

The Late Devonian Upper Kellwasser Event and entomozoacean ostracods in the Holy Cross Mountains, Poland

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Olempska, E. 2002. The Late Devonian Upper Kellwasser Event and entomozoacean ostracods in the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* 47 (2): 247–266.

Late Frasnian–Early Famennian entomozoacean ostracod assemblages from the Plucki section in the Holy Cross Mountains were studied to establish the effect of the “Kellwasser bio-event” on the planktonic biodiversity and faunal content. The composition of ostracod assemblages changes from a moderately diverse (10 species) *Entomoprimitia–Richterina–Nehdentomis–Nandania* dominated “background” assemblage characterising a pre-event interval, to an *Entomoprimitia*-assemblage during the event interval, and finally to a *Franklinella*-dominated post-event assemblage in the Middle *Palmatolepis triangularis* conodont Zone. The Frasnian–Famennian extinction caused substantial losses among entomozoacean lineages. In the Plucki section it occurred in two closely spaced steps within the *Palmatolepis linguiformis* conodont Zone. The first step, at the base of the dark cephalopod limestone (Upper Kellwasser Horizon), reduced the abundance and the species diversity of entomozoaceans to only two *Entomoprimitia* species. The vacant niche was then filled by the new, immigrant species *Entomoprimitia (Entomoprimitia) kayseri* which is dominant in the Upper Kellwasser interval. All these species were lost at the second step within the Upper Kellwasser Horizon. The entomozoaceans remained virtually absent during a long time interval between the end-Frasnian crisis and the Middle *Pa. triangularis* Zone. They reappear as new species from refugia lineages (*Franklinella*, *Nehdentomis*) and became widespread, indicating favourable ecological conditions. Some 13 species have been identified and assigned to seven genera. *Rabienella? lagowiensis* sp. nov. is proposed.

Key words: Ostracoda, Entomozoacea, Frasnian, Famennian, Upper Kellwasser Event, extinction.

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Introduction

The Frasnian–Famennian (F–F) bio-event associated with a geologically short-term reduction in global biomass and extinction of up to 80 percent of the world’s marine tropical to subtropical species, represents one of the largest Phanerozoic mass extinction events (see McLaren 1970; Raup and Sepkoski 1982; Sandberg et al. 1988; McGhee 1988, 1996; Walliser et al. 1989; Schindler 1990a, b, 1993; Buggisch 1991; Becker and House 1994; Walliser 1996; Hallam and Wignall 1997; Copper 1998; Racki 1998, 1999a, b; Racki et al. 2002; Morrow 2000). The species affected most were reefal, perireefal and shallow-water benthic organisms belonging to stromatoporoids, corals, brachiopods, and trilobites, but phytoplankton, ammonoid cephalopods, crinoids, ostracods, and conodonts were also decimated. However, the causes, and relative scaling of the F–F event, still remain subjects of controversy.

The latest Frasnian biotic turnover, during the eustatic-hypoxic Upper Kellwasser event, culminated in the presumed ecosystem collapse near the F–F transition (see discussion in McGhee 1996; Copper 1998; Racki 1998, 1999a, b). This catastrophic hypoxic episode in the Late *Palmatolepis linguiformis*

formis Zone was associated with important eustatic fluctuations: a rapid sea-level rise, quickly reversed in a catastrophic fall (Johnson et al. 1985; Sandberg et al. 1988, 1992; Muecher et al. 1996) recorded in the Upper Kellwasser Horizon (UKWH).

The bituminous limestone and black shale units of the Kellwasser horizons can be found across Europe and northern Africa in the late Frasnian, demonstrating incursions of the oxygen minimum zone into shallow water regions during critical periods of time (Buggisch 1991; Wendt and Belka 1991).

Most of the extinctions occurred at the base and during the UKW interval (Schindler 1990a, b). The sudden change of the lithology immediately above the UKWH was reconstructed (Sandberg et al. 1988; Klapper et al. 1994) as a sudden regressive event, but interpreted by Schindler (1990a) as autoclastic breccia after the event. According to Schindler (1990a, b), the shallowing begins in the uppermost part of the UKWH, before the distinct facies change.

The late Frasnian was a period of rapid diversifications and evolutionary innovations for the entomozoaceans (pelagic “finger-print” ostracods): more than 20 species have been found in the late Frasnian, between the Lower and Upper KW horizons (Groos-Uffenorde and Wang 1989; Groos-Uffenorde and Schindler 1990). The total diversity of

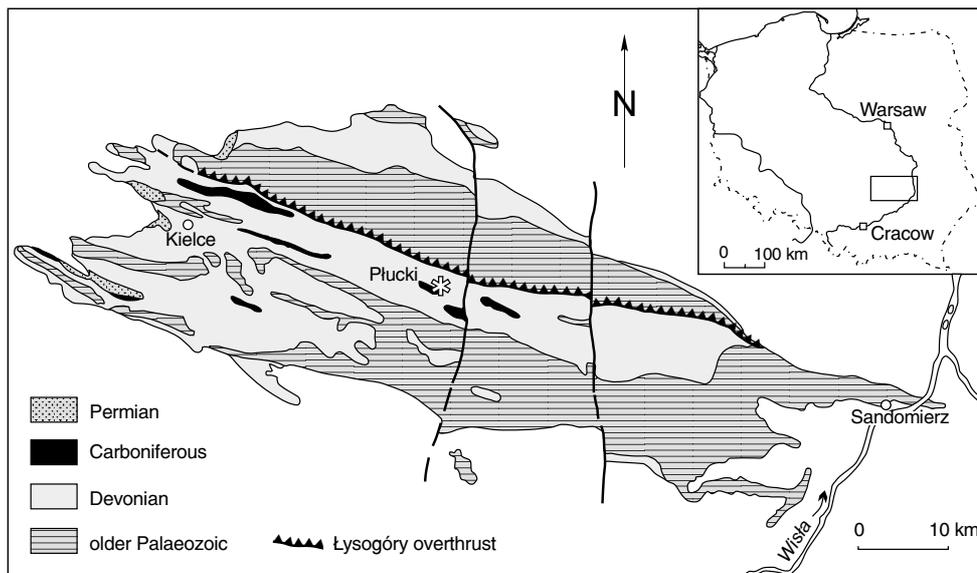


Fig. 1. Geological map of the Holy Cross Mountains and location of the Plucki section. Simplified after Racki 1993.

the Entomozoacea for the Frasnian is estimated at some 11 genera and subgenera (Groos-Uffendorfer et al. 2000).

The objective of this paper is to present the pelagic entomozocean ostracod faunal change across the F–F boundary at the Plucki section (Fig. 1), because this section displays the most complete F–F boundary beds in the Holy Cross Mountains. Another important reason is that until now, the ostracod change at the Frasnian–Famennian boundary in Poland, has only been studied in shallow settings. Definitions of various entomozocean zones and subzones recognised in Poland are briefly discussed, and correlation with sections of western Europe is proposed. However, the data were derived only from one section, and consequently may reflect a local rather than broad biogeographic patterns of extinction. It is demonstrated that for the entomozocean species, at least in low latitudes, the F–F boundary extinction was a relatively abrupt event.

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

Material and methods

The present investigation is based on 166 samples covering the uppermost 13.5 m of the late Frasnian succession and 8 m of the early Famennian, with the densest sampling through the interval of maximum turnover of species. More than 15,000 valves, carapaces and fragments of ostracod shells were extracted. The assemblages recognised are rich in juvenile as well as in large adult specimens. Entomozoceans are found in 39 samples and entomozocean-bearing horizons are most frequent in shales. The samples, each weighing about 0.5–1 kg, were disintegrated through thawing in a saturated solution of Glaubert's salt. No detailed work has been done on limestone samples below the F–F boundary because of the difficulty in extracting the entomozoceans. The dark (UKW) limestone

samples and the early Famennian limestone samples were hammered into small pieces. Each one was examined under a microscope for entomozocean specimens or moulds.

Entomozoceans extracted from the rock matrix have interirid areas often filled with sediment. They are preserved as single valves or carapaces. Preservation is poor, and commonly they are fragmented. The probably originally soft and flexible shells of entomozoceans are usually wrinkled, flattened, extended or compressed parallel to their long axis or deformed obliquely into an asymmetric shape.

Stratigraphical setting

The Plucki entomozocean-bearing mudrocks were formed in a deep intrashelf basin (outer part of the epicontinental sea) which was situated on the south-eastern edge of the Laurussian palaeocontinent (Fig. 2) in a subtropical belt at approximately 10°S palaeolatitude on the map of Scotese and McKerrow (1990).

The section is exposed in a trench situated near Łągów, about 30 km east of Kielce, in the Holy Cross Mountains (Fig. 1). The studied interval comprises the *Rabienella reichi*/*Entomoprimitia (Entomoprimitia) splendens* Interregnum, the *E. (E.) splendens* Zone, the *E. (E.) splendens*/*Franklinella (Franklinella) sigmoidale* Interregnum and the *F. (F.) sigmoidale* Zone of the entomozocean zonation (Fig. 3). This sequence consists of rhythmically bedded, commonly black and laminated marly limestones and shales ranging from the Late *Palmatolepis rhenana* to the Middle *Palmatolepis triangularis* Zone (Racki 1993; Racka 2000; Ginter 2002; Racki et al. 2002; Dzik in press). The F–F boundary is located near the top of a 30 cm thick, dark cephalopod-bivalve-homocentrid (coquine) limestone bed (Racka 2000). This bed is believed to be equivalent to the German Upper Kellwasser Limestone, a black bituminous limestone depos-

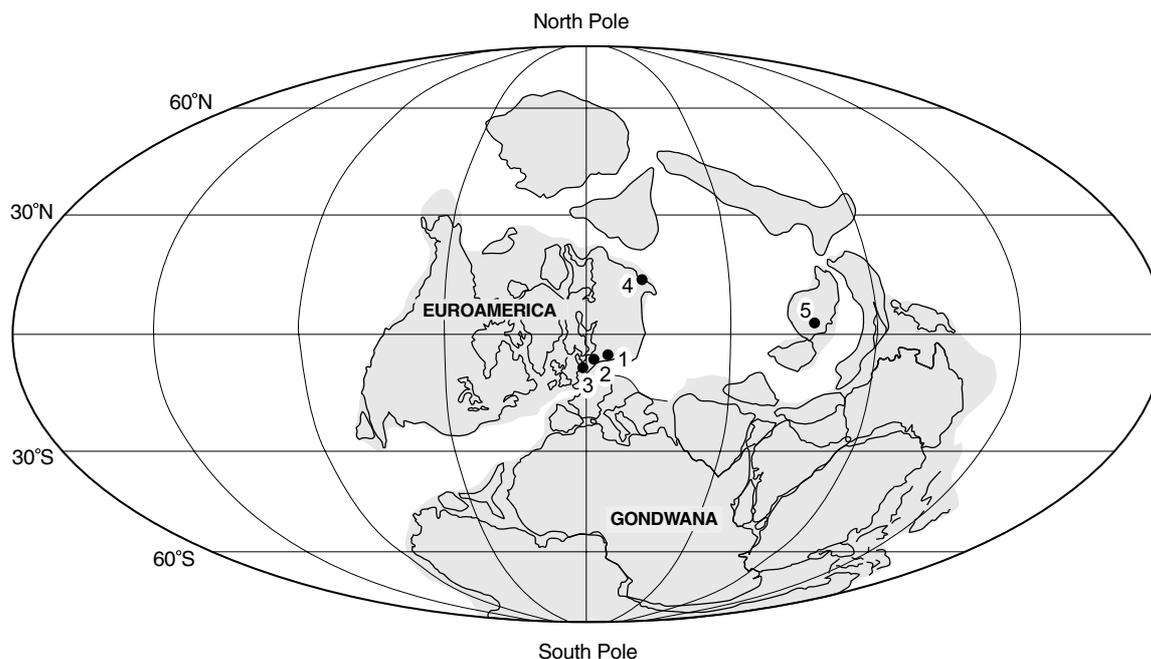


Fig. 2. Locations of studied and discussed entomozocean faunas on the Late Devonian palaeogeography map of Scotese and McKerrow (1990). 1, Holy Cross Mountains; 2, Rhenish Slate Mountains; 3, Ardennes; 4, Volga-Ural region; 5, South China.

ited under hypoxic conditions in the Kellwasser Valley in the Harz Mountains (Schindler 1990a).

