## Changes in benthic ostracod assemblages across the Devonian–Carboniferous boundary in the Holy Cross Mountains, Poland

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The Kowala section situated in the southern part of the Holy Cross Mountains represents continuous sedimentation in almost the same facies across the Devonian-Carboniferous (D-C) transition. The D-C boundary has been identified about two meters above the top of the cephalopod nodular limestone with Wocklumeria. In the transitional deposits of the latest Famennian (Prothognathodus kockeli Zone) several faunally distinct units that correspond to relative sea level changes in the area have been identified. Ostracods are abundant in the Kowala sequence. Their assemblages contain well known index species and new ones of the Thuringian and Entomozoacean ecotypes. A total of 15 probably planktonic entomozoaceans, and 64 benthic species have been identified. Healdia shangquii sp. n. and Mauryella polonica sp. n. are proposed. A major change in the ostracod fauna takes place above the limestone with Wocklumeria within the transitional interval represented by clays and claystones with tuffites in its middle part. Thuringian and Entomozoacean ecotype ostracods disappear and are replaced by more shallow water 'exotic' assemblage dominated by Healdia, Mauryella and Monoceratina species. In the early Tournaisian rocks Thuringian-, Entomozoacean- and Bairdia-type ostracods reappear with some of the same species as before, and with new Carboniferous index taxa.

Key words: Ostracoda, palaeoecology, Late Devonian, Early Carboniferous.

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## Introduction

Marine sediments of the latest Famennian display anomalous lithological, geochemical and/or faunal characteristics worldwide. Oceanic areas and many marginal basins contain dark-coloured (light gray to black) laminated organic-rich mudrocks of this



Fig. 1. A. Facies of Famennian in Poland (after Racki 1992) to show location of the Holy Cross Mountains, Kowala locality. B. Location of the studied area. Kowala trench indicated with asterisk.

age. Benthic faunas are commonly impoverished or absent in these sediments. The terminal Devonian event (Hangenberg Event) immediately postdates the main ammonoid extinction level (Walliser 1984, 1996).

The Kowala section in the Holy Cross Mountains displays the most complete D–C boundary beds. The faunal assemblage contains conodonts, cephalopods, ostracods, foraminifers, trilobites, bryozoans, and other fossil groups.

The Kowala section is situated on the southern limb of Checiny anticline in SW Holy Cross Mountains (Fig. 1).

The study sequence was exposed in an 88 meter long trench, dug directly to the north of the Kowala quarry wall. A profile of the investigated Kowala section was published by Malec (1995). The section starts with the *Palmatolepis expansa* Zone and runs to the *Siphonodella crenulata* Zone (Malec 1995). The D–C boundary cannot be established with certainty by conodonts (Malec 1995; Dzik 1997). Conodonts from the Carboniferous part of the section were studied by Dzik (1997), who revised the conodont zonation in this part of the section. The stratigraphical conodont zonation of Lane *et al.* (1980) and partly of Dzik (1997) is followed here (Figs 2, 3). The Late Devonian is represented there by biomicritic gray and brown nodular limestones with marly intercalations, with *Kalloclymenia* in the lower part and *Wocklumeria* in the higher part of the sequence (samples Ko-102–Ko-75). The D–C transitional beds are represented by yellow and gray decalcified claystones with tuffites in their middle part and the Early Carboniferous is represented by marly shales with biomicritic light-gray nodular limestones.

Ostracods of the Thuringian and Entomozoacean ecotypes (see Becker in Bandel & Becker 1975) are common faunal elements of the Devonian–Carboniferous deposits in the Kowala section. The D–C boundary interval is characterized by variation in the composition of ostracod assemblages and the abundance of some ostracod species.

The first ostracods from the Late Devonian and Early Carboniferous of Kowala were described and figured by Olempska (1979, 1981, 1991) and from the Kowala 1 borehole by Żakowa *et. al.* (1985). Since then, additional and new material preserved only in limestones and marls has been discovered while excavating the trench across the boundary.

The depositional evolution of the Holy Cross Mountains during the Devonian and Carboniferous was summarized by Szulczewski (1995).

This work was carried out at the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw (abbreviated ZPAL), where the type materials are housed.

#### Materials and methods

Eighty-four samples numbered Ko-27–Ko-121, each weighing about 1.5 kg, were collected at regular intervals from the entire Kowala section. Eighty of them yielded identifiable ostracods.

Ostracod samples were disaggregated with Na<sub>2</sub> SO<sub>4</sub> or washed only with water. All ostracods, including single valves, were counted. The number of individuals and the number of species in each sample were tabulated. The average relative abundance was computed for each species to help define ostracod assemblages and to systematically eliminate rare species from further consideration (Fig. 4). The vertical distribution of the identified taxa is shown in Fig. 2.



Fig. 2. Striatigraphical distribution of the Late Devonian–Early Carboniferous ostracod species in the Kowala section. Dotted area: interval between topmost *Wocklumeria* limestone and Devonian–Carboniferous boundary.

# Transgression–Regression cycles across the Devonian–Carboniferous boundary

According to most workers (Johnson et al. 1985, 1986; Johnson & Sandberg 1988; Walliser 1996), a regressive tendency dominated during the younger Famennian,



Fig. 2. (continued).

extensive transgression took place in the Early Carboniferous, and the main biocrisis period was characterized by significant short-term and severe eustatic sea-level fluctuations.

Johnson *et al.* (1985, 1986) and Johnson & Sandberg (1988), identified the late Fammenian–early Strunian T–R cycle IIf, consisting of two subcycles. Cycle IIf began at the base of the Lower *P. expansa* Zone with an extensive transgression. In Europe, the onset of IIf is represented by Epinette Shale and *Wocklumeria* Limestone. The global eustatic fall in sea level began in the Middle *Siphonodella praesulcata* Zone and



Fig. 3. The Devonian–Carboniferous boundary section at Kowala, Holy Cross Mountains. Detailed distribution of the ostracods in the D–C interval part of the section. The Thuringian and Entomozoacean type ostracods disappear abruptly in the Devonian and re-appears gradually in the Carboniferous.

continued through the lower three condont zones of the Carboniferous. The next major transgressive cycle began in the Lower *S. crenulata* Zone (Sandberg *et al.* 1986), corresponding to Tn2a in Europe.

The Transgression–Regression cycles around the Devonian–Carboniferous boundary in the Rhenish Slate Mountains (Rheinische Schiefergebirge) were compared with the Transgression–Regression cycles of Johnson *et al.* (1985, 1986) by Van Steenwinkel (1990, 1993a, 1993b), Flajs & Feist (1988), and Bless *et al.* (1993). A major regression starting in the Middle *S. praesulcata* conodont zone slightly below the D–C boundary and a major transgression in the early *S. crenulata* conodont zone are both generally accepted. Most authors also agree that one or more 'minor transgressions' occurred in the earliest Carboniferous *Siphonodella sulcata* through *S. sandbergi* conodont zones (Bless *et al.* 1993).

#### Devonian-Carboniferous boundary event

The Devonian–Carboniferous boundary is now defined according to conodont evolution from *Siphonodella praesulcata* to *Siphonodella sulcata* (Lane *et al.* 1980).

This boundary became of great interest due to the extinctions of many invertebrate groups which are thought to have disappeared close to the boundary. The profound faunal and lithological changes are slightly below the boundary at the base of Hangenberg Black Shale and are often called the 'D–C event boundary' or Hangenberg Event (see Walliser 1984, 1996; Johnson *et al.* 1985, 1986; Sandberg *et al.* 1986; Bless *et al.* 1993).

The profound cephalopod, conodont, and trilobite changes in many parts of the world probably coincide with the Hangenberg Event at the base of the Hangenberg Shale. These changes are connected with the world-wide disappearance of the Late Devonian cephalopod limestones and with the extinction of most of the clymenids as well as many other taxa (Walliser 1984, 1996).

Many different causes for the Devonian–Carboniferous event have been discussed, e.g. rapid sea level fluctuations, climatic oscillations, water chemistry changes and stratification of the water column among others (e.g. Walliser 1984, 1996; Flajs & Feist 1988; Bless *et al.* 1993).

According to Walliser (1984) the Devonian–Carboniferous event seems to be connected with a sudden eutrophication of the oceans in depths where the cephalopod limestones were being deposited associated with expanding of the anoxic zone.

This major global litho- and bio-event was interpreted as a response to a major fall in sea-level in the Middle *S. praesulcata* Zone interrupted by a relatively short anoxic episode with deposition of anoxic deposits taking place during the short-lived trangression (Walliser 1996).

#### Changes in ostracod assemblages across the Devonian–Carboniferous boundary in the Kowala section

The ostracod succession of the Late Devonian to the basal Tournaisian in the Holy Cross Mountains shows similarities to the faunal sequences of Germany, Spain, Morocco, Algeria and China (Becker 1981, 1987; Becker *et al.* 1993; Becker & Blumenstengel 1995; Wang 1983, 1988), but is also unique in some aspects which may reflect the regional biofacies setting.

There are not many such sections in the world in which the ostracods are represented in the critical Devonian–Carboniferous boundary interval. Pelagic entomozoacean ostracods are well documented close to the boundary in some sections in the Rhenish Slate Mountains (Groos-Uffenorde & Uffenorde 1974; Bless & Groos-Uffenorde 1984). Thuringian-type ostracods which are thin-shelled, spinose and mostly podocopine species occur in the Late Devonian–Early Carboniferous Thuringia sections (Gründel 1961, 1962; Blumenstengel 1965, 1979, 1993, 1995; Bartzch & Weyer 1979, 1982, 1985, 1986; Becker & Blumenstengel 1995), Montagne Noire (Lethiers & Feist 1991), Rhenish Slate Mountains (Becker *et al.* 1993), NE Russian Platform (Nemirovskaya *et al.* 1992; Sobolev 1995), and the Guangxi region of China (Wang 1988), but more detailed studies are not yet available.

In the Kowala section dramatic changes in ostracod abundance, species composition and diversity take place immediately above the nodular cephalopod limestone (*Wocklumeria* limestone), 2 m below the stage boundary.

#### **Benthic ostracods**

Benthic ostracod assemblages in the Kowala section are represented mostly by Thuringian-type ostracods in the Late Devonian (pre-event) and Early Carboniferous (post-event) deposits. In these assemblages the genera *Rectonaria, Rectoplacera, Orthonaria, Triplacera, Necrateria,* and *Aurigerites* are regarded as Thuringian. Thick-shelled *Bairdia* species, '*Harziella*' (abundant in some levels), *Shemonaella, Mauryella* and rare palaeocopids are probably indicative of a shallower water, high energy environment.

