Shell structure of the entomozoaceans: allegedly planktonic ostracodes of the Palaeozoic

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The prominent external ornamentation of the entomozoacean shells arises from the thin outer layer. The much thicker and structurally complicated inner layer is rarely well preserved. Three microstructural types of the inner layer are recognized: (1) poorly calcified with residual remnants of the original organic matter, (2) better calcified with oval in transverse section cavities that possibly were originally empty, or filled with an organic matter, longitudinal canals, (3) heavily calcified, in some specimens with sparite-filled remnants of cavities, which may represent only artifacts of recrystallization. The outer layer may correspond to the epicuticle and the inner layer to the endocuticle of Recent ostracodes. A hinge, slight left over right valve overlap, and marginal sculpture are identified for the first time in Famennian entomozoaceans. The mode of life remain unknown. *Richterina (Fossirichterina) uffenordeae* sp. n. and *R. (R.) goodayi* sp. n. are proposed.

Key words: Ostracoda, Entomozoacea, Late Devonian, shell structure, morphology, mode of life.

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Introduction

Entomozoacean ostracodes, with their characteristic fingerprint-like ornament, are easily obtainable in great quantities from many sequences of Silurian to Carboniferous rocks throughout the world. They reached their highest diversity in the Late Devonian and Early Carboniferous.

A zonal stratigraphic scheme based on the entomozoacean ostracodes was established by Rabien (1954, 1956) for the Late Devonian of Germany, and since that time their value for stratigraphic correlation has remained undisputed. The stratigraphic distribution of the Late Devonian and Early Carboniferous entomozoaceans has been summarized recently by Groos-Uffenorde (1984), Groos-Uffenorde & Wang (1989) and Groos-Uffenorde &

Schindler (1990). The entomozoacean zonation is easy to correlate with goniatite and conodont subdivisions.

The name Entomozoacea is still applied to the fingerprint ostracodes of pelagic facies, although the type species of the type genus (*Entomis tuberosa* Jones 1861) has proved to be a bolbozoid myodocope lacking any fingerprint sculpture (see Siveter & Vannier 1990).

The entomozoaceans were recognized for the first time and identified as ostracodes by Guido Sandberger (1842) in the Rhenish Massif. Since that time, a lot of species have been described but still very little is known regarding morphological features such as valve overlap, hinge structure, adductor muscle attachement area, ontogeny, the presence or absence of the sexual dimorphism and shell structures (see Gooday 1983). The vast majority of entomozoaceans are preserved as external and internal moulds of disarticulated carapaces.

The main objective of the present investigation was to identify the original shell structure and morphology in entomozoaceans from the Late Devonian of the Holy Cross Mountains. Species of special stratigraphic value have been chosen for the study (see Olempska 1979, and in preparation). They were collected from several localities and stratigraphic levels, and from rocks of varying lithologies.

All the studied material has been deposited in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland (abbreviated ZPAL).

Material and methods

In the Holy Cross Mountains entomozoaceans occur in limestones, argillaceous limestones, and marls. They are represented by numerous juveniles and rare adult forms. There is no evidence of transport or reworking. The calcareous valves of the carapace are frequently closed and, although strongly recrystallized, undeformed. Silicified closed carapaces and single valves were also studied. In the available material, calcareous shells of *Richterina (Richterina) striatula* (Richter 1848), *R. (R.)* cf. *tenuistriata* Kummerow 1939, and *'Entomozoe' (Nehdentomis) pseudorichterina* (Matern 1929) occur abundantly as articulated carapaces whereas the remaining species are represented by single valves and only rarely are preserved as closed carapaces. Most of the material comes from the Famennian of Kowala, Jabłonna and Łagów (Holy Cross Mountains), but some well preserved forms from other localities have been included for the purpose of comparison. The calcareous specimens were prepared mechanically. The silicified material has been extracted with acetic acid by Jerzy Dzik. In specimens without rock matrix, the outer layer of the shell is usually exfoliated and flanges broken. Therefore, for the study of shell structures, specimens partly covered by rock matrix were sectioned. The shell structure of several species was examined both under the SEM and

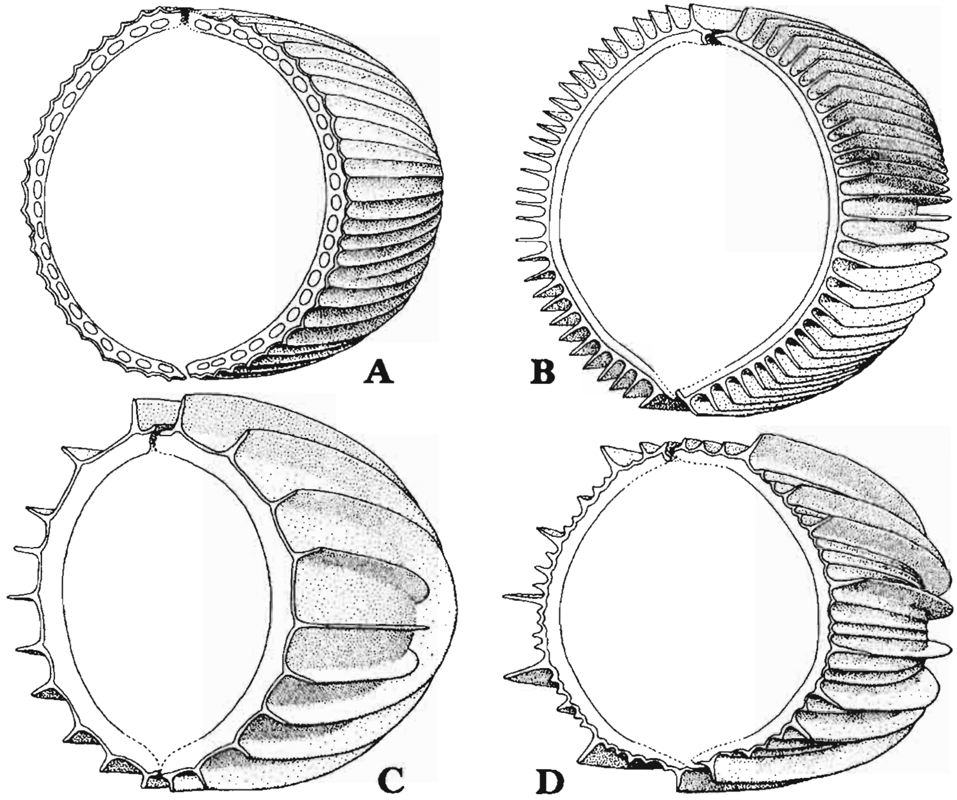

Fig. 1. Schematic drawings of transverse sections of entomozoacean carapaces. □A. *'Entomozoe' (Nehdentomis) pseudorichterina* (Matern 1929), showing the outer layer with ribs and inner layer with canals. □B. *Richterina (Richterina) striatula* (Richter 1848), showing the thin outer layer with high flanges, and the inner layer composed of fine-sized calcite cristals with probably residual organic substance. □C. *Maternella hemisphaerica* (Richter 1848), showing the outer layer with flanges and inner layer probably heavily calcified. □D. *Richterina (Fossirichterina) costata* (Richter 1869), showing thin outer layer with flanges and ribs and the inner layer which is usually strongly recrystallized.

in thin sections in transmitted light. Measurements of specimens were taken using an ocular micrometer in a binocular microscope.

Shell structure

The exoskeleton of most of ostracodes consists of four layers: the outermost thin epicuticle and beneath, the exocuticle, the endocuticle and the membraneous layer (see Sylvester-Bradley & Benson 1971, Bate & East 1972, Langer 1973, Kornicker 1981, Bate & Sheppard 1982, Okada 1982, Sohn & Kornicker 1988). However, in Recent Myodocopa, the shell consist of two parts: the epicuticle and the endocuticle (Kornicker 1969, 1981;

Bate & East 1972, Bate & Sheppard 1982, Sohn & Kornicker 1988). The outer part of the endocuticle of the myodocopids may represent in fact the exocuticle but the boundary between these two layers is either absent or indistinct (see Kornicker 1981).

Much less is known about the shell structure of entomozoacean ostracodes. They are usually considered to have had thin weakly calcified carapaces, like those of Recent Halocyprididae, and because of that poorly preserved (Rabien 1954, Gründel 1962, Becker 1977, Groos-Uffenorde & Schindler 1990, Becker & Bless 1990). Only Blumenstengel (1965, 1973) believed that entomozoaceans must have been heavily calcified. Blumenstengel based his hypothesis on the presence of thick silicified entomozoacean valves in which the original calcite was assumed to have been replaced by silica. The shell structure of *Nehdentomis nehdensis* (Matern 1929) was examined by Langer (1973) who demonstrated that the shell consists of a thin outer layer which formed the ornamentation, and an underlaying crypto- or microcrystaline layer. Specimens sectioned by Langer (1973) were poorly preserved and strongly recrystallized. He therefore suggested that these were secondary structures, the original weakly calcified shell having been completely replaced by calcite.

All the examined Polish Famennian entomozoaceans have the same general type of shell structure with a very thin outer layer that builds high projections forming the strong external ornamentation, and a thicker, more complicated inner layer (Fig. 1A-D).

Rabien (1954) and Gooday (1983) noted that, in addition to the external ornamentation, there is also ornamentation on the internal surface of entomozoacean valves corresponding to the ribs and grooves of the external surface. Groos-Uffenorde & Uffenorde (1974) suggest that the two different types of ribs present on the external moulds of *Maternella schindewolfi* (Kummerow 1939) were derived from different shell layers. Also, Becker (1977) believed there to be a thick internal chitinous layer forming the sculpture of the shell interior.

None of the entomozoacean species discussed above have ornamentation on the internal surface of the valves. Also, the internal shell surface in all silicified specimens examined during the present study was smooth. The same observation was made by Becker (1977) in the case of silicified specimens of *Maternella*. Evidently, the ornamentation on the upper surface of the inner layer was interpreted by these authors to represent the ornamentation on the internal surface of the valve.