The faunal assemblage of the Płucki section contains conodonts, cephalopods, abundant entomozoceans and homoctenids, rare brachiopods, chondrichthyan microremains, and also rare molluscs.

Entomozocean palaeoenvironments

Entomozoceans originated in the Late Silurian, differentiating rapidly into many groups and attaining their greatest peak in diversity during the Late Devonian and Early Carboniferous. The tropical and subtropical warm waters of the Palaeotethys proved to be a favourable habitat, which produced a spectacular range of entomozocean “finger-print” morphologies.

The entomozocean fauna had a high degree of cosmopolitanism. Often the same species can be found in Europe, China, North Africa, and North America. They are typically associated with outer-shelf depositional environments, but also occurred in more nearshore settings. It is generally assumed that most of the entomozocean ostracods had a planktonic or nekto-planktonic life habit, although any direct evidence for this is lacking. The life habit of the entomozoceans was extensively discussed by Gooday (1983) but still remains a subject of controversy. Almost all possible marine habitats, ranging from planktonic to benthic and from shallow to deep water have been proposed for the entomozoceans (see Casier 1987, 1992; Becker and Bless 1990; Groos-Uffenorde and

Schindler 1990; Olempska 1992; Lethiers and Casier 1995). Data on the bathymetry of ostracod assemblages and associated faunas show that the entomozoceans were apparently absent nearshore and had a strong preference for deeper environments. However, occasionally they also occur in more shallow environments together with benthic ostracods. According to Casier (1987) they were suited for living in poorly oxygenated environments.

Entomozocean stratigraphy across the Frasnian–Famennian boundary

The Frasnian entomozocean zonation in Europe was established by Rabien (1954), supplemented by Krebs and Rabien (1964) and Buggisch et al. (1978) and was mainly based on faunas from the Rhenish Slate Mts. of Germany. Supplements to these works have been added by Gooday (1978), Groos-Uffenorde and Wang (1989), Groos-Uffenorde and Schindler (1990), and the entomozocean zonation was recently summarised by Groos-Uffenorde et al. (2000).

The entomozocean zonation is mainly based on a partial ranges of species. The subdivision of the late Frasnian is based on the evolution of *Rabienella* and *Entomoprimitia*, and is named after the first occurrence of a new species. These partial ranges are mostly considered as subzones.

Entomozocean ostracods of the latest Frasnian *E. (E.) splendens* Zone in the Rhenish Slate Mts. are best seen in shale sequences. The ostracod fauna of the upper part of the *E. (E.)*

splendens Zone from dark limestones of the UKWH of the Harz Mountains (inclusive of the type locality in the Kellwasser Valley) and the Rhenish Slate Mts. is dominated by *Entomoprimitia* species but contains as well *Nehdentomis*, *Franklinella* and *Richterina* (e.g., Rabien 1954; Müller-Steffen 1965).

The boundary between the *E. (E.) splendens* and *F. (F.) sigmoidale* zones was correlated with the Middle *Pa. triangularis* conodont Zone by Buggisch et al. (1978), and followed by Gooday (1978), Casier (1982b), Bless et al. (1986), Groos-Uffendorde and Wang (1989), and Gozalo (1994). Groos-Uffendorde and Schindler (1990) and Schindler (1990a, 1993) have correlated the extinction of *Entomoprimitia (Entomoprimitia) splendens* (Waldschmidt, 1885) in a pelagic sequence near Iserlohn (Rhenish Slate Mts., Germany) with the F–F boundary (top of the *Pa. linguiformis* Zone).

The beginning of the early Famennian adaptive radiation in entomozoceans has been hitherto only rarely documented in shales from Western Europe. The earliest Famennian *F. (F.) sigmoidale* Zone was established by Raith (1968) above the *E. (E.) splendens* Zone as a total range zone in the latest Adorf “stage” (= latest tao5 of Rabien 1954) and earliest Nehden “stage” (early do II), the so-called “Adorf/Nehden Grenzhorizont”. According to Buggisch et al. (1978: 68) and Rabien (1970: 154) the upper part of the *F. (F.) sigmoidale* Zone is characterised by the co-occurrence of *Franklinella (Franklinella) sigmoidale* Müller-Steffen, 1964 and *Richterina serratostrata* (Sandberger, 1845), but *F. (F.) sigmoidale* does not continue into their *R. serratostrata/N. nehdensis* Zone.

The sections in Thuringia near Saalfeld (Blumenstengel 1959) show basically the same succession of Frasnian entomozocean faunas as the Rhenish localities, however, the *F. (F.) sigmoidale* Zone is missing near Saalfeld.

Entomozoceans of the F–F boundary stratotype at Coumiac (Montagne Noire, France) are rare. They did not survive the F–F event, and guide species have not been reported (Lethiers and Casier 1995, 1996a, b).

Changes within the entomozocean ostracods at the F–F boundary from trenches near the historical type section at Senzeilles, Dinant Basin (Belgium), have been published by Casier (1982a, 1992). The late Frasnian entomozoceans from the Volga-Ural region were also described by Polenova (1955).

The F–F entomozocean zonation from Europe was partly followed by Wang (1983, 1986, 1987, 1989) in China. However, the entomozocean-bearing sections from China have not been dated with conodonts.

Frasnian–Famennian entomozoceans of the Plucki section

The biostratigraphy of the Plucki section is based on the scheme of Rabien (1954) and on its supplements, with the addition of the *E. (E.) splendens/F. (F.) sigmoidale* Interregnum

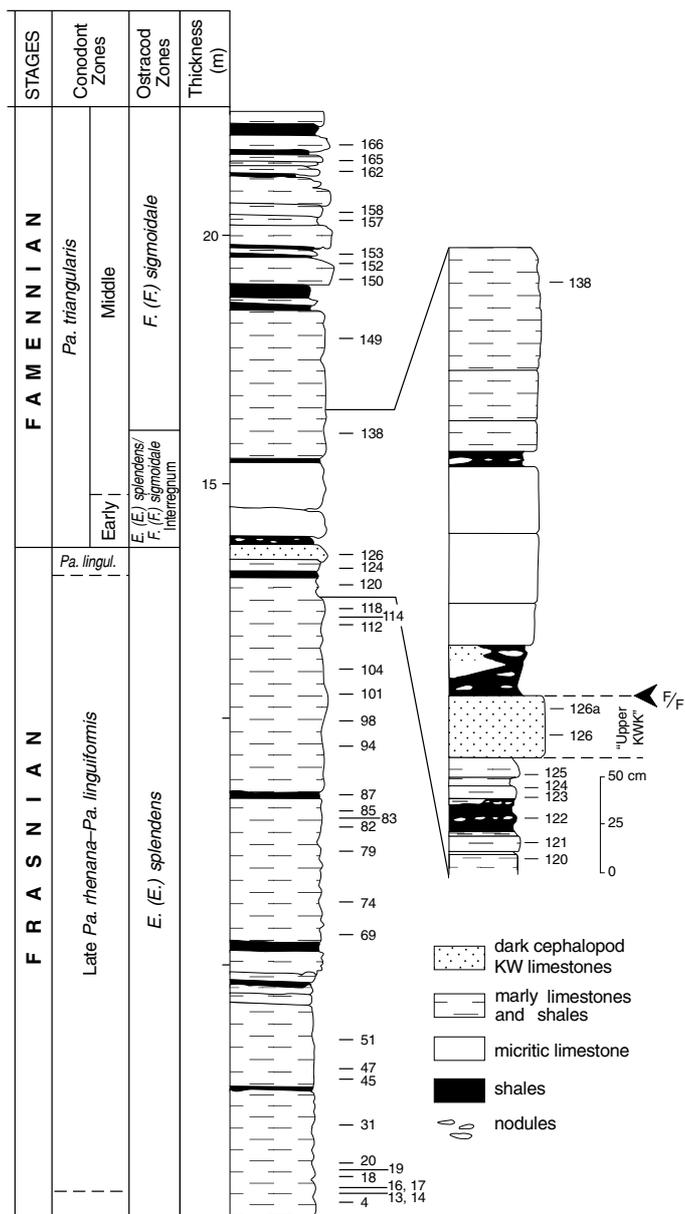


Fig. 3. Lithological column across the F–F boundary in the Plucki section.

to mark the absence of the entomozoceans in the early part of the Famennian (Fig. 3). The age of the studied sequence starts with the *R. reichi/E. (E.) splendens* Interregnum and runs to the *F. (F.) sigmoidale* Zone. Thirteen entomozocean species were recorded in the studied samples (Fig. 4).

The primary changes of the entomozocean faunas across the F–F boundary are summarised in Fig. 5. The main entomozocean bio-events and relative frequency are superimposed over the primary conceptual phases of mass extinctions, recoveries and sea-level fluctuations recognised by Kauffman and Erwin (1995), Kauffman and Harries (1996), and Johnson et al. (1985).