*Bairdia* species are common to abundant, sometimes dominant, constituting up to 70% of the relative frequency in some samples (Fig. 4).

Late Devonian pre-event assemblages. — (Samples Ko-124–Ko-74). Assemblages from the *P. expansa* Zone (samples Ko-115–Ko-110) yielded abundant ostracod fauna with over 80% of the relative abundance being represented by *Bairdia* species (*B.* ex gr. *hypsela* Rome, 1971; *B. nidensis* Olempska, 1979; *B. feliumgibba* Becker, 1982). '*Harziella' blessi* (Olempska, 1979) (up to 9% in sample Ko-115) and *Ovato-quasillites* aff. *investibus* Becker, 1987 (up to 5% in sample Ko-114 which yielded 21 species represented by 740 individuals) are also important components of the assemblages (Fig. 4).

Higher up (samples Ko-111, Ko-110), Ovatoquasillites aff. investibus constitutes 15% of ostracod specimens with the relative frequency of Bairdia species varying between 25% and 40%. The fauna represented in samples Ko-110–Ko-107 is very similar to that in the underlying strata and the diversity is also comparable, but there is an increased percentage of 'Harziella' blessi (40% in sample Ko-109 and 24% in sample Ko-107). In this part of the section, Shemonaella sp. make up 6–10%. Rectonariids (Rectonaria inclinata Gründel, 1961, Rectonaria muelleri Gründel, 1961, Rectoplacera aff. robusta Blumenstengel, 1965, Orthonaria neotridentifer Lethiers & Feist, 1991, and Aurigerites blumenstengeli Olempska, 1979) do not make up more than a few percent (1–5%), and Orthonaria gruendeli makes up 5%. Healdiids with Healdia anterodepressa Blumenstengel, 1965 and Timorhealdia aff. nitidula (Rh. Richter, 1869) make up 5–15% of the sample.



Fig. 4. Frequency distribution of the most common ostracod species across the Devonian–Carboniferous boundary of the Kowala section.

Assemblages from samples Ko-105–Ko-100 yielded species similar to the underlying beds with the bairdiids dominating: *Bairdia* ex gr. *hypsela*, *B.* sp. 1, *B. nidensis* (max. 70% in sample Ko-101). '*Harziella' blessi* is also comparatively numerous (max. 42% in sample Ko-100). It is important to note the disappearance of *Healdia anterodepressa* (the last specimens were found in sample Ko-101), since this species was thought to be disappearing at the Devonian–Carboniferous boundary. Samples from this interval contain 130–230 individuals each. Rectonariids occur in high diversity (10–15 species) but in low relative frequency (0.5–5.0% each species).

A profound ostracod faunal change takes place higher up (samples Ko-99, Ko-98) in the black shale layer (Fig. 4). The ostracod assemblage there is dominated by quasillitids with *Ovatoquasillites*? sp. which make up 60% of the total content. Samples Ko-97–Ko-88 are characterized by low numbers and diversity (< 100 individuals in each sample). The ostracods are also poorly preserved and partly decalcified. The first appearance of *Healdia thuringensis* Gründel, 1961 occurs in sample Ko-89.

The assemblage from sample Ko-87 is very rich in entomozoaceans (> 300 individuals) but poor in benthic species (10 species, 50 individuals) with *Acratia rostrataformis* Schevtsov, 1964 dominating (30%).

The top of the *Wocklumeria* limestone (samples Ko-77–Ko-75) yielded rich and diverse benthic ostracod assemblage (800–1000 individuals per sample and 27 species). New immigrant species *Tetrasacullus triloculi* Blumenstengel, 1979, *Ceratacratia cerata* Blumenstengel, 1965, '*Pribylites*' sp., *Polycope* cf. *sphaerula* (Grün-

del, 1961), appear there. Rectonariids also increase in abundance there. In sample Ko-77 Orthonaria rectagona (Gründel, 1962) makes up 30%, Timorhealdia aff. nitidula - 13%, and Aurigerites blumenstengeli - 13\%, but Bairdia species continue to be an important part of the assemblage (15–17%).

**Devonian–Carboniferous event assemblage** (Samples Ko-74–Ko-57). — There is an abrupt and extensive change in the benthic ostracod assemblage just above the limestone with *Wocklumeria* (Figs 2, 3). Thuringian-type forms as well as *Bairdia* species disappear (the last specimens were found in sample Ko-75). Only isolated and poorly preserved specimens of *Shemonaella* sp., *'Selebratina'* aff. *angustocristata* Blumenstengel, 1965, and *Amphissites* sp. 1 have been found in samples above the limestone. This critical interval is situated between samples Ko-74 and Ko-58 and is about 2 m thick. A major lithologic change is also observed: in this interval the section is represented by clays and claystones with tuffites in its middle part (Fig. 5).

There is also an abrupt change in the macrofauna above the *Wocklumeria* limestone in the Kowala section. Clymenids, trilobites and bryozoans, abundant in the nodular limestone, disappear at this level. However, one small poorly preserved fragment of *Biloclymenia*? sp. (J. Dzik, personal communication) has been found in sample Ko-72. This sample, taken a few centimetres above the limestone (Ko-74), was the last containing abundant entomozoacean fauna (Fig. 3).

In sample Ko-73 there are abundant skeletal remains of fish, wood fragments, radiolarians and a mass occurrence of silicified unicellular algae (probably leiospheres) as well as abundant juvenile ammonoids. A frequently observed fossil in this interval is the bivalve *Guerichia*. Acutimitoceras faunas appear slightly higher (samples Ko-69–Ko-64).

In the sample Ko-64 a new 'exotic' ostracod assemblage (*Healdia shangquii* sp. n., *Mauryella polonica* sp. n. and *Monoceratina* sp.) appears. Only one species (*Shemonaella* sp.) from underlying beds continues to occur. The new assemblage is poor in species (only 4 species occur), but rich in individuals. Sample Ko-65 yielded more than 300 individuals with *Healdia shangqii* dominating, making up 75%.

Only *Healdia shangquii* continues to the Carboniferous, whereas *Mauryella polonica* and *Monoceratina* sp. as well as *Shemonaella* sp. dissappear close to its base.

**Carboniferous assemblage** (Samples Ko-56–Ko-27). — Thuringian-type ostracods and *Bairdia* species reappear again in the Carboniferous deposits with almost the same or closely related species. Only a few spinose species disappear while some new Carboniferous species appear (Figs 2, 3).

In the sample Ko-58, poor in species and specimens, Thuringian- and Entomozoacean-type ostracods reappear.

The first appearance of *Richterina (Richterina) latior* Rabien, 1960 and unnumerous benthic *Aurigerites* sp. and *Microcheilinella bushminae* Olempska, 1981 make their appearance in the assemblage from sample Ko-58 and *Healdia shangquii* continues.

In the overlying black shale (8–10 cm thick, sample Ko-57) there are poorly preserved, decalcified *Amphissites* sp. 2 and *Coryellina grandis* Robinson, 1978.

Higher up (samples Ko-56–Ko-53), the ostracod abundance and diversity gradually increase. *Bairdia* ex gr. *hypsela* reappears and *Bairdia venterba* Gründel, 1961 appears



Fig. 5. Thin-sections of the rocks from the Devonian–Carboniferous boundary interval of Kowala section. A. Boundary between vitroclastic tuff and crystalloclastic tuff; sample Ko-66;  $\times$  6. B. A crystalloclastic tuff, 8 cm thick layer between sample Ko-68 and Ko-69;  $\times$  6. C. Homogeneous micrite with laminae of bioclastic material; sample Ko-60;  $\times$  8. D. Laminated radiolarian biomicrite; sample Ko-59;  $\times$  6.

for the first time in sample Ko-56, making up 50% of the assemblage while *H. shangquii* makes up 11%. Rectonariids are represented there by the Devonian species *R. inclinata* (15%) and *R. muelleri* (1–3%), but new Carboniferous species also appear including *Necrateria trapezoidalis* (Gründel, 1962), *Aurigerites* sp. up to 30%, and *Shivaella* sp. 1.

Still higher (samples Ko-53–Ko-45), the entomozoaceans gradually increase in abundance and *Bairdia* species represent a very small percentage of the assemblages. *Healdia shangquii* is the dominant species in this part of the section (up to 38% in sample Ko-48). There is a complete gradation between early forms of *Microcheilinella bushminae* (Fig. 17A, B) with small spines on the posteroventral part of the carapace and *Microcheilinella aculeata* Buschmina, 1975 (Fig. 17C, E) with a large posteroventral spine on the right valve. *Orthonaria* cf. *berna* (Gründel, 1962) appears in sample Ko-53 and *B. felumgibba* reappears. *Rectoplacera*? sp. n. 1 appears in sample Ko-50. The abundance of *Bairdia* species varies in different samples, reaching from 20% in sample Ko-56 to 2% in Ko-50. *Healdia thuringensis* reappears in sample Ko-45 and *Ovatoquasillites slowikensis* (Olempska, 1981) appears.

Rectonariids increase in abundance and diversity in assemblages from samples Ko-45–Ko-38, together comprising 65% of samples Ko-39–Ko-40 (*R. muelleri*, *R. inclinata*, *O.* cf. *berna*, *Triplacera triquetra*, *Rectoplacera*? sp. n., *Rectoplacera*? sp. 1, and *Aurigerites* sp.).

One poorly preserved specimen of *Polycope* cf. *sphaerula* was found in sample Ko-34.

In the upper part of the section (*S. sandbergi* Zone, samples Ko-33–Ko-27), the abundance and diversity of benthic species decreases and the abundance of entomozoacean species increases.

## Discussion

The distribution of Thuringian-type ostracod assemblages was strongly determined by the environment. According to Becker (1982), Becker & Bless (1990) and Becker & Blumenstengel (1995), the Thuringian-type ostracods inhabited low-energy environments. A rather deep, calm, cold and oxygen deficient biotope with a high amount of dissolved silica was proposed for them by Lethiers & Crasquin (1987), Lethiers & Feist (1991), and Bless *et al.* (1986). In the opinion of Raymond & Lethiers (1990), the installation of benthic spinous ostracod fauna (Thuringian ecotype) in the late Famennian Palaeotethys correlated to an invasion of cold deep-water currents that originated in the glacial north-Gondwanian area. In their opinion, the Thuringian ostracods are typical of a deep, cool, poorly-oxygenated environment rich in dissolved silica. According to Kozur (1991) the upper depth limit for Thuringian ostracods (paleopsychrospheric ostracods according to Gründel & Kozur 1975 and Kozur 1991) was between 200 and 500 m. They lived in a stable environment in a two-layered ocean with unrestricted connections (Kozur 1991). Dreesen *et al.* (1985), Bless (1987), and Bless (1992) suggested that low-energy conditions were more important than depth.

