Emergence and collapse of the Frasnian conodont and ammonoid communities in the Holy Cross Mountains, Poland

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The dominant factor in faunal succession of conodonts in the Frasnian of Poland is the apparent immigration of species originating allopatrically in other regions. Each immigration event usually changes the population variability of a local species (character displacement). Only a few lineages show their phyletic evolution within the studied area. Attempts to distinguish conodont species on the basis of platform element shape failed in some of the latest Frasnian palmatolepidids. Even at the apparatus-based generic level, certain ramiform elements of the apparatus appear much more diagnostic than the platforms. Correlative value of the late Frasnian palmatolepidids of unknown apparatus structure is thus questionable. The evolution of platform elements in *Ancyrodella* offers a more solid basis for age determination although their great population variability makes resolution rather low and requires the population approach. The panderodontids *Belodella*(?) *tenuiserrata* sp., *B. minutidentata* sp. nov., *B. robustidentata* sp. nov., prioniodontid *Icriodus kielcensis* sp. nov., enigmatic monospecific Playfordiidae fam. nov., prioniodinids *Dyminodina planidentata* gen. et sp. nov., *D. anterodenticulata* sp. nov., *D. kovalensis* sp. nov., *Pluckidina kielcensis* gen. et sp. nov., *P. slupiensis* sp. nov., *P. robustipegmata* sp. nov., and *P. lagoviensis* sp. nov., derived polygnathid *Avignathus bifurcatus* sp. nov., probably secondarily simplified polygnathid *Nicollidina* gen. nov., and palmatolepidids *Kielcelepis* gen. nov., *Lagovilepis* gen. nov. and *Klapperilepis* gen. nov. are proposed.

Key words: Conodonta, Ammonoidea, Devonian, evolution, Holy Cross Mountains, Poland.

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Contents

Introduction

The conodont chordates and ammonoid cephalopod molluscs have one of the most complete fossil records among pelagic organisms of the Palaeozoic. They may thus serve as useful markers of the changes that took place in pelagic ecosystems at system boundaries, especially catastrophic environmental events associated with replacement of faunas. The most publicised of the Devonian "extinctions" is that at the Frasnian–Famennian boundary of the Late Devonian which resulted in the world-wide collapse of the great stromatoporoid-coral reefs. In pelagic environments this "extinction" is generally believed to correspond to the world-wide environmental event of the Upper Kellwasser Limestone Horizon (e.g., Walliser et al. 1989; McGhee 1996; Racki 1998; Hallam and Wignall 1999; Gong et al. 2001; House 2002). The Devonian ammonoids and conodonts have been extensively studied in the north European part of the Variscan orogenic belt and in Russia. The faunas in the area in between, represented by the Holy Cross Mountains (Fig. 1A), remain relatively poorly known, although the first Frasnian conodonts have been identified and described from there already by Wolska (1967), with subsequent monographic treatment by Szulczewski (1971), supplemented by Narkiewicz (1978; Narkiewicz and Narkiewicz 1992), Baliński (1979), Matyja and Narkiewicz (1995), and a series of works by Racki (1985, 1990, 1993; Racki et al. 1993).

In the Holy Cross Mountains the Upper Kellwasserkalk black cephalopod limestone horizon is well developed in weakly tectonized exposures and abounds in conodonts and cephalopods. It terminates an epoch of flourishing of benthic shallow-water and pelagic life in the area that began in the Early Devonian with the Emsian sea-level rise and transgression (Racki 1990; Szulczewski 1993). Nowhere in the area, however, are pelagic environments continuously represented in the fossil record. Instead, there is a series of brief incursions of pelagic biofacies with conodont and cephalopod communities. These incursions are of special interest, as the standard biostratigraphic divisions are based on their distribution.

In the present paper the conodonts and ammonoids from horizons in the Holy Cross Mountains accessible to study in the last few decades are reviewed. This begins from a brief presentation of the pre-Frasnian background of the faunal evolution of pelagic communities in the area (Figs. 1–3), and ends with presentation of some evidence on the earliest Famennian (Figs. 46–49).

In the case of conodonts an attempt to make their fossil record biologically meaningful will be presented, based on apparatus reconstructions and biometric studies of stratigraphically important species. Ranges of species will be estimated in terms of population, as it has been already proven that application of the typological (vertical) species concept makes age correlation unreliable (Dzik 1995). The succession of conodonts will be interpreted in terms of possible phyletic transformations, ecological shifts, and resulting character displacement in population variability. Ammonoid faunas from several horizons are illustrated and provisionally determined taxonomically. Some faunas are rich in specimens which allow quantitative studies of faunal dynamics, especially in the interval immediately preceding the end of the Frasnian.

The main part of the paper documents the reconstruction of conodont apparatuses and reviews ammonoid faunas. The conodont succession in a few well-sampled sections is the basis for age correlation, with ammonoids of only secondary importance. A preliminary subdivision of the Frasnian into time units based on the inferred phyletic evolution in the *Ancyrodella* lineage is used to correlate the studied sections (Fig. 4). No precise interregional correlation is advised until the actual course of evolution of *Ancyrodella* and species identity of the associated palmatolepidids is reliably established, based on biologically meaningful population approach and apparatus studies in their type areas.

Illustrated specimens are housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (abbreviated ZPAL).

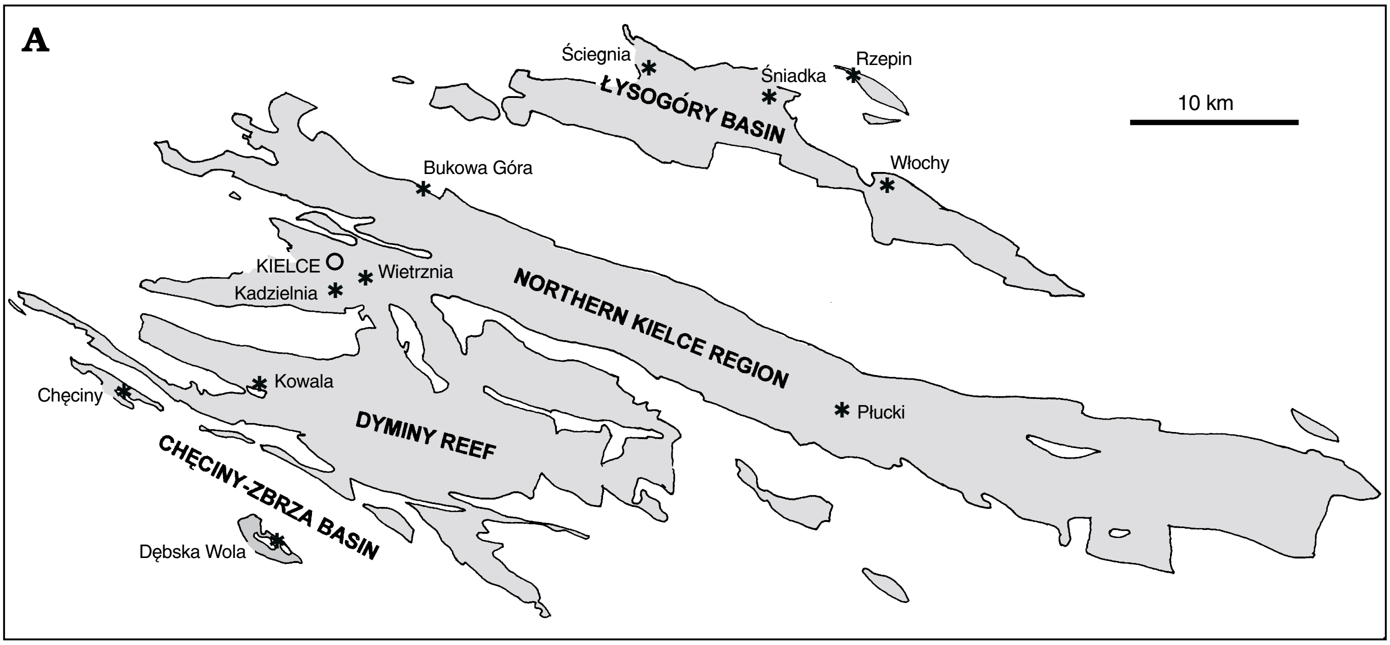
Methods

The conodont samples were dissolved in acetic (pure limestone) or formic (marls, dolomitized limestones) acids. Always there was less acid added than necessary to dissolve the carbonate and this provided some buffering. The residue was passed through a 1 mm sieve to remove acid-resistant flakes of the shale and undissolved limestone pieces. After being dried, the large fraction was screened for extremely large specimens. The remaining fraction was decanted, instead of sieved, to avoid loss of very small elements and breakage of extremely fragile ones.

The specimens are held loose in plastic slides (Franke Zellen) instead of being glued onto paper, as is the American standard. The reason for this is that gluing of a very large number of specimens is time consuming and makes turning out and segregation of specimens difficult. It is also dangerous for fragile specimens.

