 1970; ?*Graphiodactylus gyripunctuatus* Kummerow, 1939; *Richterina (Maternella) rabieni* Gründel, 1961; *Maternella rotundata* Tschigova, 1977; *Graphiodactylus schindewolfi* Kummerow, 1939 (= *Richterina (Maternella) circumcostatula* Koch, 1970); *Richterina (Maternella) seilerensis* Koch, 1970; *Richterina (Maternella) steinachensis* Gründel, 1961; *Maternella* sp. 4 *sensu* Groos-Uffenorde, 1974.

The list is the same as that given by Gründel (1979, p. 757) except for (i) the inclusion of *M. rotundata*, (ii) the exclusion of *R. (M.) pfaffenbergensis*, and (iii) the confirmation of the synonymy between *R. (M.) circumcostatula* and *G. schindewolfi*. As discussed by Gründel (1979, p. 758), *R. (R.) ampla* Gründel, 1963 may belong in this subgenus.

Maternella (Steinachella) schindewolfi (Kummerow, 1939)

v* 1939 *Graphiodactylus schindewolfi* Kummerow, pp. 33-34, pl. 3, fig. 10.

1970 *Richterina (Maternella) circumcostatula* Koch, pp. 722-724, pl. 9, figs. 3-4.

v. 1974 *Maternella schindewolfi* (Kummerow, 1939); Groos-Uffenorde, pp. 78-79, pl. 2, figs. 1-3.

Material studied. Twenty-nine specimens: locality WS3 (AD2700, 2710, 2711, 2729E, 2729F, 2730, 2730A, 2730B, 2730C, 2737, 2740, 2753, 2754A, 2766, 2767, 2768, 2768A, 2768B, 2769).

Dimensions.

	Number of specimens	Range	Mean
Length (mm)	12	0.95-1.75	1.30
Height (mm)	12	0.70-1.20	0.98
L/H ratio	12	1.18-1.48	1.32

Diagnosis. Species of *Maternella (Steinachella)* with numerous concentric ribs, very fine and closely spaced in inner part of valve, becoming more widely spaced towards margin. In centre of valve fine ribbing is arranged about axis at angle of 45-90° to long axis; outside immediate centre, ribbing is parallel to margin. There is no muscle patch.

Description of British material. The lateral outline is broadly and asymmetrically oval. The dorsal margin is gently curved and the ventral margin rather strongly curved. The posterior end is broadly and symmetrically rounded and the anterior end is more narrowly rounded with the extremity above the mid-point. The surface

bears about sixty concentric ribs across the height of the valve. In the outer part they are relatively strong with a spacing of 0.025–0.035 mm, and conform to the margin. Towards the centre, the ribs become very fine and closely spaced (0.012–0.015 mm) and usually follow an approximately subtriangular course, except in the immediate centre where they are arranged in an oval, the long axis of which lies at 45–90° to the length of the valve. However, in one specimen the inner ribbing is oval rather than subtriangular and the long axis is arranged horizontally. The tendency for coarser outer ribbing to pass into finer ribbing is not uniform in all directions. In some parts of the valve, usually near one end, fine ribs may persist to near the margin, while elsewhere the coarser ribbing extends inwards to half-way between the margin and the mid-point. Thus, over the outer quarter to one-half of the valve surface, areas of fine ribbing give way to areas of coarser ribbing. At the junction between these two types of ornament, the coarse ribs rapidly become narrow and pass into fine ribs between which are intercalated additional fine ribs. A muscle attachment area has not been observed. Internal moulds have fairly strong ribbing similar to that on the outer surface.

Discussion. Groos-Uffenorde (1974, p. 78) regarded *Richterina (Maternella) circumcostatula* as a junior synonym of *Graphiodactylus schindewolfi* but the synonymy was questioned by Gründel (1979, p. 758). According to Kummerow's (1939, pl. 3, fig. 10) illustration, *G. schindewolfi* has a more elongate lateral outline and inner, fine ribbing which is arranged about an approximately horizontal axis, rather than obliquely or dorso-ventrally as in *R. (M.) circumcostatula*. The ornamentation of the British specimens conforms well with the *R. (M.) circumcostatula* pattern except in one case (described above) where it is more similar to that of *G. schindewolfi*. Groos-Uffenorde (1974, pl. 2, fig. 1) illustrated an external mould having a moderately elongate carapace and ornamentation resembling the *G. schindewolfi* pattern fairly closely. My notes on the holotype of *G. schindewolfi* (an internal mould), examined in 1974 before the publication of Groos-Uffenorde's and Gründel's papers, record that the ribbing, although difficult to see, is close to that of *R. (M.) circumcostatula*. For these reasons it seems likely that the holotype of *G. schindewolfi* falls within the morphological range of *R. (M.) circumcostatula* and the synonymy of these two species is therefore accepted.

In the specimens described by Koch (1970) and Groos-Uffenorde (1974) the outer ribs are more widely spaced and more sharply differentiated from the fine inner ribbing than in the British material. It is considered that these differences arise from intraspecific variability and are of no taxonomic significance.

Although not clearly shown in Gründel's (1961, pl. 12, fig. 1a, b) figures, the holotype of *M. (S.) steinachensis* Gründel, 1961 has ribs which, in the centre, are arranged about an axis lying at approximately 40° to the length of the valve. This is very similar to the arrangement in *M. (S.) schindewolfi*. The only significant difference between the two species is the uniform strength of the ribbing in *M. (S.) steinachensis*.

Distribution. South-western England, Rheinische Schiefergebirge.