Fig. 6. A. Amphissites sp. 1. Carapace ZPAL O.XXXIX/19 in left lateral view; × 45; sample Ko-122. B. Amphissites sp. 2. Carapace ZPAL O.XXXIX/111 in left lateral view; × 45; sample Ko-32. C. Villozona



villosa villosa (Gründel, 1961). Right valve in lateral view, ZPAL O.XXXIX/123; × 55; sample Ko-45. **D**. Kirkbya sp. Left valve in lateral view, ZPAL O.XXXIX/16; × 90; sample Ko-44. **E**. Amphissites centronotus (Ulrich & Bassler, 1906). Carapace ZPAL O.XXXIX/150 in right lateral view; × 70; sample Ko-39. **F-G**. Coryellina grandis Robinson, 1978. **F**. Carapace ZPAL O.XXXIX/125 in dorsal view; × 60; sample Ko-45. **G**. Carapace ZPAL O.XXXIX/124 in right lateral view; × 70; sample Ko-45. **H**, **I**. 'Selebratina' sp. 1 (sensu Olempska 1979). **H**. Carapace ZPAL O.XXXIX/266, × 60; sample Ko-115. **I**. Left valve in lateral view, ZPAL O.XXXIX/67; × 60; sample Ko-76. **J**. 'Selebratina' aff. angustocristata Blumenstengel, 1965. Right valve in lateral view, ZPAL O.XXXIX/50; × 60; sample Ko-76. **K**. Coryellina grandis Robinson, 1978. Right valve in lateral view, ZPAL O.XXXIX/351; × 60; sample Ko-27.



Fig. 7. A–C. 'Fellerites' bohlenensis Gründel, 1962. A. Inside view of left valve, ZPAL O.XXXIX/3; × 60; sample Ko-108. B. Carapace ZPAL O.XXXIX/185 in left lateral view; × 60; sample Ko-38. C. Carapace ZPAL O.XXXIX/177 in left lateral view; × 55; sample Ko-38. D–F. Shemonaella sp. D. Carapace ZPAL O.XXXIX/353 in dorsal view; × 80; sample Ko-76. E. Carapace ZPAL O.XXXIX/190 in right lateral view; × 80; sample Ko-77. F. Inside view of left valve, ZPAL O.XXXIX/257; × 80; sample Ko-108. G. Shivaella? sp. 2. Right valve in lateral view, ZPAL O.XXXIX/38; × 120; sample Ko-56. H, I. Shivaella sp. 1. H. Carapace ZPAL O.XXXIX/24 in in right lateral view; × 45; sample Ko-45. I. Carapace ZPAL O.XXXIX/348 in left lateral view; × 60; sample Ko-58.

It seems that the Late Devonian and early Tournaisian Thuringian-type ostracod assemblages from the Kowala section were probably much more shallow water oriented than other Devonian Thuringian assemblages (e.g. from Thuringia, Rhenish Slate Mountains, and China). Shallow water, thick-shelled species such as bairdiids, podocopids without spines such as *Ampuloides* and '*Harziella*' and paraparchitaceans are abundant. The absence of tricorniinids usually present in deeper water Thuringian assemblages supplies further confirmation of a shallowing setting. The entomozoaceans are present in nearly all Thuringian assemblages.

Near the Devonian–Carboniferous boundary there is a changeover from fauna dominated by podocopids (*Wocklumeria* limestone) to that dominated by palaeocopids (Ko-73–Ko-66) and in the upper part of boundary interval the fauna is dominated by metacopids and palaeocopids (Ko-65–Ko-60).

The 'exotic' species of the event assemblage (*Mauryella polonica, Healdia shangquii, Monoceratina* sp.) are unusual for the Thuringian ecotype. Rare species of *Mauryella* Ulrich & Bassler, 1923 occur in the Late Devonian and Early Carboniferous deposits of N-America. In Europe, the impoverished, mixed assemblage of the Thuringian ecotype and 'exotic' forms (also with *Mauryella*) were observed in the NW wall of Drewer Quarry (Sauerland). This assemblage has been identified in the Stockum level above the Hangenberg Shale and below the Devonian–Carboniferous boundary (Becker & Blumenstengel 1995: figs 6, 8). The assemblage from the Stockum layer of Drewer can be correlated with the event assemblage from samples Ko-65–Ko-60 of the Kowala section and related to shallower water and relatively high energy conditions.

The dominance of metacopids (*Healdia shangquii*) in the event assemblage is thought to be evidence of a reduced oxygen environment. Metacopids and palaeocopids are believed to be filter-feeders (Lethiers & Whatley 1994). After the event, the filter-feeders declined to their former relative insignificance while the podocopids gradually achieved their former diversity. According to Whatley (1990, 1995) and Lethiers & Whatley (1994) there is a simple biological explanation of the survival of the filter-feeding metacopids, platycopids and palaeocopids in reduced oxygen environments. The metacopids and platycopids have more 'branchial' plates on their appendages than the podocopids do and can, therefore, cope with reduced oxygen levels better because they are able to circulate larger volumes of water.

The Carboniferous ostracod assemblages return to their normal diversity and composition similar as in the *Wocklumeria* limestone. The Carboniferous assemblage is probably much deeper-water than the Devonian one. Rectonariids occur there in greater diversiy and in the upper part of the section (*S. sandbergi* Zone) entomozoaceans dominate in the assemblage. The Devonian podocopids which are probably representatives of shallower water environments or highly specialized forms (thick shelled *Ampuloides*, '*Harziella*') disappear at the D–C event beds and do not reappear in the Carboniferous. The only ones which occur above the topmost *Wocklumeria* limestone are rare '*Selebratina*' aff. *angustocristata*, *Shemonaella* sp., and *Amphissites* sp. 1. Some highly specialized and short-lived Devonian rectonariids (*Ceratacratia cerata*, *Cristanaria cristata*), as in Thuringian sections (Blumenstengel 1993) and NE Russian Platform (Sobolev 1995), disappear at the top of the *Wocklumeria* limestone.

## Succession of entomozoacean ostracods

Complete and well dated studies on Devonian-Carboniferous boundary sections with entomozoacean ostracods have been done only in Northern and Central Europe (Chillaton area in England; Hasselbach Valley, Stockum and Sallfeld in Germany), but the distribution of entomozoaceans varies between these four sections (cf. Bless & Groos-Uffenorde 1984).

The Famennian zonation of Rabien (1954) was supplemented by the *M. hemisphaerica/R. (R.) latior* Interregnum of Rabien (1960). This was supported by Groos-Uffenorde & Uffenorde (1974) and Bless & Groos-Uffenorde (1984), Bless *et al.* (1986) but called into doubt in Thuringia by Bartzsch & Weyer (1980, 1982). According to Blumenstengel (1993), *M. hemisphaerica* (Richter, 1848) extends up to the last fossiliferous layer of the *Wocklumeria* stage in Thuringia and *Richterina (R.) latior* first occurs in the first layer of the *Gattendorfia* stage. *M. hemisphaerica/R. (R.) latior* Interregnum is not discernible here and Late Devonian entomozoacean assemblages are separated from the Early Carboniferous assemblages by an unfossiliferous interval: the 'Hangender Quarzit'.

In the continuous Devonian–Carboniferous sections in Licun and Lanxu of the Guangxi region of China there is only an interval of over 10 cm between the top of the M. hemisphaerica–M. dichotoma Zone and the base of the R. (R.) latior Zone (Wang 1983).

Late Devonian pre-event assemblage. — The entomozoacean assemblage of the Upper *M. hemisphaerica–M. dichotoma* Zone consists predominantly of frequent *Richterina (R.) striatula* (Richter, 1848), *Richterina (R.) costata* (Richter, 1869), *Maternella hemisphaerica*, and sparse *Maternella dichotoma* (Paeckelman, 1913) and *Kuzmianella* sp.

In the *Wocklumeria* limestone entomozoaceans are numerous and occur slightly later (last specimens in sample Ko-74) than benthic ostracods (last specimens in sample Ko-75) (see Fig. 3).

**Event assemblage.** — Just above the *Wocklumeria* limestone in marls of sample Ko-74, *R. (R.) striatula* and *R. (R.) costata* are still abundant but *M. hemisphaerica* is absent. It disappeared earlier at the top of *Wocklumeria* limestone (last *M. hemisphaerica* is in sample Ko-76).

The *M. hemisphaerica/R. (R.) latior* Interregnum *sensu* Bless & Groos-Uffenorde (1984) begins here. The *M. hemisphaerica/R. (R.) latior* Interregnum extends from sample Ko-74 to Ko-59 in the Kowala section (Fig. 3).

Only three entomozoacean species occur in the *M. hemisphaerica/R. (R.) latior* Interregnum in the Stockum section (Rhenish Slate Mountains, Germany): *Maternella* sp. n. 3, *Maternella* sp. 4 and *Maternella circumcostata* (see Groos-Uffenorde & Uffenorde 1974; Bless & Groos-Uffenorde 1984).

Carboniferous assemblage. — In sample Ko-58 R. (R.) latior appears slightly earlier than Siphonodella sulcata.

Similarly, *R. (R.) latior* also appears slightly earlier than *S. sulcata* in sections of Donbas, the southern Urals, northern regions of the Volga-Urals district and Mugodar (Bless & Groos-Uffenorde 1984). In northwestern Europe *R. (R.) latior* appears a little above the first appearance of *S. sulcata* (Bless & Groos-Uffenorde 1984).

In samples Ko-40–Ko-39 (S. sandbergi Zone) two new entomozoaceans appear: Ungerella sp. n. and Maternella sp. 1.

In the Carboniferous part of the sequence entomozoaceans are less abundant in the *S. sulcata* and *S. duplicata* Zones, but become abundant in the *S. sandbergi* Zone, being represented mostly by different *Maternella* species [*Maternella* (*Zagoroundella*) schindewolfi (Kummerow, 1939); *M. (Z.) arcuata* Gründel, 1961; *M. steinachensis* Gründel, 1961; *M. sp.*]. There are no Devonian type entomozoacean species in the Carboniferous part of the sequence in the Kowala section.