Measurements have been done not on actual specimens but on their contour drawings made with a microscope drawing apparatus. For the measurements, the specimens of palmatolepidids were first arranged in rows. Their most stable orientation is with the denticle row (carina) vertical but the drawing apparatus shows the view from the right ocular, that is slightly oblique. Potentially it would be possible to make specimens vertical in such view but the distortion does not seem significant as long as all specimens were drawn under the same angle. To assure this the, lobes of all specimens, both dextral and sinistral, were oriented towards right while delineated.

The notation system for the conodont apparatus follows here the proposal of Purnell et al. (2000). To avoid misunderstanding, the Jeppson's symbols (see Dzik 1991b) are added



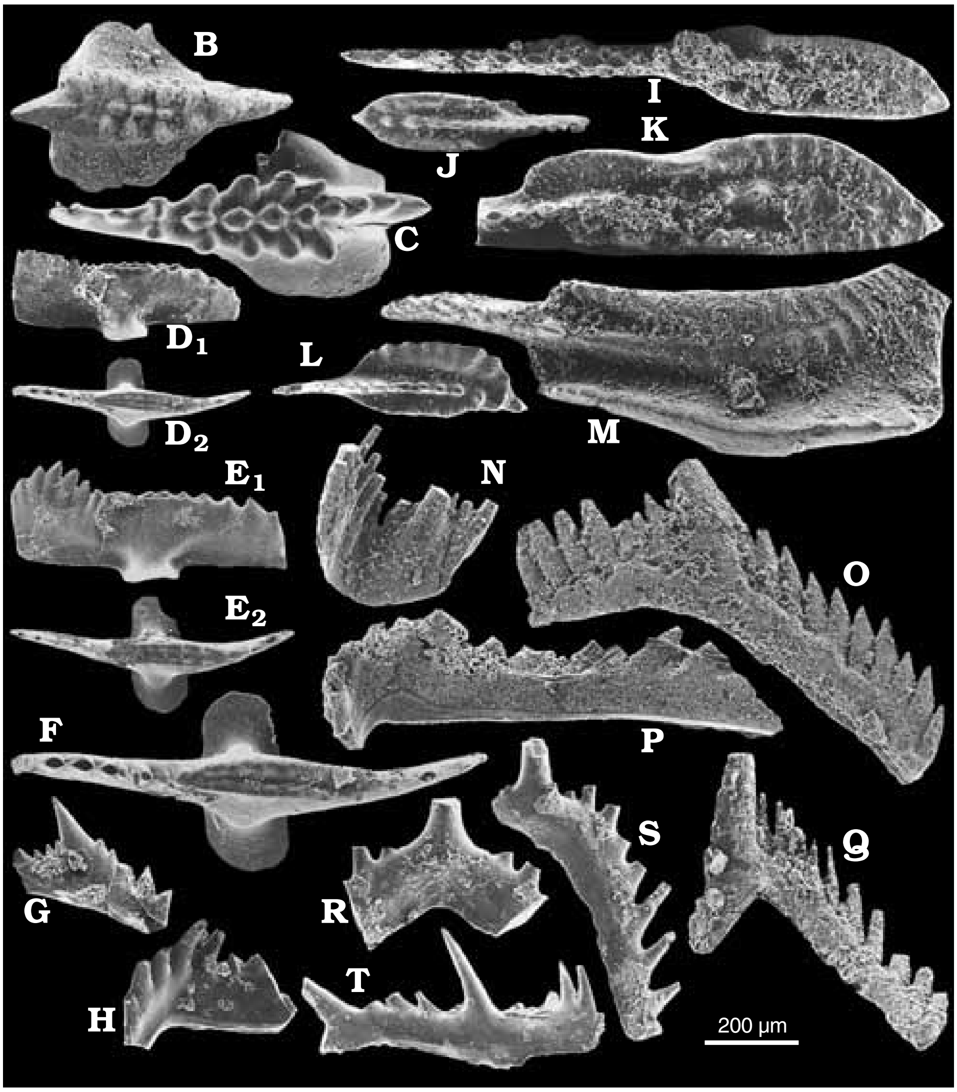


Fig. 1. **A**. Geographic position of the localities discussed in the text within the Devonian outcrops in the Holy Cross Mountains, central Poland. **B**–**T**. Eifelian conodonts from the area. **B**. *Icriodus* sp. (ex gr. *I. struvei* Weddige, 1977), P$_1$ (sp) element ZPAL CXVI/956, Dębska Wola. **C**. *Icriodus brevis* Stauffer, 1940, P$_1$ element ZPAL CXVI/763, sample Sn-1, Skały Formation, Śniadka. **D**–**H**. *Bipennatus bipennatus* (Bischoff and Ziegler, 1957), P$_1$ elements ZPAL CXVI/764 (**D**), 765 (**E**), 766 (**F**), also possibly belonging to this species P$_2$ (oz) element ZPAL CXVI/767 (**G**), S$_{3–4}$ (ke-hi) element ZPAL CXVI/769 (**H**), same sample. **I**–**K**, **N**–**Q**. *Polygnathus timorensis* Klapper, Philip, and Jackson, 1970, P$_1$ elements ZPAL CXVI/774 (**I**), 775 (**J**), 777 (**K**), S$_1$ (lo) element ZPAL CXVI/778 (**N**), P$_2$ element ZPAL CXVI/776 (**O**), S$_{3–4}$ element ZPAL CXVI/780 (**P**), M (ne) element ZPAL CXVI/781 (**Q**), sample Sn-2, same locality. **L**–**M**, **T**. *Parapolygnathus linguiformis* (Hinde, 1879), juvenile P$_1$ element ZPAL CXVI/766 (**L**), sample Sn-1 and mature ZPAL CXVI/777 (**M**), sample Sn-2, S$_2$ element ZPAL CXVI/770 (**T**), sample Sn-1, same locality. **R**, **S**. *Ligonodina pectinata* Bassler, 1925, S$_2$ (pl) element ZPAL CXVI/768 and S$_2$ element ZPAL CXVI/771, sample Sn-1, same locality.

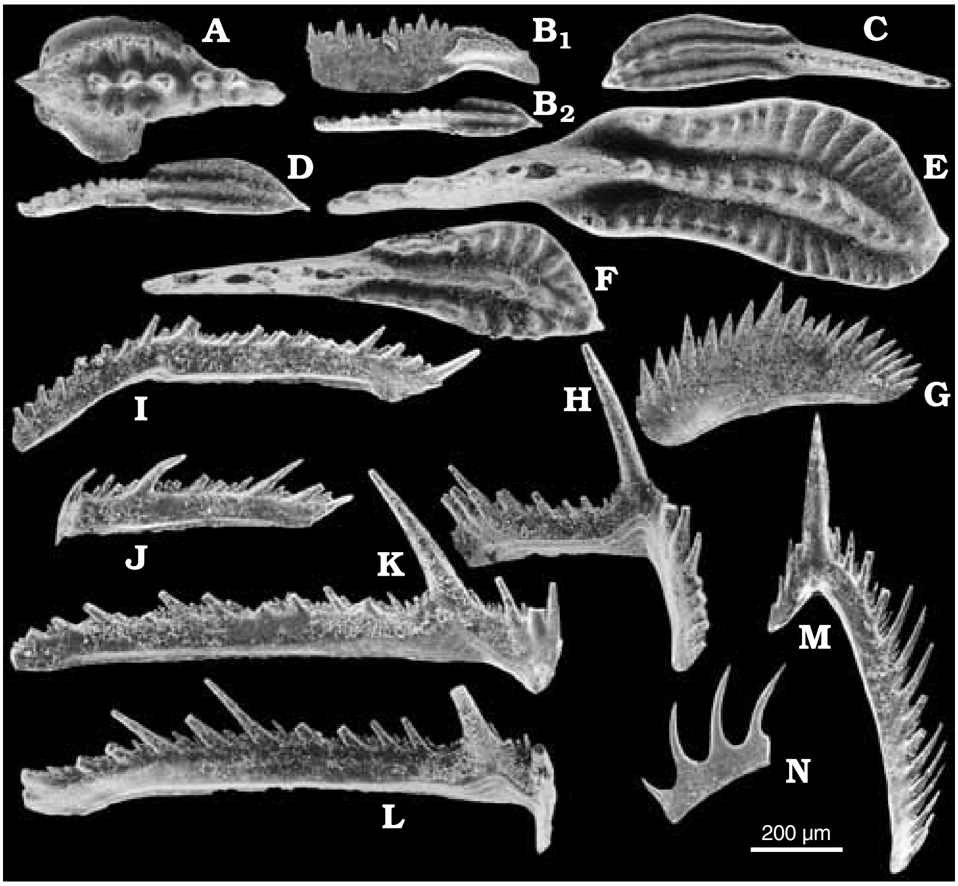


Fig. 2. Late Givetian conodonts from the Holy Cross Mountains. **A**. *Icriodus* sp. (ex gr. *I. subterminus* Youngquist, 1947), P_1 (sp) element ZPAL CXVI/942, sample 492F-1; Góra Zamkowa section at Chęciny. **B**–**M**. *Polygnathus dubius* Hinde 1879 → *Polygnathus aequalis* Klapper and Lane, 1985 (= *Polygnathus* sp. A Racki, 1992), P_1 elements ZPAL CXVI/948 (**B**), 946 (**C**; juvenile), 947 (**D**), 944 (**E**), 945 (**F**), P_2 (oz) element ZPAL CXVI/949 (**G**), S_0 (tr) element ZPAL CXVI/950 (**H**), S_2 (pl) element ZPAL CXVI/951 (**I**), S_1 (lo) element ZPAL CXVI/952 (**J**), S_{3-4} (ke-hi) elements ZPAL CXVI/953 and 954 (**K**, **L**), and M (ne) element ZPAL CXVI/955 (**M**), same sample. **N**. Unidentifiable prioniodinid element ZPAL CXVI/943, same sample.

in brackets. Descriptives for orientation of all elements are based on their serial homology with the platform series elements, not on probable actual orientation in the apparatus.