Maternella (Steinachella) seilerensis Koch, 1970

Text-fig. 9A–D

* 1970 *Maternella seilerensis* Koch, pp. 725–726, pl. 10, fig. 2.

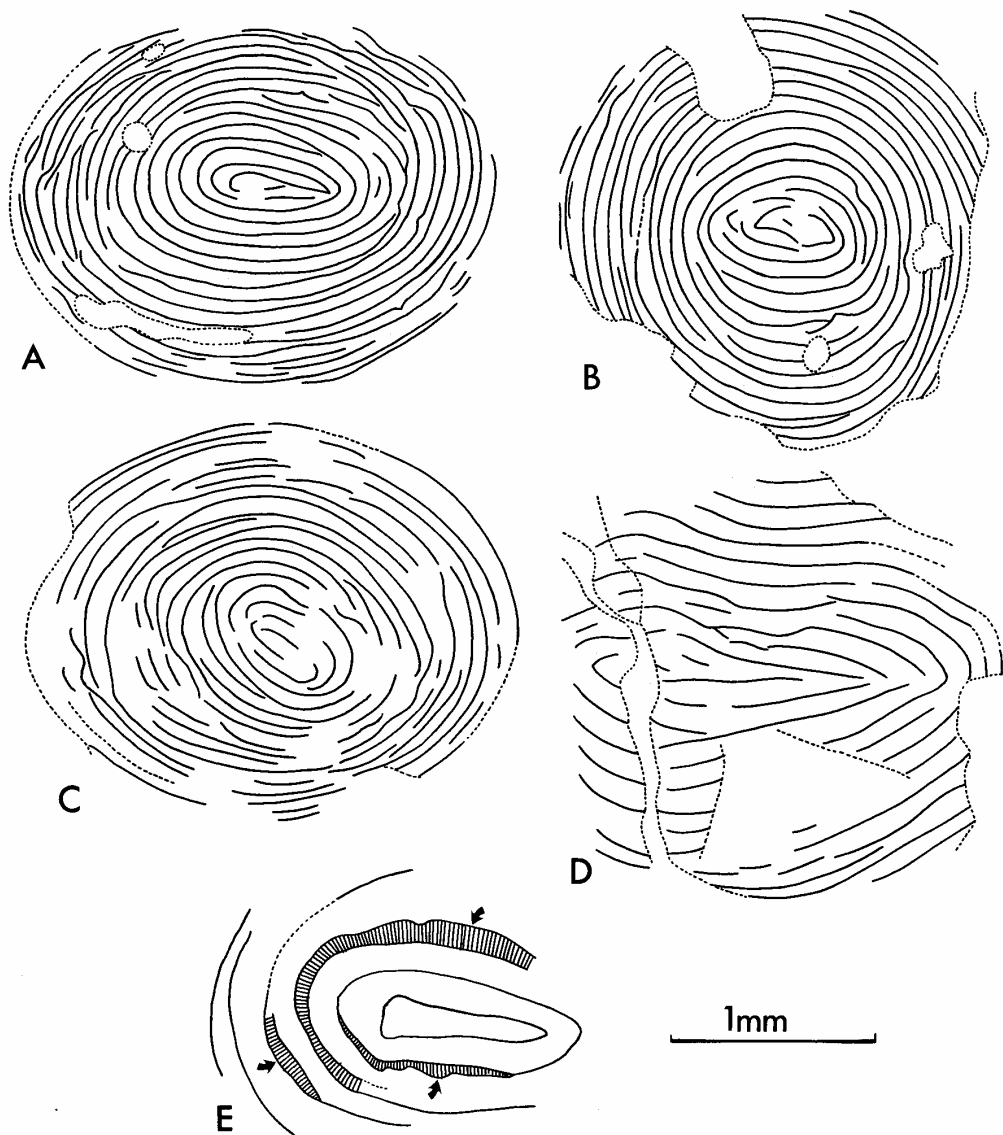
v. 1974 *Maternella* sp. 4 *sensu* Groos-Uffenorde, p. 80, pl. 2, fig. 7; pl. 4, fig. 6.

Material studied. Twenty-three specimens: locality WS3 (AD2732, 2738, 2751, 2758, 2759, 2761, 2764, 2765, 2767–2770, 2770A).

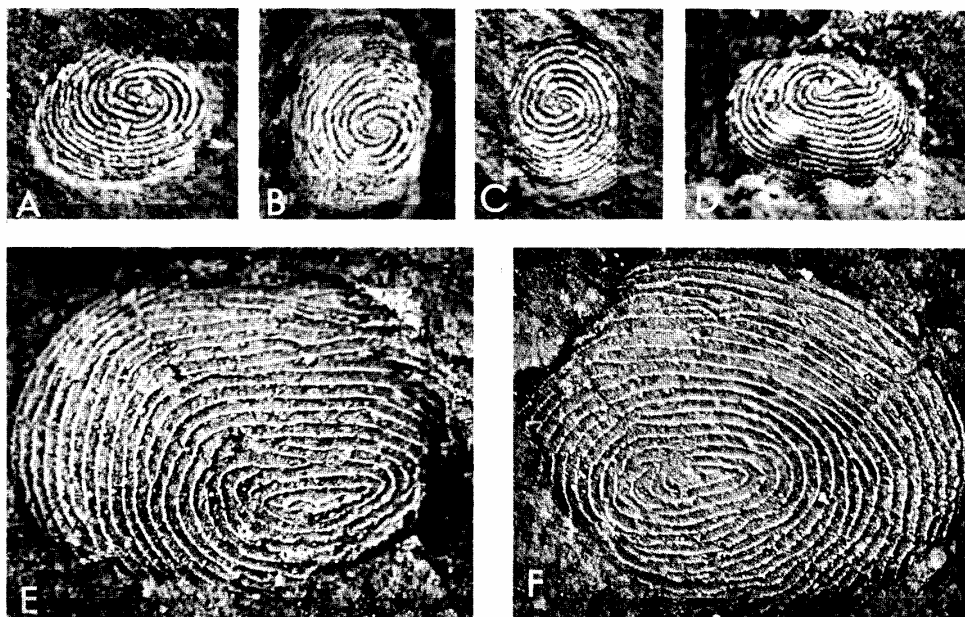
Dimensions.