There is an important change between the Devonian and Carboniferous entomozoaceans at the species level but not at higher taxonomic levels. The distribution of entomozoacean ostracods in the Kowala section confirm their zonation in Europe.

#### **Palaeoenvironmental remarks**

The long-term influence of the Hangenberg Event on the global ostracod distribution was rather insignificant. The ostracod assemblages of the do VI and cu I are rich in species. The overall regression during the Middle *S. praesulcata* time was accompanied by a short decline and turnover in benthic ostracods in the Holy Cross Mountains. Comparable changes in entomozoaceans occurred slightly later. The Kowala faunal changes were local biotic events but could be closely associated with the well known D–C extinctions.

Three main episodes can be distinguished in ostracod succession around the Devonian–Carboniferous boundary in the Kowala section:

(1) The top of the *Woclumeria* limestone is marked by an overall decrease in ostracod diversity. All podocopids disappeared while only a few palaeocopids survived and adapted to the rapidly changing environments. The disappearance of planktonic entomozoaceans post-dates the major change in benthic species. Abundant leiospheres occur at the base of the event interval in the Kowala section. In the geological record they demonstrate a capability for surviving widespread extinctions which affected phytoplankton groups, e.g. acritarchs. Their occurence often is interpreted as a result of a density stratification of the water column after a reduction in surface water salinity (Loh *et al.* 1986; Riegel *et al.* 1986).

A poor oxygenation of the bottom water probably resulted from density stratification of the water column and sluggish circulation in basinal area.

In South America (Parnaiba Basin), deposits correlated with the LE–LN spore zones (latest Famennian) are interpreted as glacial/interglacial deposits (Loboziak *et al.* 1992, 1993). Perhaps there is a causal connection between the begining of this glaciation and the minor regression at the end of the sedimentation of the *Wocklumeria* Limestone and the decrease in faunal diversity.

According to Flajs & Feist (1988), it is possible that the melting of inland ice could have affected the salinity of the surface water at the time of the D–C boundary, but there is no evidence of large inland ice-sheets. It is also possible that salinity was lowered by river runoff, and the presence of common wood fragments in the layer with abundant leiospheres supports this.

The slightly longer existence of abundant entomozoaceans in comparison with benthic assemblages indicate that the surface waters remained oxygenated longer compared to the bottom waters. The disappearance of entomozoaceans in the Kowala section may be due to lowered salinity of the surface waters, but it is possible that entomozoaceans might have also lived in deeper waters and an expansion of the oxygen minimum zone in the water column caused their disappearance. Vertical and horizontal distribution of planktonic ostracods in the water column depends on many factors, e.g. temperature, salinity, pH, water depth, nutrients and oxygen level. Major changes in these factors may have led to the extinction of the most sensitive groups. The disappearance of *Maternella hemisphaerica* along with the benthic ostracods may be connected with its necto-benthic mode of live, postulated by several authors (see Becker & Bless 1990; Gooday 1983; Olempska 1991).

The great abundance of juvenile cephalopod specimens in samples Ko-73–Ko-72 combined with the absence of benthic organisms also suggests the presence of an oxygen depleted zone.

(2) The next episode was the immigration of new 'exotic' benthic ostracods unusual to the Thuringian ecotype and probably indicating shallower water conditions.

It is difficult to judge whether the samples represent a more shallow water assemblage or a remnant of filter-feeding ostracods which could survive in 'difficult' dysaerobic conditions (Whatley 1990, 1995; Lethiers & Whatley 1994).

The radiolarians common in samples Ko-69–Ko-64 provide support for a deepening trend within the basin.

(3) At the begining of the Carboniferous the global sea-level returned to the pre-event level and remained very high in the Early Carboniferous. There was a progressive recolonization of bottom area and water column by the Thuringian- and Entomozoacean-type ostracods at this time.

The Hangenberg anoxic event did not result in a global extinction of the Thuringian-type ostracods but only in their local dissapearance in some areas. The regressive phase at the begining of the Middle *S. praesulcata* Zone caused the extinction of thick-shelled taxa (*Tetrasacculus triloculi, Ampuloides pumillus, 'Harziella' blessi*) in the Kowala area. The Thuringian assemblages may have persisted during a time of crisis in well oxygenated peripheral refuges of their formerly widespread habitat area. They reappeared as Lazarus taxa later in the Carboniferous in shelf environments. The subsequent transgression in the *S. sulcata* Zone permitted recolonization of the shelf from the marginal refuges. They reappeared together with new taxa. Possible refuges of Thuringian ostracods were probably the deeper waters of, for example, Montagne Noire (Lethiers & Feist 1991) and Rhenish Massif (Becker *et al.* 1993; Becker & Blumenstengel 1995) regions where they occur in the sediments deposited between the Hangenberg Shale and the D–C boundary.

Oscillation of the oxygen depleted layer may have caused this bio-event, thus contributing to a stepwise dissapearance of certain taxa.

Fig. 8. A–C. Healdia anterodepressa Blumenstengel, 1965. A. Carapace ZPAL O.XXXIX/5 in right lateral view; × 45; sample Ko-105. B. Carapace ZPAL O.XXXIX/5 in dorsal view; × 36; sample Ko-105. C. Carapace ZPAL O.XXXIX/6 in ventral view; × 45; sample Ko-105. D–F. Healdia thuringensis Gründel, 1961. D. Carapace ZPAL O.XXXIX/205 in right lateral view; × 50; sample Ko-38. E. Carapace ZPAL O.XXXIX/196 in dorsal view; × 55; sample Ko-37. F. Carapace ZPAL O.XXXIX/198 in ventral view; × 55; sample Ko-36. G–I. Timorhealdia aff. nitidula (Rh. Richter, 1869). G. Carapace ZPAL O.XXXIX/230 in right lateral view; × 95; sample Ko-76. H. Carapace ZPAL O.XXXIX/231 in dorsal view;



 $\times$  95; sample Ko-76. I. Carapace ZPAL O.XXXIX/232 in ventral view;  $\times$  95; sample Ko-76. J–M. *Timorhealdia nitidula nitidula* (Rh. Richter, 1869). J. Carapace ZPAL O.XXXIX/187 in right lateral view;  $\times$  80; sample Ko-38. K. Carapace ZPAL O.XXXIX/184 in right lateral view;  $\times$  60; sample Ko-38. L. Carapace ZPAL O.XXXIX/361 in left lateral view;  $\times$  60; sample Ko-36. M. Carapace ZPAL O.XXXIX/184 in ventral view;  $\times$  60; sample Ko-38.

## **Review of identified species**

There are difficulties in comparing the usually silicified Thuringian-type ostracod fauna from western Europe with the calcareous carapaces extracted from limestones and marls in the Holy Cross Mountains. Ostracods are quite common in most samples from the Kowala section, but not always well preserved. Except for rare separate valves, they are closed, making examination of their internal features difficult. The genera are successively presented in alphabetic order.

Acratia cooperi Gründel, 1962. — In the Kowala section this species (Fig. 19G) occurs only in the *Gattendorfia* stage (samples Ko-45–Ko-27). The species is known from the Early Carboniferous (cu I) of Thuringia (Gründel 1961, 1962; Bartzch & Weyer 1986); cu I of the Rhenish Massif (Becker et al. 1993); cu I of the Montagne Noire (Lethiers & Feist 1991); cu I of Algeria (Becker 1987) and cu I (*S. sandbergi* Zone) of China (Wang 1988).

Acratia rostrataformis Schevtsov, 1964. — This species (Fig. 19F) occurs in the Kowala section in the Devonian pre-event deposits (samples Ko-115–Ko-75), most abundantly in sample Ko-87. It is also known from the Late Devonian (do II) of Thuringia (Blumenstengel 1969); do III–V of the Cantabrian Mountains (Becker 1981); do VI of Morocco and Early Carboniferous (cu I) of Algeria (Becker 1987).

Amphissites centronotus (Ulrich & Bassler, 1906). — In Kowala the species (Fig. 6E) occurs in the S. sandbergi Zone (samples Ko-40–Ko-27). This species or homeomorphic forms are known from the Early to Late Carboniferous of N. Spain, the Carnic Alps, Thuringia, N. America and China. According to Shi Cong-quang (1982) A. blumenstengeli Gründel, 1962 and A. mosquensis Posner, 1951, are conspecific with A. centronotus.

*Amphissites* sp. 1. — Poorly preserved specimens (Fig. 6A) occur in many samples in the Devonian pre-event and the lower part of the event interval of the Kowala section (last found in sample Ko-69).

Amphissites sp. 2. — This species (Fig. 6B) occurs in samples of the S. sulcata up to the S. sandbergi Zone.

Ampuloides pumillus Olempska, 1979. — This species (Fig. 18E, F) occurs only in the Devonian pre-event part of the Kowala section (samples Ko-114–Ko-75).

*Aurigerites blumenstengeli* Olempska, 1979. — This species (Fig. 16A–G) occurs in the Kowala section in the Devonian pre-event part (samples Ko-114–Ko-75) and Carboniferous (samples Ko-50–Ko-45). It is represented by a relatively large number of specimens of younger moult stages. The posterodorsal spine of the left valve appears in older moult stages and is absent in younger ones. In specimens illustrated by Olempska (1979: pl. 28: 4) the posterodorsal spine was very small and probably represented the shell of an early instar. Specimens in the Early Carboniferous of Montagne Noire with larger posterodorsal spine were classified as subspecies *A. blumenstengeli nigermontanus* by Lethiers & Feist (1991: pl. 3: 16–18). Their material probably does not represent adult specimens.

This species is known from the Late Devonian (do V) of the Cantabrian Mountains (Becker 1981), do VI of Thuringia (Bartzsch & Weyer 1985); do VI-cu I of Morocco (Becker 1987) and cu I of the Pyrenees (Lethiers 1985).

Aurigerites sp. — Specimens of A. sp. differ (Fig. 16H, I) from A. blumenstengeli in the absence of a dorsal spine and a more rounded posterior ridge. They are more similar to specimens described by Olempska (1981) as A. aff. texanus than to A. blumenstengeli. A. obernitzensis Gründel, 1961 illustrated by Lethiers & Feist (1991), is similar to specimens of Aurigerites sp. from Kowala. Specimens from the Tournaisian of the Karaganda Basin with a similar posterior ridge and small posterodorsal spine were classified by Buschmina (1977) as Aurigerites kazakhstanicus Buschmina, 1977. In Kowala it occurs in Carboniferous part of the section.