Outer layer.– In all species examined the outer layer is very thin. Undulations and high lamellar projections of this layer form the strong external shell ornamentation, largely in the form of flanges and ribs (Figs 3-5). The flanges are extremely high, extending out at right angles to the valve surface (Figs 3F, 5C). In *Richterina (Fossirichterina) costata* (Richter 1869), *R. (F.) unispinosa* Olempska 1979, *R. (F.) uffenordeae* and *Richterina (Richterina) goodayi*, the flanges of 'primary ribs' (in the sense of Rabien 1954 and Gooday 1983) are considerably higher than those of 'secondary

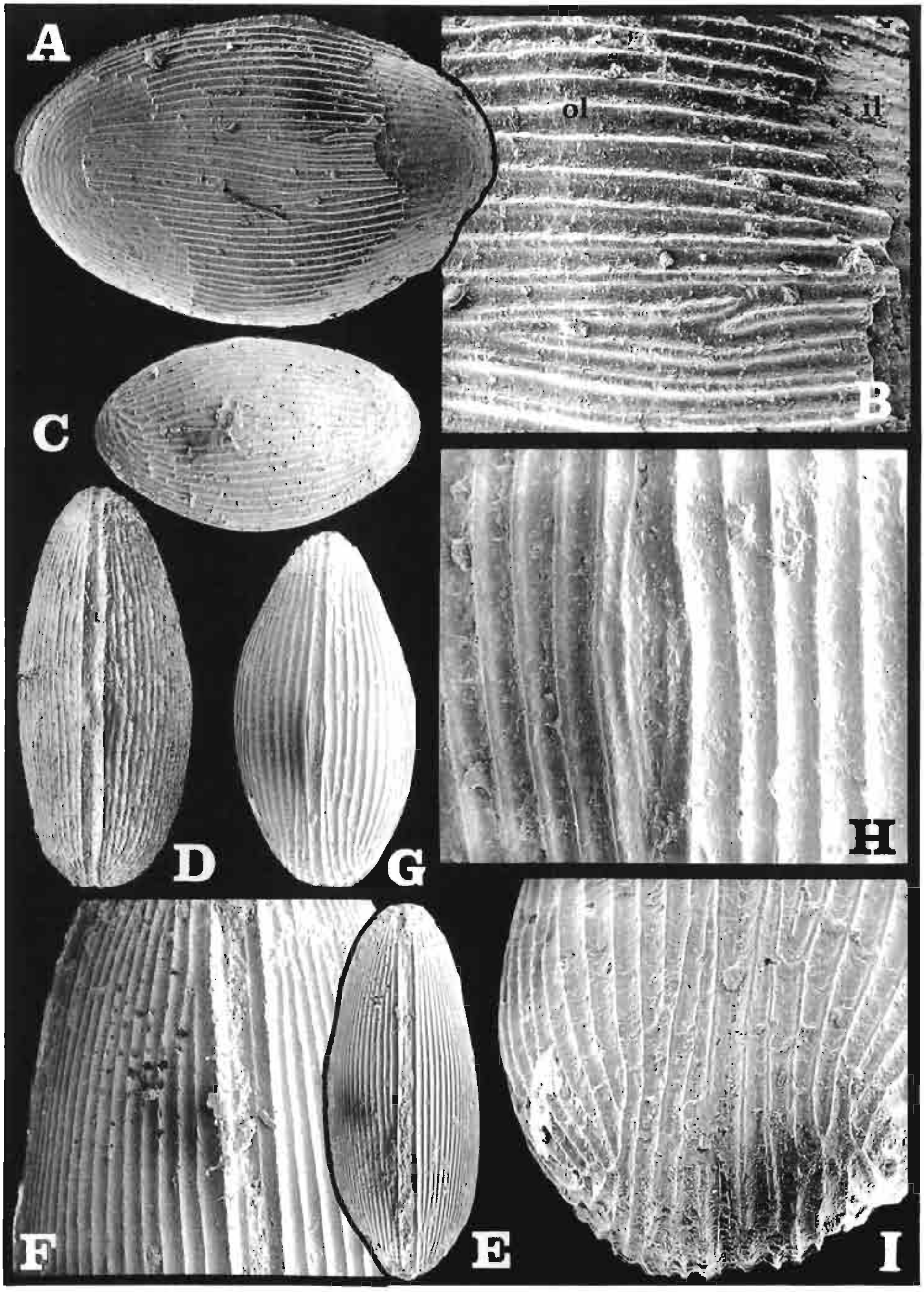

Fig. 2. *Richterina (Richterina) striatula* (Richter 1848), late Famennian, Kowala, Holy Cross Mountains, Poland. ☐A. Right valve in lateral view, ZPAL O.XV/231, × 66. ☐B. Detail of A, × 200. ☐C. Carapace in left lateral view, ZPAL O.XV/214, × 66. ☐D. Carapace in dorsal view, ZPAL O.XV/209, × 33. ☐E. Carapace in ventral view, ZPAL O.XV/64, × 33. ☐F. Detail of E, × 80. ☐G. Carapace in dorsal view, juvenile specimen, ZPAL O.XV/195, × 70. ☐H. Detail of G, hinge structure, × 250. ☐I. Detail of G, dorsal-posterior view, × 200.

ribs' (Figs 4C-D, 10, 11). Sections of the carapaces of *R. (R.) striatula* and *R. (R.)* cf. *tenuistriata* show the outer layer forming flanges which are extremely high and all of the same height (Fig. 3). Flanges of *Maternella hemisphaerica* (Figs 7, 8) and *M. dichotoma* (Paeckelmann 1913) are not so high but also of the same height.

The thickness of the outer layer, as seen in thin sections, is very small between ribs and flanges and varies among species, reaching up to 1-3 μm in *R. (R.) striatula* (Fig. 3), 5-6 μm in *M. hemisphaerica* (Figs 7-8), and 2 μm in *'Entomozoe' (Nehdentomis) pseudorichterina* (Fig. 6).

The outer layer has an amorphous transparent appearance in thin sections and appears as a single unit. In sections of *R. (R.) striatula* shells, very thin spaces about 0.5-1.0 μm thick, perpendicular to the surface of the outer layer, are visible between flanges. In mechanically prepared single valves there is a tendency for a thin outer layer to be exfoliated together with the rock matrix. The lower surface of the outer layer then makes an 'external mould' whereas the ornamented upper surface of the inner layer makes an 'internal mould'. In many specimens investigated by SEM, the partly preserved outer layer and the flanges are clearly visible at the boundary between the rock matrix and the shell (Figs 4, 5, 6, 9). Usually flanges are broken and removed during mechanical preparation.

The extremely high flanges in *R. (R.) striatula* tend to be deformed without breakage (Fig. 3E, F). The uniform deformation directions suggest an process occurring after burial probably due to sediment compaction.

Inner layer.– Interior to the ornament-bearing outer layer there is a thicker inner layer. The thickness of the inner layer varies among species, from 20-30 μm in *R. (R.) striatula*, to 40-60 μm in *M. hemisphaerica*, 50-60 μm in *R. (F.) semen* (Jones 1895) and 30-40 μm in *'E.' (N.) pseudorichterina*. In *R. (R.) striatula*, the inner layer is of uniform thickness although it can not be traced near the dorsal and ventral margins. In *M. hemisphaerica* the inner layer is also of uniform thickness close to the margins of the valve.

The upper surface of the inner layer, visible when the outer layer has been exfoliated, is covered by a 'secondary' ornamentation corresponding to the flanges and ribs of the outer layer. This ornamentation is not as strong as that on the external surface of the valve, the peaks of the ribs usually being rounded. In *R. (R.) striatula* and *R. (R.)* cf. *tenuistriata*, the upper surface of the inner layer is weakly striated or almost smooth, looking as a typical 'internal mould'. The smooth surface of the 'internal mould' in *R. (R.) striatula* was also observed by Gooday (1983).

The microstructure of the inner layer varies among species. The following three types of the inner layer structure have been identified:

Type 1. The inner layer, 20-30 μm thick, is composed of a mosaic of finely crystalline calcite with inclusions, presumably of residual organic substance (Fig. 3A). This type of inner layer is developed in *R. (R.) striatula* and probably in *R. (R.)* cf. *tenuistriata*. The upper surface of the inner layer in these species is almost smooth (Fig. 3E, F). The inner layer in one isolated valve of *R. (R.) striatula* from late Famennian marls of the Kowala