	Number of specimens	Range	Mean
Length (mm)	7	0.45–0.80	0.65
Height (mm)	7	0.40–0.65	0.51
L/H ratio	7	1.20–1.37	1.27

Diagnosis. Rather small species of *Maternella (Steinachella)* with circular to broadly oval outline. Surface bears two to three spiral ribs running approximately parallel to margin; twenty-two to



TEXT-FIG. 8. A-C, *Maternella (Steinachella)* sp. 1. A, ZO4390, external mould. B, ZO4394, external mould. C, ZO4391, internal mould. D, *Maternella (Maternella)* sp. 5 *sensu* Groos-Uffendorde (1974), AD2695, internal mould. E, *Maternella* (?Subgenus) *pfaffenbergensis* Gründel, 1961. AD2717, internal mould, arrows indicate distal (outer) edges of flange-like ribs.



TEXT-FIG. 9. A-D *Maternella (Steinachella) seilerensis* Koch, 1970. A, AD2770A, external mould, maximum dimension 0.70 mm. B, AD2769, internal mould, maximum dimension 0.90 mm. C, AD2770, latex cast of external mould, maximum dimension 0.50 mm. D, AD2769, latex cast of external mould, maximum dimension 0.75 mm. E, F, *Maternella (Steinachella)* sp. 1. E, ZO4390, maximum dimension 2.15 mm. F, ZO4391, maximum dimension 2.25 mm.

thirty-six ribs can be counted across height of valve. Rib spacing decreases towards margin. Small, central muscle patch developed.

Description of British Material

Adults. The lateral outline is broadly oval. The surface bears two to three broad, spirally arranged ribs, separated by narrow intercostal grooves. The ribs make three to four revolutions and twenty-six to thirty-six can be counted across the height of the valve. They follow an almost circular to moderately oval course with a spacing of 0.028–0.035 mm near the centre, decreasing to 0.022–0.025 mm towards the margin. A number of ribs bifurcate. At the centre of the valve is a small muscle patch, 0.04–0.06 mm in diameter. The ornamentation of internal moulds is similar to that of the external surface.

Juveniles. A small, nearly circular specimen, 0.45 mm in diameter, with about twenty-five ribs, is probably a juvenile.

Discussion. In his description of *M. seilerensis* Koch (1970, p. 725) states that the ornamentation comprises an inner spiral rib which is finer than the outer concentric ribbing. It was because of this that Groos-Uffenorde (1974, p. 80) separated *M. seilerensis* from *Maternella* sp. 4 in which the outer ribbing is finer than the inner. However, Koch's (1970, pl. 10, fig. 2) photograph of the holotype does not correspond to his description because the outer ribs are clearly more closely spaced than the inner ribs. The holotype differs from Groos-Uffenorde's form, and from most of the British material, in having a more circular outline, but this may be an ontogenetic effect since the smallest British specimen (slightly smaller than the holotype) is also nearly circular.

Distribution. South-western England, Rheinische Schiefergebirge.

Maternella (Steinachella) sp. 1

Text-figs. 8A-C, 9E, F

Material studied. Five specimens: locality BLF1 (ZO4390, 4391, 4394).*Dimensions.*

Length (mm)	Height (mm)	L/H ratio
2.37	1.92	1.23
2.37	1.92	1.23
2.32	2.02	1.14
> 2.25	> 1.75	—

Description. The lateral outline is broadly oval. Details are unknown but the ribbing pattern suggests that the anterior end is more narrowly rounded than the posterior end. The surface bears narrow ribs, separated by broader intercostal grooves and following a spiral course which is more narrowly rounded at the anterior end and apparently conforms to the margin. There are thirty-four to forty-two ribs across the height of the valve with a spacing between 0.042 and 0.060 mm. A number of ribs are intercalated or bifurcate. Internal moulds bear a vague ornamentation of indistinct ribs.

Variation. In three specimens, the central ribbing follows an elongate oval course (text-fig. 8A) but in two specimens it is less elongate (text-fig. 8B). One internal mould is unusual because the ribs in the inner part of the valve are arranged about an axis lying at approximately 45° to the horizontal (text-fig. 8C).

Discussion. This distinctive ostracod has a ribbing pattern similar to that of *M. (M.) sp. aff. circumcostata sensu* Groos-Uffenorde (1974) but is rather larger and, more importantly, the ribs are considerably narrower, rather than broader than the intercostal grooves. *M. (S.) sp. 1* is distinguished from *M. (S.) geniceraensis* Jordan and Bless, 1970 by the greater regularity of the ribbing, by the smaller number of ribs, and, in at least some specimens, by the somewhat more elongate course of the central ribbing.

Distribution. South-western England.

Maternella (?Subgenus) pfaffenbergensis Gründel, 1961

Text-fig. 8E

- v* 1961 *Richterina (Maternella) pfaffenbergensis* Gründel, pp. 131-132, pl. 12, fig. 5.
v. 1974 *Maternella pfaffenbergensis* Gründel, 1961; Groos-Uffenorde, p. 78, pl. 2, fig. 4.