Populational approach to the species-level taxonomy is used here and taxa are defined on the basis of the most specific characters within the apparatus, irrespective of whether the most characteristic element is easy to recover (bears a platform) or not. In the population and apparatus approach morphology alone is not enough to determine the species identity of a specimen. It may happen that this is done despite its morphology. Instead, its position within the range of population variability and/or co-occurrence in the same sample with specimens showing characters enabling identification with the type population of the species are relied upon.

In age-determination the evolutionary method (Dzik 1995), here referred to as chronophyletics, is used. Although its resolution is rather low, reliability is higher than if correlation is based on faunal changes caused by ecological factors. Chronophyletics can be supplemented by methods referring to ecologically controlled composition of species assemblages (e.g., Dzik 1999), thus to more or less sophisticated versions of the old principle of homotaxy (Dzik 1995). Such correlations can be precise but usually reliable only locally. The graphic correlation method, advocated by Klapper and Becker (1999), is among them. Taking apart taphonomic factors, ranges of species observed in rocks correspond to the time span between their immigration to the area and local extinction. Except for extremely rare cases when an arbitrary boundary between successive chronospecies is defined, the range of a species is controlled exclusively by ecological factors and have nothing to do with its evolution (see Dzik 1995 for review of the problem). Homotaxy may thus allow some approximation to isochrones only in two extreme, rarely met cases: (1) when factors controlling the distribution act synchronously over large areas, or (2) when the phyletic evolution of a species with a wide geographic range can be traced (and associated species do not change). To make distinction between age correlation based on evolution and on environmental changes, a hierarchical approach is followed here: precise (but not especially reliable) ecostratigraphic content is included in the rough (but unrepeatable) chronophyletic frame.

Ammonoids are too rare in the Holy Cross Mountains and their taxonomy is too poorly known to be of use in age correlation of the Frasnian strata. Unfortunately, there are problems also with using conodonts for correlation. All the generally accepted conodont biostratigraphic subdivisions of the Frasnian are based on the supposed phylogeny of the palmatolepidids (Ziegler and Sandberg 1990; Klapper and Becker 1999). Actually, evolutionary origin of no single species of the palmatolepidids has been documented. With a few exceptions (Klapper and Foster 1993), no references to the apparatus structure has been made to determine species. As will be

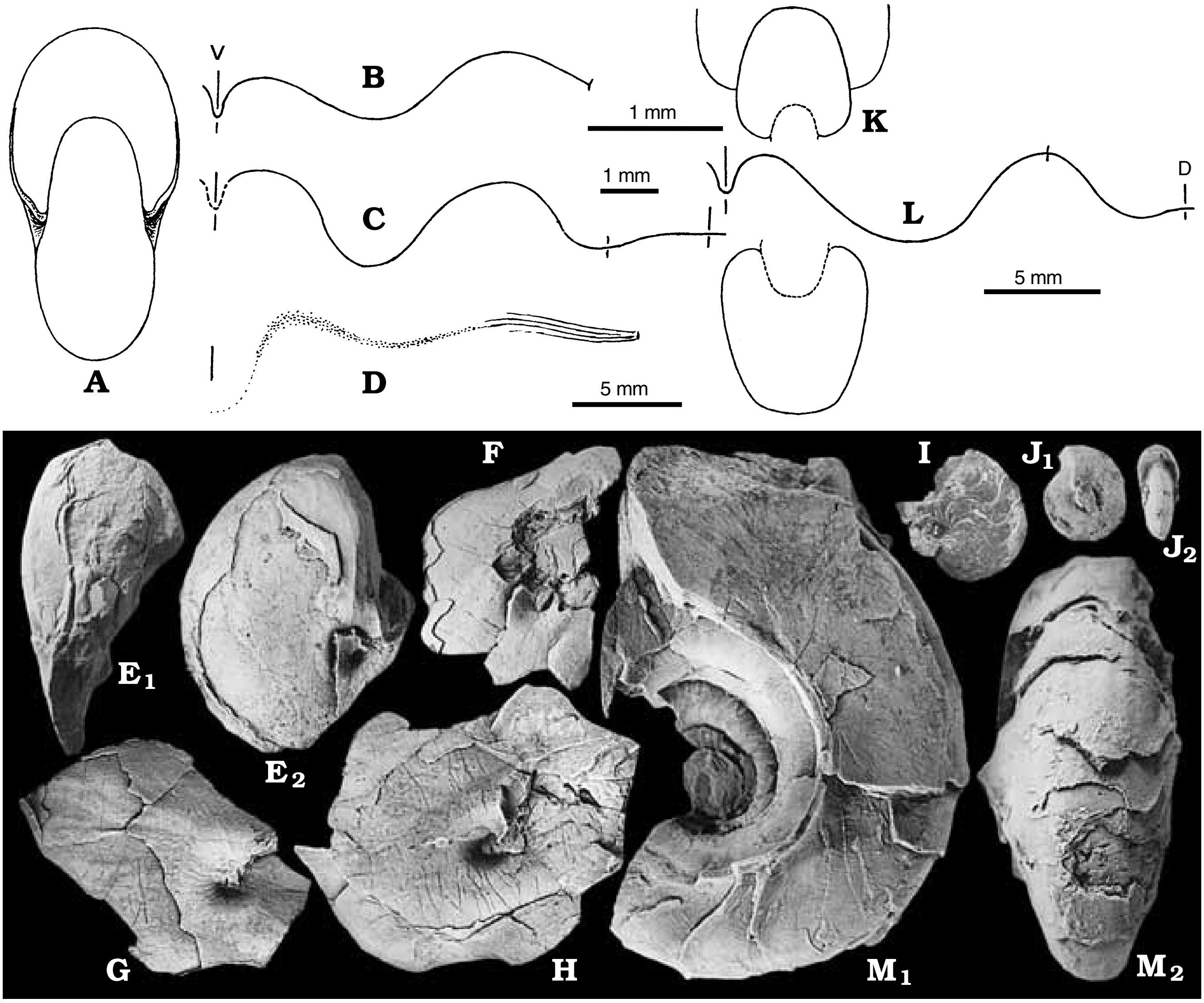


Fig. 3. Ammonoids from the Skały Formation cropping out in an abandoned quarry near old water mill at Śniadka (exposure 6a of Sobolew 1909), 1 m below sample Sn-1. **A**–**J**. *Holzapfeloceras* sp. aff. *H. croyi* House, 1978; restored conch proportions (**A**), sutures (**B**, **C**; based on specimens ZPAL AmVII/97 and 487, respectively), growth lines (**D**; based on ZPAL AmVII/490), shell preserved three-dimensionally in concretion (**E**; ZPAL AmVII/485), crushed specimens showing partially preserved suture (**F**; ZPAL AmVII/484) and growth lines (**G**, **H**; ZPAL AmVII/490 and 488), and phragmocone fragments with preserved septa (**I**, **J**; ZPAL AmVII/487 and 79); all × 2 except for **J** which is × 3 . **K**–**M**. *Agoniatites* sp., possibly *A. vanuxemi* (Hall, 1879); specimen ZPAL AmVII/483; restored cross section (**K**), suture (**L**), and actual specimen (**M**), × 2.

shown below, the platform P_1 (sp) elements alone cannot be used to reliably identify a species. This makes both literature data on species ranges and their species rank taxonomic identifications tentative at best. Consequently, the alleged evolutionary basis of the subdivisions (Ziegler and Sandberg 1990) is hardly reliable.