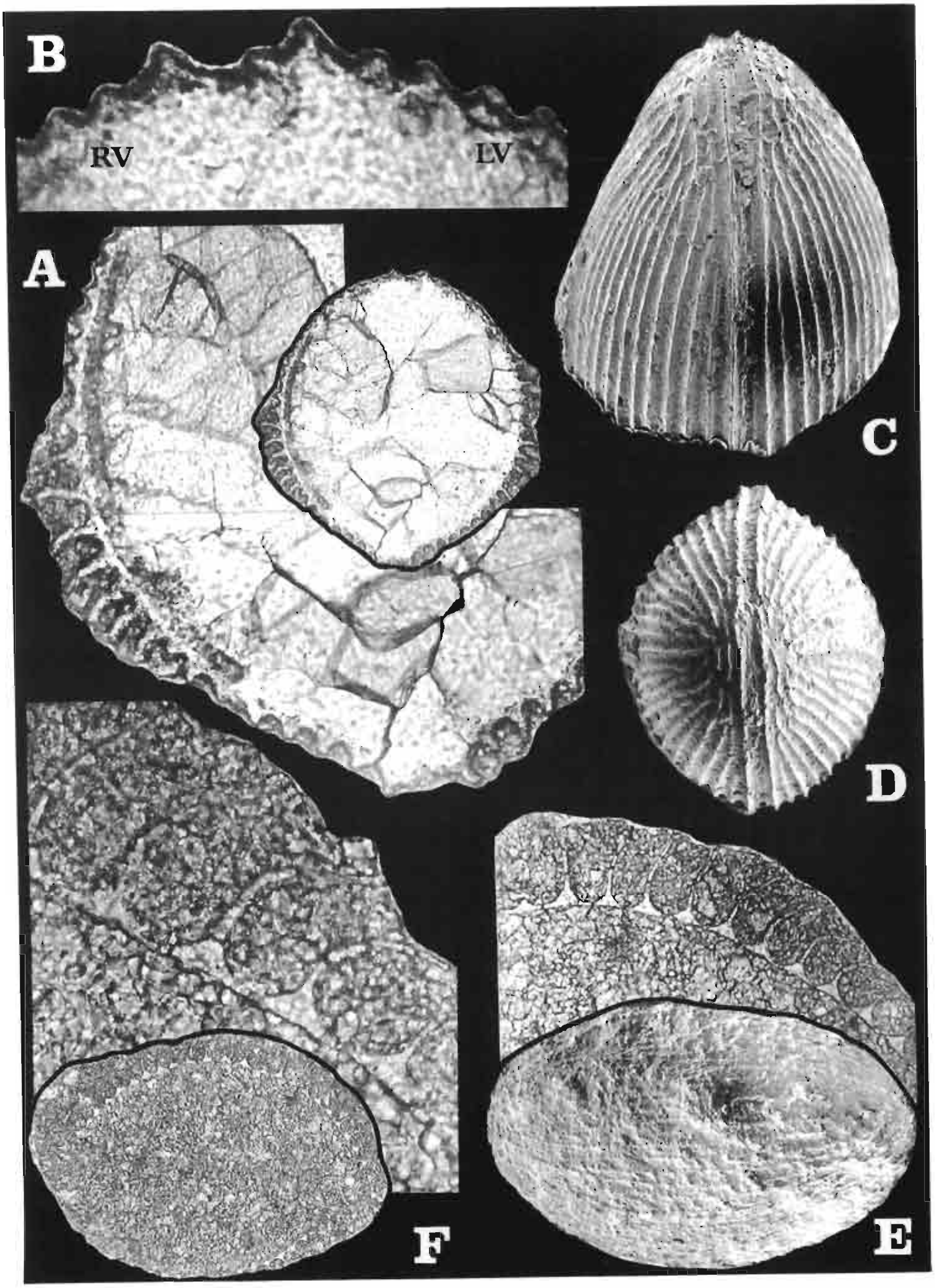

Fig. 3. A-D. *Richterina (Richterina) striatula* (Richter 1848), late Famennian, Kowala. ❑A. Carapace, thin section showing the outer layer and partly preserved inner layer, ZPAL O.XV/246, × 55, × 120. ❑B. Detail of A, showing the hinge structure, × 345. ❑C. Anterior end of carapace in dorsal view, ZPAL O.XV/196, × 108. ❑D. Carapace, anterior end, ZPAL O.XV/196, × 77. E - F. *Richterina (Richterina)* cf. *tenuistriata* Kummerow 1939, late Famennian, Kowala. ❑E. Carapace, right lateral view before sectioning, ZPAL O.XV/202, × 66. ❑F. Thin section of E, × 130, × 330.

section was pale brown in transmitted light and contrasted well with the clear, transparent outer layer. The brownish coloration seems to be a result of inclusions of residual organic substance.

In thin sections, closed carapaces of *R. (R.) striatula* are filled with calcite cement having plane intercrystalline boundaries and with an increase of crystal size away from the surface of the shell. The recrystallization in closed carapaces may be confined to parts of the inner layer (Fig. 3A). In other cases, recrystallization is coarse and all the inner layer is destroyed (Fig. 4C). The inner layer, initially composed of micron-sized calcite (micrite), is now transected, or wholly replaced, by sparry calcite.

It seems that the inner layer of *R. (R.) striatula* and *R. (R.)* cf. *tenuistriata*, and probably also *R. (F.) costata* and other species of *R. (Fossirichterina)*, was poorly calcified. The inner layer structure of *R. (F.) costata* is not well known, and requires further study.

Type 2. The inner layer, 30-40 μm thick, is distinctly ornamented on the upper surface. In the inner part of the layer, oval brown fields are visible in thin sections (Fig. 6H, I). The rest of the layer is composd of sparry calcite. The lower boundary of the layer is poorly visible, probably because it is more coarsely recrystallized. The oval fields seem to represent sections of longitudinal canals (or chambers) that originally contained organic substance or were empty. This type of inner layer was identified in *'E.' (N.) pseudorichterina*.

Type 3. The inner layer, 50-60 μm thick, consist of sparry crystals, in some specimens arranged in a way suggestive of fields similar to those described above (Fig. 7E, F). The outer surface of the layer is indistinctly ornamented. The inner surface is well delimited in specimens from marls (Fig. 7F). This type of inner layer structure was observed in *M. hemisphaerica* and *M. dichotoma*. Specimens of *M. hemisphaerica* and *M. dichotoma* are rather well preserved, thick and not coarsely recrystallized, suggesting that this type of the inner layer was much more heavily calcified than the others.

The preservation of the inner layer strongly depends on the rock matrix. Usually, the inner layer is strongly recrystallized in limestones. The secondary crystals are easily recognizable by their large size and their arrangement, usually with the longer axis of the crystals perpendicular to the surface of the outer layer. The spar crystals are often similar in diameter. The inner boundary of the inner layer is usually poorly visible in strongly recrystallized specimens (Figs 7D, 8C). Occasionally, single valves preserved in marls are well preserved, but due to the fragility of the material it is difficult to produce acceptable thin sections, especially in the case of *R. (R.) striatula*. In all specimens of *R. (F.) semen*, *R. (F.) costata*, *R. (F.) unispinosa* and *R. (F.) uffenordeae* examined , the inner layer, being coarsely recrystallized, is composed of neomorphic sparry calcite crystals. As a result the inner boundary of the layer is often indistinct (Fig. 9A, H).

Discussion.– The epicuticle in Recent ostracodes consists exclusively of organic substance while the endocuticle is heavily calcified in benthonic

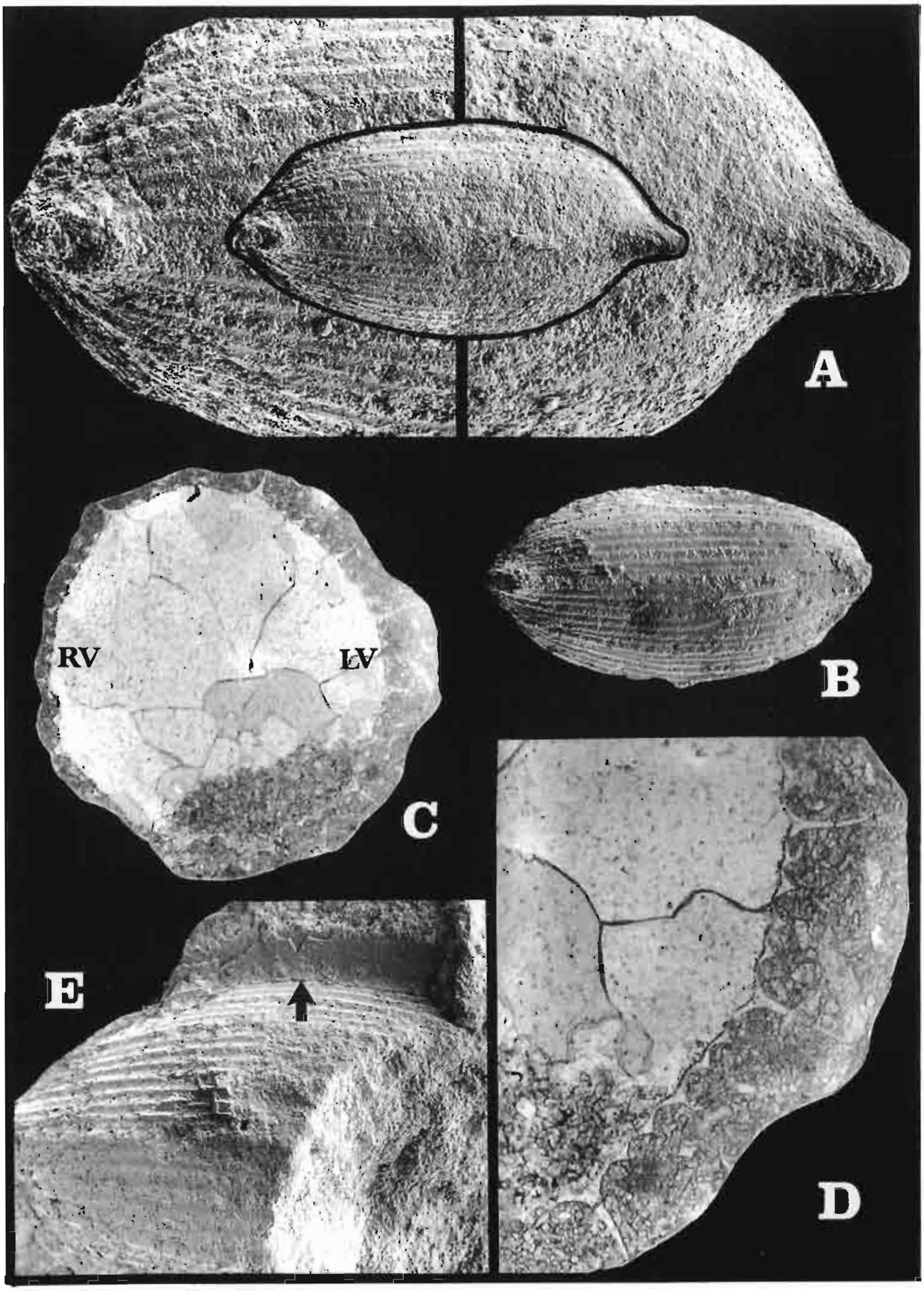

Fig. 4. *Richterina (Fossirichterina) costata* (Richter 1869), late Famennian, Kowala. ❑A. Right valve in lateral view, ZPAL O.XV/237, × 40; detail of ends, × 100. ❑B. Right valve in lateral view, ZPAL O.XV/224, × 40. ❑C, D. Thin section, only outer layer visible, inner layer completely recrystallized, ZPAL O.XV/247, × 53. D. Detail of C, × 137. ❑E. Flange on the primary rib, fragments of the outer layer visible, ZPAL O.XV/197, × 66.

and poorly calcified in planktonic ostracodes (Bate & East 1972, Kornicker 1981, Sohn & Kornicker 1988). The epicuticle, as indicated by Sohn & Kornicker (1988), appears to lack any internally differentiated substructures. According to Kornicker (1981) the surface ornamentation (often as strong ridges) in many Recent Cylindroleberididae (*Asteropterigion, Asteropella, Actinoseta, Pteromeniscus, Omegasterope*) is produced by the epicuticle. Moreover, in some of the Cylindroleberididae the ornamentation (fossae) of the upper surface of the endocuticle is not always visible in SEM micrographs, being hidden under a layer of epicuticle (Kornicker 1981). Kornicker (1981: p. 59) interpreted the amber-coloured outer layer in the cross section of *Cyclasterope hendersoni* Brady 1897, illustrated by Harding (1965: Fig. 7), to be equivalent to the epicuticle. Bate & Sheppard (1982: Pl. 9, 10: 3) noted that the striae forming the reticulation on the surface of *Halocypris inflata* (Dana 1849) are seen in cross-sections as small projections of the epicuticle.