The major characteristics of the extinction and important associated palaeoecologic changes of the entomozocean faunas include successively:

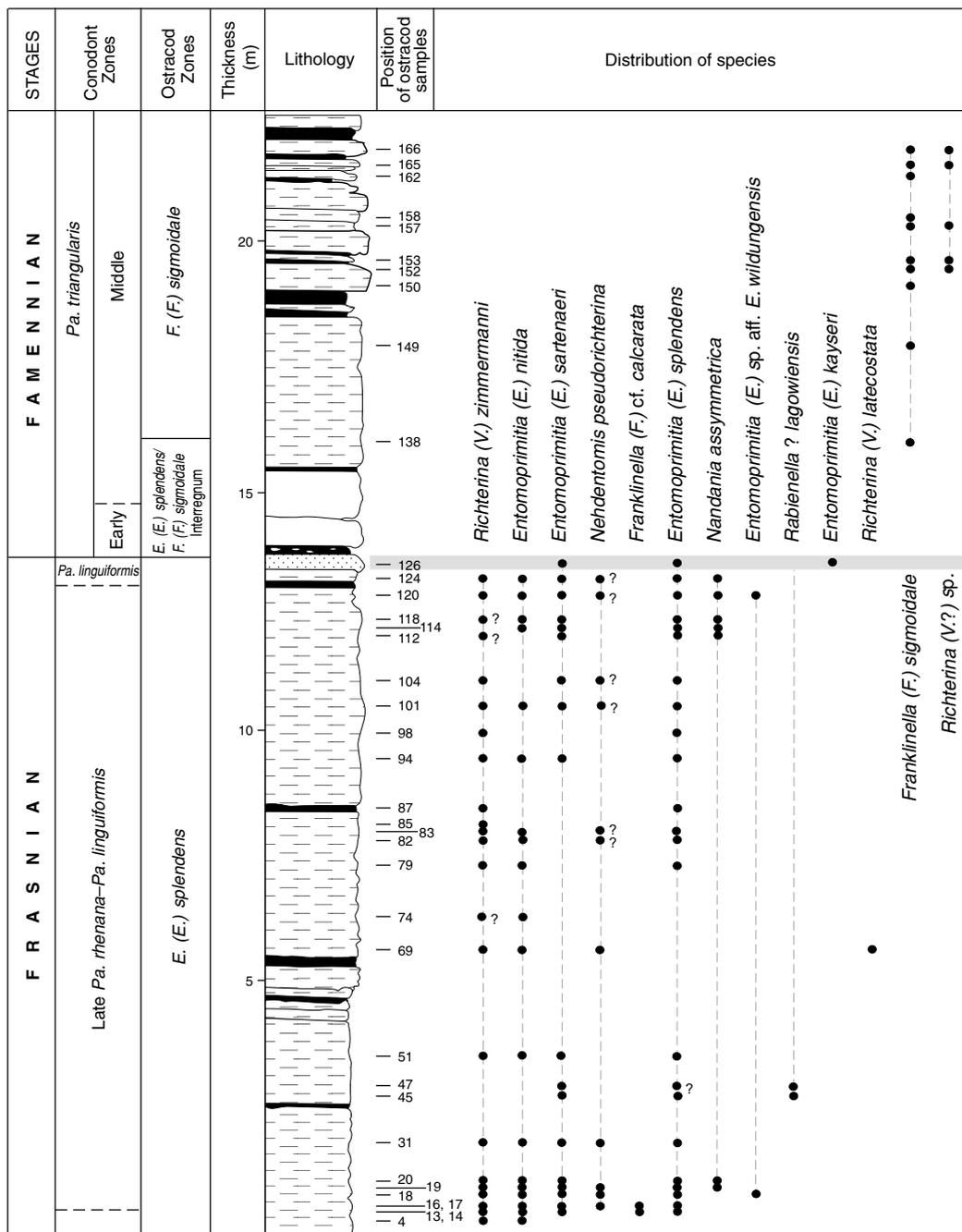


Fig. 4. Entomozoacean distribution across the Frasnian–Famennian boundary in the Plucki section.

Late Frasnian “background” entomozoacean fauna.—

The late Frasnian entomozoacean fauna was dominated by species of huge populations sizes with global distribution within tropical and subtropical ocean water masses. Species had short biostratigraphical ranges, reflecting rapid evolutionary rates. In most stratigraphically complete late Frasnian sections worldwide, there are usually 8–13 entomozoacean species within each entomozoacean (sub-) zone (Rabien 1954; Casier 1975, 1982a; Wang 1983, 1989; Groos-Uffenorde and Wang 1989).

Species origination rates within the genera *Rabienella*, *Entomoprimitia*, *Richteria*, *Nehdentomis* and *Nandania*

balanced extinction rates over the interval between the Lower and Upper Kellwasser Horizons (see also Groos-Uffenorde and Wang 1989).

Generic composition plots show that the entomoprimitid-richterinid biofacies dominated offshore palaeogeographic settings just below the UKWH. The net diversity of entomozoaceans in the Plucki section below the UKWH remained relatively moderate (10 species), however, in the opinion of the present writer, there are several cryptic species within this fauna.

In the lowermost part of the Plucki section (sample P-4), monospecific association of *Richteria (Volkina) zimmer-*

manni (Volk, 1939) is present. Probably this part of the section represents the upper part of the *R. reichi*/*E. (E.) splendens* Interregnum.

The *E. (E.) splendens* Zone spans the total range of *Entomoprimitia (Entomoprimitia) splendens* (Waldschmidt, 1885). At Płucki this species range from 20 m (sample P-13) below the F–F boundary to the upper part of the cephalopod limestone (UKW) layer (sample P-126a).

The entomozocean ostracod assemblages of the *E. (E.) splendens* Zone below the UKW layer, are abundant in specimens but moderately diversified and consist of the nominal species, *Entomoprimitia (Entomoprimitia) sartenaeri* Casier, 1975, *Entomoprimitia (Entomoprimitia) nitida* (Roemer, 1850), *R. (V.) zimmermanni*, *Nandania assymetrica* (Koch, 1967), *Nehdentomis pseudorichterina* (Matern, 1929), and scarce *Franklinella (Franklinella) cf. calcarata* (Richter, 1856), *Entomoprimitia (Entomoprimitia) sp. aff. E. (E.) wildungensis* (Matern, 1929), *Rabienella? lagowiensis* sp. nov., and *Richterina (Volkina) latecostata* Rabien, 1954.

In the middle part of the section (samples P-15, P-16, P-19) rare cypridinaceans (Myodocopida) represented by *Polenovia pseudomagna* (Stewart and Hendrix, 1945) and *Palaeophilomedes? sp.* occur. Benthic ostracods represented by primitiopsacean species occur in sample P-14.

The morphological studies of several traditionally recognised species, especially *E. (E.) splendens* and *E. (E.) sartenaeri*, have shown that there is a great variability and that several morphotypes occur in each “species”, which differ in ribbing pattern and density of ribs. They likely represent clusters of related species. Probably these species actually consist of numerous cryptic species, but it seems probable that some of them also represent sexual dimorphs. Four species: *R. (V.) zimmermanni*, *E. (E.) nitida*, *E. (E.) splendens*, and *E. (E.) sartenaeri* dominate the entomozocean assemblage in the interval below the UKWH (Fig. 5).

The base of the section (samples P-4 to P-13) is characterised by the dominance of *R. (V.) zimmermanni*, whose relative frequency is nearly 100 percent, and only two poorly preserved specimens of *E. (E.) nitida* have been found. In samples P-13 to P-31, *E. (E.) nitida* and *R. (V.) zimmermanni* each comprises about 30 percent of the content of the assemblage. The remaining species (*E. (E.) sartenaeri*, *N. pseudorichterina*, *F. (F.) cf. calcarata*, *E. (E.) splendens*, *N. assymetrica* and *E. (E.) sp. aff. E. (E.) wildungensis*) do not exceed a few percent of each sample contents. The most significant change in the composition of entomozocean assemblage took place in samples P-45 and P-47. These samples are dominated by *E. (E.) sartenaeri*, which comprises more than 95 percent of the total content. *E. (E.) splendens* is present in small numbers.

Entomozocean assemblage from sample P-51 is dominated by *E. (E.) nitida* but *R. (V.) zimmermanni*, *E. (E.) sartenaeri*, *E. (E.) splendens* constitute a very small percentage of the assemblage. Samples P-69 to P-118 are dominated by *R. (V.) zimmermanni*.

In samples P-120 to P-125 just below the UKWH, the entomozoceans are very abundant, represented by juvenile

and adult specimens. Four species: *E. (E.) nitida*, *E. (E.) sartenaeri*, *E. (E.) splendens* and *Nandania assymetrica*, dominate in this part of the section.

There is no gradual decrease in entomozocean abundance and diversity towards the top of the Frasnian in the Płucki section.

Entomozocean fauna of the Płucki section is comparable with that of the “Cypridinen-Schiefer” of Germany, which have been interpreted as pelagic fauna in typical sediments of a “Stillwasser” facies deposited in a relatively deep marine basin, with poorly oxygenated and dark bottom surface (Rabien 1956).

Entomozoceans of the Upper Kellwasser Event Horizon.—This horizon, a 30 cm thick limestone, show characteristic associations of faunal elements such as bivalve *Buchiola*, goniatite *Crickites*, orthocone nautiloids, homotenenids in huge numbers, and rare entomozoceans. It represents the uppermost part of the *Pa. linguiformis* Zone and the top of the layer represents the Early *Pa. triangularis* Zone.

An examination of the species richness and of the abundance shows a substantial change in the distribution of taxa that corresponds to the main extinction (Figs. 4, 5). At the base of the dark cephalopod limestone layer (UKWH) the diversity of entomozoceans declines rapidly in the Płucki section. The base of this layer marks the final extinction of eight entomozocean species, and the only survivors were *E. (E.) splendens* and *E. (E.) sartenaeri*. In the UKWH, *Entomoprimitia (Entomoprimitia) kayseri* (Waldschmidt, 1885) an “exotic” species for the Płucki section appeared and became dominant in this interval (samples P-126, P-126a; Figs. 4, 5). This species is also abundant in the UKWH in German sections. The appearance of *E. (E.) kayseri* in the Płucki section seems to be associated with the short-term transgressive pulse recognised by Johnson et al. (1985) and Sandberg et al. (1988) in the *Pa. linguiformis* Zone. Finally, all entomozocean species disappeared near the top of the UKWH (above the sample P-126a).

The F–F boundary at the Płucki section can be identified near the top of the cephalopod limestone layer by the appearance of *Palmatolepis triangularis* (Racka 2000; Dzik in press).

The main extinction step and the substantial drop in entomozocean diversity in the Płucki section differ from UKWH sections in Germany, but they coincide with the beginning of the kenoxic conditions of the UKWH. However, multicausal factors appear responsible for the entomozocean extinction bio-event.

Appearance of anoxic/kenoxic waters in shallower settings coincide with major short-term sea-level oscillation and climatic changes (Sandberg et al. 1988, 1992; McGhee 1989, 1996; Buggisch 1991; Joachimski and Buggisch 1993, 1996; Racki 1998, 1999a, b) probably in relation to a global cooling (Copper 1998). The timing of the onset and the duration of the anoxia are probably slightly different at different areas (see discussion in Bratton et al. 1999). It appears that ento-