Instead of relying on questionable standards, I prefer to use perhaps the less precise but more trustworthy evidence on the evolution of Frasnian conodonts. The lineages which seem to offer such record in the early Frasnian are those of *Ancyrodella* and *Mesotaxis*. The more or less reliably documented evolutionary origin of the nominal species is used to define beginning of particular zones (or rather chrones; Fig. 4). Obviously, even in this case the available evidence is incomplete and strongly biased by different approaches to the basic data. Most of the taxa are based on the vertical species concept which results in artificial "speciations" and overlapping of ranges (see e.g., Dzik 1991a). It is not easy to "translate" such published evidence into populationally understood and biologically meaningful data. Some doubts always remain whether we are truly dealing with segments of evolutionary lineages or rather bunches of sympatric species of unknown origins. Some promising progress has been done, at least in respect to *Ancyrodella*.

The main objective of the present work is to separate phyletic evolution from effects of migration.

Pre-Frasnian roots of the conodonts and ammonoids in the Holy Cross Mountains

The Early Devonian was an epoch of coarse clastic sedimentation in the area of the Holy Cross Mountains. There is no environmental continuity with the fine clastic sedimentation of the Late Silurian and possibly earliest Devonian. All the pelagic organisms represented by fossils in the Middle Devonian and Frasnian strata immigrated to the area from the Variscan open sea during transgressive episodes starting in the latest Early Devonian. These seem to be world-wide correlatable, as already suggested for the Holy Cross Mountains Devonian succession by earlier authors (e.g., Racki 1993). Names of the events used by Becker and House (1994b) are followed here.

The only pre-Frasnian locality with a reasonable number of ammonoids and conodonts which is now accessible to study is the exposure at Śniadka near Bodzentyn, presumably representing the upper part of the Skały Formation (Sobolew 1909). This is an abandoned quarry near an old water mill at Śniadka. The strata there are overturned (Kłossowski 1985). The oldest unit, exposed at the eastern end of the ravine which opens to the Psarka creek valley near the exposure, is a dark shale with thin marly intercalations and a few beds of a crinoidal limestone with corals. They are succeeded down the ravine with a few metres of bedded limestone with thin shaly intercalations which gradually increase their contribution to the rock thickness. In the quarry there is almost exclusively a clayey shale, with a few thin limestone beds. These *Eoreticularia* brachiopod-rich limestone intercalations contain only numerous coniform fish teeth. The last intercalation, with *Schelwienella* (sample Sn-1: Table 1), yielded an assemblage of conodonts (Fig. 1C–S) associated with rare fish teeth which indicate a relatively shallow-water assemblage. The shale, which follows down the wall of the Śniadka exposure contains a diverse benthic assemblage dominated by the bivalve *Ctenodonta* and gastropods, and a horizon with psammosteid agnathans and goniatites. In the marly limestone intercalation exposed at the southern end of the exposure, 8.5 m from the *Schelwienella* bed (sample Sn-2), only conodonts occur. Apparently this marks the peak of the sea level rise. The Skały Formation is correlated with the Eifelian/Givetian boundary by pelagic tentaculites (Dzik 1981). Pelagic strata with Givetian ammonoids, once studied by Sobolew (1909) in the same area, are no longer exposed.

The only abundant Late Givetian conodont assemblages at my disposal are from Góra Zamkowa in the southern Chęciny facies region (Racki 1992: table 1). The Kostomłoty quarries in the northern Łysogóry facies region (Racki 1985; Racki et al. 1985) show well the transition from a massive limestone deposited during the *Polygnathus varcus* Zone to marls with limestone intercalations of the *Klapperina disparilis* Zone (Racki 1985). Unfortunately, the samples were inadequate for apparatus study.

The terminal Emsian eustatic rise.—In the Holy Cross Mountains, the first expression of the onset of sea level rise after the Early Devonian lowstand (Johnson et al. 1985) was the deposition of the Bukowa Shale Formation in the northern Łysogóry facies belt (Szulczewski 1993). No pelagic organisms have yet been reported from the formation, which is dated as terminal Emsian on the basis of brachiopod and benthic ostracod assemblages (goniatites mentioned by Malec 1990 seem to represent rather misidentified bellerophontids). Apparently, the Bukowa Shale Formation originated in the same eustatic event at the Emsian–Eifelian boundary, which controlled formation of the famous fossiliferous Hunsrück slates in Germany (Bartels et al. 1998). The overlying Kapkazy Formation is a shallow-water sediment. The shallowing was hardly a result of the basin being filled with sediments, as the unit thickness of a few metres is too small for this.

The oldest Devonian conodonts in the Holy Cross Mountains occur in an exposure near Kolonia Rzepin on the right bank of the Świślina creek, in a sandy limestone overlying sandstone (Bednarczyk et al. 1983). The conodonts from Rzepin, dominated by generalised *Icriodus* of the *I. corniger* Wittekindt, 1965 group (Bednarczyk et al. 1983: fig. 4), are of very limited correlative value. The form is a member of the *I. corniger* → *I. struvei* lineage that unfortunately does not show any apparent evolutionary transformations in the morphology of the icrion or shape of the basal cone (Weddige and Ziegler 1979). The precise position of the Rzepin horizon in the Bodzentyn syncline remains thus to be solved. According to Malec (1990), the Bukowa Shale Formation corresponds in age to the Grzegorzowice Formation in the Grzegorzowice-Skały region. He claims findings of the *Polygnathus patulus* Zone conodonts in the formation. The Grzegorzowice Formation is overlain by carbonate rock units, with no sandstone. This would imply that the limestone facies disappeared westward in the area. Szulczewski (1993) considers the Bukowa Shale and Grzegorzowice Formations to represent separate eustatic events, the latter a Mid-Eifelian episode.

Mid-Eifelian eustatic rise.—The next eustatic rise impulse seems thus to correspond to the shaly Grzegorzowice Formation (Szulczewski 1993). An icriodontid faunule from the Dębska Wola section in the Zbrza facies region (sample collected by Tomasz Prejbisz, M.Sc.) and in the Jurkowice quarry in eastern part of the Holy Cross Region probably documents this invasion of conodonts to the Holy Cross Mountains. At Dębska Wola the icriodontids (Fig. 1B) are associated with possibly planktonic bellerophontids *Tropidodiscus* (Dzik 1997: fig. 8.5C); at both localities the nautiloid cephalopod *Tripleuroceras* is also known (Dzik 1984: pl. 20).

Kačak event.—The first incursion of pelagic tentaculites (Dzik 1981), goniatites (Fig. 3), and more diverse conodont assemblage (Fig. 1C–T) to the Holy Cross Mountains area took place when the shaly Skały Formation was deposited in the northern Łysogóry facies belt. The most precise dating of these strata is based on identification of *Nowakia otomari*, a representative of the fast evolving pelagic tentaculite lineage