**Bairdia feliumgibba Becker, 1982.** — This species (Fig. 20H, I) occurs in the Devonian preevent part (Fig. 20H) and in the Carboniferous part (Fig. 20I) of the Kowala section [= B.(B.) aff.galinae sensu Olempska 1981]. It is known also from the Early Carboniferous (S. sandbergi Zone)



Fig. 9. All specimens from sample Ko-65. A–C. *Mauryella polonica* sp. n. A. Holotype, carapace ZPAL O.XXXIX/81 in right lateral view;  $\times$  85. B. Carapace ZPAL O.XXXIX/172 in ventral view;  $\times$  80. C. Juvelile carapace ZPAL O.XXXIX/320 in left lateral view;  $\times$  85. D–E. *Monoceratina* sp. D. Carapace ZPAL O.XXXIX/119 in right lateral view;  $\times$  100. E. Carapace ZPAL O.XXXIX/235 in right lateral view;  $\times$  90. F–J. *Healdia shangquii* sp. n. F. Holotype, carapace ZPAL O.XXXIX/13 in right lateral view;  $\times$  90. G. Carapace ZPAL O.XXXIX/299 in left lateral view;  $\times$  90. H. Carapace ZPAL O.XXXIX/357 in left lateral view;  $\times$  90. I. Carapace ZPAL O.XXXIX/173 in ventral view;  $\times$  80. J. Carapace ZPAL O.XXXIX/32 in right lateral view;  $\times$  85.

of China (Wang 1988); do I – cu I of Thuringia (Gründel 1961; Blumenstengel 1979; Bartzch & Weyer 1985); the late *S. praesulcata–S. duplicata* Zones of the Rhenish Massif (Becker *et al.* 1993); cu II of the Montagne Noire (Lethiers & Feist 1991); do III–V of the Cantabrian Mountains (Becker 1982); do IV – cu II of Harz (Müller-Steffen 1965); do V of Moravia (Dvorak *et al.* 1986); do VI of the Pyrenees (Delvolvé & Lethiers 1986); do VI of Morocco and cu I of Algeria (Becker 1987).

**Bairdia** ex gr. hypsela Rome, 1971. — In Kowala this species (Fig. 20A, J) is abundant in the *Wocklumeria* limestone (Fig. 20A) and in the Tournaisian (Fig. 20J). Closely related species are known from do III–IV of the Cantabrian Mountains (Becker 1982); do VI – cu I of Thuringia (Gründel 1961; Blumenstengel 1965, 1979); do VI of Morocco; cu I of Algeria (Becker 1987) and S. praesulcata–S. sandbergi Zones of the Rhenish Massif (Becker *et al.* 1993).

**Bairdia nidensis** Olempska, 1979. — This rare species (Fig. 20B) occurs in Kowala only in the lower part of the section (samples Ko-115–Ko-87). It is also known from do III–IV of the Cantabrian Mountains (Becker 1982); do VI – cu I of the Rhenish Massif (Becker *et al.* 1993) and do VI of Morocco (Becker 1987).

**Bairdia venterba Gründel, 1961.** — In Kowala this species (Fig. 20D) occurs only in samples Ko-53–Ko-34. It is known also from the Early Carboniferous (cu I) of Thuringia (Gründel 1961, 1962; Blumenstengel 1993); cu I of the Rhenish Massif (Becker *et al.* 1993); the Early Carboniferous of China (Wang 1988); cu I of the Montagne Noire (Lethiers & Feist 1991) and cu I of Algeria (Becker 1987).

**Bairdia** sp. 1. — This species (Fig. 20C) is common in Kowala in samples Ko-110–Ko-100. It is similar in its lateral outline to the Carboniferous *B. venterba*.

**Bairdia** sp. 2. — This species (Fig. 20E) is characterized by its slightly concave centrodorsal margin. In Kowala it occurs only in sample Ko-56.

**Bairdia sp. 3**. — In the Kowala section this species (Fig. 20K) has been found in sample Ko-27. From congeneric species it differs in its almost straight, truncated posterior margin.

**Beecheroscapha?** sp. — This species (Fig. 20F) differs from others assigned to the genus in having a pointed posterior end in the mid-half of the valve and bearing a posteroventrally located large spine and having its anterior end pointed anterodorsally and terminating in a delicate spine. The spine at the posterior end is somewhat similar to that in *Beecheroscapha puanensis* Becker & Wang, 1992 from the Early and Middle Devonian of China. A ridge along its ventral margin also makes it different from congeneric species. In Kowala it occurs only in sample Ko-27.

**Bohlenatia rhenothuria Becker, 1993** (= *B. banfensis* Olempska, 1981). — This species (Fig. 20G) occurs only in the Tournaisian part of the Kowala sequence (sample Ko-38). It is known also from the *Gattendorfia* stage of Thuringia (Gründel 1961, 1962; Blumenstengel 1993) and the Early Carboniferous (*S. duplicata–S. sandbergi* Zones) of the Rhenish Massif (Becker *et al.* 1993).

It also appears in impoverished mixed ostracod fauna at the Stockum level in the Drewer Quarry, Rhenish Massif (Becker & Blumenstengel 1995).

*Ceratacratia cerata* Blumenstengel, 1965. — This rare species (Fig. 19H, I) occurs in the Kowala section only in the Devonian pre-event part of the section (samples Ko-114–Ko-76). It is also known from the Late Devonian (do II–VI) of Thuringia (Blumenstengel 1965, 1993; Bartzch & Weyer 1979); do III–V of the Cantabrian Mountains (Becker 1982); do V of Moravia; do VI of Harz; do VI of the Pyrenees (Delvolvé & Lethiers 1986) and do VI of Morocco (Becker 1987).

*Coryellina grandis* Robinson, 1979. — This species (Fig. 6F, G, K) occurs in the Carboniferous part of the Kowala section (*S. sulcata* up to the *S. sandbergi* Zone, samples Ko-57–Ko-27). It is also known from the Tournaisian of the British Isles (Robinson 1979).

*Cristanaria cristata* (Blumenstengel, 1965). — In the Kowala section this species (Fig. 12A–E) occurs only in the upper part of the *Wocklumeria* limestone (samples Ko-76–Ko-77). Specimens from Kowala represent young instars and they have only a posterodorsal spine on the left valve. They differ from the adult specimens illustrated by Blumenstengel (1965, 1979) from Thuringia in having antero-



Fig. 10. A, B. Ovatoquasillites aff. investibus Becker, 1987. A. Right valve in lateral view, ZPAL O.XXXIX/4; × 45; sample Ko-107. B. Inside view of left valve, ZPAL O.XXXIX/1; × 45; sample Ko-110. C, D. Ovatoquasillites slowikensis (Olempska, 1981). C. Carapace ZPAL O.XXXIX/311 in right lateral view; × 55; sample Ko-39. D. Inside view of left valve, ZPAL O.XXXIX/27; × 55; sample Ko-45. E. Ovatoquasillites? sp. Carapace ZPAL O.XXXIX/278 in right lateral view; × 60; sample Ko-114. F. Knoxiella? sp. Left valve in lateral view, ZPAL O.XXXIX/245; × 80; sample Ko-99. G, H. Praepilatina adamczaki Olempska, 1979. G. Carapace ZPAL O.XXXIX/87 in left lateral view; × 70; sample Ko-107. H. Carapace ZPAL O.XXXIX/312 in right lateral view; × 90; sample Ko-39.

and posterodorsal spines on the left valve. This species is known from do VI of Thuringia (Blumenstengel 1979; Bartzch & Weyer 1986) and the late Famennian of the Russian Platform (Sobolev 1995).



Fig. 11. A, B. Rectonaria inclinata Gründel, 1961. A. Carapace ZPAL O.XXXIX/307 in right lateral view; × 120; sample Ko-109. B. Carapace ZPAL O.XXXIX/37 in right lateral view; × 90; sample Ko-50. C, D. Rectonaria muelleri Gründel, 1961. C. Right valve in lateral view, ZPAL O.XXXIX/233; × 95; sample Ko-77. D. Carapace ZPAL O.XXXIX/28 in right lateral view; × 80; sample Ko-45. E–I. Triplacera triquetra Gründel, 1961. E. Carapace ZPAL O.XXXIX/129 in right lateral view; × 60; sample Ko-114. F. Right valve in lateral view, ZPAL O.XXXIX/129 in right lateral view; × 60; sample Ko-114. F. Right valve in lateral view; × 60; sample Ko-114. H. Carapace ZPAL O.XXXIX/128 in dorsal view; × 60; sample Ko-114. I. Carapace ZPAL O.XXXIX/311 in ventral view; × 45; sample Ko-48. J. Rectonaria inclinata Gründel, 1961. Carapace ZPAL O.XXXIX/306 in ventral view; × 85; sample Ko-50.



Fig. 12. A–E. Cristanaria cristata (Blumenstengel, 1965). A. Carapace ZPAL O.XXXIX/188 in left lateral view; × 80; sample Ko-77. B. Carapace ZPAL O.XXXIX/70 in dorsal view; × 60; sample Ko-77. C. Carapace ZPAL O.XXXIX/8 in ventral view; × 60; sample Ko-76. D. Carapace ZPAL O.XXXIX/70 in right lateral view; × 60; sample Ko-77. E. Carapace ZPAL O.XXXIX/39 in ventral view; × 60; sample Ko-75. F–H. *Rectoplacera* aff. *robusta* Blumenstengel, 1965. F. Carapace ZPAL O.XXXIX/301 in right lateral view; × 85; sample Ko-103. G. Carapace ZPAL O.XXXIX/162 in dorsal view; × 60; sample Ko-103. H. Carapace ZPAL O.XXXIX/307 in ventral view; × 60; sample Ko-111. I–L. *Olempskaella ventrospina* Blumenstengel, 1995 I. Right valve in lateral view; ZPAL O.XXXIX/260; × 60; sample Ko-77. J. Right valve in lateral view; ZPAL O.XXXIX/261; × 60; sample Ko-77. K. Right valve in lateral view; ZPAL O.XXXIX/261; × 60; sample Ko-103.