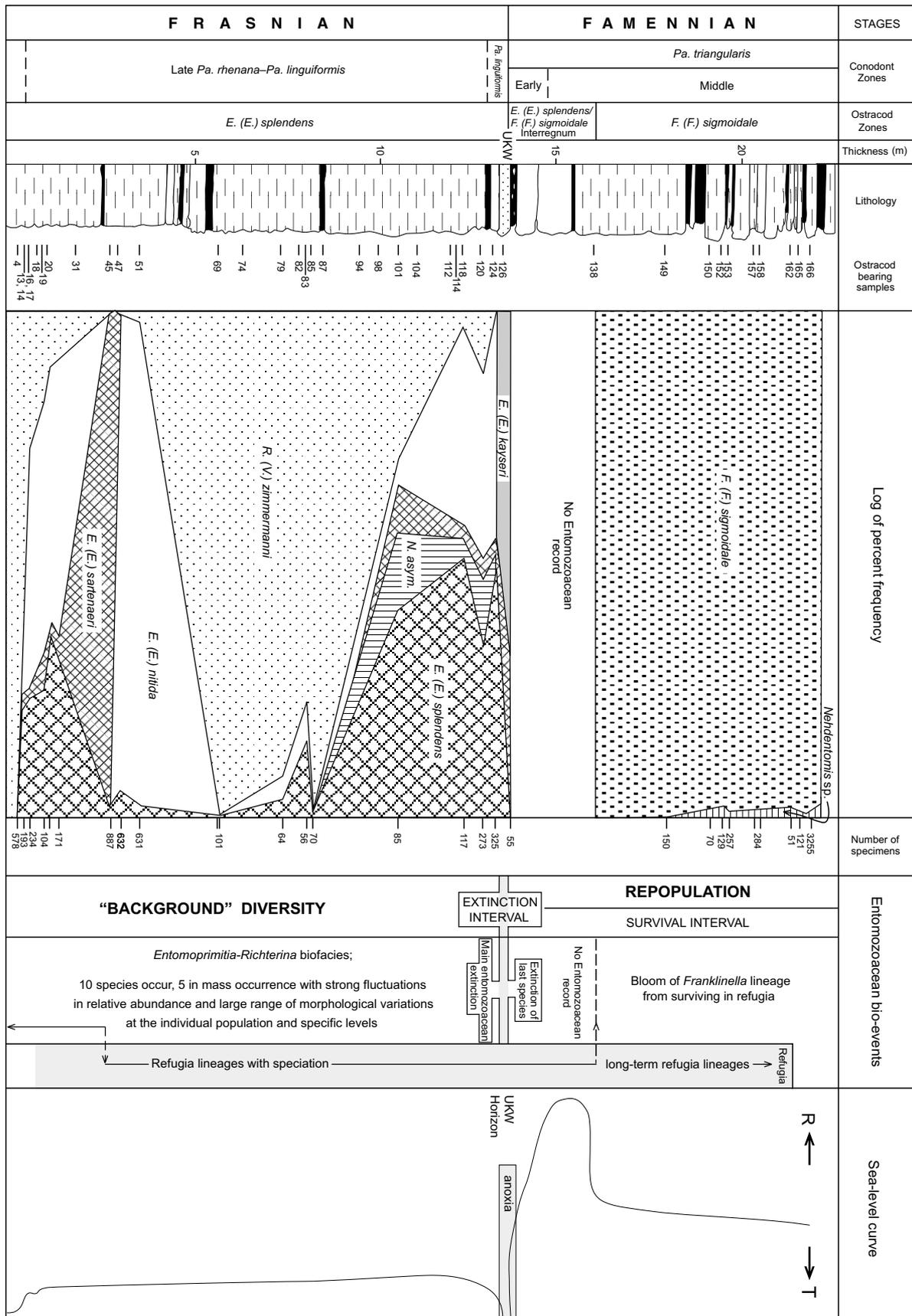


Fig. 5. The main entomozoacean bio-events and relative frequency superimposed over the primary conceptual phases of mass extinctions, recoveries and sea-level fluctuations recognised by Kauffman and Erwin (1995), Kauffman and Harries (1996) and Johnson et al. (1985).

mozoaceans preferred deeper water environments and probably oxygen-deficient habitat (Casier 1987), and that they were affected at the beginning of the rapidly rising bottom-water anoxia into the water column. This was responsible for the disappearance of species and of their habitats before the species could repopulate by long-distance dispersal (see also Norris 2000).

The data based on the detailed stratigraphic range of benthic ostracods from several F–F boundary sections in Europe and N-America, show that more than 70 percent of all marine benthic ostracod species abruptly disappeared close to the F–F boundary in lower latitudes (Casier 1992; Lethiers and Casier 1996a, b, 1999; Casier and Lethiers 1998a, b; Lethiers et al. 1998; Casier et al. 1996, 1997, 1999, 2000).

The stepwise character of the UKW extinction in the German sections at Steinbruch Schmidt (Kellerwald) and Aeke valley (Harz Mts.) was demonstrated by Walliser et al. (1989), Schindler (1990a, b, 1993), and Groos-Uffendorde and Schindler (1990). According to these authors, the step they call $\beta 2$ marks the most prominent change within the UKWH in Steinbruch Schmidt section with the extinction of gephoroceratids and of two *Entomoprimitia* species *E. (E.) splendens* and *E. (E.) kayseri*, and the reduction of homocatenids.

The study of the F–F ostracod fauna in the Schmidt quarry by Casier and Lethiers (1998a) and Casier et al. (1999) has shown that the mass extinction of the benthic ostracods took place in the last 5 cm of the UKWH and that this thickness is in accordance with a duration of some thousand years for the mass extinction as estimated by Sandberg et al. (1988).

Early Famennian repopulation interval.—The earliest Famennian post-extinction interval is characterised by the absence of entomozocean fauna in the lowermost part of the Famennian (early and lower part of the Middle *Pa. triangularis* Zone, samples P-127 to P-138) of the Płucki section. The *E. (E.) splendens*/*F. (F.) sigmoidale* Interregnum spans the interval from the last appearance (sample P-126a) of *E. (E.) splendens* to the first appearance (sample P-138) of *F. (F.) sigmoidale*. At Płucki this interval extends from the top of the UKWH to 2 m above the F–F boundary. In the investigated region, entomozoaceans reappeared in the Middle *Pa. triangularis* Zone, more than 0.5 m.y. after the end-Frasnian extinction according to Sandberg and Ziegler (1996) conodont based biochronology. The recovering entomozoaceans include mainly *F. (F.) sigmoidale*, which marked a post-extinction abundance bloom and comprises almost 100 percent of the total content, and very rare *Nehdentomis* sp. specimens. The genus *Franklinella* strongly dominated early Famennian basinal marine assemblages in the Palaeotethys.

The rapid colonisation of the ecospace by the *Franklinella* species after a long interval without obvious biota seems to be associated with the beginning of the early Famennian transgression (T-R Cycle IId) as established by Johnson et al. (1985), and Sandberg et al. (1988, 1992). A high number of *Franklinella* reflects the transition to a more open marine environment associated with this eustatic sea-level rise. The appearance of entomozoaceans could also be due to oceanographic factors such as a return to well oxygenated water masses and also to biological factors such as the opportunistic occupation of the niche spaces vacated by other entomozoaceans, species that were casualties of the extinction in the latest Frasnian.

It appears that *Franklinella*- and *Nehdentomis*-lineages survived the Upper Kellwasser crisis in refugia.

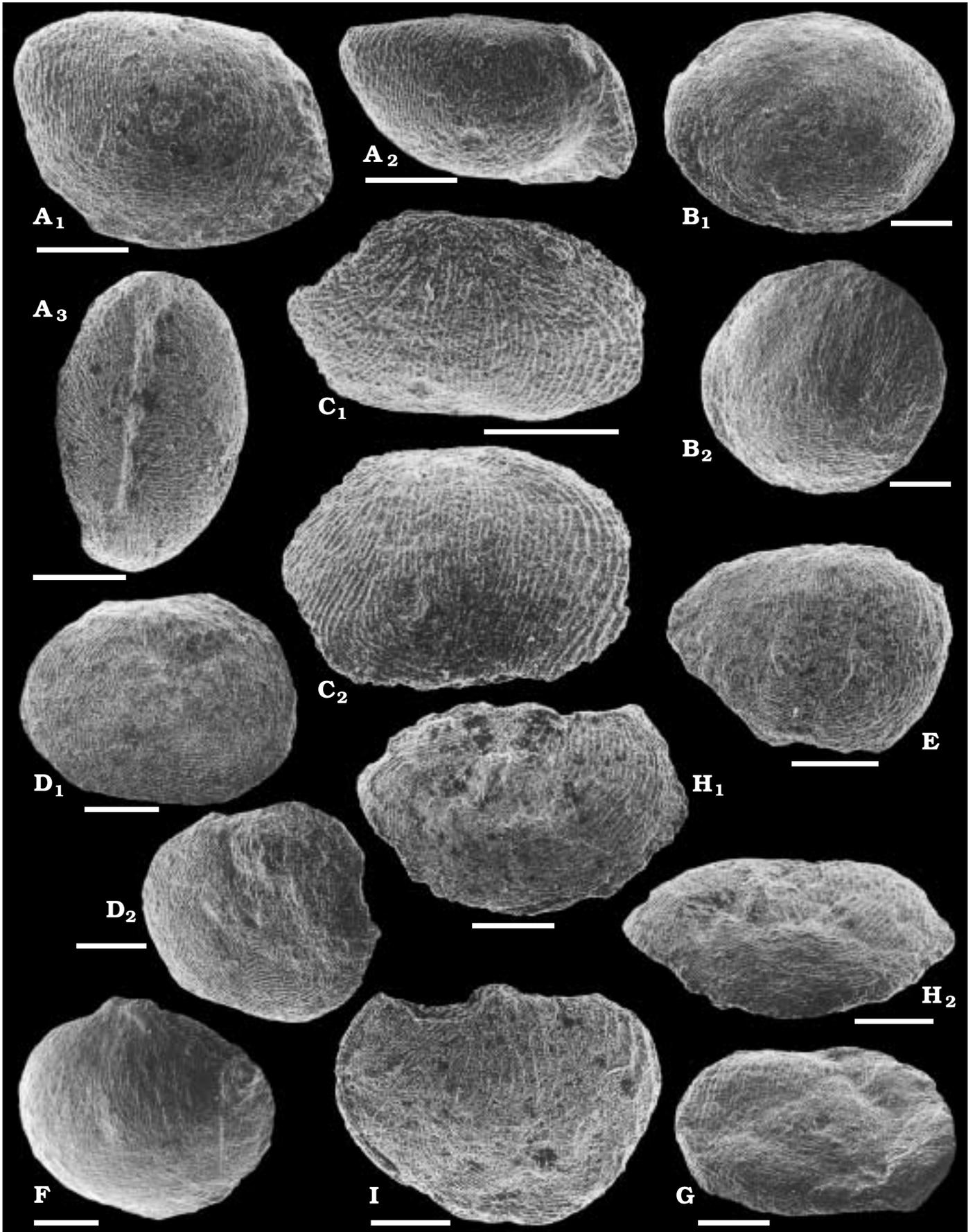
It is suggested therefore, that the Famennian Palaeotethys entomozoaceans fauna is the product of migration of Lazarus taxa from refugia, and from radiations of new taxa, which took place at those times of relatively high sea level. Unfavourable ecological conditions (oxygen depletion or concomitant nutrient poisoning) in the early and lower part of the Middle *Pa. triangularis* Zone may explain why no immediate radiation of entomozoaceans occurred.

However, the absence of the entomozoaceans in the earliest Famennian might also have been an artefact based on collection failures (sample too small to recover uncommon taxa), or due to a local absence of a particular community.

In the opinion of Kauffman and Erwin (1995), Kauffman and Harries (1996), Harries et al. (1996), who define the different survival “strategies”, taxa that disappear from the fossil record (Lazarus taxa) during mass extinction for a significant time interval and then reappear only after the crisis has passed, possibly migrate into refugia habitats or were reduced to small populations which survived the extinction but were unlikely to be collected as fossils. The refugia taxa occupied very small to very large (e.g., deep-sea habitats) protected habitats, which were permanently isolated or left behind by long-term shifts in Earth environments (Kauffman and Harries 1996).