Thus, as in the entomozoaceans, the external shell ornamentation of living ostracods is produced by projections of a thin outer layer. When specimens of Recent myodocopids are freeze-dried there is a tendency for the epicuticle to peel off; in entomozoaceans the outer layer also easily falls off from the inner layer.

The thin outer layer of the entomozoaceans may correspond to the epicuticle of Recent ostracodes. The thicker inner layer appears to correspond to the endocuticle of Recent myodocopids. Despite some similarities, the shell structures of Recent myodocopids and entomozoacean ostracodes remain different. Recent myodocopids differ from the entomozoaceans in having a thinner epicuticle, although the thickness of this layer is known only in few Recent species.

The relatively good preservation of the outer layer in entomozoaceans, compared with the usually strongly recrystallized inner layer, suggests that the outer layer was strongly sclerotized and probably partly calcified. The presence of strongly curved flanges suggests that they were flexibile in life. An early post-mortem mineralization of rather flimsy shell is also possible.

According to Bate & East (1972) the absence of epicuticular layer in fossil ostracodes suggest that this layer was never calcified although Herrig (1987) reported the presence of fossil epicuticular layer in *Ogmoconchella adenticulata* (Pietrzeniuk 1961) from the Late Domerian of Grimmen near Greifswald.

Sohn & Kornicker (1988) identified five primary components of endocuticle in myodocopid ostracodes: laminate, columnar, fine granular, coarse granular and homogenous. With few exceptions, pelagic Myodocopida have a laminate endocuticle, benthonic species may have a combination of one to four components in the endocuticle (Sohn & Kornicker 1988). The endocuticle is heavily calcified in all ostracodes except the planktonic Halocyprididae which possess non-calcareous or weakly calcified carapaces.

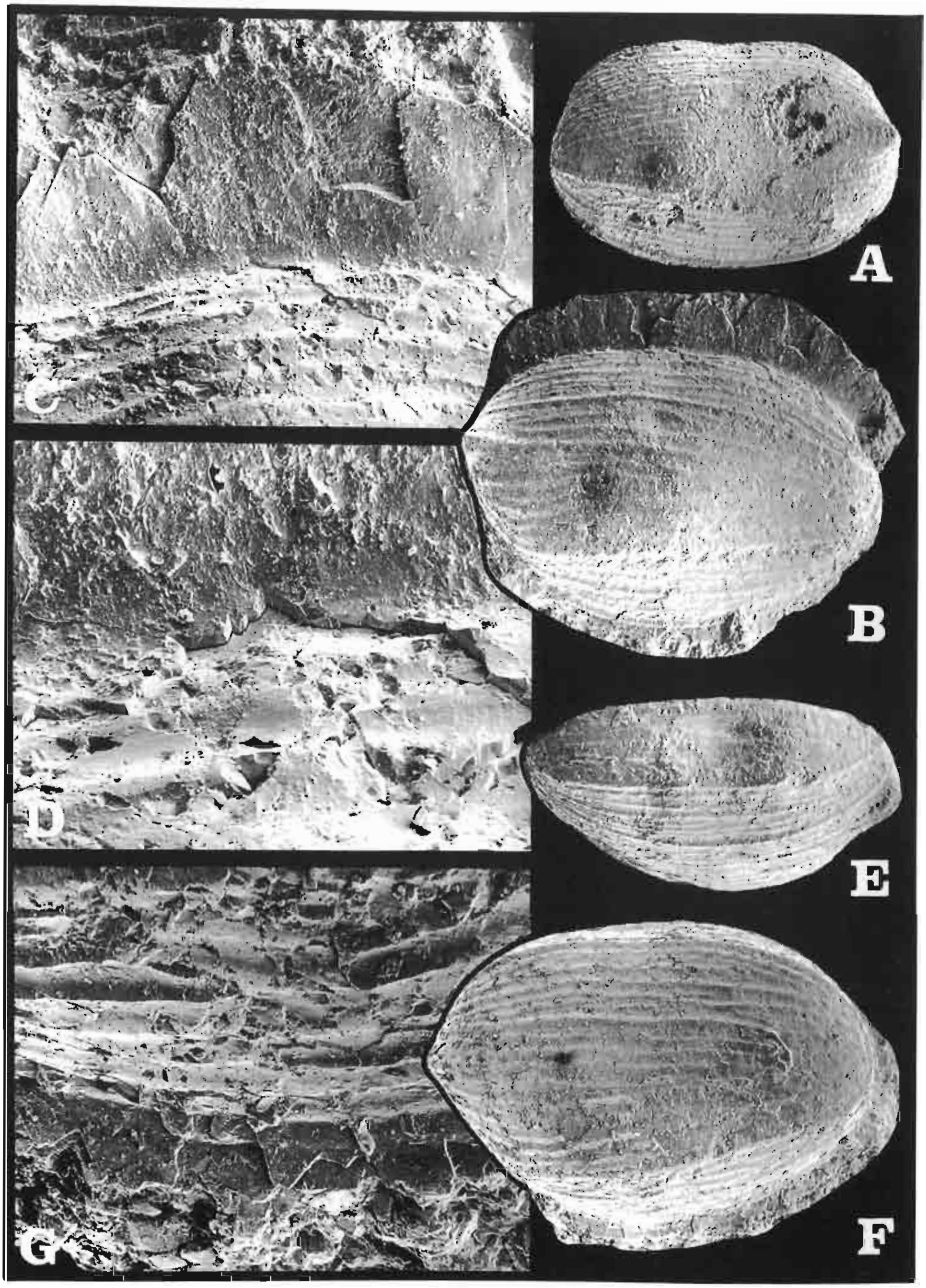

Fig. 5. *Richterina (Fossirichterina) uffenordeae* sp. n., Lower *M. hemisphaerica-M. dichotoma* Zone, Famennian, Kowala. ❑A. Right valve in lateral view, upper surface of the inner layer visible, ZPAL O.XV/182, × 40. ❑B-D. Left valve in lateral view, high flange on the upper primary rib and partly preserved outer layer is visible, ZPAL O.XV/177, × 66. C. Detail of B, showing the outer layer with flange, × 200. D. Detail of C, outer layer and upper surface of the inner layer is visible, × 660. ❑E. Right valve in dorsal view, ZPAL O.XV/183, × 40. ❑F, G. Left valve in lateral view, holotype ZPAL O.XV/184, × 66. G. Detail of F, ventral marginal rib with partly preserved outer layer, × 330.

The degree of calcification of the inner layer in entomozoaceans is difficult to determine, but evidently it was poorly calcified in some species like *R. (R.) striatula, R. (R.)* cf. *tenuistriata, R. (F.) costata, F. (F.) unispinosa, R. (F.) semen, R. (F.) uffenordeae*, and much stronger calcified in others (*M. hemisphaerica, M. dichotoma*). In *R. (R.) latior* and other species the valve material is sometimes torn, suggesting that it was weakly calcified (Gooday 1983). Specimens of *R. (F.) semen* often show plastic deformation of valves, suggestive of some elasticity.

The functional significance of the proposed longitudinal canals, within *'E.' (N.) pseudorichterina* is not clear. They may have assisted in exchange of respiratory gases. Such a function could have been important for entomozoaceans in stagnant and possibly dysaerobic waters. It is also possible that they had a buoyancy function or perphaps served to make the shell lighter and thinner, thereby increasing the economy of the carapace design.

The mineralogy of Recent myodocopid shells remains poorly known. According to Roseboom (*in* Sohn & Kornicker 1969: p. 103, 1988: p. 246) the shell of *Vargula hilgendorfii* (Muller 1890) contains monohydrocalcite ($CaCO_3 \cdot H_2O$), which is an unstable mineral. Calcite nodules are common components of Recent myodocopid shells (Kornicker 1981, Sohn & Kornicker 1969, 1988; Bate & Sheppard 1982) and may ocasionally form in myodocopid shells while animal is still alive or shortly after death (Sohn & Kornicker 1988). Among a few thousands specimens examined, no traces of crystalline nodules on the surface of the outer and inner layer have been identified, but it cannot be excluded that the oval fields in the carapace of *M. hemisphaerica* are actually post-mortem artifacts.

Carapace morphology

Orientation of the carapace.– The position of adductorial sulcus (nuchal furrow) is regarded by most authors as decisive for determinig the orientation of entomozoaceans. However, the sulcus is absent in most late Famennian species and the true orientation of the carapaces in these forms is difficult to determine. The anterior-posterior and often dorsal-