'Fellerites' bohlenensis Gründel, 1962 (= Fellerites sp. 1 sensu Olempska 1981). — Two poorly preserved specimens were identified in samples Ko-108 and Ko-105 and rare specimens occur in the *S. sandbergi* Zone in sample Ko-38 (Fig. 7A–C). This species has been reported from the Late Devonian (do V–VI) of the Rhenish Massif (Becker *et al.* 1993); the latest Devonian (do VI) of Morocco (Becker 1987) and from the Early Carboniferous (cu I) of Thuringia (Gründel 1961, 1962).

'Harziella' blessi (Olempska, 1979). — This species (Fig. 18C, D) occurs in the entire pre-event Devonian part of the Kowala section. The closely related 'Harziella' ornata Müller-Steffen, 1965, is known from do VI of Thuringia (Blumenstengel 1979), and the NE Russian Platform (Sobolev 1995).

*Healdia anterodepressa* Blumenstengel, 1965. — In the Kowala section this species (Fig. 8A–C) disappears above sample Ko-102 (*P. expansa* Zone). In Thuringia (Blumentengel 1993) it extends to the Upper Quarzite (D–C boundary). The species is also known from do VI of Morocco (Becker 1987) and do IV–VI of Thuringia (Blumenstengel 1965, 1979, 1993; Bartzch & Weyer 1979, 1985, 1986).

#### *Healdia shangquii* sp. n.

Fig. 9F-J.

Holotype: ZPAL O.XXXIX/13; Fig. 9F.

Type horizon: Protognathodus kockeli Zone.

Type locality: Kowala, Holy Cross Mountains, Poland.

Derivation of the name: In honour of Dr. Wang Shang-qi from Nanking, China.

Diagnosis: *Healdia* species with small anterior spines on both valves and strongly convex dorsal margin.

**Remarks.** — It is most similar to *Healdia ratra* Gründel, 1961 but differs in the presence of small spines at the anterior end of both valves (*H. ratra* has a spine only on the left valve). The new species differs from *T.* aff. *nitidula* in the lateral outline of its valves and a larger overlapping area along the ventral margin.

In Kowala it occurs from the upper part of the event interval (sample Ko-68) and continues through the entire Carboniferous part of the section.

*Healdia thuringensis* Gründel, 1961. — In the Kowala section this species (Fig. 8D–F) appears in sample Ko-93 and continues its appearance to the top of *Wocklumeria* limestone (sample Ko-75). It reappears in the Carboniferous sample Ko-43. This species is also known from do VI to cu II of Thuringia (Gründel 1961, 1962, 1963; Bartz & Weyer 1986).

It occurs in Montagne Noire in cu I (Lethirs & Feist 1991). In the Rhenish Massif (Drewer Quarry) it occurs from the Late *S. praesulcata* Zone to the *S. sandbergi* Zone (Becker *et al.*1993; Becker & Blumenstengel 1995).

*Kirkbya* sp. — One specimen (Fig. 6D) was found in sample Ko-44 (*S. duplicata* Zone). It is similar to *Kirkbya? cornuta* Robinson, 1978 from the Brigantian (Visean) of the British Isles (Robinson 1978) but differs in lacking an anterodorsal spine.

Knoxiella? sp. — This species (Fig. 10F) occurs only in the black shale layer (sample Ko-99).

*Mauryella polonica* sp. n. Fig.9A–C. Holotype: ZPAL O.XXXIX/81; Fig. 9A. Type horizon: *Protognathodus kockeli* Zone.

Fig. 13. A–E. Orthonaria neotridentifer Lethiers & Feist, 1991. A. Carapace ZPAL O.XXXIX/166 in right lateral view; × 70; sample Ko-76. B. Carapace ZPAL O.XXXIX/332 in dorsal view; × 80; sample Ko-76. C. Carapace ZPAL O.XXXIX/166 in ventral view; × 70; sample Ko-76. D. Carapace ZPAL O.XXXIX/362 in right lateral view; × 90; sample Ko-36. E. Carapace ZPAL O.XXXIX/363 in ventral view; × 90; sample



Ko-36. **F**–**H**. *Rectoplacera*? sp.n. 1. **F**. Carapace ZPAL O.XXXIX/15 in right lateral view; × 90; sample Ko-45. **G**. Carapace ZPAL O.XXXIX/15 in dorsal view; × 90; sample Ko-45. **H**. Carapace ZPAL O.XXXIX/271 in ventral view; × 90; sample Ko-45. I–L. *Rectoplacera neoelongata* Blumenstengel, 1979. **I**. Carapace ZPAL O.XXXIX/7 in right lateral view; × 60; sample Ko-76. **J**. Carapace ZPAL O.XXXIX/7 in dorsal view; × 60; sample Ko-76. **K**. Carapace ZPAL O.XXXIX/10 in ventral view; × 60; sample Ko-76. **L**. Carapace ZPAL O.XXXIX/2 in right lateral view; × 60; sample Ko-76. **L**. Carapace ZPAL O.XXXIX/2 in right lateral view; × 60; sample Ko-710.

Type locality: Kowala, Holy Cross Mountains, Poland.

Derivation of the name: From the latin *polonica*, meaning Polish.

Diagnosis: *Mauryella* species with reticulate surface and six nodes on the lateral surface: the three dorsal nodes are almost equal, anterodorsally displaced median node subdued and the two ventral nodes are larger than the dorsal nodes.

**Remarks.** — This species is very similar to the type species of the genus *M. mammillata* Ulrich & Bassler, 1923, but differs in the relative dimensions of its nodes. From *Mauryella* sp. illustrated by Becker & Blumenstengel (1995) from the Stockum layer of Drewer Quarry, Rhenish Massif, this species differs in having much smaller nodes. *Evlanovia* cf. *tichonovitchi* Egorov, 1950, described by Lethiers (1981: pl. 1: 3, 4) from the latest Devonian (do VI) of Western Canada possibly also represents this genus.

*Microcheilinella aculeata* Buschmina, 1975. — This species (Fig. 17C–E) occurs in Kowala in the Carboniferous part of the section (samples Ko-43–Ko-27). It is also known from the Early Carboniferous of the Kolyma Massif (Buschmina 1975). This species is similar in the presence of a spine and in its lateral outline to *Grammia elongata* Kotschetkova, 1980 from the Tournaisian of the S. Urals (Kotschetkova 1980).

*Microcheilinella bushminae* Olempska, 1981. — This species (Fig. 17A, B) occurs in Kowala in samples Ko-56–Ko-50 (*S. sulcata* Zone). It is also known from the Early Carboniferous (*S. sandbergi* Zone) of the Wangyou Formation in Nandan of Guangxi, China (Wang 1988).

**Monoceratinia sp.** — This species (Fig. 9D, E) occurs in Kowala only in sample Ko-65 (*Protognathodus kockeli* Zone). It is similar in its lateral ornamentation of thin ridges to *Monoceratina virgata* Green, 1963 from the early Mississippian of Alberta, classified by Kozur (1985) to his genus *Striatobythoceratina*. It is also similar to *Monoceratina simakovi* Bless, 1984 from the middle Tournaisian of the Omolon region, NE-Russia (Shilo *et al.* 1984).

Necrateria trapezoidalis (Gründel, 1962). — This species (Fig. 17F, G) occurs in Kowala in S. sulcata –S. sandbergi Zones (samples Ko-56–Ko-27). It is also known from cu I of Thuringia (Gründel 1962; Blumenstengel 1965); cu I of Moravia (Dvorak et al. 1986); do VI – cu I of Morocco and Algeria (Becker 1987).

*Olempskaella ventrospina* Blumenstengel, 1995. — This rare species (Fig. 12I–L) occurs in the upper part of the Devonian pre-event part of the section (samples Ko-111–Ko-77). It is also known from do VI of Thuringia (Blumenstengel 1995).

*Orthonaria gruendeli* Olempska, 1979. — This species (Fig. 15E, F) occurs in the *Wocklumeria* limestone (samples Ko-77–Ko-76).

Orthonaria cf. berna (Gründel, 1962). — The spine on the left valve of the Kowala specimens (Fig. 15G, H) is slightly closer to the ventral margin than in the holotype. This species possesses two spines on the posterior part of its right valve and one on posterior part of the left valve. O. cf. berna is closely related to the stratigraphically older O. gruendeli, but differs in having only one posterior spine on its left valve. In Kowala it occurs only in the earliest Carboniferous, S. sulcata–S. duplicata Zones (samples Ko-50–Ko-44). In Thuringia it occurs in the Gattendorfia stage (Gründel 1962).

*Orthonaria neotridentifer* Lethiers & Feist, 1991. — This species (Fig. 13A–E) occurs in Kowala in the Devonian pre-event part of the section (samples Ko-115–Ko-75) and the post-event Carboniferous part (samples Ko-53–Ko-36). It is also known from cu I of Montagne Noire (Lethiers & Feist 1991).

It is similar in its lateral outline to Rectoplacera neoelongata Blumenstengel, 1979.

**Orthonaria rectagona** (Gründel, 1962). — This species (Fig. 14A–C) is abundant in the Devonian pre-event part of the section and rare in the Tournaisian of Kowala.

It is also known from do VI – cu I of Thuringia (Gründel 1962; Blumenstengel 1993); do VI of Morocco and do VI – cu I of Algeria (Becker 1987) and the late Famennian of the NE Russian Platform (Sobolev 1995).



Fig. 14. A–C. Orthonaria rectagona (Gründel, 1962). A. Carapace ZPAL O.XXXIX/240 in right lateral view; × 95; sample Ko-77. B. Carapace ZPAL O.XXXIX/330 in dorsal view; × 70; sample Ko-76. C. Carapace ZPAL O.XXXIX/239 in ventral view; × 70; sample Ko-77. D, E. Rectoplacera? sp. n. 2. D. Left valve in lateral view; ZPAL O.XXXIX/258; × 80; sample Ko-77. E. Left valve in lateral view; ZPAL O.XXXIX/259; × 60; sample Ko-77. F, G. Rectoplacera? sp. 1. Carapace ZPAL O.XXXIX/305, × 80; sample Ko-38. F. Right lateral view. G. Dorsal view. H, I. Rectoplacera sp. 2. Carapace ZPAL O.XXXIX/276; × 110; sample Ko-107. H. Dorsal view. I. Right lateral view.