The ancestral *Franklinella*-lineage was represented in the late Frasnian pre-event interval in many sequences by *Franklinella (F.) calcarata*, a rare and relatively small sized species. The descendant *F. (F.) sigmoidale* is an abundant and relatively large-sized species. In terms of the repopulation modes, ranging from surviving taxa to new species from newly evolved lineages (Kauffman and Erwin 1995; Kauffman and Harries 1996), the early Famennian was dominated by new species from surviving *Franklinella*-lineage. This lineage represents a slowly evolving conservative group, abundant in specimens in the late Givetian/early Frasnian, and in the early Famennian,

Fig. 6. *Entomoprimitia (Entomoprimitia) splendens* (Waldschmidt, 1885). **A₁–A₃**. Carapace ZPAL O.52/40 in left lateral view, dorsal oblique view and dorsal view; sample P-120. **B₁, B₂**. Carapace ZPAL O.52/64 in left lateral and oblique views; sample P-120. **C₁, C₂**. Right valve ZPAL O.52/7 in oblique dorsal and lateral views; sample P-114. **D₁, D₂**. Left valve ZPAL O.52/78 in lateral and oblique views; sample P-120. **E**. Left valve ZPAL O.52/74 in lateral view; sample P-118. **F**. Right valve ZPAL O.52/65 in oblique anterior view; sample P-120. **G**. Right valve ZPAL O.52/72 in oblique ventral view; sample P-118. **H₁, H₂**. Right valve ZPAL O.52/50 in lateral and oblique ventral view; sample P-16. **I**. Carapace ZPAL O.52/23 in right lateral view; sample P-124. Scale bars 500 μ m.



disappearing in refugia for middle and late Famennian and re-appearing for a short time before their final decline in the Early Carboniferous. It is in accordance with Jablonski's (1986a, b) hypothesis that most of the assumed survivors of mass extinctions belong to clades characterised by very slow evolutionary rates and long taxa duration.

Literature data on the Famennian *Entomoprimitia* (*Entomoprimitia*) occurrences are essentially not confirmed during this study. So, at least "typical" *Entomoprimitia* (*Entomoprimitia*) species vanished as a biomass during the catastrophic regression near the F–F boundary, but *Entomoprimitia* (*Reptiprimitia*) survive the F–F boundary (probably as refugia taxon) and continued its evolution in the Famennian.

In South China some species of *Richterina*–*Nehdentomis*–*Nandania*-lineages (*R. (V.) zimmermanni*, *N. assymetrica*, *N. pseudophtalma*, *N. tenera*) survived the F–F event (Wang 1989: table 1). Buggisch et al. (1983: 125) also listed the presence of *Nandania pseudophtalma* (Volk, 1939) in the Lower *Pa. triangularis* Zone of Diana section (Rhenish Slate Mts.).

The post extinction Famennian recovery phase looks less like a phase of explosive radiation, but more like a gradual, protracted, but very limited long-term recovery (see also Rabien 1954; Müller-Steffen 1964, 1965; Raith 1968; Olempska 1979, 1997). The entomozoceans radiations began in the *Pa. crepida* conodont Zone, where species populations of *Richterina*–*Nehdentomis*–*Maternella*-lineages increased significantly and became abundant in the fossil record in deeper water settings.

The peak of recovery and adaptative radiation of entomozoceans occurred in the Early Carboniferous and led the peak of F–F extinction by about 10 m.y. The Early Carboniferous radiation of entomozocean fauna continued the evolution of *Richterina*- and *Maternella*-lineages (Groos-Uffenorde and Uffenorde 1974; Wang 1989; Olempska 1997), but also some refugia taxons (*Franklinella*, *Waldeckella*) reappeared. It is in accordance with Kirchner and Weil (2000) and Erwin (2000) studies on biotic recoveries after five Phanerozoic mass extinctions, which show that the peak in recovery of biodiversity seems to lag the peak of extinction by about ten million years.

Review of identified ostracod species and description of a new species

Superfamily Entomozoacea Přibyl, 1951

Family Entomozoidae Přibyl, 1951

Genus *Entomoprimitia* Kummerow, 1939

Subgenus *Entomoprimitia* (*Entomoprimitia*)

Kummerow, 1939

***Entomoprimitia* (*Entomoprimitia*) *splendens* (Waldschmidt, 1885).**—This species (Figs. 6A–I, 10C–E) is common in the pre-event part of the Plucki section. It occurs also in the

Kowala section (samples Kw-117–130; see also Vishnevskaya et al. 2002: figs. 1, 2). Some well preserved complete carapaces and single valves were recovered, but the majority of specimens are poorly preserved single valves. The specimens of *E. (E.) splendens* from Plucki are marked by a considerable degree of variability. There are three rather distinct forms which seems to be within the range of variation of *E. (E.) splendens*. They mostly differ in the arrangement and spacing of the ribs. Form 1 (Fig. 6B–G) is characterised by a lateral outline broadly oval. The dorsal margin is slightly curved and the ventral margin is gently rounded. The anterior end is more narrowly rounded than the posterior end. The muscle pit is prominent and circular. The surface bears about 40 fine ribs of equal strength, concentrically arranged around the muscle pit. The intercalated and bifurcating ribs are present. The inner ribs are curved and join each other near the dorsal margin. In well preserved specimens it is visible that the outer ribs with very narrow intercostal spaces run concentrically parallel and close to the dorsal margin. The variable numbers of ribs are deflected outwards in a sigmoidale fashion towards the anterior and posterior margins below the mid-height. The intercostal spaces are slightly wider in the anterior part of the carapace. Specimens of *E. (E.) splendens* from the UKWH (Fig. 10C–E) are probably juvenile forms. They are similar to those illustrated by Matern (1929: pl. 1: 5a–c), Blumenstengel (1959: pl. 2: 8), Casier (1982a: pl. 1: 3), and those illustrated by Casier and Lethiers (1998a: fig. 3d).

Form 2 (Fig. 6A) is distinguished by the almost straight dorsal margin and slightly trembling ribs.

Form 3 (Fig. 6H–I) is characterised by densely spaced ribs in the posterior part of the carapace and wide intercostal spaces in the anterior part of the carapace. Ribs in the posterior part of the carapace run at a slight angle to the inner rib surrounding the round and deep muscle pit. This form is somewhat similar to *Entomoprimitia* (*Reptiprimitia*) species, from which it may be distinguished by the absence of sulcus. It seems to be possible that form 3 should be excluded from *E. (E.) splendens*, but the poor state of preservation of specimens available, precludes the possibility of separating new species.

Considerable intraspecific variability of the taxon has already been pointed out by other authors (Rabien 1954; Groos-Uffenorde 1984) who described narrow and coarsely ribbed forms. Similar is the case of the material under study in which differences may be observed which are even more distinct than those described by these authors. The polymorphism observed within this species is also present in several other species, especially in *E. (E.) sartenaeri*. It seems possible that *Entomoprimitia* (*E.*) *rotundata* (Polenova, 1955) from the late Frasnian of the Volga-Ural region (Polenova 1955: pl. 14: 2) should be included in *E. (E.) splendens*, but taken as a precursor of *E. (E.) splendens* by Krebs and Rabien (1964: 97).

Range and occurrence.—This species is restricted to the late Frasnian, *E. (E.) splendens* Zone, of Europe (Rhenish Slate Mts., Harz Mts., Thuringia, Ardennes, Great Britain, Holy Cross Mts.), and South China.

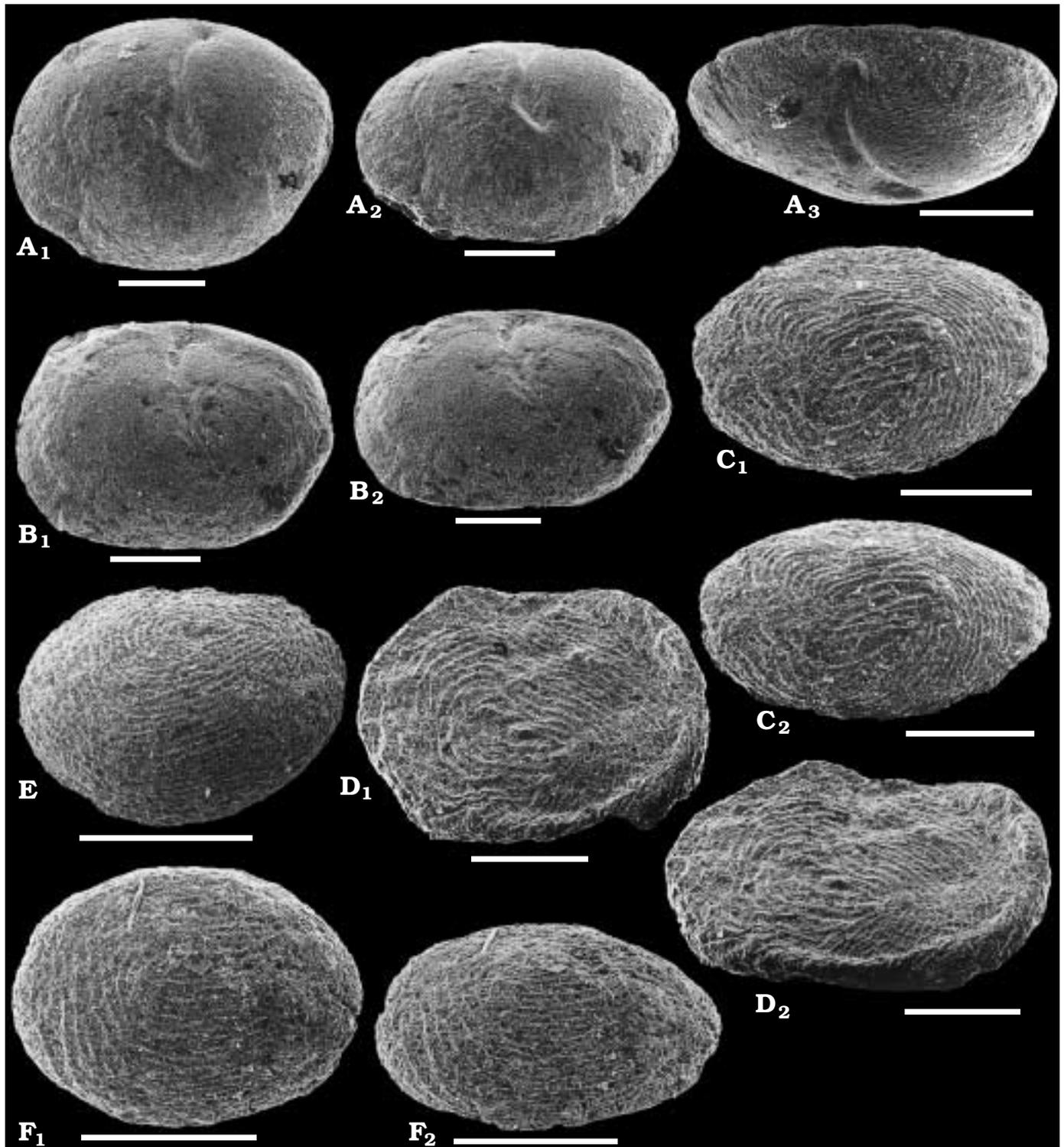


Fig. 7. **A, B.** *Entomoprimitia (Entomoprimitia) nitida* (Roemer, 1850). **A₁–A₃**. Right valve ZPAL O.52/32 in lateral, oblique ventral and oblique dorsal views; sample P-120. **B₁, B₂**. Carapace ZPAL O.52/25 in right lateral and oblique ventral views; sample P-14. **C, D.** *Rabiennella? lagowiensis* sp. nov. **C₁, C₂**. Right valve, holotype ZPAL O.52/76 in lateral and oblique ventral views; sample P-a. **E, F.** *Entomoprimitia (Entomoprimitia)* sp. aff. *E. (E.) wildungensis* (Matern, 1929). **E**. Carapace ZPAL O.52/68 in right oblique ventral view; sample P-112. **F₁, F₂**. Right valve ZPAL O.52/37 in lateral and oblique ventral views; sample P-120. Scale bars 500 μ m.