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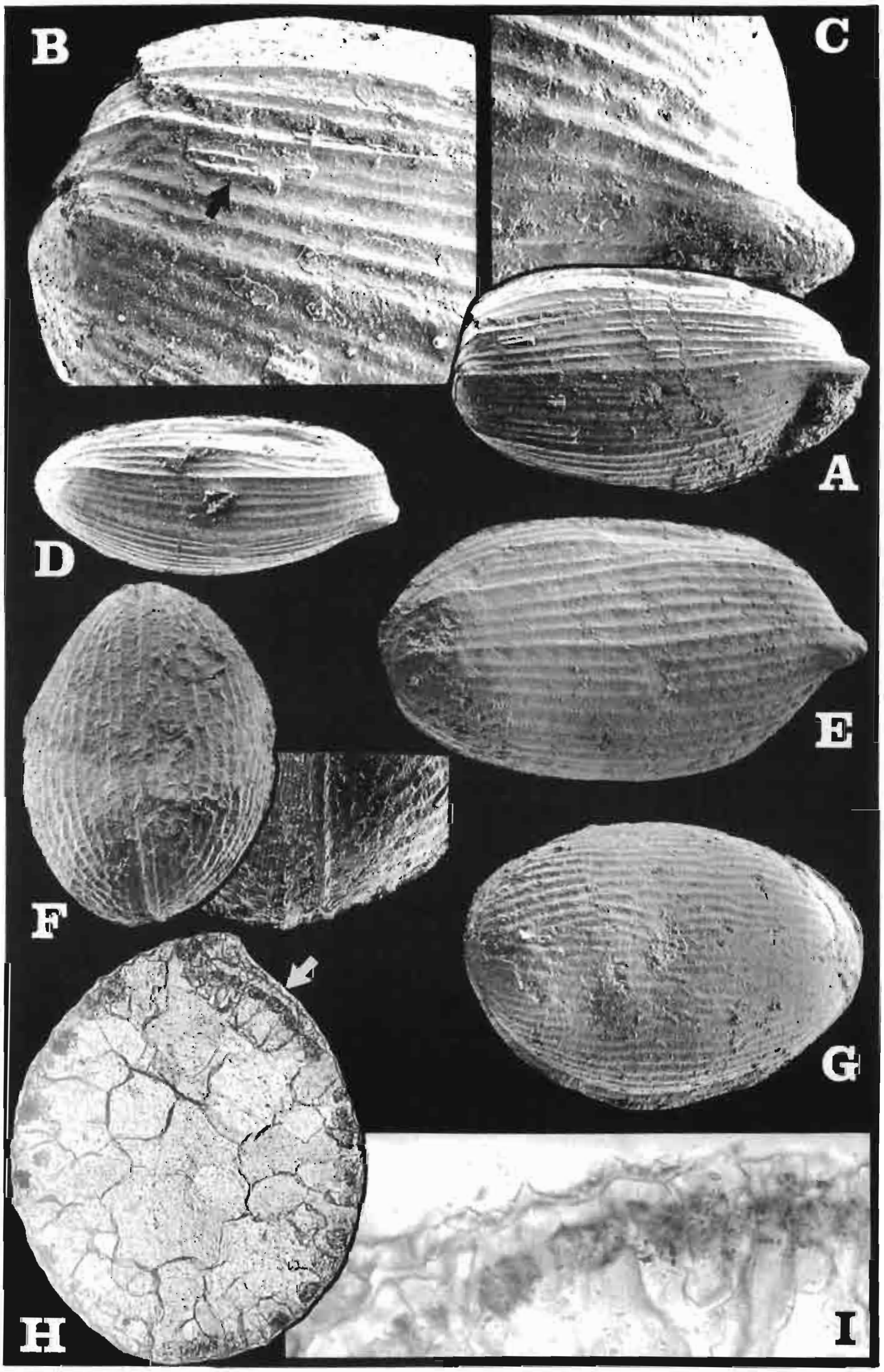
Fig. 6. A-E. *Richterina (Fossirichterina) unispinosa* Olempska 1979, late Famennian, Kowala. □A-C. Right valve in lateral view, upper surface of the inner layer and fragments of the outer layer are visible, ZPAL O.XV/187, × 33. B. Detail of posterior end, fragments of the outer layer indicated by an arrow, × 100. C. Detail of anterior end, × 133. □D. Right valve in dorsal view, ZPAL O.XV/188, × 40. □E. Right valve in lateral view juvenile specimen, upper surface of the inner layer, ZPAL O.XV/241, × 66. F-I. *'Entomozoe' (Nehdentomis) pseudorichterina* (Matern 1929), early Famennian, Jabłonna. □F. Carapace in dorsal view, juvenile specimen, ZPAL O.XV/229, × 66; detail of posterior end × 100. □G. Carapace in left lateral view, ZPAL O.XV/243, × 40. □H, I. Carapace, thin section, partly preserved outer layer and inner layer, the location of I indicated by an arrow, ZPAL O.XV/248, × 83. I. Detail of H, showing the thin outer layer and inner layer with oval structures, × 466.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ventral orientation is almost impossible to determine in moulds. In some species of *Maternella, 'Entomozoe' (Nehdentomis), Entomoprimitia*, a slight antero-ventral indentation of the margin is present. Concerning the anterior-posterior orientation of *Richterina (Richterina)* and *Richterina (Fossirichterina)* carapaces, there are several characteristics which suggest that the wider end of the carapace, as seen in dorsal view, is the posterior one. As seen in lateral view, the posterior end is also slightly broader. The evidence for this interpretation is as follows: (1) the hinge structure is situated in the wider part of the carapace (Fig. 2D, G), (2) the adductor muscle attachement area visible on the upper surface of the inner layer in *R. (Fossirichterina)* species and poorly visible in *R. (Richterina)* is situated slightly towards the narrower end, close to mid-length of the carapaces, beneath the dorsal depression, (3) the dorsal depression in *R. (Fossirichterina)* species is situated closer to the narrower end of the carapace.

Spines may also be helpful in orienting carapaces. The spine at the anterior end of *R. (F.) costata* is larger than that at the oposite posterior end. Spines developed only at one end of the carapace, they are usually situated anteriorly *[R. (F.) usispinosa, R. (F.) uffenordeae, R. (R.) goodayi].*

In cross sections, the carapaces of *R. (R.) striatula, R. (F.) costata, M. hemisphaerica* and *M. dichotoma* are almost symmetrical, with the position of the greathest width approximately at the mid-height. All of the closed entomozoaceans carapaces have a straight contact line between the two valves when examined in their dorsal and ventral aspects.

Valve overlap and hinge structure.– Entomozoaceans are usually considered to have valves of equal size (Rabien 1954, Gooday 1983), although Langer (1973) found that in *Nehdentomis nehdensis* (Matern 1929) the right valve projects beyond the left valve along the dorsal margin. It is possible that Langer (1973: Pl. 8: 2) assumed a dorsal-ventral orientation of the carapace that is actually opposite to the real one.

Thin sections of closed carapaces of *R. (R.) striatula, R. (R.)* cf. *tenuistriata, R. (F.) costata*, and also silicified specimens of *R. (R.) goodayi*, preserved as closed or slightly open carapaces (Figs 3, 4, 10, 11), show that the left valve is slightly larger and overlaps the right one along the whole free margin. In some specimens of *R. (R.) striatula*, the left valve slightly protrudes beyond the right one along the dorsal margin and the right valve protrudes beyond the left one along its ventral margin (Fig. 3D). However, this may be due to a slight dislocation of the valves, which often occurs in entomozoaceans.

Until recently it was considered that the valves of entomozoacean ostracodes were joined in life by an organic or perphaps chitinous membrane without any hinge structure (Gooday 1983). However, well developed hinge structures occur in several of the studied species. The hinge was identified in thin sections of closed carapaces of *R. (R.) striatula* and *R. (F.) costata* (Figs 3, 4). The left valve shows a semicircular structure (hinge groove ?), its counterpart on the right valve is a straight continuation of the outer margin. In thin sections the hinge structure is seen to be built

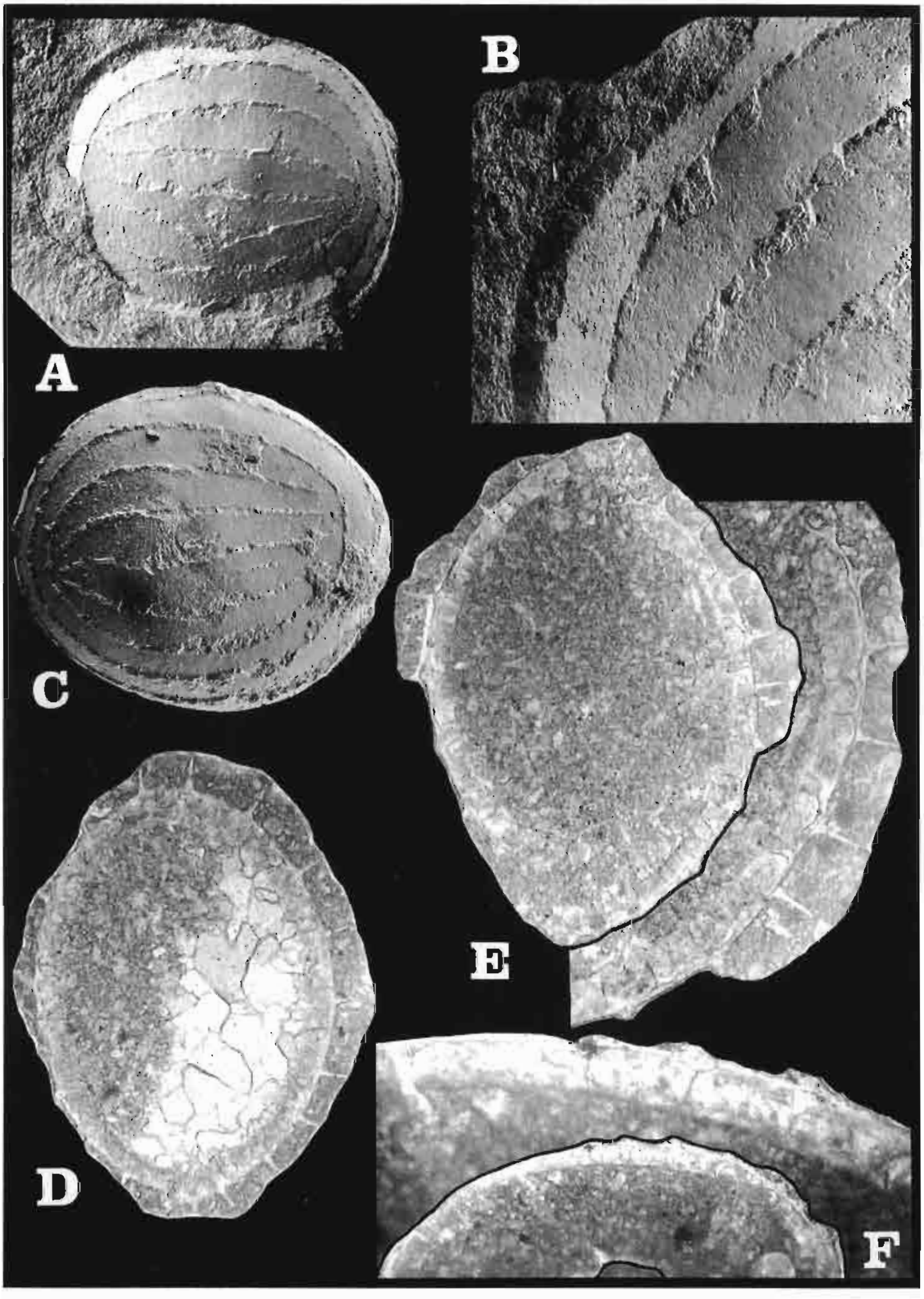

Fig. 7. *Maternella hemisphaerica* (Richter 1848), late Famennian, Kowala. ❑A, B. Left valve in lateral view, ZPAL O.XV/236, × 40. B. Detail of A, outer layer preserved, one flange preserved, others broken, × 100. ❑C. Right valve in lateral view, ZPAL O.XV/235, × 40. ❑D. Thin section of the carapace, ZPAL O.XV/249, × 53. ❑E. Thin section of the carapace, ZPAL O.XV/250, × 53, detail × 84. ❑F. Thin section of the valve, ZPAL O.XV/251, × 60, detail × 160.

from the outer layer. The inner layer was recrystallized near the dorsal margin in all examined specimens. No single valve with the hinge preserved have been found. However, the hinge as observed in dorsal view of closed carapaces of *R. (R.) striatula* and *R. (R.)* cf. *tenuistriata* is developed in the posterior part of the dorsal margin (Fig. 2D, G), and its position is marked by a thin additional ridge on the left valve and slightly concave marginal ridge on the right (Fig. 2G, H). The ridge on the left valve is longer in juvenile specimens than in later growth stages (Fig. 2D, G) where it is very short and close to the mid-length. All the closed carapaces of *Maternella* examined in thin sections are slightly dislocated with the hinge structure destroyed.