Diagnosis. Large species (length up to 2 mm), with broadly oval lateral outline, anterior end more narrowly rounded than posterior. Surface bears few flange-like ribs which follow elongate spiral or concentric course, more narrowly rounded at anterior end. There are five to six ribs between central muscle patch and margin. Rib spacing is very wide: 0.15-0.20 mm. (Modified after Gründel 1961.)

Material studied. Seven incomplete specimens: locality WS3 (AD2714, 2716, 2717, 2756, 2757).

Dimensions.

Length (mm)	Height (mm)	L/H ratio
1.80	1.50	1.20
1.85	1.55	1.19
1.90	1.70	1.12

Description of British material. The lateral outline is not preserved. The surface bears one or more spiral or concentric flange-like ribs extending to a height of >0.10 mm. Between the centre and margin of the valve there are at least four ribs separated by broad, flat intercostal spaces, and following a course which is more strongly curved on the ventral side and more narrowly rounded at the anterior end. Near the valve centre there may be one or two intercalated ribs. The rib spacing varies from 0.11 to 0.20 mm. The ribs deviate around a large circular central muscle patch, about 0.20 mm in diameter. Internal moulds are ornamented by a shallow spiral groove corresponding to the rib on the outer surface.

Discussion. The subgeneric placement of this species is problematical. It conforms to the diagnosis of *M. (Steinachella)* in having spirally or concentrically arranged ribs. On the other hand, *M. pfaffenbergensis* has at least two characters in common with species of *M. (Maternella)*: the flange-like structure of the ribs and their drawing out parallel to the long axis of the valve. Gründel (1979, p. 758) regarded it as being a morphological link between *M. (M.) hemisphaerica* (Rh. Richter, 1848) and *M. (S.) rabieni*. *R. (M.) gruendeli* Koch, 1970, is a closely similar species in which the ornamentation is intermediate between that of *M. (M.) hemisphaerica* and *M. (?Subgenus) pfaffenbergensis*.

Distribution. South-western England, Rheinische Schiefergebirge, Thüringia.

KUZMINAELLA Tschigova, 1977

Type species. *Kuzminaella venusta* Tschigova, 1977.

Diagnosis. Similar to *Maternella* but with ribs following irregular, swirling course. Cross-ribs may be developed.

?*Kuzminaella* sp.

Text-fig. 10

Material studied. Single, fragmentary external mould (AD2728) and part of corresponding internal mould (AD2727): locality WS3.

Dimension. The maximum dimension of the fragment is 3.45 mm.

Description. The fragment is basically semicircular in outline, the curved border being the original margin of the valve. It is slightly buckled tectonically and the external mould is disrupted by a tear-like dislocation. The surface bears ribs (spacing 0.045–0.095 mm) following an irregular, curved course with no clear pattern. They run parallel to the margin for a short distance, but in general impinge upon the margin at a shallow angle. There are numerous intercalated ribs. Examined in detail, the 'ribs' are seen to comprise several elements. Narrow, irregular, flange-like ribs extend out from the valve surface and to one side of these are much broader, low, ridge-like structures (broad, shallow grooves on the external mould) which are separated from the next flange-like rib by a somewhat broader intercostal groove. The broad ridges become less prominent towards the margin.

Remarks. The disorganized, rather swirling ribbing pattern of this fragment is similar to that of *Kuzminaella* (see particularly Tschigova 1977, pl. xiii, fig. 6), although the specimen is considerably larger than any of Tschigova's (1977) species.

Subfamily ENTOMOPRIMITIINAE Gründel, 1962

Diagnosis. Lateral outline usually asymmetrical and broadly oval with clearly developed straight dorsal margin. Ribs arranged concentrically, usually following elliptical or triangular pattern around sculpture centre. (After Gründel 1962, p. 1203.)

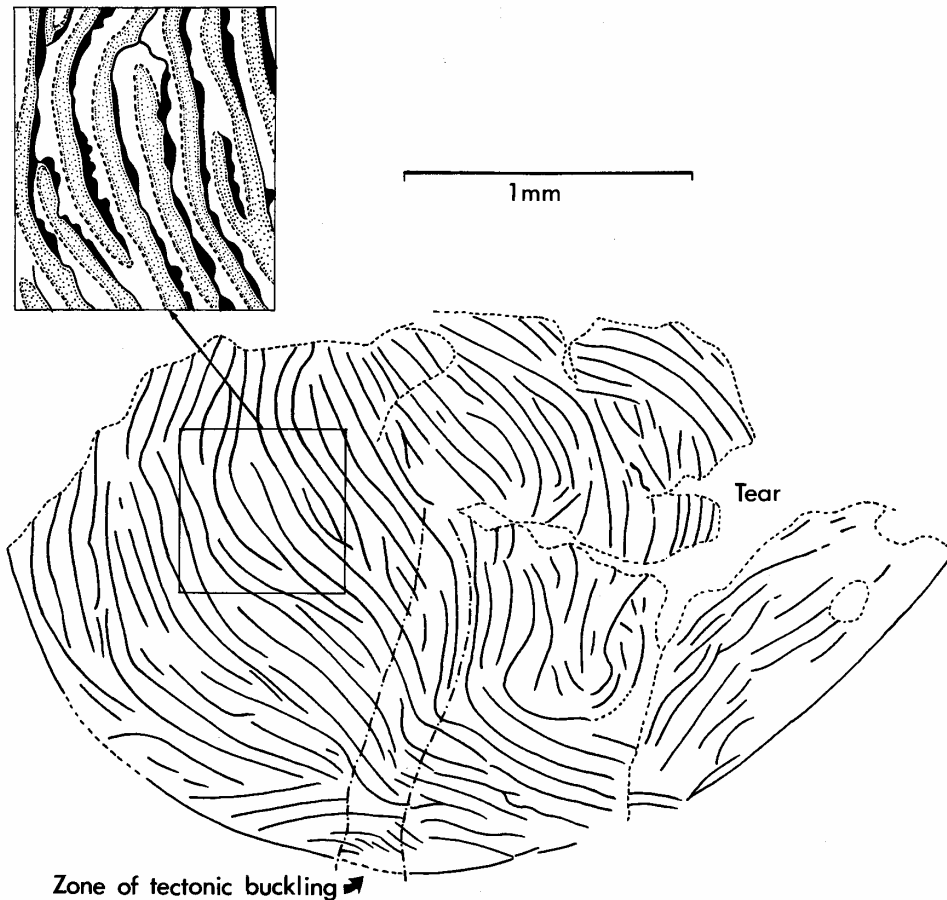
Discussion. The Entomoprimitiinae includes two genera and their subgenera: *Entomoprimitia* (*Entomoprimitia*) Kummerow, 1939; *E. (Reptiprimitia)* Gründel, 1962; *Bertillonella* (*Bertillonella*) Stewart and Hendrix, 1945; *B. (Rabienella)* Gründel, 1962.