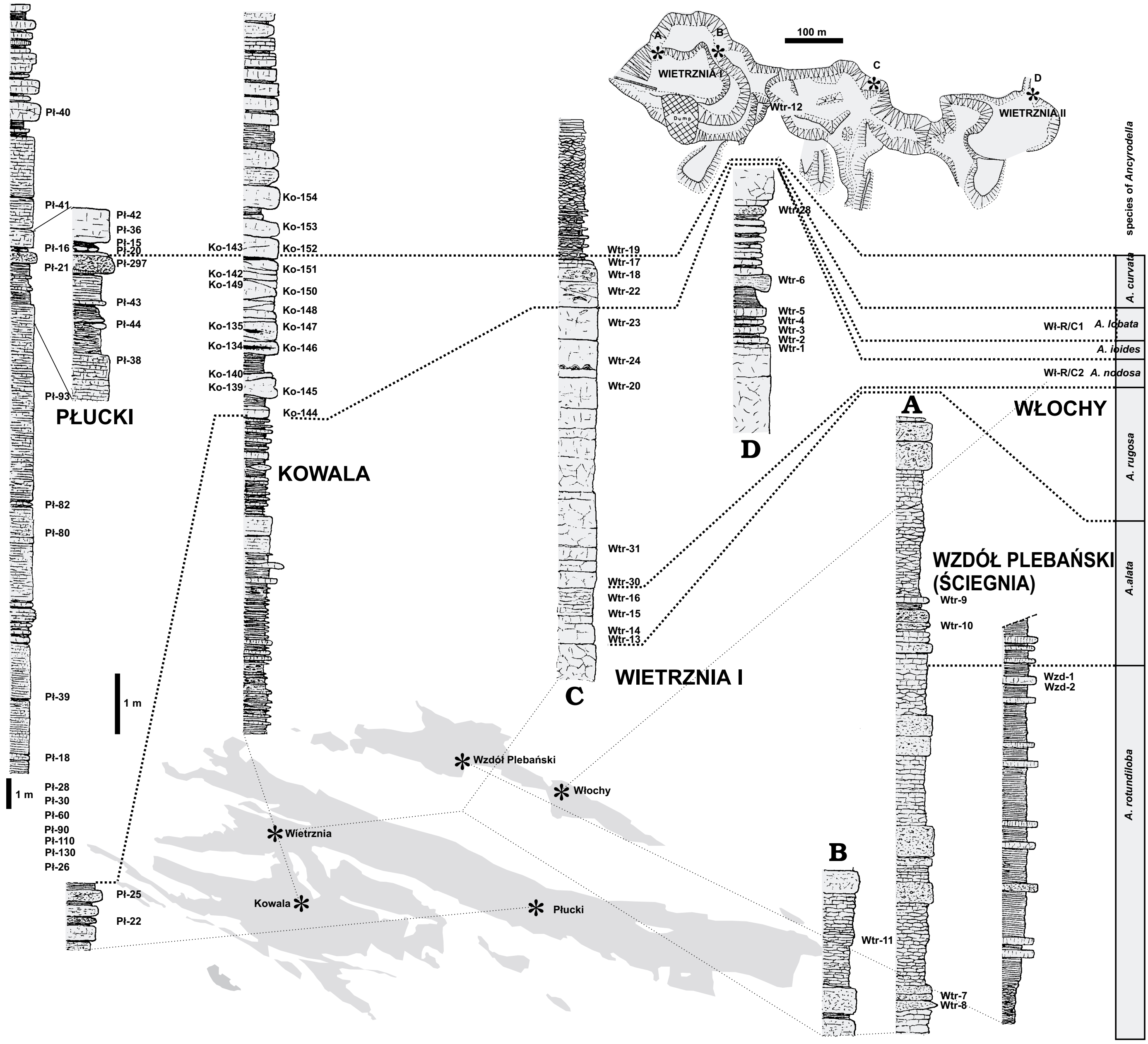


Fig. 4. Correlation of studied sections of the Frasnian in the Holy Cross Mountains, Poland and position of conodont samples and ammonoid-bearing horizons. Note that the complete section of the Płucki main trench (extreme left) is drawn in different scale; samples between Pł-25 and Pł-18 come from small trenches. Above is a map of the Wietrznia quarries with locations of the sampled sections; the basal part of the section, with *Ancyrodella soluta*, has not been sampled because of low frequency of conodont elements (see Racki 1993); provisional zonation based on other *Ancyrodella* species is shown. Kowala section was measured at the eastern end of the quarry, the highest exploitation level. **A**. Wietrznia 1d of Racki et al. (1993; Racki and Bultynck 1993). **B**. Wietrznia 1e. **C**. Wietrznia block D of Szulczewski (1989). **D**. Wietrznia II.

(Dzik 1981) indicative of the "otomari Event" of Walliser (1996; Kačak event of Becker and House 1994b). Incursions of pelagic tentaculites to the Holy Cross Mountains were too rare, however, to rely on them exclusively. Of crucial importance is thus the evolution of *Polygnathus*, several species of which occur in the Skały Formation (Malec and Turnau 1997). Most of the published phylogenetic evidence on *Polygnathus* use the typologic (vertical) species concept and it is not easy to extract biological reality from the nomenclatorial overburden. The population approach followed here may thus suffer from the lack of any reliable reference standard.

The origins and early evolution of *Polygnathus* is relatively well recognised and widely used in correlation of the Devonian strata starting from the Emsian (Klapper 1971; Klapper and Johnson 1975; Bultynck 1989; Yolkin et al. 1994; Bełka et al. 1999). The ancestral form of the lineage is *P. pireneae* Boersma, 1974 with relatively narrow platform of fusiform contour, the subsequent stage in the evolution (*P.*

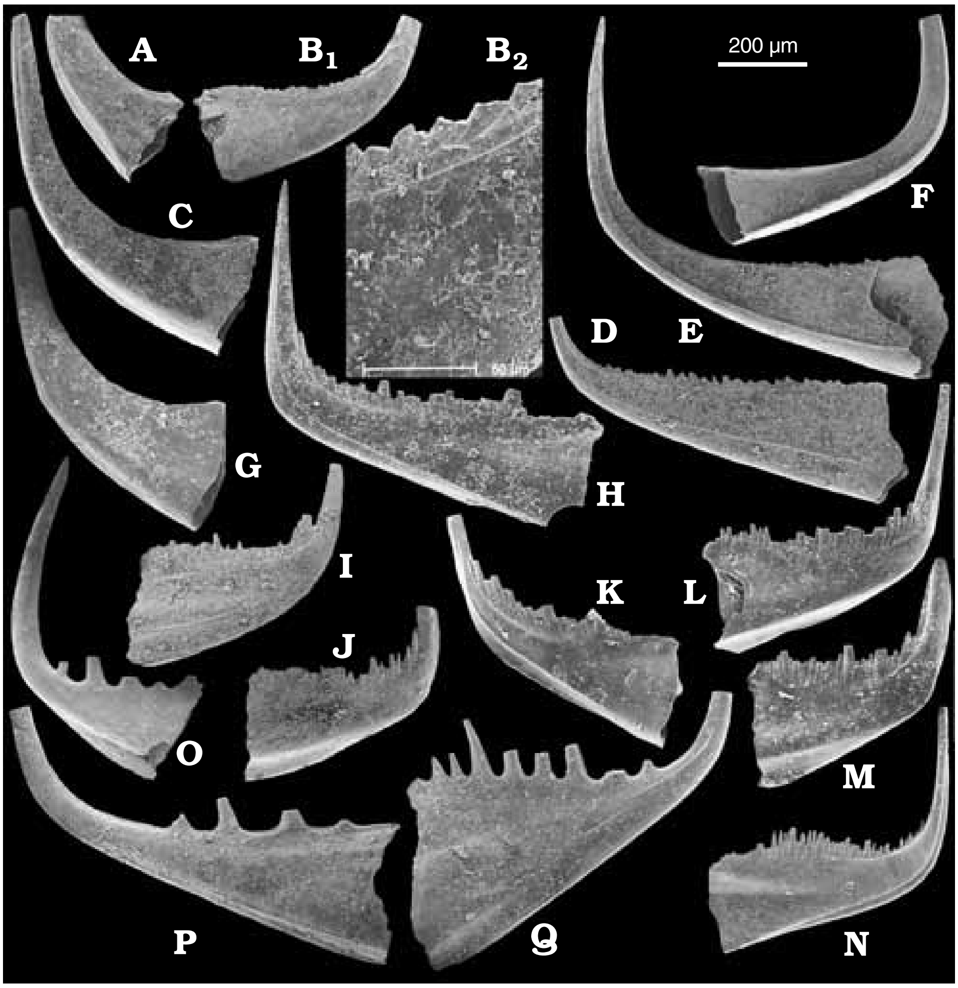


Fig. 5. Frasnian belodellids from the Holy Cross Mountains. **A**, **B**. *Belodella tenuiserrata* sp. nov., M (ne) element ZPAL CXVI/683 (**A**) and S_4 (hi) element ZPAL CXVI/684 (**B**, holotype; B_2, detail of denticulation), sample Wtr-5, Wietrznia II quarry in Kielce, mid-Frasnian. **C**–**F**. *Belodella minutidentata* sp. nov., M element ZPAL CXVI/691 (**C**), S_0 (tr) element ZPAL CXVI/692 (**D**; holotype), lo-pl element ZPAL CXVI/693 (**E**) and S_4 (hi) element ZPAL CXVI/694 (**F**), same sample. **G**–**N**. *Belodella devonica* (Stauffer, 1940), M (ne) element ZPAL CXVI/579 (**G**), S_{1-2} (lo-pl) element ZPAL CXVI/584, 583, and 582 (**H**, **L**, **M**), S_4 element ZPAL CXVI/587 (**K**), P_{1-2} (oz-sp) elements ZPAL CXVI/689 and 690 (**I**, **J**) and S_0 (tr) element ZPAL CXVI/688 (**N**) from sample Wtr-5. **O**–**Q**. *Belodella robustidentata* sp. nov., P_{1-2} element ZPAL CXVI/687 (**O**), S_{1-2} element ZPAL CXVI/689 (**P**), and S_0 element ZPAL CXVI/686 (**Q**; holotype).

kitabicus Yolkin et al., 1994) delimiting the base of the Emsian (Yolkin et al. 1994). In the subsequent Emsian evolution, the transverse ridges at the dorsal end of the platform gradually merge, finally passing uninterrupted across the carina (*P. excavatus* → *P. perbonus* transition; Yolkin et al. 1994). An inversion of the basal cavity marks the origin of *P. inversus*. It is generally assumed that the inversion occurred independently and more or less synchronously also in other early *Polygnathus* lineages. Among them, that of *P. ensensis* → *P. timorensis* → *P. ansatus* Ziegler and Klapper, 1976 is of crucial importance in dating the Givetian strata in the studied area. In the course of its evolution the free edges of the platform, which are originally strongly denticulated, became smooth on one side, with the smooth area separated by a geniculation, and then on both sides (Ziegler et al. 1976; Austin et al. 1985). The origin of *P. timorensis* defines the beginning of the *Polygnathus varcus* Zone (Ziegler et al. 1976) and its first subzone, the end of which is defined by the next evolutionary change in the lineage (Bultynck 1987). Unfortunately, taxonomic identifications of such morphologically simple specimens are problematic, as is the case with the morphotype of *P. ansatus* (= *P. hemiansatus* Bultynck, 1987) proposed to mark the base of the Givetian (questioned by Sparling 1999).