Marginal sculpture.– Silicified specimens of *R. (R.) goodayi* possess a marginal sculpture similar to that in some other Palaeozoic ostracodes (palaeocopids). There is a relatively thin marginal ridge on the larger left valve and an admarginal ridge on the right (Figs 10, 11). *R. (R.) striatula, R. (R.)* cf. *tenuistriata* and *R. (F.) semen* have an indistinct narrow admarginal ridge on the right valve. In many entomozoaceans there is an outermost ridge, which may be compared with an adventral structure which continues around the entire valve margin. Such a ridge is well developed in *R. (R.) striatula, R. (R.)* cf. *tenuistriata, R. (F.) costata* and *M. hemisphaerica*. Groos-Uffenorde (1984) already noted the presence of the adventral structure in *Entomoprimitia sandbergeri* (Matern 1929) but suggested that this species should be excluded from the entomozoaceans and transfered to the palaeocopids.

Muscle scars.– The adductor muscle attachment area is represented in *R. (F.) costata, R. (F.) unispinosa* and *R. (F.) uffenordeae* by a circular pit, which occurs near the centre of the valve or slightly in front of the mid-length. It is relatively small, indistinct and seems to be actually a single muscle spot, interrupting only one or two ribs of the shell surface. The adductor muscle attachement area in *R. (F.) semen* was described by Gooday (1978, 1983) as an oval or rounded area ith 30-50 tiny round muscle scars. The adductor attachement area in specimens of *R. (F.) semen* from the Holy Cross Mountains was observed in hundreds of specimens but it is difficult to say whereas it is really the same as that described by Gooday (1978). Even if the muscle attachement area in the largest specimens is similar to that described by Gooday, the number of scars seems to be smaller.

The presence or absence of the adductor muscle attachment area is one of the most important taxonomic features of entomozoacean ostracodes, especially among *R. (Richterina) - R. (Fossirichterina)* species. Often, even in closely related species, some specimens possess the muscle pit whereas others do not (e.g. *R. (F.) intercostata - R. (R.) eocostata*, specimens of *R. (F.) costata* with and without muscle pit). In silicified specimens of *R. (R.) goodayi* whenever the outer layer is preserved, the adductor muscle pit is not visible. Specimens with the outer layer partly corroded exhibit a small muscle pit. A similar feature was also observed in *R. (R.) striatula* which is preserved either as closed carapaces without any visible muscle patch or

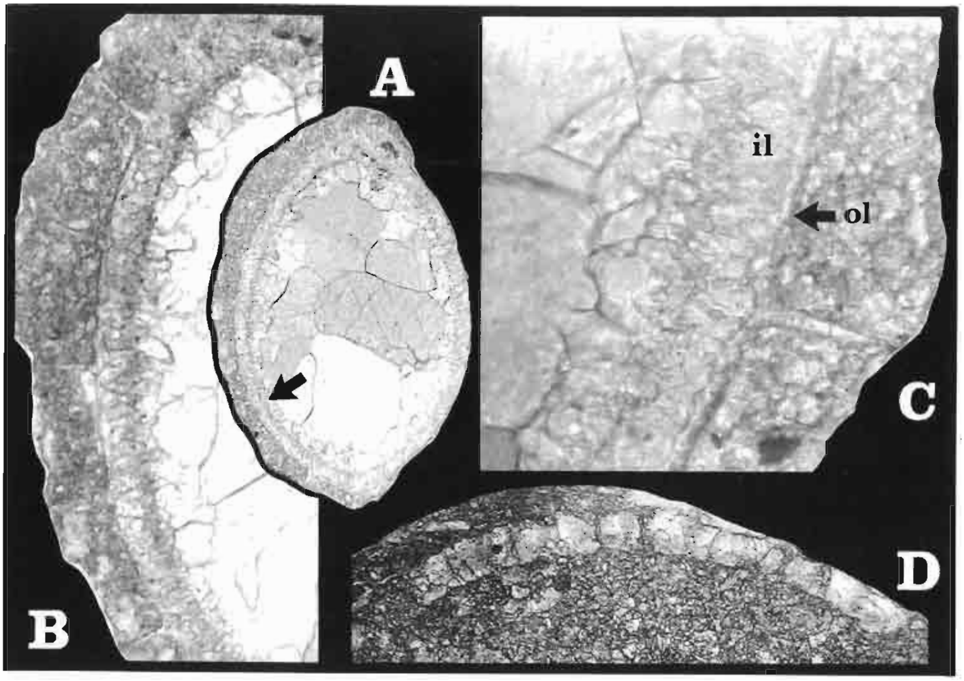

Fig. 8. *Maternella hemisphaerica* (Richter 1848), late Famennian, Kowala. ❑A. Thin section of the carapace, ZPAL O.XV/252, × 53. The location of C indicated by an arrow. ❑B. Detail of A, outer layer with flanges visible and inner layer partly recrystallized, × 150. ❑C. Detail of A, × 454. ❑D. Thin section of the valve, inner layer preserved, outer layer visible in part covered by the rock matrix, ZPAL O.XV/253, × 90.

as single valves with an exfoliated outer layer showing a small muscle patch on the upper surface of the inner layer. It is possible that even smaller muscle pits do not interrupting any ribs remain unidentified on the valve surface.

Details of the central muscle attachement scar are also not visible in reflected light or in SEM micrograph in some Recent myodocopids. The scar is visible only when the outer layer is removed (Kornicker 1981).

Rabien (1954) and Tschigova (1977) noted the presence of an elongate dorsal depression in *Volkina* and *Rabienites* species, respectively. As suggested by Rabien (1954) and Gooday (1983), this structure may be homologous to the dorsal muscle scar area of some other ostracodes. The presence of the dorsal depression was also observed in the Holy Cross Mountains material of *R. (F.) costata* (Fig. 4A, B), *R. (F.) unispinosa* (Fig. 6A, D, E), *R. (F.) uffenordeae* (Fig. 5E,) and *R. (F.) semen* (Fig. 9B, E). The dorsal depression, as well as the muscle pit, is better visible on the upper surface of the inner layer. A similar elongate dorsal depression was also identified in *Richteria* and *Nehdentomis*, in which the adductorial sulcus is strongly or weakly developed. The dorsal depression in these species is situated at the end of the adductorial sulcus. It is possible, that the dorsal depression in the anterior part of the dorsal margin in *Volkina*, *Rabienites* and

Fossirichterina is a remnant of the adductorial sulcus (nuchal furrow) and may indicate sulcate ancestor. Probably, it was the area where strong muscles of the first two appendages were attached.

Conclusions.– The Entomozoacea Přibyl 1950 have been placed in various suborders e.g. Cladocopina (Zanina & Polenova 1960, Pokorný 1978, Groos-Uffenorde & Wang 1989), Myodocopina (Sylvester-Bradley 1961), and Entomozoocopina (Gründel 1969) of the superorder Myodocopa. They have been compared also to the Thaumatocypridacea (Groos-Uffenorde 1991) and Polycopacea (Kozur 1972, Neale 1983). Recently Siveter & Vannier (1990) concluded that entomozoaceans 'are clearly the most atypical of all of the ostracode groups which traditionally have been assigned to the Myodocopida and their true taxonomic position may be well elsewhere' but 'if anything, have more in common with the myodocopid myodocopes'.

Although the shell structure of the entomozoacean ostracodes is similar to that of the Recent myodocopids, their morphology in several respect is quite different from other typical myodocope groups. The entomozoaceans do not have any rostrum or rostral incisure. The marginal sculpture, although poorly known in the entomozoaceans, are similar to that in the palaeocopids. It may be that the entomozoacean ancestors are actually among the Lower Palaeozoic palaeocopids.