***Entomoprimitia (Entomoprimitia) nitida* (Roemer, 1850).**— This large species (Fig. 7A, B), up to 1.85 mm in length and 1.60 mm in height, with a finely-ribbing surface pattern is

common in the pre-event part of the Plucki section (samples P-13 to P-124). The shell is equally convex and the dorsal margin is straight. The anterior and posterior ends are

rounded, the posterior one more broadly. The adductorial sulcus is long and wide and reaches below the mid-height of the carapace. In its ventral part, the sulcus is curved antero-ventrally, and expands into an elongated muscle pit. A low indistinct ridge-like elevation usually surrounds the ventral part of the sulcus in adult forms. The deep depression is present in the dorsal part of the sulcus. The surface bears 40–50 fine, narrow ribs of equal strength, concentrically arranged around the sulcus and the muscle pit. A few bifurcatory and intercalatory ribs are usually present.

Specimens from Płucki differ from those illustrated by Rabien (1954: pl. 3: 24) and Müller-Steffen (1964: pl. 18: 2) in having a longer and wider sulcus. They are quite similar to the specimens of *E. (E.) nitida* illustrated by Casier (1975: pl. 3: 1) from the Matagne Formation of Belgium. It seems possible that *Entomoprimitia (E.) sarailensis* (Polenova, 1955) from the late Frasnian of the Volga-Ural region (Polenova 1955: pl. 14: 1) should be included in this species, as proposed by Krebs and Rabien (1964).

Range and occurrence.—This species is known from the middle and late Frasnian, *Waldeckella cicatricosa* up to the *E. (E.) splendens* zones, of Europe and South China.

***Entomoprimitia (Entomoprimitia) sartenaeri* Casier, 1975.**

—This species (Figs. 8A–H, 10B) occurs in the pre-event and event part of the Płucki section. (samples P-4 to P-126). This relatively large-sized species (up to 2.3 mm in length), shows a rather high degree of variation in the ribbing pattern, partly due to the slight deformations of the carapace. It is characterised by the broadly oval lateral outline of the carapace, slightly convex to almost straight dorsal margin, and deep circular muscle pit. The surface bears 15 to 25 concentric but sigmoidally deflected ribs. In the material from the Płucki section there are specimens closely similar to the holotype (Fig. 8B–D, G), but also specimens with more densely spaced ribs (Fig. 8A), and specimens having intercostal spacing between inner ribs wider than between outer ribs (Fig. 8H, I). It seems that *Entomoprimitia (E.)* aff. *spiralis* (Martynova in Polenova, 1955) from late Frasnian of the Volga-Ural region (Polenova 1955: pl. 13: 4) should be included in *E. (E.) sartenaeri*.

Range and occurrence.—This species is known from the middle and late Frasnian, *W. cicatricosa/Rabienella barandei* Interregnum up to the *E. (E.) splendens* Zone of Europe and South China, however, Buggisch et al. (1978) noted *E. (E.) variostrata* (= *sartenaeri*) vel *kayseri* from the early Famennian, *F. (F.) sigmoidale* Zone.

***Entomoprimitia (Entomoprimitia) kayseri* (Waldschmidt, 1885).**—This species (Fig. 10A) occurs in the Płucki section

only in the UKWH (sample P-126a). Probably only juvenile specimens are present. Specimens from Płucki possess ten concentric outer ribs, partly divided, and four to five longitudinal ribs in the middle part of the carapace. The dorsal margin is long and almost straight, and the ventral margin is slightly convex. A large swelling is present in the posterodorsal part of the carapace and a small preadductorial node is present before the sulcal depression. The sulcus is shallow and short.

Rabien (1954) and Groos-Uffenorde (1984: pl. 2: 9, 10) described two forms of this species: a smaller coarsely ribbed form and a much larger narrow ribbed form. Specimens from the Płucki section are most similar to the coarsely ribbed form *sensu* Rabien (1954).

Range and occurrences.—This is one of the most characteristic species in the UKWH. It is abundant in the upper part of the Kellwasser Horizon in the Steinbruch Schmidt section, Rhenish Slate Mts., Aeketal and Kellwasser-Tal sections in the Harz Mts. (Walliser et al. 1989; Groos-Uffenorde and Schindler 1990; Schindler 1990a, b; 1993; Casier and Lethiers 1998a). However, in the Rhenish Slate Mts., it occurs also below the UKWH (Rabien 1954; Buggisch et al. 1980; Schindler 1993). This species occurs also in the Neuville section in the southern part of the Dinant Basin, Belgium (Casier 1982a).

***Entomoprimitia (Entomoprimitia) sp. aff. E. (E.) wildungensis* (Matern, 1929).**—This rare species (Fig. 7E, F) in Płucki occurs only in samples P-18 and P-120. It is most similar in its concentrically arranged outer ribs and longitudinally elongated inner ribs to the *E. (E.) wildungensis* illustrated by Matern (1929: pl. 1: 4a–c).

Range and occurrences.—This species occurs in the Płucki section in the late Frasnian, below the UKWH, *E. (E.) splendens* Zone.

Genus *Rabienella* Gründel, 1962

***Rabienella? lagowiensis* sp. nov.**

Fig. 7C, D.

Holotype: ZPAL O. 52/76; Fig. 7C.

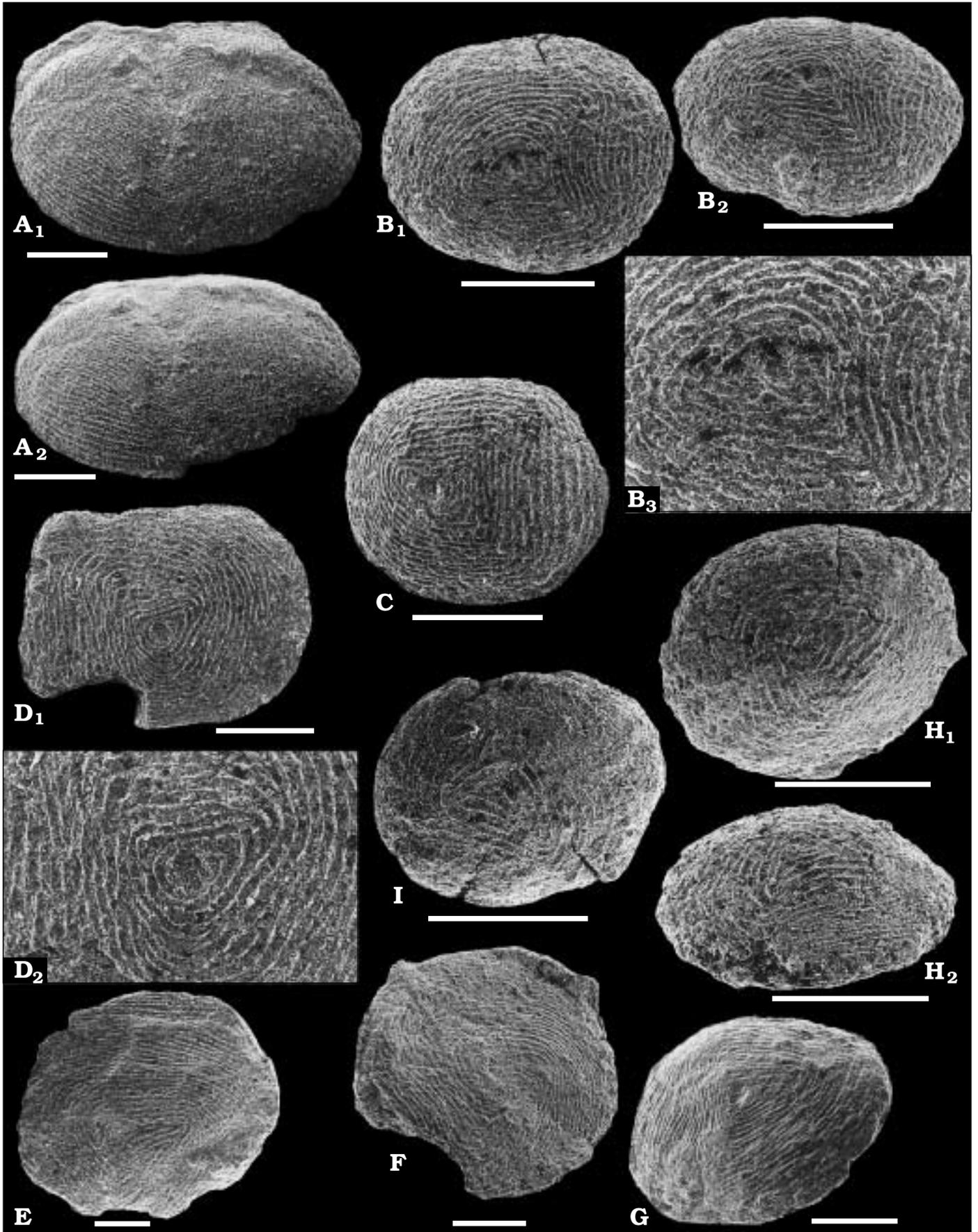
Type horizon: Latest Frasnian, *E. (E.) splendens* Zone.

Type locality: Płucki, Holy Cross Mountains, Poland.

Derivation of the name: From Łagów, a town in the Holy Cross Mountains.

Diagnosis.—Medium-sized *Rabienella* (length up to 1.7 mm) differs from other species of the genus in having numerous concentric ribs of equal strength, and in the asymmetrical ribs pattern in the anteroventral part of the carapace: the outer ribs turn toward the ventral margin, and those in the posteroventral part join them at an acute angle.

Fig. 8. *Entomoprimitia (Entomoprimitia) sartenaeri* Casier, 1975. **A₁, A₂**. Left valve ZPAL O.52/5 in lateral and oblique ventral views; sample P-120. **B₁–B₃**. Left valve ZPAL O.52/58 in lateral, oblique ventral views and details of ornamentation; sample P-120. **C**. Left valve ZPAL O.52/44 in oblique posterior view; sample P-124. **D₁, D₂**. Right valve ZPAL O.52/48 in lateral view and details of ornamentation; sample P-118. **E**. Carapace ZPAL O.52/19 in lateral view, slightly deformed; sample P-47. **F**. Carapace ZPAL O.52/61 in lateral view; sample P-45. **G**. Left valve ZPAL O.52/80 in oblique posterior view; sample P-45. **H₁, H₂**. Left valve ZPAL O.52/33 in lateral and oblique ventral view; sample P-17. **I**. Right valve ZPAL O.52/24 in lateral view; sample P-124. Scale bars 500 µm.