P. timorensis, associated with specimens of the typical population of *Parapolygnathus linguiformis* (Hinde, 1879) (see Ziegler et al. 1976; Mawson and Talent 1989; Talent and Mawson 1994) widely occurs in the Skały Formation (Fig. 1I–K, N–Q; Malec and Turnau 1997). The way in which the conodonts invaded the area in the Kačak sea level rise is traceable at Śniadka. The topmost of the brachiopod-rich limestone intercalations at the exposure, corresponding to 6a of Sobolew (1909) (sample Sn-1: Table 1), yielded a conodont assemblage dominated with *Icriodus brevis* Stauffer, 1940 (almost 70%; see Ziegler et al. 1976) and *Bipennatus bipennatus* (Bischoff and Ziegler, 1957) (Fig. 1D–H). In the marly limestone intercalation exposed at the southern end of the exposure, 8.5 m from the *Schelwienella* bed (sample Sn-2), fish remains and *Bipennatus* are missing, *Icriodus* is rare, and *P. linguiformis* together with *P. timorensis* is the dominant conodont species (Fig. 1L–M, S). Poorly preserved specimens of *Belodella* and a prioniodinid (Fig. 1R–S) enrich the assemblage (composed almost exclusively of polygnathids) which apparently marks the peak of the sea level rise.

According to Mawson (1993) and Talent and Mawson (1994) *B. bipennatus* is only a homeomorph of the Early Devonian *Eognathodus*, that originated from *Pandorinellina* in

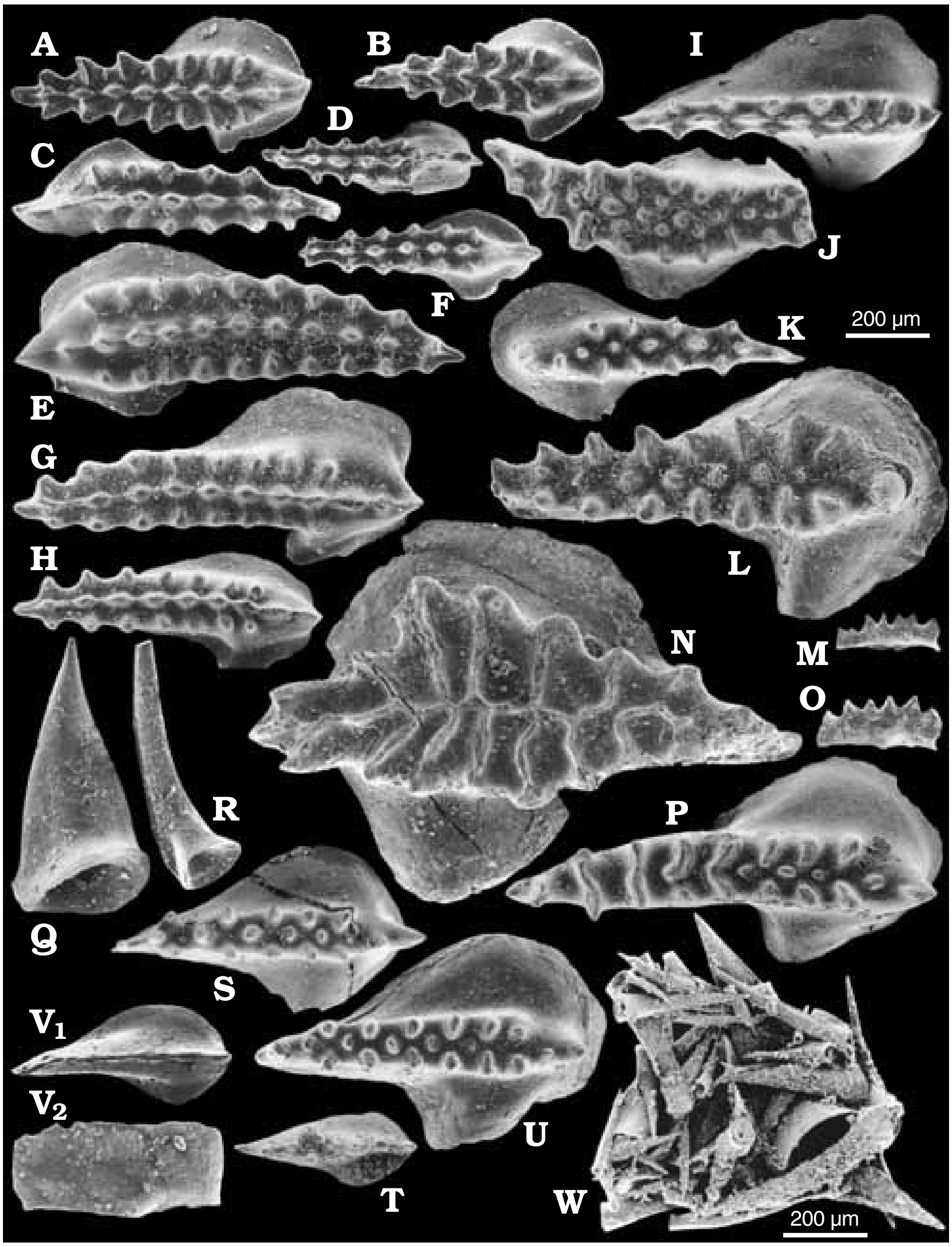


Fig. 6. Frasnian and earliest Famennian icriodontids from the Holy Cross Mountains. **A–D**. *Icriodus expansus* Branson and Mehl, 1938 from the Early Frasnian of Wietrznia (**A**, **B**; sample Wtr-11) and Włochy (**C**, **D**; sample Wł-R/A1), P_1 (sp) elements ZPAL CXVI/1039, 1038, 861, and 862, respectively. **E–H**. *Icriodus symmetricus* Branson and Mehl, 1934 from the mid-Frasnian of Wietrznia, samples Wtr-9 (**E**, **F**) and Wtr-13 (**G**, **H**), P_1 (sp) elements ZPAL CXVI/1058, 1059, 1059, 1056, respectively. **I**, **J**. *Icriodus kielcensis* sp. nov. from the mid-Frasnian of Wietrznia, sample Wtr-5, P_1 elements ZPAL CXVI/714 (holotype) and 1210. **K–M**, **Q**. *Icriodus elegantulus* Stauffer, 1938 from the lower cephalopod limestone at Płucki, sample Pł-22, P_1 elements ZPAL CXVI/ 590, 578, and 592 (juvenile), and possible P_2 (oz) element ZPAL CXVI/593 (**Q**). **N–P**, **R**. *Icriodus iowensis* Youngquist and Peterson, 1947 from the Upper Kellwasserkalk at Płucki, sample Pł-391, P_1 elements ZPAL CXVI/ 424, 969, 426, and denticle of a ramiform element ZPAL CXVI/430 (**R**). **S–W**. *Icriodus alternatus* Branson and Mehl, 1934 from the base of the Famennian Płucki, sample Pł-16, P_1 elements ZPAL CXVI/1004, 1003, 1005, and cluster of coniform denticles ZPAL CXVI/1002 (**W**). **V**. *Pelekysgnathus planus* Sannemann, 1955 from the Upper Kellwasserkalk at Płucki, sample Pł-391; P_1 element ZPAL CXVI/968 in occlusal and lateral views.

the Late Emsian, somewhat preceding the formation of platform in the *Polygnathus* lineage (Lane and Ormiston 1979: fig. 6). Bischoff and Argent (1990) reported specimens transitional between *E. sulcatus* and *Polygnathus pireneae* and partially restored apparatus of *Eognathodus* which, if correct, would make *Eognathodus* a member of the Spathognathodontidae (biramous S_0 elements!). A wide icrion with transverse ridges developed in the *Bipennatus* lineage in the Early Givetian *P. varcus* Zone.

The second polygnathid lineage of some correlative value is that of *Parapolygnthus linguiformis*. According to Klapper (1971; the view somewhat modified by Weddige and Ziegler 1979) in the course of its evolution the characteristic flange-like rostral margin of the platform expanded gradually. It developed independently from, and later than in, superficially similar *Polygnathus serotinus* Telford, 1975, which has an expanded basal cavity. *Polygnathus perbonus* Philip, 1965, ancestral to both those lineages (Yolkin et al. 1994), had the apparatus transitional between *Polygnathus* and *Parapolygnathus* (Klapper and Philip 1971). The Śniadka specimens represent the final stage in *P. linguiformis* lineage development, which is consistent with their co-occurrence with *P. timorensis* (see also Weary and Harris 1994; Lazreq 1999).