Entomozoacean life habits

It is generally assumed that most of the entomozoacean ostracodes had a planktonic life habit, similar to that of Recent Halocyprididae, although direct evidence for this is lacking. The life habits of the entomozoaceans was extensively discussed by Gooday (1983) but it still remain a subject of controversy. Almost all possible marine habitats, ranging from planktonic to benthonic and from shallow to deep water (see Bless *et al.* 1986, Casier 1987, Groos-Uffenorde & Schindler 1990, Becker & Bless 1990), have been proposed for the entomozoaceans. Extremely fragile, thin ornamentation over the whole carapace is apparently inconsistent with a benthonic mode of life since the ornamentation would have been damaged by mechanical interaction with detrital particles. The extremely high flanges, as noted also by Gooday (1983), may be rather an adaptation to the planktonic

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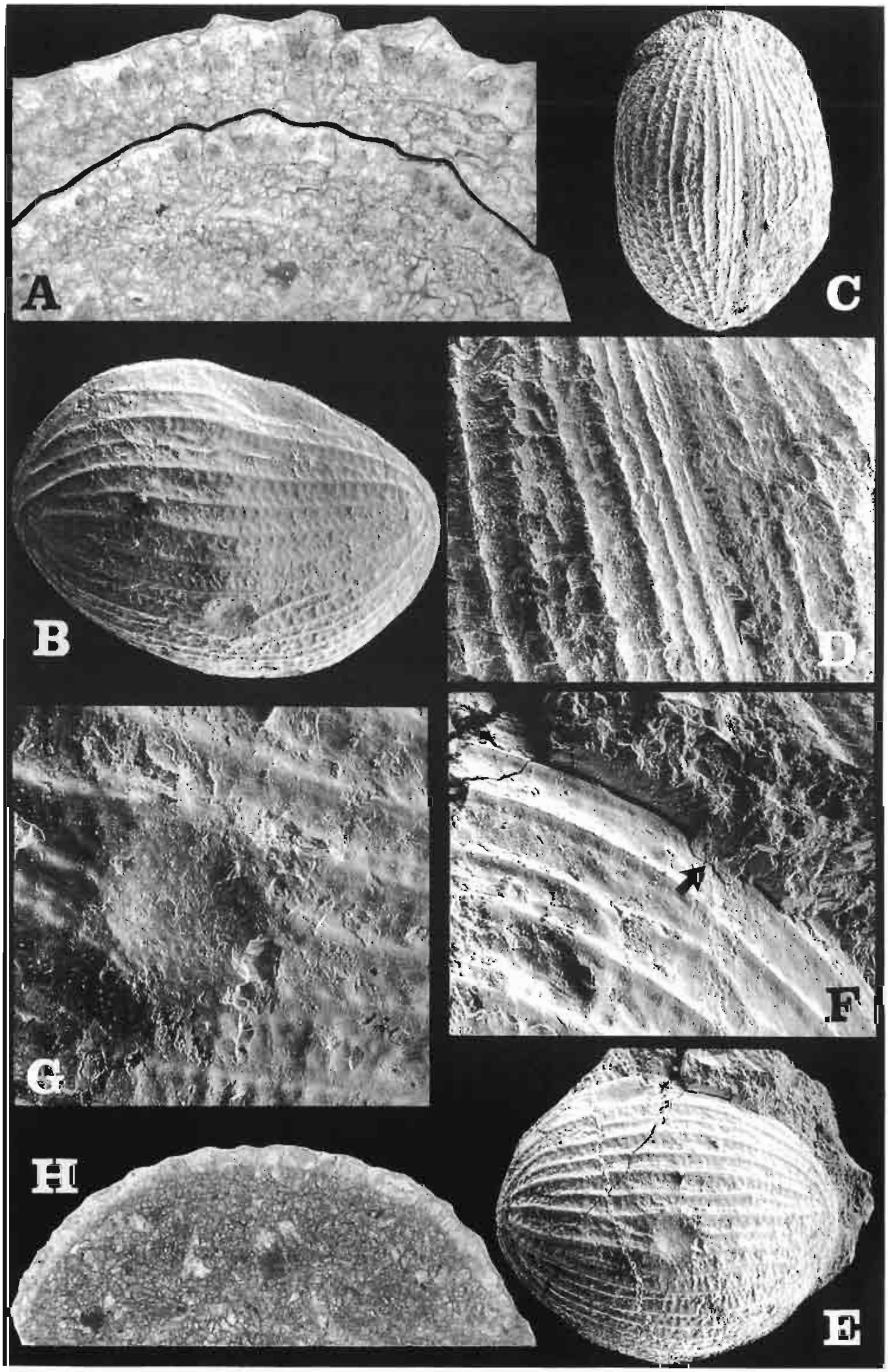
Fig. 9. *Richterina (Fossirichterina) semen* (Jones 1895), late Famennian, Kowala. ❑A. Thin section of the valve, only the inner layer preserved, the outer layer exfoliated. ZPAL O.XV/254, × 73, detail × 166. ❑B. Right valve in dorsal-oblique view, ZPAL O.XV/173, × 40. ❑C, D. Carapace in ventral view, juvenile specimen, ZPAL O.XV/228, × 40. D. Detail of C, × 133. ❑E-G. Left valve in lateral view, ZPAL O.XV/171, × 33. F. Detail of E, small fragments of the outer layer and flange visible near the rock matrix, × 133. G. Detail of E, muscle scar visible, × 133. ❑H. Thin section of the valve, inner layer only preserved, the outer layer completely exfoliated, ZPAL O.XV/255, × 63.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mode of life. Very high flanges on the external surface clearly reinforced the poorly calcified exoskeleton of such forms as *R. (Richterina)* and *R. (Fossirichterina)*. Such structures significantly increase the thickness of the cuticle and strengthen the exoskeleton by forming a mechanical meshwork over the external surface.

Data on the bathymetry of ostracode assemblages and associated faunas show that the entomozoaceans were apparently absent nearshore and had a strong preference for deeper environments (cf. Groos-Uffenorde & Schindler 1990). There is no direct evidence for a planktonic mode of life for entomozoaceans with rather heavily calcified shells and relatively short flanges such as *M. hemisphaerica, M. dichotoma* or *'E.' (N.) pseudorichterina*. For these species probably an epi-planktonic as well as plankto-benthonic mode of life is conceivable. Species with very high flanges and poorly calcified shells (species of subgenera *Richterina* and *Fossirichterina*) could be planktonic.

Descriptions of new species

Richterina (Fossirichterina) uffenordeae sp. n.
Fig. 5A-G.
Holotype: Left valve, ZPAL O.XV/184, Fig. 5F.
Type horizon: Lower *M. hemisphaerica - M. dichotoma* Zone, Famennian.
Type locality: Trench south of Kowala, Holy Cross Mountains, Poland.
Derivation of the name: In honour of Dr. Helga Groos-Uffenorde, German researcher of Palaeozoic ostracodes.

Diagnosis.– Lateral outline subrhomboidal. Surface with 2 longitudinal primary ribs connected with each other and running parallel to posterior margin. Between primary ribs there are 10-15 secondary ribs. Single short spine developed in anterior end in mid-height of the valve. Surface above upper primary rib and below lower primary rib strongly flattened. Elongate dorsal depression in front of mid-length. Muscle pit shallow.

Material.– Several tens of left and right valves. The outer layer with flanges only fragmentarily preserved.

Description.– The dorsal margin of the carapace is almost straight, ventral margin gently convex. The posterior end is broader. The anterior end has a short spine in mid-height. Shell surface bears 2 primary ribs, which run subparallel to the dorsal and ventral margins and then connect with each other posteriorly and run parallel to the posterior margin. High flanges are preserved on primary ribs in some specimens (Fig. 5C). Between the

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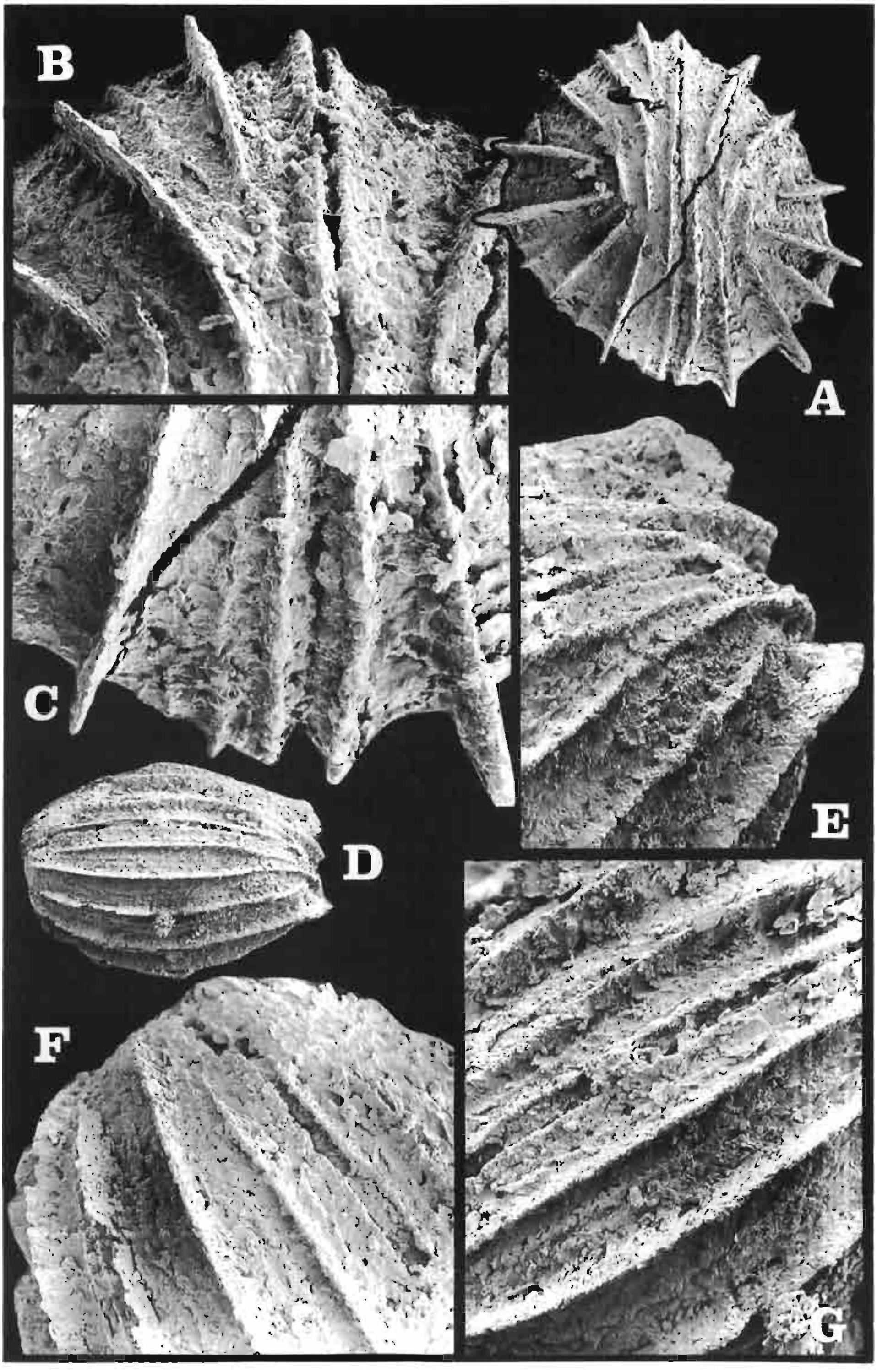
Fig. 10. *Richterina (Richterina) goodayi* sp. n., *Palmatolepis trachytera* Zone, Famennian, Łagów. □A-C. Posterior end of the carapace, ZPAL O.XV/301, × 66. B, C. Details of A, × 200. □D-G. Carapace in ventral view, juvenile specimen, ZPAL O.XV/302, × 40. E. Detail of D, anterior end in ventral view, × 133. F. Detail of D, posterior end, × 133. G. Detail of D, contact margin, × 133.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primary ribs the lateral surface covered by 10-15 longitudinal secondary ribs. Outside the primary ribs there is one concentric rib developed around the shell and marginal ridge (flange) developed close to whole free margin. There are 2-3 additional secondary ribs between each of the primary ribs, concentric rib and marginal ridge. The surface above the upper primary rib and below the lower primary rib is strongly flattened, giving a trapezoidal appearance in transverse section. Small shallow muscle pit developed slightly in front of the mid-length and slightly above mid-height. An elongate dorsal depression developed near the dorsal margin at mid-length or slightly in front of it.