Genus BERTILLONELLA Stewart and Hendrix, 1945

1954 *Waldeckella* Rabien.

Type species. *Bertillonella subcircularis* Stewart and Hendrix, 1945.

Diagnosis. Lateral outline asymmetrical and broadly oval to droplet-shaped with short, straight dorsal margin and anterior end more gently rounded than posterior end. Sulcus-like depression in anterior one-third of dorsal margin. Concentric ribs arranged in elliptical, subtriangular, or



TEXT-FIG. 10. ?*Kuzminaella* sp., AD2728, external mould. The inset shows the ornamentation in more detail: the black areas are the exposed faces of flange-like ribs; the stippled areas are shallow depressions; the white areas are low ridges.

subrectangular course around muscle patch: one species with rows of minute spines centred around antero-dorsal sculpture centre. (Based on Rabien 1954, p. 150.)

Discussion. The broader end of the carapace in *Bertilionella* has been interpreted as the anterior. This orientation, which is based on the position nearer the broader end of the dorsal depression (?rudimentary sulcus), should be regarded as questionable because in all other entomozoceans with asymmetrical outlines, including *Entomoprimitia*, the anterior end is narrower than the posterior end.

Subgenus BERTILIONELLA (BERTILIONELLA) Stewart and Hendrix, 1945

Diagnosis. Lateral outline asymmetrical and broadly oval. Concentric ribs arranged in elliptical course around muscle patch with long axis of ellipse parallel, or at right angles to long axis of carapace. (Based on Gründel 1962, p. 1200.)

Bertillonella (Bertillonella) sp. 2 sensu Groos-Uffenerde, 1974

v. 1974 *Bertillonella (Waldeckella) sp. 2 sensu Groos-Uffenerde, p. 73, text-fig. 4.*

Material studied. Nine strongly deformed internal and external moulds: locality TS1 (AD3721, 3722, 3727, 3729, 3730).

Dimensions.

	Number of specimens	Range	Mean
Length (mm)	6	0.45-0.70	0.59
Height (mm)	6	0.50-0.85	0.62
L/H ratio	6	0.59-1.30	0.90

Description of British material. The outline is unknown. The height of the valve is approximately equal to the length or occasionally exceeds the length, probably as the result of tectonic distortion. The surface bears several spirally arranged ribs which follow an oval course, at right angles to the length of the valve. Between twenty-four and thirty-two ribs can be counted across the height. The rib spacing ranges from 0.022 to 0.030 mm. Weak cross-ribs may be developed. A muscle patch has not been observed. Internal moulds are indistinctly ornamented.

Discussion. The strongly deformed British material compares well with that of Groos-Uffenerde (1974). This small form is distinguished from species of *Maternella* by the arrangement of the ribbing about a dorsal-ventral axis.

Distribution. South-western England, Rheinische Schiefergebirge.

Family RHOMBOENTOMOZOIDAE Gründel, 1962

Type genus. *Rhombentomozoe* Přibyl, 1949.

Diagnosis. Valves of apparently equal size. Lateral outline triangular to subquadrate, sometimes broadly egg-shaped. Straight dorsal margin usually well developed, sometimes corresponding to greatest carapace length; dorsal angles distinct or rounded. Sulcus always present, usually strongly developed, often extending across more than half of valve surface. Muscle attachment area absent. Spines may be developed near margin. Ornamentation comprises longitudinal ribs arranged parallel to dorsal margin, some outer ribs may be parallel to ends of valve. Surface occasionally smooth. (Slightly modified after Gründel 1962, p. 1198.)

Discussion. In addition to the type genus, the family includes *Pseudoentomozoe* Přibyl, 1949, *Ungerella* Livental, 1948, and possibly *Vltavina* Bouček, 1936. It is distinguished from the Entomozoidae by the generally triangular to subquadrate lateral outline and the long, straight dorsal margin.

Genus UNGERELLA Livental, 1948

1954 *Franklinella* Rabien, 1954.

Type species. *Cypridina calcarata* Rh. Richter, 1856.