Fig. 15. A–D. Paragerodia subtrapezoidalis Wang, 1988. A, B. Carapace ZPAL O.XXXIX/237 in right lateroventral and lateral views; × 95; sample Ko-76. C, D. Carapace ZPAL O.XXXIX/314 in right lateral and lateroventral views; × 90; sample Ko-40. E, F. Orthonaria gruendeli Olempska, 1979. E. Carapace ZPAL O.XXXIX/228 in left lateral view; × 120; sample Ko-76. F. Carapace ZPAL O.XXXIX/9 in right lateral view; × 120; sample Ko-77. G, H. Orthonaria cf. berna (Gründel, 1962). G. Carapace ZPAL O.XXXIX/226 in right lateral view; × 120; sample Ko-50. H. Carapace ZPAL O.XXXIX/333 in left lateral view; × 150; sample Ko-50.

**Ovatoquasillites aff. investibus Becker, 1987.** — This species (Fig. 10A, B) is most similar in its smooth lateral surface to *Ovatoquasillites investibus* Becker, 1987 from do VI of Algeria. It is possible that it represents a new subspecies. It occurs in Kowala only in the Devonian pre-event part of the section (samples Ko-114–Ko-82).



Fig. 16. A–G. Aurigerites blumenstengeli Olempska, 1979. A. Carapace ZPAL O.XXXIX/191 in right lateral view; × 80; sample Ko-77. B. Juvenile carapace ZPAL O.XXXIX/254 in right lateral view; × 80; sample Ko-77. C. Juvenile carapace ZPAL O.XXXIX/255 in right lateral view; × 80; sample Ko-77. D. Juvenile carapace ZPAL O.XXXIX/349 in right lateral view; × 80; sample Ko-58. E. Juvenile carapace ZPAL O.XXXIX/349 in right lateral view; × 80; sample Ko-58. E. Juvenile carapace ZPAL O.XXXIX/256 in right lateral view; × 80; sample Ko-77. F. Carapace ZPAL O.XXXIX/259 in dorsal view; × 80; sample Ko-76. G. Carapace ZPAL O.XXXIX/170 in ventral view; slightly open; × 80; sample Ko-76. H. I. Aurigerites sp. H. Carapace ZPAL O.XXXIX/36 in right lateral view; × 85; sample Ko-50. I. Carapace ZPAL O.XXXIX/146 in right lateral view; × 70; sample Ko-50.

*Ovatoquasillites slowikensis* (Olempska, 1981). — This species (Fig. 10C) is most similar to *Ovatoquasillites blaszyki* Becker, 1987 from do VI – cu I of the Rhenish Massif (Becker *et al.* 1993) and cu I of Algeria (Becker 1987). It occurs in the Carboniferous part of the Kowala section (samples Ko-45–Ko-36).



Fig. 17. A, B. *Microcheilinella bushminae* Olempska, 1981. A. Carapace ZPAL O.XXXIX/148 in right lateral view; × 110; sample Ko-50. B. Carapace ZPAL O.XXXIX/147 in ventral view; × 110; sample Ko-50. C-E. *Microcheilinella aculeata* Buschmina, 1979. C. Carapace ZPAL O.XXXIX/202 in right lateral view; × 100; sample Ko-35. D. Carapace ZPAL O.XXXIX/303 in dorsal view; × 110; sample Ko-38. E. Carapace ZPAL O.XXXIX/304 in ventral view; × 110; sample Ko-38. F, G. *Necrateria trapezoidalis* (Gründel, 1962). F. Carapace ZPAL O.XXXIX/334 in right lateral view; × 60; sample Ko-53. G. Carapace ZPAL O.XXXIX/25 in right lateral view; × 60; sample Ko-45.

**Ovatoquassilites?** sp. — This species (Fig. 10E) occurs abundantly only in the thin black shale layer (sample Ko-99).

**Paragerodia subtrapezoidalis Wang, 1988** (= Healdianella aff. bispinosa sensu Olempska 1979). — This species (Fig. 15A–D) occurs in the Devonian pre-event part (samples Ko-110–Ko-76, Fig. 15A, B) and in the *Gattendorfia* stage (samples Ko-45–Ko-36; Fig. 15C, D) in the Kowala section. It is also known from the Early Carboniferous (*S. sandbergi* Zone) of China (Wang 1988) and do VI – cu I of Montagne Noire (Lethiers & Feist 1991).

**Polycope cf. sphaerula (Gründel, 1961).** — This species (Fig. 18A, B) is common in the *Wocklumeria* limestone (samples Ko-91–Ko-75) in Kowala, and one poorly preserved specimen has been found in sample Ko-34 (*S. sandbergi* Zone). It is known from the Late Devonian and Early Carboniferous of Thuringia (Gründel 1961, 1962); in the Late *S. praesulcata* to the *S. sandbergi* Zone of the Rhenish Massif (Becker *et al.* 1993) and cu I of China (Wang 1988). In Drewer Quarry (Sauerland) it is known from the Stockum level (Becker & Blumenstengel 1995).

**Praepilatina adamczaki Olempska, 1979.** — This rare species (Fig. 10G, H) was found in sample Ko-107 (Fig. 10G). It is more common in the Carboniferous part of the section in samples Ko-40–Ko-38 (Fig.10H). It occurs also in the Late Devonian (do III – do V) of the Cantabrian Mountains (Becker 1981); do VI of the Pyrenees (Delvolvé & Lethiers 1986); do VI – cu I of Montagne Noire (Lethiers & Feist 1991); cu I (*S. sandbergi* Zone) of the Guangxi region, China (Wang 1988) and the Late Devonian–Early Carboniferous (*S. praesulcata–S. sandbergi* Zones) of the Rhenish Massif (Becker *et al.* 1993).

'Pribylites'? aff. elongatus Blumenstengel, 1965. — This species (Fig. 19B–D) occurs in Kowala only in the Wocklumeria limestone (samples Ko-77–Ko-75). It is most similar in its lateral outline to 'Pribylites' elongatus Blumenstengel, 1965, illustrated by Becker et al. (1993: pl. 4: 5–18) from the cu I (S. sulcata–S. sandbergi Zones) of the Rhenish Massif and Becker (1981: pl. 1: 17–18) from do V of the Cantabrian Mountains. Specimens illustrated by Becker et al. (1993) differ from the holotype in lacking dorsal spines which are present in the specimens illustrated by Blumenstengel (1965). Becker's specimens probably represent a new species. The Kowala specimens are also similar in their lateral outline and reticulate ornamentation to Amicus sp. described by Lethiers & Feist (1991) from cu I of Montagne Noire.

**Rectonaria inclinata Gründel, 1961.** — This species (Fig. 11A, B, J) occurs in Kowala in all pre-event Devonian and post-event Carboniferous parts of the section. It is also known from do V – cu I of Thuringia (Gründel 1961; Blumenstengel 1965, 1979, 1993; Bartzch & Weyer 1979, 1985, 1986); cu I – cu II of Montagne Noire (Lethiers & Feist 1991); do V of the Cantabrian Mountains (Becker 1981); do VI of the Rhenish Massif (Becker *et al.* 1993); cu I (*S. sandbergi* Zone) of the Guanxi region, China (Wang 1988) and cu I of Algeria (Becker 1987).

**Rectonaria muelleri Gründel, 1961. — This is one of the most characteristic species (Fig. 11C, D) in the Thuringian type assemblages from the Late Devonian and Early Carboniferous. In Kowala it occurs in all the Devonian pre-event parts of the section and reappears in the Carboniferous in sample Ko-56 (lower part of the** *S. sulcata* **Zone). It is also known from do I – cu I of Thuringia (Gründel 1961; Blumenstengel 1965, 1979, 1993; Bartzch & Weyer 1979, 1985, 1986); the Early Carboniferous (***S. sandbergi***) of the Wangyou Formation of the Guangxi region, China (Wang 1988); do VI of Morocco and do VI – cu I of Algeria (Becker 1987); do VI – cu I of Montagne Noire (Lethiers & Feist 1991); do III – do IV of the Cantabrian Mountains (Becker 1981); do V, cu I of Moravia (Dvorak** *et al.* **1986); do VI of Pyrenees (Delvolvé & Lethiers 1986) and the Rhenish Massif (Becker** *et al.* **1993). It is also known from the impoverished ostracod fauna of the Stockum level in Saalfeld (lowermost Upper** *S. praesulcata* **Zone) (Becker & Blumenstengel 1995).** 

*Rectoplacera neoelongata* Blumenstengel, 1979. — This species (Fig. 13I–L) is similar to *Rectoplacera* sp. described by Kotschetkova (1980) from the late Tournaisian of the S. Urals. It occurs in Kowala in the Devonian pre-event part of the section (samples Ko-110–Ko-76). It is also known from do VI of Thuringia (Blumenstengel 1979).

**Rectoplacera** aff. robusta Blumenstengel, 1965 (sensu Olempska 1979). — This species(Fig. 12F–H) occurs in Kowala in the lower part of the section.

**Rectoplacera? sp. n. 1.** — This species (Fig. 13F–H) is very similar to *Triplacera oblonga* Wang, 1988 in the shape of its posterior ridge, but differs from it in having shorter posterior spines. It is also possible that *Triplacera (N.?) gattendorfina* Gründel, 1962 from the *Gattendorfia* stage of Thuringia is based on juvenile specimens of this species. *T.(N.?) gattendorfina* differs in lacking a dorsal spine,



Fig. 18. A, B. *Polycope* cf. *sphaerula* (Gründel, 1961). A. Right valve in lateral view; ZPAL O.XXXIX/68; × 120; sample Ko-76. B. Left valve in lateral view; ZPAL O.XXXIX/69; × 120; sample Ko-76. C, D. *'Harziella' blessi* (Olempska, 1979). C. Carapace ZPAL O.XXXIX/314 in right lateral view; × 90; sample Ko-77. D. Carapace ZPAL O.XXXIX/313 in ventral view; × 90; sample Ko-76. E, F. *Ampuloides pumillus* Olempska, 1979. E. Carapace ZPAL O.XXXIX/316; × 90; sample Ko-76. F. Carapace ZPAL O.XXXIX/315 in ventral view; × 90; sample Ko-76. G–I. *Tetrasacculus triloculi* Blumenstengel, 1979. G. Carapace ZPAL O.XXXIX/40 in right lateral view; × 60; sample Ko-77. H. Carapace ZPAL O.XXXIX/160 in ventral view; × 70; sample Ko-103. I. Right female valve in ventral view; ZPAL O.XXXIX/44; × 75; sample Ko-76.

but this spine develops in the pre-adult instars. It occurs in Kowala in the Carboniferous part of the section (samples Ko-50–Ko-34).