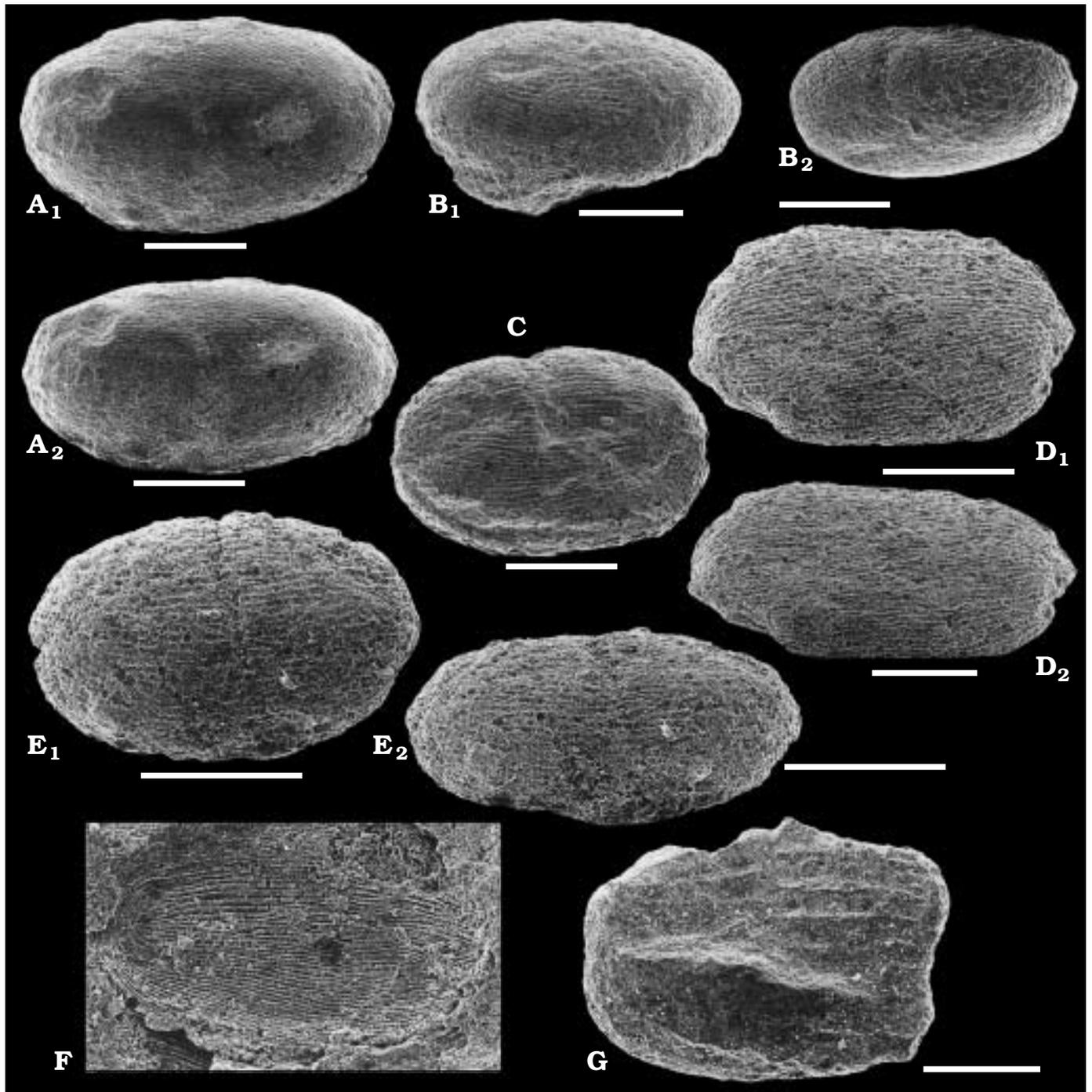


Fig. 9. **A, B.** *Nandania asymmetrica* (Koch, 1967) **A₁, A₂**. Left valve ZPAL O.52/83 in lateral and oblique ventral views; sample P-20. **B₁, B₂**. Right valve ZPAL O.52/82 in lateral and oblique dorsal views; sample P-120. **C–E.** *Richterina (Volkina) zimmermanni* (Volk, 1939). **C.** Left valve ZPAL O.52/84 in lateral view; sample P-18. **D1–D2.** Right valve ZPAL O.52/59 in lateral and oblique ventral views; sample P-83. **E₁, E₂**. Right valve ZPAL O.52/38 in lateral and oblique ventral views; sample P-15. **F.** *Nehdentomis pseudorichterina* (Matern, 1929). Internal mould of left valve ZPAL O.52/47 in lateral view; sample P-18. **G.** *Franklinella (Franklinella) cf. calcarata* (Richter, 1856). Right valve ZPAL O.52/16 in lateral view; sample P-13. Scale bars 500 µm.

Material.—25 specimens.

Description.—The lateral outline is broadly oval. The dorsal and ventral margins are gently curved. The posterior end is more broadly rounded than the anterior end. The surface bears approximately 18 - 20 ribs of equal strength. The inner ribs run concentrically and are slightly lenslike. The outer

ribs are parallel to the dorsal, anterior and posterior margins. In the anteroventral part of the carapace, the outer ribs turn toward the ventral margin, and those in the posteroventral part join them at an acute angle.

Remarks.—This species is most similar in the ribbing pattern to *Rabienella? barrandei* (Richter, 1869).

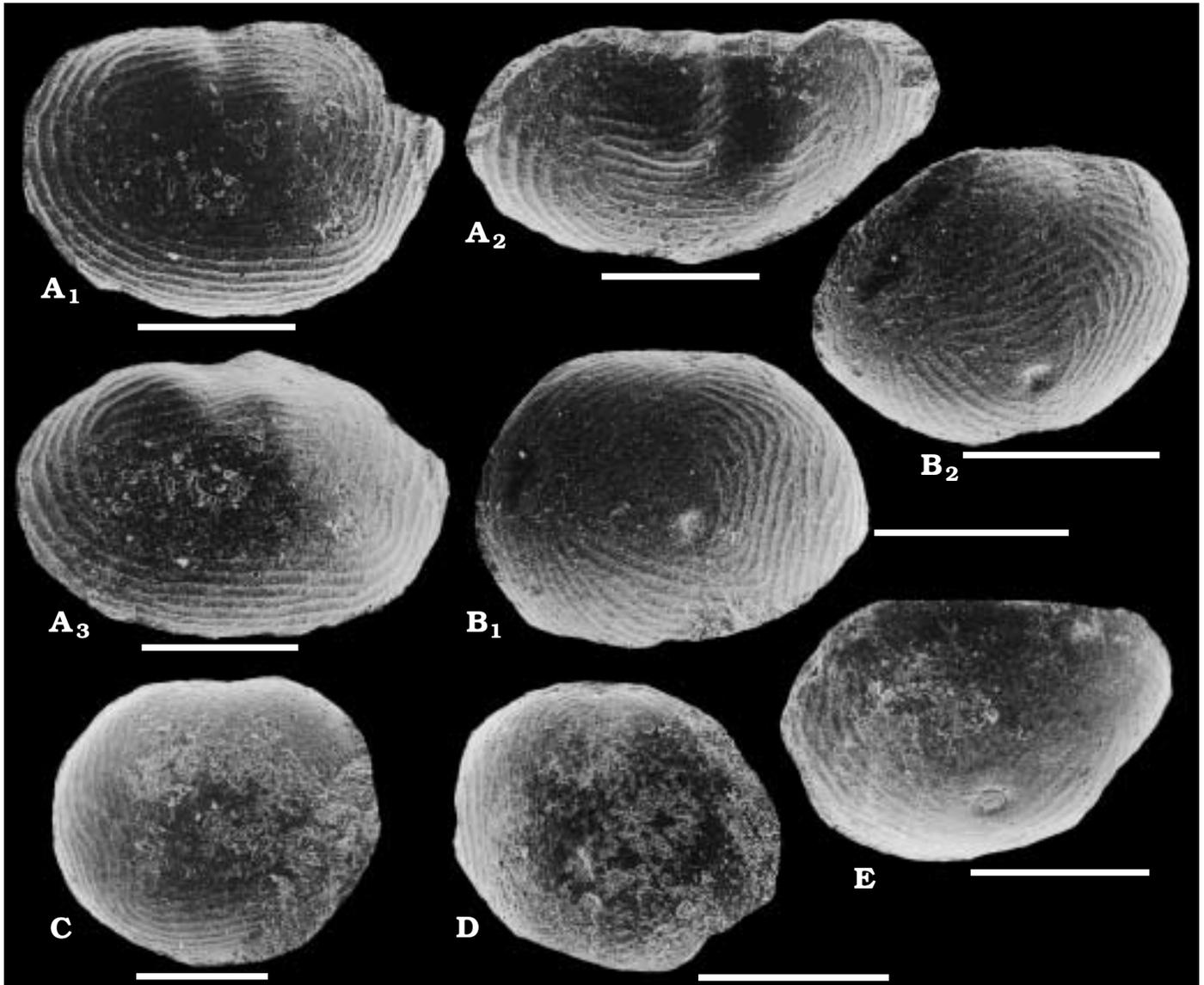


Fig. 10. Entomozoacean species from the Upper Kellwasser Horizon (sample P-126, 126a). **A₁–A₃**. *Entomoprimitia (Entomoprimitia) kayseri* (Waldschmidt, 1885). Right valve ZPAL O.52/23 in lateral, oblique dorsal and oblique ventral views. **B₁, B₂**. *Entomoprimitia (Entomoprimitia) sartenaeri* Casier, 1975. Right valve ZPAL O.52/29 in lateral and oblique dorsal views. **C–E**. *Entomoprimitia (Entomoprimitia) splendens* (Waldschmidt, 1885). **C**. Left valve ZPAL O.52/24 in lateral view. **D**. Right valve ZPAL O.52/17 in lateral view. **E**. Left valve ZPAL O.52/18 in oblique dorsal view. Scale bars 500 μ m.

Range and occurrence.—This species occurs in the late Frasnian of the Plucki section (samples P-45, P-47), below the UKWH, *E. (E.) splendens* Zone.

Genus *Nehdentomis* Matern, 1929

Nehdentomis pseudorichterina (Matern, 1929).—All the specimens (Fig. 9F) from the Plucki section included in this species are poorly preserved. The lateral outline of this species is asymmetrically oval, the dorsal margin is slightly curved and the ventral margin is more strongly curved. The posterior end is broadly and symmetrically rounded, the anterior end is more narrowly and asymmetrically rounded. The greatest height is in the anterior third. The surface bears 28–35 longitudinal ribs, those in the dorsal part of the valve run straight, and

those in the ventral part are slightly curved with some ending against the innermost dorsal rib. Four to five ribs run concentrically and parallel to margins. Bifurcations of ribs is present. The sulcus is short and weak. The muscle pit is well developed and circular, lying just in front of the middle. A slight indentation of the anteroventral part of the margin is present.

Range and occurrence.—This species is common in the middle and late Frasnian, *W. cicatricosa*–*E. (E.) splendens* zones, and in the early Famennian of Europe (Germany, Poland, Great Britain, Belgium, Spain); late Frasnian of Sahara, Algeria; late Frasnian of the Volga-Ural region, Russia; late Frasnian–early Famennian of China.

Nehdentomis sp.—This poorly preserved and rare species (Fig. 12F) occurs in the early Famennian (samples P-152 to

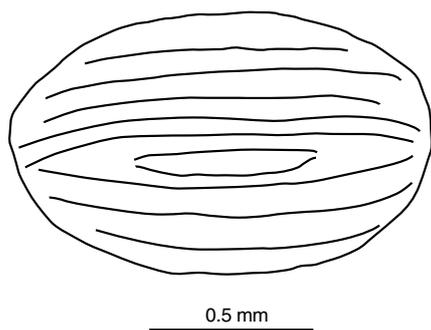


Fig. 11. Schematic drawing of *Richterina (Volkina) latecostata* Rabien, 1954. Sample P-69.