Remarks.– *R. (F.) uffenordeae* sp. n. is closely related to *R. (F.) unispinosa*, but differs from it in strongly flattened surface above and below the primary ribs and shorter but wider anterior spine. *R. (F.) uffenordeae* is also similar to *R. (F.) submoravica* Wang 1984, from the lower Famennian of China (Wang 1984), but differs in having flattened surface in dorsal and ventral regions, as well as the presence of a short spine in mid-height. However, the illustrated specimens of *R. (F.) submoravica* are poorly preserved and comparison with them is difficult.

Distribution.– Only the type locality.

Richterina (Richterina) goodayi sp. n.

Figs 10, 11.

Holotype: Right valve, ZPAL O.XV/306, Fig. 11H.

Type horizon: Conodont *Palmatolepis trachytera* Zone, Famennian.

Type locality: Łagów, Holy Cross Mountains, Poland.

Derivation of the name: In honour of Dr. Andrew Gooday, British researcher of Palaeozoic entomozoaceans.

Diagnosis.– Subcircular in lateral outline. Dorsal and ventral margins slightly convex. Surface with one concentric flange around the entire margin, and 4-6 high flanges, betwen each of which are 1-2 additional and lower ribs. Small protrusion at anterior end of the central lateral flange on each valve.

Material.– 50 carapaces and several silicified valves.

Description.– The posterior end of the carapace is broadly curved. Anterior end is narrower and with a small protrusion at the end of the central lateral flange. The shell surface bears one concentric marginal flange and 4-6 high longitudinal flanges, between each of which are 1-2 additional low flanges. Central muscle pit absent at the exterior surface. The greatest

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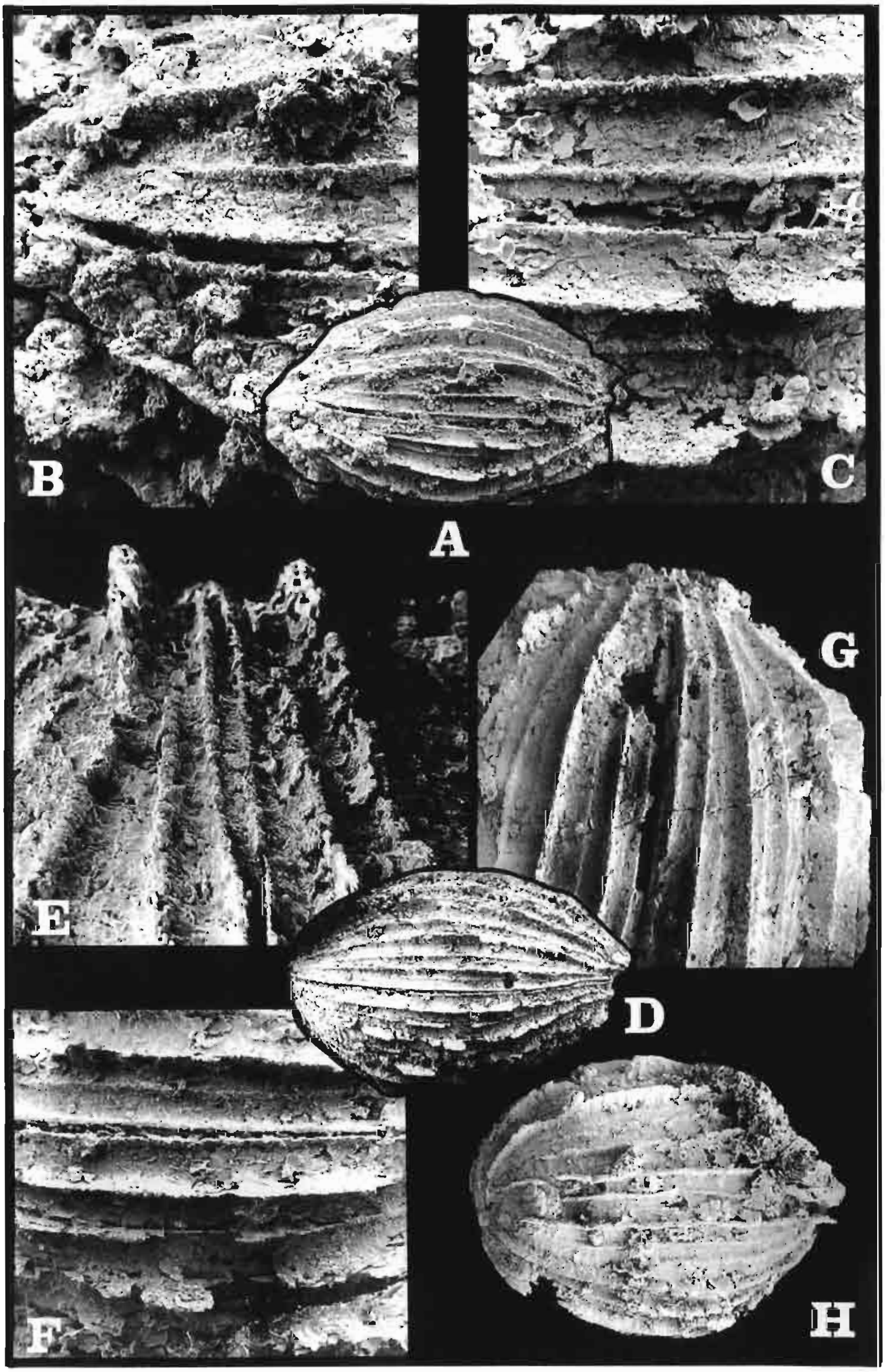
Fig. 11. *Richterina (Richterina) goodayi* sp. n., *Palmatolepis trachytera* Zone, Famennian, Łagów. ❑A-C. Carapace in ventral view, ZPAL O.XV/303, × 30. B, C. Details of A, ventral margin, × 133. ❑D-F. Carapace in ventral view, ZPAL O.XV/304, × 27. E. Detail of D, anterior end in ventral view, × 200. F. Detail of D, ventral contact margin visible, × 66. ❑G. Posterior end in ventral view, ZPAL O.XV/305, × 100. ❑H. Right valve in lateral view, holotype ZPAL O.XV/306, × 33.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width is located slightly behind the mid-length. Narrow marginal ridge is present on the left valve and admarginal ridge on the right.
Remarks.– *R. (R.) goodayi* sp.n. is closely related to *R. (R.) eocostata* Wang 1983 from the *R. (R.) eocostata* Zone (middle Famennian) of south China (Wang 1983, 1984), from which it differs in the presence of the protrusion in the anterior end of the valves.
Distribution.– Only the type locality.

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Streszczenie

Dewońskie małżoraczki z rodziny Entomozoidae znajdowane są najczęściej jako odciski skorupek, w związku z czym zarówno ich budowa jak i pozycja systematyczna nie są w pełni jasne.

Szlify cienkie wykonane z unikalnie zachowanych wapiennych skorupek i pancerzyków górnodewońskich entomozoidów z Gór Świętokrzyskich wykazały, że skorupki te zbudowane są z dwu wyraźnie różniących się warstw. Bardzo cienka warstwa zewnętrzna tworzy rozbudowaną ornamentację typu "finger-print" na powierzchni skorupek entomozoidów. Pomiędzy wysokimi żebrami warstwa zewnętrzna osiąga grubość 1-2 μm u *R. (R.) striatula* i *R. (R.)* cf. *tenuistriata*, 5-6 μm u *M. hemisphaerica* i *M. dichotoma* oraz 2 μm u *'E.' (N.) pseudorichterina*. Pod warstwą zewnętrzną znajduje się gruba warstwa wewnętrzna osiągająca 20-30 μm u *R. (R.) striatula*, 40-60 μm u *M. hemisphaerica* i *R. (F.) semen* oraz 30-40 μm u *'E.' (N.) pseudorichterina*. Górna powierzchnia warstwy wewnętrznej pokryta jest delikatną ornamentacją odpowiadającą ornamentacji zewnetrznej. Warstwa wewnętrzna różni się budową oraz stopniem kalcyfikacji u poszczególnych gatunków.

Przez porównanie ze współczesnymi małżoraczkami z rzędu Myodocopa wysunięto hipotezę, że zewnętrzna warstwa skorupek entomozoidów odpowiada epikutikuli współczesnych małżoraczków, natomiast warstwa wewnętrzna endokutikuli. Występowanie zwapniałej epikutikuli poza nielicznymi wyjątkami nie było dotychczas znane u kopalnych małżoraczków.

Opisano po raz pierwszy struktury zawiasowe, struktury marginalne oraz sposób obejmowania się skorupek entomozoidów, cechy mające istotne znaczenie taksonomiczne. Zasugerowano pochodzenie entomozoidów od dolnopaleozoicznych małżoraczków z rzędu Palaeocopida.

Model życia entomozoidów jest w literaturze przedmiotem wielu kontrowersji przy przeważającym poglądzie o planktonicznym trybie życia większości gatunków. Budowa skorupek entomozoidów przemawia za planktonicznym trybem życia gatunków o słabo zwapniałej warstwie wewnętrznej (*R. (R.) striatula, R. (R.)* cf. *tenuistriata, R. (F.) costata, R. (F.) unispinosa, R. (F.) uffenordeae*) oraz nekto-bentonicznym dla gatunków o większym stopniu kalcyfikacji tej warstwy (*M. hemisphaerica, M. dichotoma*).