Diagnosis. Carapace thin and weakly calcified. Lateral outline broadly egg-shaped, subquadrate, or triangular with greatest height in middle to anterior third and greatest length above mid-height. Straight dorsal margin usually clearly developed. Dorsal angles rounded. Anterior end more broadly rounded than posterior end. Sulcus prominent and deep, beginning in middle dorsal margin and curving across more than three-quarters of valve surface. Valve bears two obliquely directed spines, larger one situated at antero-ventral corner, smaller one postero-dorsal; antero-ventral spine is often in line with end of sulcus. Surface bears longitudinal ribs, some of which converge towards spines, others continue parallel to ends of valve. Number, spacing, and precise arrangement of ribs varies widely. (Modified after Rabien's 1954, p. 46 diagnosis of *Franklinella*.)

Discussion. *Ungerella* differs from *Rhombentomozoe* in the presence of two (antero-ventral and postero-dorsal) spines rather than one (ventral) spine. *Pseudoentomozoe* lacks spines and, like *Rhombentomozoe*, it has a more triangular outline than *Ungerella*.

Ungerella aff. *postmulticostata* Groos-Uffenorde, 1974

Text-figs. 11A, B

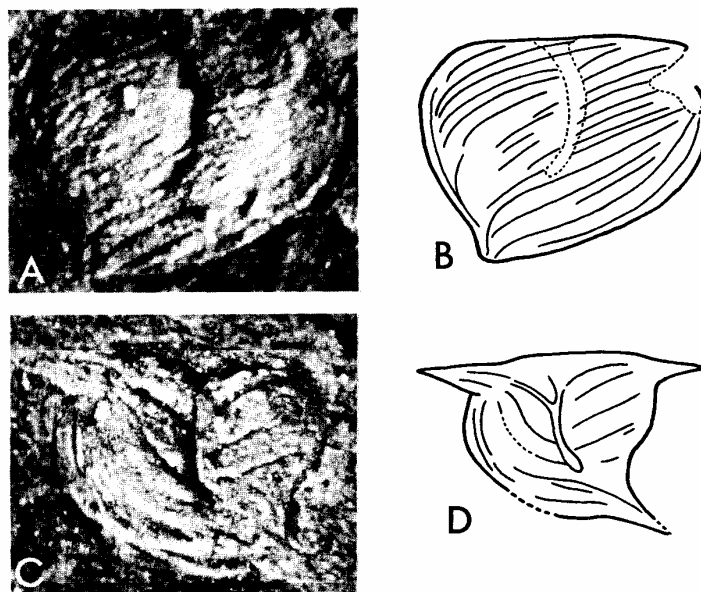
Material studied. Nine specimens: locality WS3 (AD2731, 2768, 2769, 2770).

Dimensions.

	Number of specimens	Range	Mean
Length (mm)	6	0.35-0.55	0.48
Height (mm)	6	0.25-0.45	0.37
L/H ratio	6	1.22-1.50	1.31

Description. The lateral outline is rounded and approximately subquadrate. The dorsal margin is fairly straight and occupies more than three-quarters of the valve length. The posterior end is rather more narrowly rounded than the anterior end and joins the gently curved ventral margin evenly. Just below the postero-dorsal margin is a short, conical spine which is directed slightly outwards and upwards. A similar spine arises from just inside the antero-ventral margin. The narrow, fairly deep sulcus extends across two-thirds to three-quarters of the valve surface and its lower part is directly in line with the antero-ventral spine.

The surface bears sixteen to eighteen narrow ribs separated by wider, flat intercostal spaces. The ribs run longitudinally, parallel, or at a slight angle to the dorsal margin and tend to converge towards the spines. One or two ribs are concentric around the posterior end and one rib runs parallel to the anterior end. There is no deviation of the ribs across the sulcus. The rib spacing ranges from 0.022 to 0.025 mm. Internal moulds are ornamented by shallow grooves which correspond to the ribs on the external surface.



TEXT-FIG. 11. A, B, *Ungerella* aff. *postmulticostata* Groos-Uffenorde, 1974, AD2769. A, photograph of internal mould, maximum dimension 0.50 mm and B, interpretation. C, D, *Ungerella stockumensis* Groos-Uffenorde, 1974, AD2768. C, Photograph of internal mould and D, interpretation.

Discussion. The British specimens are close to *U. postmulticostata* but are usually smaller, with a less elongate lateral outline, fewer longitudinal ribs, and a rather more prominent postero-dorsal spine.

Ungerella stockumensis Groos-Uffenorde, 1974

Text-fig. 11c, d

v* *Ungerella stockumensis* Groos-Uffenorde, p. 84, pl. 5, figs. 1-2, text-fig. 7.6-11.

Material studied. Six specimens: locality WS3 (AD2768, 2768A, 2769, 2770).

Dimensions.

Length (mm)	Height (mm)	L/H ratio
0.60	0.43	1.39
0.55	—	—
0.57	0.43	1.33
>0.40	0.37	—
0.60	0.37	1.62

Diagnosis. Medium-sized *Ungerella* with very well-developed ventral spine, few narrow ribs, and broad intercostal spaces. On both sides, ribs make more or less acute angle with sulcus. (After Groos-Uffenorde, 1974.)

Description of British material. The lateral outline is approximately subquadrate with a long and fairly straight dorsal margin. The best-preserved internal and corresponding external moulds bear two large spines at the ends of the dorsal margin. The prominent antero-ventral spine projects out at an angle of about 45° to the dorsal margin for at least 0.15 mm. The sulcus is well developed, narrow, and deep, extending across two-thirds to three-quarters of the valve surface and, at its ventral end, directly in line with the antero-ventral spine.