P-166) part of the Plucki section. The ribbing pattern with longitudinal ribs in the middle part of the valve and parallel to the posterior end somewhat resembles those of *N. pseudo-richterina*.

Genus *Nandania* Wang, 1989

Nandania asymmetrica (Koch, 1967).—This species (Fig. 9A, B) occurs in the Plucki section in the pre-event interval (samples P-19, P-20, and P-112 to P-124). The lateral outline of this species is elongate oval. The posterior and anterior ends are broadly rounded and the dorsal and ventral margins are gently curved. The sulcus is almost absent, and the shallow muscle pit is only occasionally developed. The longitudinal depression runs in mid-height from the muscle pit towards the posterior margin. The surface bears 30–40 longitudinal ribs. Between four and five ribs run parallel to the posterior end and three to four run parallel to the anterior end. Cross ribs are often developed. This species is very similar to *Nandania pseudophthalma* from the Frasnian of Germany (Rabien 1954), Spain (Gozalo 1994), Belgium (Casier 1975), and China (Wang 1989), but differs in the absence of the sulcus.

Range and occurrences.—Originally this species was described from the Famennian (Nehden-Stufe) of Sauerland, Germany (Koch 1967). It occurs also in the early Famennian of Great Britain (Goody 1978), but it is also known from the late Frasnian and early Famennian of South China (Wang 1989).

Genus *Richterina* Gürich, 1896

Subgenus *Richterina (Volkina)* Rabien, 1954

Richterina (Volkina) zimmermanni (Volk, 1939).—This species (Fig. 9C–E) occurs in the pre-event part of the section. Its lateral outline is elongate oval, and both ends are almost equally rounded. A shallow dorsal depression is present. The muscle pit is absent. The surface bears 30–35 narrow longitudinal ribs of equal strength. Ribs are concentrically arranged around the anterior margin. In the posterior part of the carapace, two or three inner dorsal ribs usually join the corresponding ventral ribs at an acute angle. Outer dorsal and ventral ribs are almost parallel to the margins. In poorly preserved specimens with an invisible muscle pit, it is difficult to

distinguish between *R. (V.) zimmermanni* and *N. pseudo-richterina*.

Range and occurrence.—This species is known from the middle and late Frasnian, *W. cicatricosa* Zone up to the *E. (E.) splendens* Zone, of Europe (Rhenish Slate Mts., Harz Mts., Thuringia, Spain, Montagne Noire, Ardennes, Holy Cross Mts.), N-Africa (Sahara, Algeria), N-America (Ohio) and South China. However, in China it occurs also in the early Famennian, *F. (F.) sigmoidale* Zone.

Richterina (Volkina) latecostata Rabien, 1954.—This rare species (Fig. 11) is restricted to the middle part of the Plucki section (sample P-69). Its lateral outline is elongately oval, the dorsal margin is gently curved, and the ventral margin is more curved. The anterior and posterior ends are rather narrowly and equally rounded. The surface bears six to seven longitudinal ribs separated by wide intercostal grooves. In the dorsal part of the carapace, ribs are almost straight, and in the ventral part, they are more strongly curved. A few intercalated ribs are present.

Range and occurrence.—This species is known from the latest Frasnian, *E. (E.) splendens* Zone, of Europe.

Family Rhomboentomozoidea Gründel, 1962

Genus *Franklinella* Stewart and Hendrix, 1945

Franklinella (Franklinella) sigmoidale Müller-Steffen, 1964.

—This species (Fig. 12A–E) is abundant in the post-event part of the Plucki section (samples P-138 to P-166). Its lateral outline is subquadrate, and the dorsal margin is long and straight. The posterior end is more narrowly rounded than the anterior end, and the ventral margin is gently curved. The sulcus is narrow and extends from the dorsal margin to below the mid-height. In the posterodorsal part of the carapace, a small, conical spine, directed slightly outwards and upwards, occurs. A similar but larger spine occurs in the anteroventral part of the carapace. The surface bears eight to ten longitudinal narrow ribs with wide intercostal spaces, which run at a slight angle to the dorsal margin and tend to converge towards the spines. Some intercalated ribs are also present. Three ribs are concentric and parallel to the posterior margin and two are parallel to the anterior margin.

Range and occurrence.—This species occurs in the early Famennian, *F. (F.) sigmoidale* Zone, of Europe (Rhenish Slate Mts., Harz Mts., Holy Cross Mts.) and South China. However in South China it is also noted from the Early *R. serratostrata*–*N. nehdenensis* Zone.

Franklinella (Franklinella) cf. calcarata (Richter, 1856).—

This rare and small (up to 1 mm long) species (Fig. 9G) has been found in samples P-13 and P-17. The surface bears five longitudinal ribs with wide intercostal spaces. Small spines are present in the posterodorsal and the anteroventral parts of the carapace, the anteroventral spines are broken in all specimens. The sulcus is very poorly developed.

Range and occurrence.—This species is known from the middle and late Frasnian, *W. cicatricosa* Zone up to *E. (E.)*

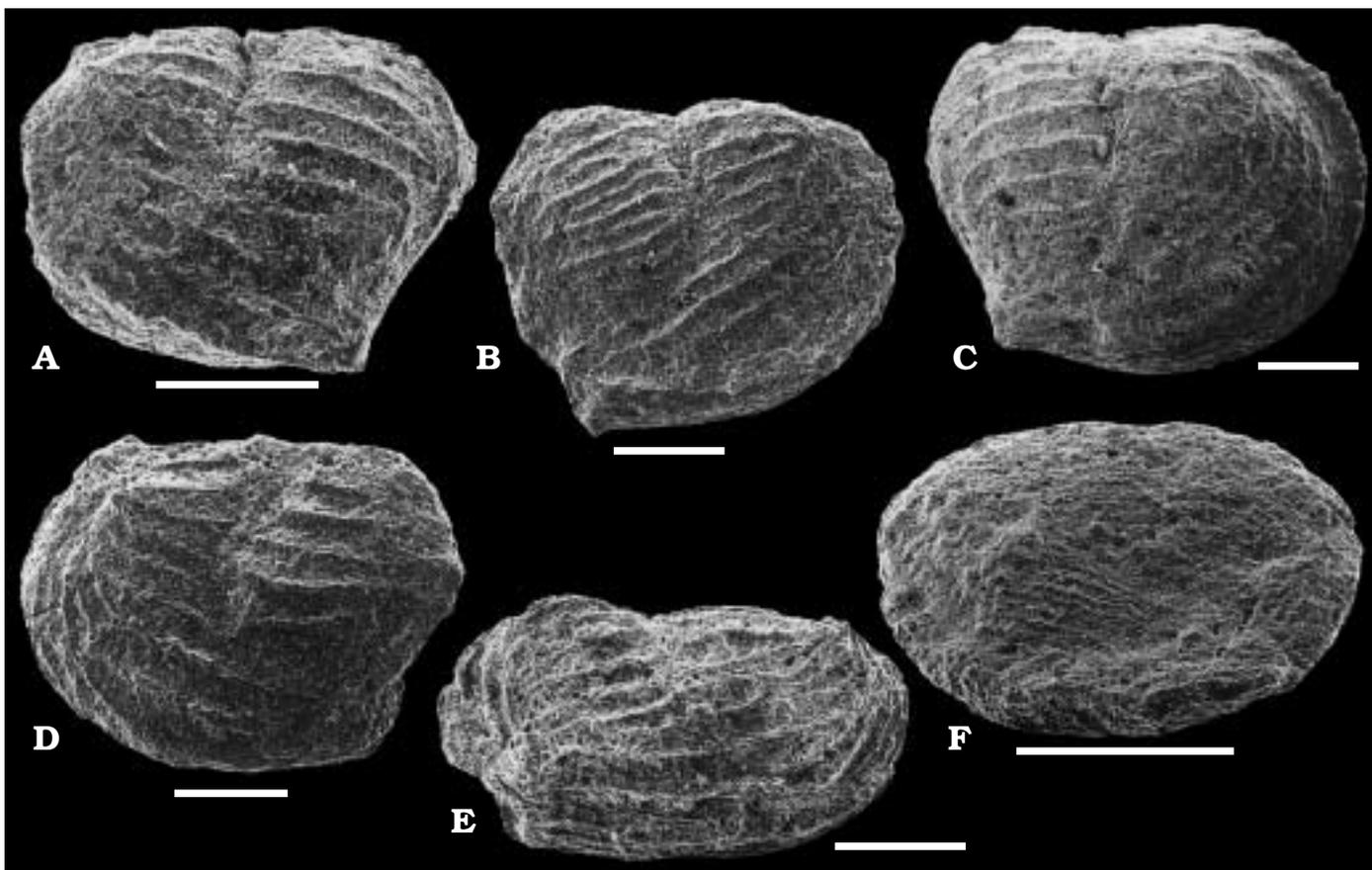


Fig. 12. A–E. *Franklinella* (*Franklinella*) *sigmoidale* Müller-Steffen, 1964. A. Carapace ZPAL O.52/12 in right lateral view; sample P-152. B. Carapace ZPAL O.52/1 in left lateral view; sample P-157. C. Left valve ZPAL O.52/13 in lateral view; sample P-152. D. Right valve ZPAL O.52/2 in lateral view; sample P-157. E. Left valve ZPAL O.52/78 in oblique ventral view. F. *Nehdentomis* sp. Carapace ZPAL O.52/22 in left lateral view; sample P-166. Scale bars 500 μm .

splendens Zone, of Europe and South China. However it is also noted from the early Famennian, *F. (F.) sigmoidale* Zone.

Summary and conclusion

The entomozoacean faunal change across the F–F boundary in the Plucki section, Holy Cross Mountains shows the following characteristics:

The overall reduction in species number in the latest Frasnian occurs in two steps: (a) a few species of planktonic entomozoaceans became extinct at the base of the Upper Kellwasser Horizon (upper part of the *E. (E.) splendens* Zone), (b) the main extinction of entomozoacean species was within the UKWH.

The appearance of the new immigrant species *E. (E.) kayseri* in the UKWH coincides with a short-term transgressive pulse in the *Pa. linguiformis* Zone.

The final extinction of entomozoacean species at the F–F boundary coincides with the short-term regressive pulse recognised by Johnson et al. (1985) and Sandberg et al.

(1988), however, multicausal factors appear to be responsible for this extinction bio-event.

The absence of entomozoaceans in the earliest Famennian was probably the result of ecological conditions.

An entirely new assemblage composed of abundant *Franklinella (F.) sigmoidale* and rare specimens of *Nehdentomis* sp. appeared in the Middle *Pa. triangularis* conodont Zone. The *Franklinella*- and *Nehdentomis*-lineages might survive stressed environmental conditions in refugia.

There is a correlation between the appearance of entomozoaceans in the early Famennian and the beginning of the transgressive pulse recognised in the Middle *Pa. triangularis* Zone by Johnson et al. (1985).

Acknowledgements

I would like to thank Dr. Helga Groos-Uffenorde (Institute und Museum für Geologie und Paläontologie, Göttingen) and Dr. Jean-Georges Casier (L'Institut royal des Sciences naturelles de Belgique) for helpful comments and suggestions on the manuscript. Research was partly supported by the Committee of Scientific Research in Poland (grant 6P04D 02413).

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