In the middle Skały Formation of the Grzegorzowice Skały section, located eastward, the *Polygnathus*-dominated assemblage contains also *Polygnathus pseudofoliatus* Wittekindt, 1966 (Malec and Turnau 1997). Mawson and Talent (1989: 237) commented on population variability of *P. pseudofoliatus* which is a long-ranging species.

Sobolew (1909) reported an occurrence of indetermin-

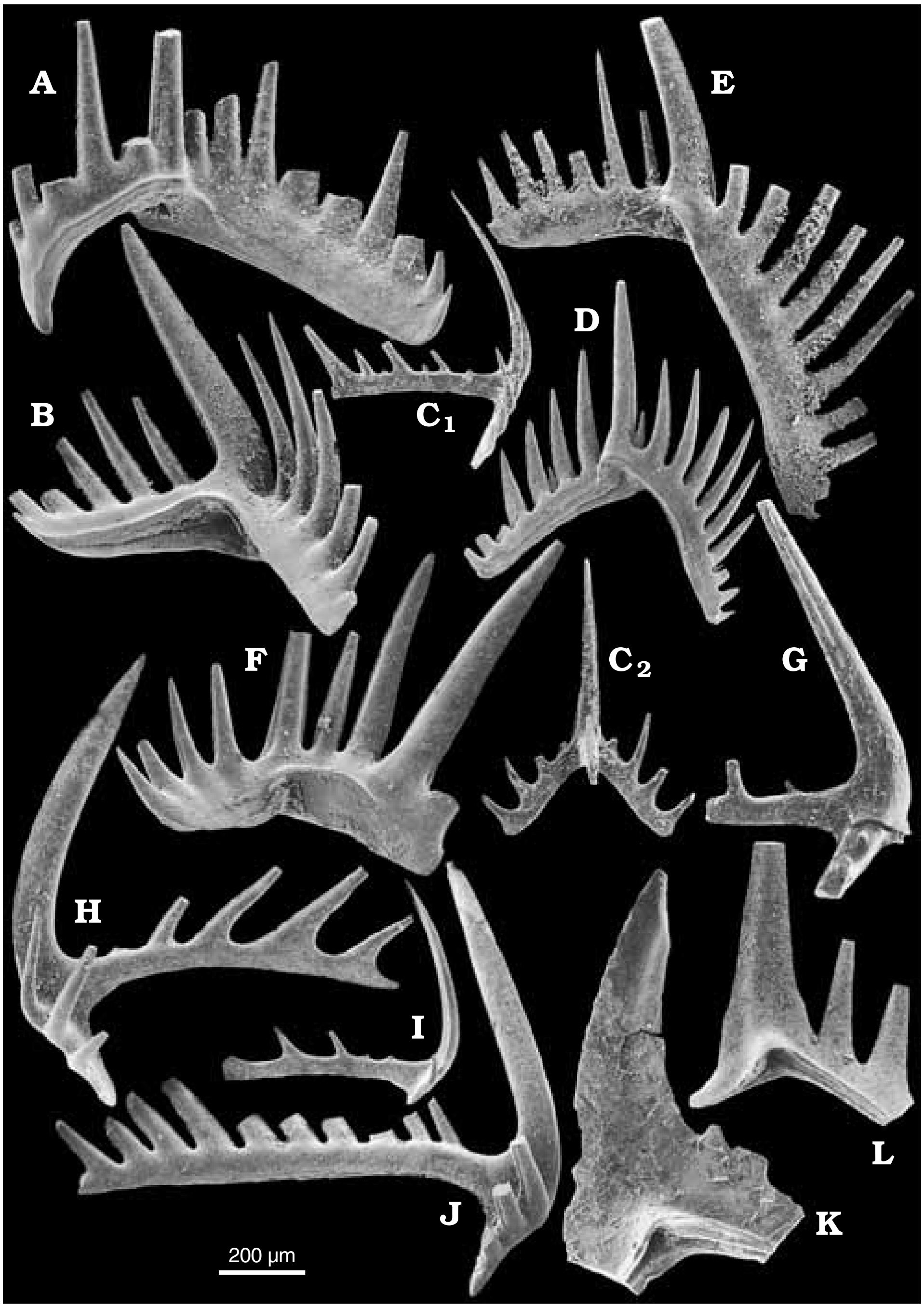


Fig. 7. The prioniodinid *Ligonodina pectinata* Bassler, 1925 from the Frasnian of the Holy Cross Mountains. **A**, **C**, **H**, **I**. Late Frasnian population from the lower cephalopod limestone at Płucki (sample Pł-22); P_1 (sp) element ZPAL CXVI/ 621 (**A**), S_0 (tr) elements ZPAL CXVI/618 and 617 (**C**, **I**), and S_4 (hi) element ZPAL CXVI/622 (H). **B**, **E**, **F**, **I**, **J**. Population from the mid-Frasnian of Wietrznia (sample Wtr-5), S_1 (lo) element ZPAL CXVI/698 (**B**, **I**), P_2 (oz) element ZPAL CXVI/695 (**E**), S_2 (pl) element ZPAL CXVI/704 (**F**), and S_4 element ZPAL CXVI/699 (**J**). **D**, **L**. Population from the mid-Frasnian of Wietrznia (sample Wtr-13), S_2 element ZPAL CXVI/830 (**D**) and M (ne) element ZPAL CXVI/832 (**L**). **G**, **K**. Population from the early Frasnian of Włochy (sample Wł R/A1), S0 element ZPAL CXVI/866 (**G**) and M (ne) element ZPAL CXVI/870 (**K**).

able goniatites with closed umbilicus in his exposure 6a at Śniadka (based on a slab of "goniatite shale" collected by Aleksander Michalski presumably at this locality) which fits its identification with the abandoned quarry sampled by myself. The ammonoids are the most common in the middle between samples Sn-1 and Sn-2, where they co-occur with the orthoceratid nautiloids (Dzik 1984), psammosteid agnathans, various benthic molluscs and trilobites. Among published illustrations, the specimen from Sobolew's exposure $5b_3$ classified by himself (Sobolew 1909: pl. 3: 11) as *Sobolewia rotella* (Holzapfel, 1985), a Givetian species, is closely similar to specimens collected by myself. One of them, partially preserved as a limestone concretion, shows the original conch proportions, in another one the suture is visible. The course of growth lines can be safely traced only near umbilicus, the shape of aperture can be inferred from growth irregularities on the conch surface (Fig. 3A–J). This limited evidence clearly indicates that the goniatites belong to a species of *Holzapfeloceras*. In its closed umbilicus the species differs from the type species of the genus, *H. convolutum* (Holzapfel, 1895), the type horizon of which is the Early Givetian Odershäuser Limestone of Germany (Becker and House 1994b: 97), but resembles *H. croyi* House, 1978 which is different in a more discoidal conch shape and deeper sutural