The surface bears six or seven narrow, flange-like ribs separated by broad intercostal spaces. Behind the sulcus four ribs follow a curved course, parallel to the posterior and ventral margins; at least one of these ribs continues on to the antero-ventral spine. One or two of the more dorsal ribs on the posterior side of the sulcus run at an angle of 45° or less to the dorsal margin. In front of the sulcus the ribs are approximately straight and follow a more nearly longitudinal course at an angle of 20 to 30° to the dorsal margin, ending against the anterior margin and the sulcus. The rib spacing varies from 0.075 to 0.10 mm. Between the main ribs, there may be a number of very narrow, closely spaced riblets. Internal moulds are ornamented by shallow grooves which correspond to the ribs on the external surface.

Discussion. The presence of what appear to be spines at both the anterior and posterior ends of the dorsal margin is of particular interest because ungerellids with three spines have been reliably documented only once (Rabien 1954, p. 61, in several specimens of *Franklinella?* (= *Ungerella*) aff. *calcarata*; see also p. 48). However, the additional antero-dorsal spine is visible in only one of the specimens and its exact nature is uncertain. Apart from the possible development of two dorsal spines, the British specimens agree well with Groos-Uffenorde's (1974) description of *Ungerella stockumensis*.

Distribution. South-western England, Rheinische Schiefergebirge.

THE STRATIGRAPHIC DISTRIBUTION OF CARBONIFEROUS ENTOMOZOACEA

European distribution. In Europe, Carboniferous entomozoaceans have usually been collected from relatively restricted sections although in many cases the ostracod-bearing horizons can be dated by means of conodonts or ammonoids. By combining sections, it is therefore possible to establish the general stratigraphic distribution of species within the system (Groos-Uffenorde, in press) and demonstrate that the Entomozoacea range just into the upper Carboniferous but are most abundant and diverse in the Tournaisian.

The number (ignoring accepted synonymies and cf. determinations) of named species and open nomenclature forms of different genera described from the topmost upper Devonian and different stratigraphic divisions of the Carboniferous in Europe are set out in Table 1. According to this compilation, there is apparently little fundamental change in the entomozocean fauna across the Devonian–Carboniferous boundary apart from the appearance of numerous new species of *Maternella* in the lower Tournaisian and the reappearance of the Frasnian and lower Famennian genera *Bertillonella* and *Ungerella*. This agrees with the conclusion of Groos-Uffendorde (in press) that 'in spite of the occurrence of new species there is no prominent biotic change at the Devonian–Carboniferous boundary within the entomozoids . . .'.

TABLE 1. Number of named species and open nomenclature forms of entomozoceans described from different stratigraphic divisions in the upper Devonian and Carboniferous. The divisions are: A, *Eumorphoceras* Stufe of ammonoid chronology (Namurian A); B, *crenistrina* conodont zone (lower Tournaisian); C, *Pericyclus* Stufe (upper Tournaisian–lower Viséan); D, *latior* ostracod Zone (lower Tournaisian); E, upper *hemisphaerica-dichotoma* ostracod Zone (topmost Famennian).

Division	<i>Entomozoe</i>	<i>Maternella</i>	<i>Richterina</i>	<i>Truyolsina</i>	<i>Bertillonella</i>	<i>Entomoprimitia</i>	<i>Ungerella</i>
A	—	—	—	5*	—	—	—
B	—	1	—	—	—	—	—
C	—	4	6	—	—	1	1
D	—	16	5	—	3	—	4
E	2	6	4	—	—	1	—

* Including two subspecies.

In contrast to the plethora of entomozocean zones spanning the upper Devonian, only the *latior* Zone of Rabien (1960), which is broadly equivalent to the *Gattendorfia* Stufe of ammonoid chronology, is generally recognized within the Carboniferous. Rabien (1960) found that this zone was separated from the upper Devonian *hemisphaerica-dichotoma* Zone by a horizon characterized by a reduced number of entomozocean species and the abundant occurrence of *R. (R.) costata* and *R. (R.) striatula*. He termed this interval, which apparently includes the Devonian–Carboniferous boundary, the *hemisphaerica-latior* Interregnum. The most complete Carboniferous section with entomozoceans, and the only one actually spanning the lower boundary of the system, was exposed by trenching at Stockum in the Rheinische Schiefergebirge (Alberti *et al.* 1974; Groos-Uffendorde 1974). The ages of the ostracod-bearing layers in these trenches are accurately controlled by conodonts. The *hemisphaerica-dichotoma* Zone, the *hemisphaerica-latior* Interregnum, and the *latior* Zone can be recognized and an additional, hitherto undocumented, entomozocean fauna, comprising *M. (M.) circumcostata*, *M. (M.)* n. sp. 3, and *M. (S.)* sp. 4, is intercalated between the Interregnum and the *latior* Zone. *R. (R.) latior* itself, instead of persisting through most of CuI as it does in other parts of the Rheinische Schiefergebirge and in Thüringia, occurs only in the lower part of this division at Stockum. The upper part of CuI is characterized instead by the abundant occurrence of *M. (M.)* cf. *arcuata*, *M. (M.) clathrata*, and *M. (S.) schindewolfi*.