**Rectoplacera**? sp. n. 2. — This species (Fig. 14D, E) differs from other *Rectoplacera* species in the reticulate surface of the valves. It occurs in Kowala in the *Wocklumeria* limestone (sample Ko-77).

**Rectoplacera? sp. 1.** — This species (Fig. 14F, G) differs from other *Rectoplacera* species in its convex ventral margin. It occurs in the Carboniferous part of the Kowala section (samples Ko-39–Ko-34).



Fig. 19. A. Palaeocopida gen. indet. Carapace ZPAL O.XXXIX/48 in right lateral view; × 60; sample Ko-76. B–D. 'Pribylites'? aff. elongatus Blumenstengel, 1965 B. Right valve in lateral view; ZPAL O.XXXIX/168; × 110; sample Ko-76. C. Right valve in lateral view; ZPAL O.XXXIX/318; × 110; sample Ko-77. D. Right valve in lateral view; ZPAL O.XXXIX/321; × 110; sample Ko-76. E. Tricornina sp. Right valve in lateral view; ZPAL O.XXXIX/308 in right lateral view; × 55; sample Ko-75. G. Acratia cooperi Gründel, 1962. Carapace ZPAL O.XXXIX/186 in right lateral view; × 60; sample Ko-76. I. Ceratacratia cerata Blumenstengel, 1965. H. Carapace ZPAL O.XXXIX/238 in right lateral view; × 95; sample Ko-76. I. Left valve in lateral view; ZPAL O.XXXIX/192; × 120; sample Ko-77.

*Rectoplacera* sp. 2. — This species (Fig. 14H, I) occurs in the lower part of the Kowala section (samples Ko-107, Ko-105).

'Selebratina' sp. 1 (sensu Olempska 1979). — The lack of the sulcus in the median part of the valve is very characteristic for this species (Fig. 6H, I). A long spine on the dorso-posterior part of

the right valve is present in well preserved specimens (Fig. 6H). This species occurs in all the Devonian pre-event parts of the Kowala section.

'Selebratina' aff. angustocristata Blumenstengel, 1965 (sensu Becker et al. 1993). — This species (Fig. 6J) occurs in Kowala in the *Wocklumeria* limestone (samples Ko-100–Ko-76) and at the base of the event interval (last in sample Ko-69). Similar specimens were found in the Carboniferous part of the section (sample Ko-27). It has been reported also from the Early Carboniferous (*S. duplicata–S. sandbergi* Zones) from the Rhenish Massif (Becker et al. 1993).

Shemonaella sp. — This species (Fig. 7D–F) is similar in the lateral outline to *Paraparchites* sp. illustrated by Blumenstengel (1995) from do VI of Thuringia. It is common in the Devonian pre-event part of the Kowala section (samples Ko-115–Ko-90), and occurs rarely in the event interval. The last specimens occur in sample Ko-65.

*Shivaella* **sp. 1** (*sensu* Olempska 1981). — This species (Fig. 7H, I) occurs in Kowala in the Carboniferous (samples Ko-56–Ko-38) part of the section. It is also known from the *Gattendorfia* stage (cu I) of Montagne Noire (Lethiers & Feist 1991).

**Shivaella? sp. 2.** — This species (Fig. 7G) differs from *Shivaella* sp. 1 in the lateral outline of its valves and the presence of a dorsal spine close to the dorsal margin. It is also smaller at comparable stages. Three specimens were found in sample Ko-56 (*S. sulcata* Zone).

*Tetrasacculus triloculi* Blumenstengel, 1979. — This rare species (Fig. 18G–I) in Kowala occurs only in the *Wocklumeria* limestone (samples Ko-103–Ko-76). It has been reported from the *Wocklumeria* stage (Upper *Clymenia* beds) of Thuringia (Blumenstengel 1979, 1993) and the late Famennian of NE Russian Platform (Sobolev 1995). According to Blumenstengel (1993), the absence of *Tetrasacculus* in the *Gattendorfia* stage in Thuringia may be related to a facies dependancy.

*Timorhealdia nitidula nitidula* (Rh. Richter, 1869). — This subspecies (Fig. 8J–L) occurs in Kowala in the Tournaisian part of the section (samples Ko-53–Ko-36). It is also known from cu I –II of Thuringia, the Late *S. praesulcata–S. sandbergi* Zones of the Rhenish Massif (Becker *et al.* 1993), Montagne Noire (Lethiers & Feist 1991) and cu I of Algeria (Becker 1987).

*Timorhealdia* aff. *nitidula* (Rh. Richter, 1869) (= *Marginohealdia* sp. *sensu* Olempska 1979). — In Kowala this species (Fig. 8G–I) occurs in the Devonian pre-event part of the section (samples Ko-115–Ko-75).

*Tricornina* sp. — This rare species (Fig. 19E) occurs in the Kowala section only in the *Wock-lumeria* limestone (samples Ko-75–Ko-76).

*Triplacera triquetra* Gründel, 1961. — This rare species (Fig. 11E–I) occurs in Kowala in the Devonian pre-event part of the section (samples Ko-114–Ko-77) and reappears in the Carboniferous (samples Ko-48–Ko-27). The species is also known from the late Famennian and Early Carboniferous (*Gattendorfia* stage) of Thuringia (Gründel 1962; Blumenstengel 1965, 1979, 1993); from the Early Carboniferous (*S. sandbergi* Zone) of the Wangyou Formation, China (Wang 1988) and probably from the *Pericyclus* stage (cu II) of Thuringia (Gründel 1963).

Villozona villosa villosa (Gründel, 1961). — This subspecies (Fig. 6C) occurs in Kowala only in samples Ko-45-Ko-38 (S. duplicata-S. sandbergi Zones). Two subspecies, V. villosa praecursor

Fig. 20. A. Bairdia ex gr. hypsela Rome, 1971. Carapace ZPAL O.XXXIX/29 in right lateral view; × 45; sample Ko-45. B. Bairdia nidensis Olempska, 1979. Carapace ZPAL O.XXXIX/129 in right lateral view; × 50; sample Ko-76. C. Bairdia sp. 1. Carapace ZPAL O.XXXIX/352 in right lateral view; × 60; sample Ko-109. D. Bairdia venterba Gründel, 1961. Carapace ZPAL O.XXXIX/355 in right lateral view; × 60; sample Ko-40. E. Bairdia sp. 2. Carapace ZPAL O.XXXIX/149 in right lateral view; × 57; sample Ko-56.
F. Beecheroscapha? sp. Left valve in lateral view; ZPAL O.XXXIX/136; × 66; sample Ko-27. G. Bohlenatia rhenothuria Becker, 1993. Left valve in lateral view; ZPAL O.XXXIX/136; × 54; sample Ko-38. H, I. Bairdia feliumgibba Becker, 1982. H. Carapace ZPAL O.XXXIX/234 in right lateral view; × 72; sample Ko-40. J. Bairdia



ex gr. *hypsela* Rome, 1971. Carapace ZPAL O.XXXIX/181 in right lateral view; × 54; sample Ko-38. **K**. *Bairdia* sp. 3. Carapace ZPAL O.XXXIX/144 in right lateral view; × 72; sample Ko-27. **L**. *Youngiella* aff. *calvata* (Green, 1963). Left valve in lateral view; ZPAL O.XXXIX/241; × 96; sample Ko-50.

(Bartzsch & Weyer, 1980) and V. villosa villosa (Gründel, 1961) are distinguished by differences of inner carina. According to Blumenstengel (1993), V. villosa praecursor occurs only in the Wocklumeria stage and V. villosa villosa in the Gattendorfia stage. V. villosa villosa is also known from cu I of Thuringia (Gründel 1961; Blumenstengel 1979, 1993); the Early Carboniferous of Guanxi, China (Wang 1988; Becker & Wang 1992) and cu I of Montagne Noire (Lethiers & Feist 1991). V. villosa cf. villosa was also described from do VI – cu I of Algeria (Becker 1987).

Youngiella aff. calvata (Green, 1963). — This rare species (Fig. 20L) was found in samples Ko-50, Ko-46 (S. sulcata Zone) of the Kowala section.

A similar species was noted from Strunian of N. France by Lethiers & Bouquillon (1986: pl. 2: 2).

**Palaeocopida gen. indet.** — This form (Fig. 19A) occurs in the Kowala section only in the *Wocklumeria* limestone (samples Ko-90–Ko-76).

#### Entomozoacean ostracods

A full systematic treatment of the Devonian–Carboniferous entomozoaceans will be given in a later publication (Olempska, in preparation).

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## Zmiany bentosowych zespołów małżoraczkowych na granicy dewon-karbon w Górach Świętokrzyskich

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#### Streszczenie

Profil utworów późnego dewonu i wczesnego karbonu w miejscowości Kowala w południowej części Gór Świętokrzyskich zachowuje ciągłość na granicy dewon-karbon. Granica ta została określona na podstawie konodontów (Dzik 1997) i małżoraczków, około 2 m powyżej stropu wapieni głowonogowych z *Wocklumeria*. W osadach najwyższego famenu (poziom *Prothognathodus kockeli*) stwierdzono szereg zmian fauny, które prawdopodobnie wywołane zostały względnymi zmianami poziomu morza.

Zespół małżoraczków z Kowali zawiera dobrze znane gatunki przewodnie jak również nowe formy małżoraczków bentosowych reprezentujących tzw. ekotyp turyngijski, składający się głównie z kolczastych podokopidów oraz planktonicznych małżoraczków ekotypu entomozoidowego. Stwierdzono występowanie 15 gatunków planktonicznych entomozoidów oraz 64 gatunki małżoraczków bentosowych. Opisano dwa nowe gatunki *Healdia shangquii* sp. n. i *Mauryella polonica* sp. n.

Główną zmianę składu gatunkowego w zespole małżoraczkowym stwierdzono powyżej stropu wapieni głowonogowych z *Wocklumeria*, w osadach przejściowych reprezentowanych przez mułowce z tufitami w części środkowej. Małżoraczki typu turyngijskiego i entomozoidowego są zastąpione w tych osadach przez zespół bardziej płytkowodny, zdominowany przez gatunki rodzajów *Healdia, Mauryella* i *Monoceratina*. We wczesnym turneju powracają zespoły typu turyngijskiego, entomozoidowego oraz liczne gatunki rodzaju *Bairdia*. Fauna wczesnego turneju reprezentowana jest zarówno przez gatunki dewońskie jak i nowe formy typowe dla wczesnego karbonu.