The proposed introduction by Becker and Bless (1974, p. 11) of a '*R. (R.)* aff. *latior*-Zeit', which is supposed to be equivalent to the middle–upper Tournaisian and part of the Viséan (approximately CuII, the *Pericyclus*-Stufe of ammonoid chronology), has been challenged by Groos-Uffendorde (in press) on the grounds that *R. (R.)* aff. *latior* includes several species, none of which is common. *M. (S.) geniceraensis* appears to be characteristic of most of CuII and has recently (Hauser, in Groos-Uffendorde, in press) been discovered in the lower part of CuIII (CuIIIa, the *crenistrina* Zone of conodont chronology = upper Viséan). However, it would be premature to establish a '*geniceraensis*-Zone' to succeed the *latior* Zone because entomozoceans have not yet been found at the base of CuII (Groos-Uffendorde, in press).

The last documented occurrence of *M. (S.) geniceraensis* is followed by an interval, corresponding to the topmost Viséan and basal Namurian, which has so far failed to yield entomozoceans. The youngest known representatives of the group occur in the basal upper Carboniferous (Namurian A) of northern Spain (Becker 1975, 1976) and are assigned to a distinct genus, *Truyolsina*.

I agree with the conclusion of Sanchez de Posada (1977, p. 72) and Groos-Uffendorde (in press) that although the Entomozoacea seem to be of stratigraphic use in some European lower Carboniferous strata, much work remains to be done.

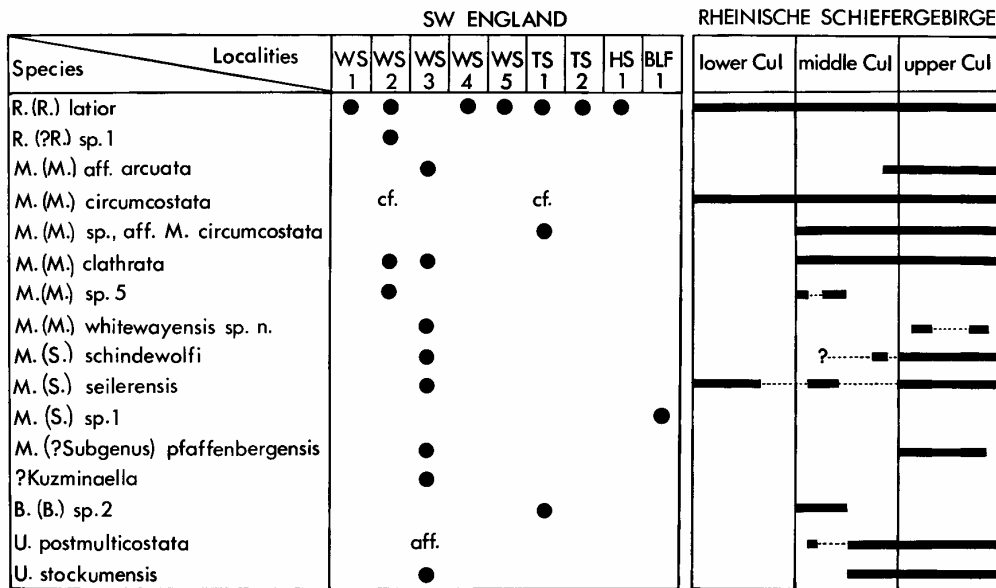
The British assemblages. The Entomozoacea described in this paper show a striking correspondence with the species recorded by Groos-Uffenorde (1974) from Stockum. With the exception of three rare forms—*R. (R.)* sp. 1, *M. (S.)* sp. 1, and ?*Kuzminaella* sp.—all the species which occur in Devon also occur at Stockum.

Text-fig. 12 summarizes the distribution of lower Carboniferous entomozoaceans among the nine British localities, together with the stratigraphic ranges given by Groos-Uffenorde (1974) for the same species in the Rheinische Schiefergebirge. On the basis of this comparison, the locality WS3 assemblage from the Whiteway Barton trench exposure can be confidently assigned to the upper *Gattendorfia* Stufe (CuI). The overlying strata with *R. (R.) latior* (localities WS4 and 5) presumably also belong to this division while a middle *Gattendorfia* Stufe age seems likely for the beds at locality WS2 in which there occur none of the species characteristic of the upper division. The presence of *B. (B.)* sp. 2 with *R. (R.) latior* at locality TS1 suggests that the middle part of CuI is also represented in the Trusham Shale.

The sparse entomozoacean fauna from the Hyner Shale includes only *R. (R.) latior* and hence is impossible to assign to any particular level within *Gattendorfia* Stufe. The age of the locality in the Bampton Limestone Formation which yielded *M. (S.)* sp. 1. is uncertain. However, the similarity of this species to *M. (M.)* sp. aff., *M. circumcostata*, and *M. (S.) geniceraensis* suggest that the upper part of the *Gattendorfia* Stufe, or perhaps the overlying *Pericyclus* Stufe, is represented here.

Acknowledgements. I particularly thank Dr. E. B. Selwood who supervised this project and gave much helpful advice and encouragement. I am grateful to Drs. H. Groos-Uffenorde, H. Malz, Professor A. J. Müller, and Dr. A. Rabien who allowed me access to museum material and to Drs. Groos-Uffenorde and A. Rabien for helpful discussion. Drs. M. V. Angel, Groos-Uffenorde, Selwood, and M. Whiteley commented critically on the manuscript. Special thanks also go to Mrs. A. Williams and Mr. A. Gray for their considerable patience and care in preparing several versions of the typescript and photographs respectively.

This project was supported by a N.E.R.C. Studentship, and funds for travelling were provided by a British Council Fellowship.



TEXT-FIG. 12. Distribution of entomozoacean species in Devon and their stratigraphic ranges in the Rheinische Schiefergebirge according to Groos-Uffenorde (1974, tables 4, 5; in press, fig. 5).

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Typescript received 30 November 1981
Revised typescript received 22 February 1983

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