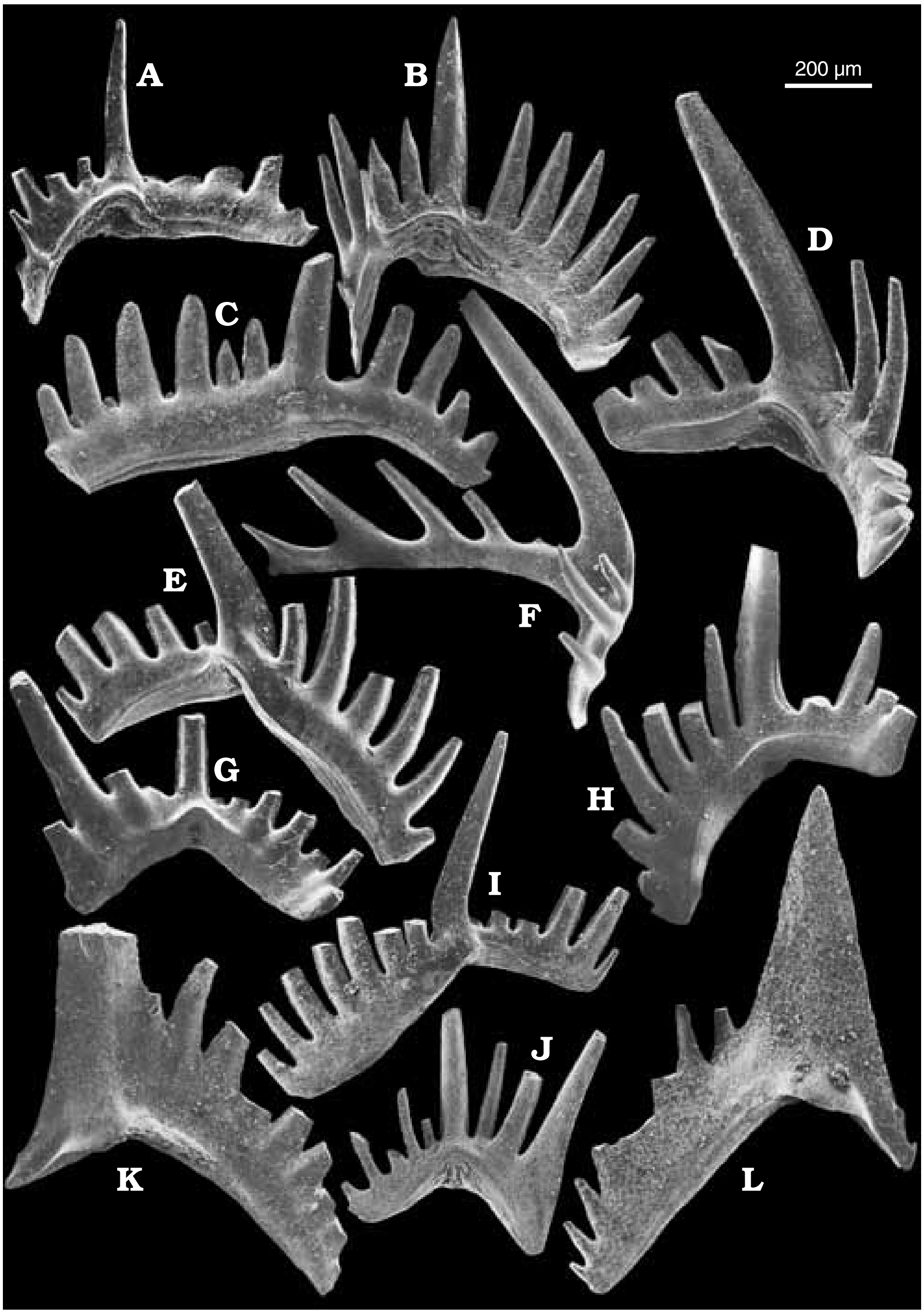


Fig. 8. The prioniodinid *Ligonodina pectinata* Bassler, 1925 from the latest Frasnian (Upper Kellwasserkalk; sample Pł-391) of Płucki in the Holy Cross Mountains, P_1 (sp) elements ZPAL CXVI/973, 401 and 402 (**A**–**C**), P_2 (oz) elements ZPAL CXVI/971 and 419 (**D**, **H**), S_1 (lo) elements ZPAL CXVI/970 and 408 (**E**, **I**), S_{3-4} (hi) element ZPAL CXVI/975 (**F**), S_2 (pl) elements ZPAL CXVI/974 and 416 (**G**, **J**), and M (ne) elements ZPAL CXVI/423 and 976 (**K**, **L**).

lobes (see House 1978). Becker and House (1994b) suggested that *H. convolutum* belongs actually to the earliest tornoceratid *Parodiceras* (in fact its types are associated with a rather advanced, involute *Agoniatites*). *Parodiceras* and *Holzapfeloceras* are homeomorphs differing in their septal early ontogeny (the former being probably derived from an unknown anarcestid; House and Price 1985) which cannot be traced in the Śniadka material. Poorly preserved but apparently conspecific specimens occur in the coeval Kačak Shale of Bohemia (Chlupač and Turek 1983). According to Becker and House (1994b) *Holzapfeloceras* is a descendant of the openly umbilicate *Werneroceras*; the closed umbilicus in so early strata makes it similar rather to *Sobolewia* reported by Belka et al. (1999: 17) well within the Eifelian.

Together with *Holzapfeloceras* a single specimen of *Agoniatites* has been found in the quarry at Śniadka (Fig. 3K–M). Possibly the juvenile specimens with large protoconchs illustrated by Sobolew (1909: pl. 4: 1–2) belong the the same species. Less certain is identity of the relatively large incomplete specimens illustrated by Gürich (1896: pl. 13: 3a–d) and juvenile specimen considered by Sobolew (1909: pl. 8: 3) to come from the same horizon and to be conspecific. In being relatively widely umbilicate and with smooth shell surface it resembles closely specimens from the

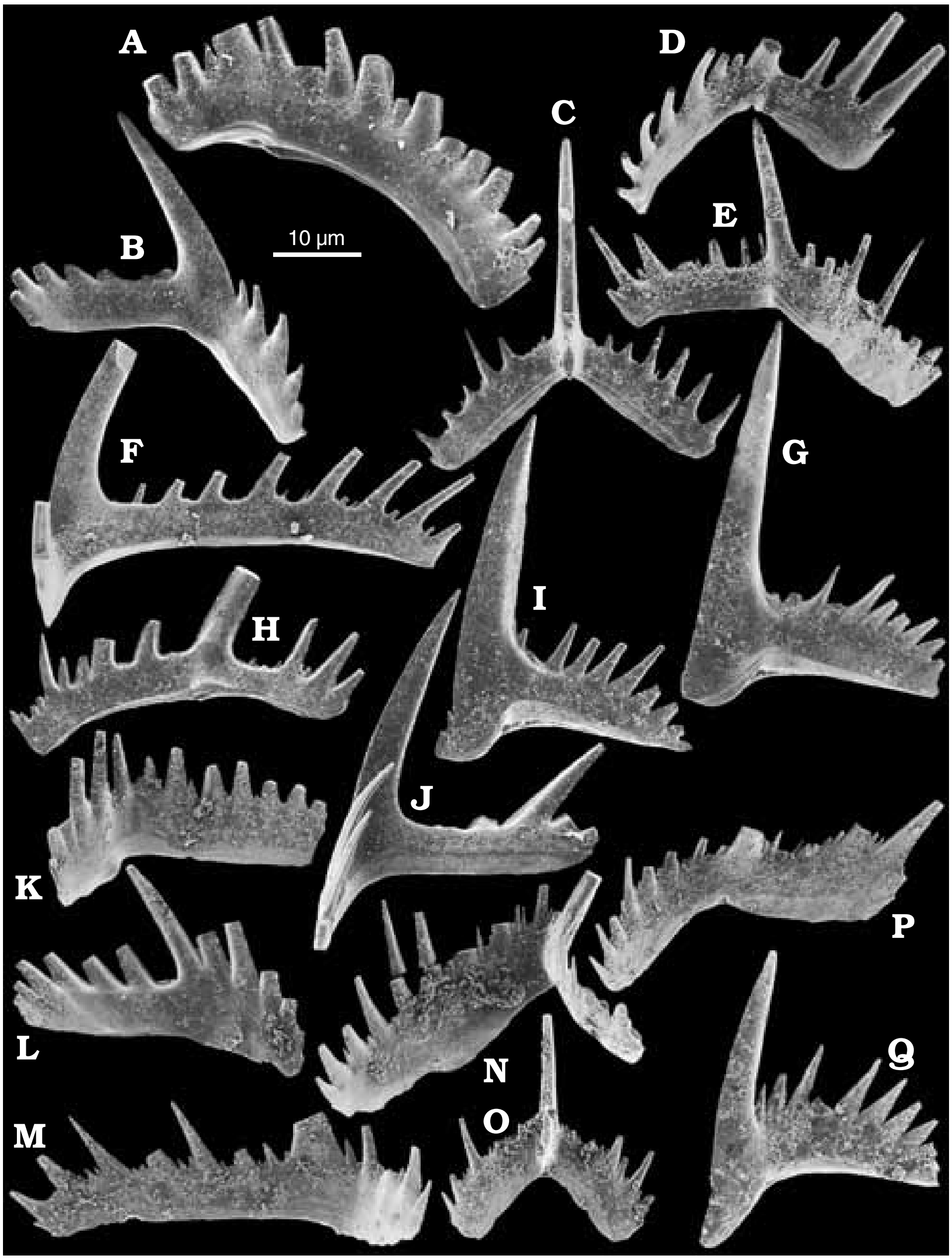


Fig. 9. The prioniodinid *Dyminodina* gen. nov. from the Frasnian of the Holy Cross Mountains. **A–I**, **O–Q**. *Dyminodina planidentata* sp. nov. **A–I**. Lower cephalopod limestone at Płucki population (sample Pł-22), P_1 (sp) element ZPAL CXVI/598 (**A**), P_2 (oz) element ZPAL CXVI/599 (**B**), S_0 (tr) element ZPAL CXVI/601 (**C**), S_2 (pl) element ZPAL CXVI/604 (**D**), S_1 (lo) element ZPAL CXVI/602 (**E**), S_4 (hi) element ZPAL CXVI/603 (**F**), and M (ne) element ZPAL CXVI/606 (**G**; holotype). **O–Q**. Early Frasnian population from Wietrznia (sample Wtr-5), S_4 element ZPAL CXVI/712 (**P**), and M (ne) element ZPAL CXVI/713 (**Q**). **H–J**. *Dyminodina anterodenticulata* sp. nov. from the Upper Kellwasserkalk at Płucki (sample Pł-391), P_1 element ZPAL CXVI/391 (**H**), M (ne) elements ZPAL CXVI/390 (**I**; holotype), and P_2 element ZPAL CXVI/402 (**J**). **K–Q**. *Dyminodina kovalensis* sp. nov. from the topmost Frasnian at the Kowala Quarry, sample Ko-151, P_1 element ZPAL CXVI/1191 (**K**), P_2 element ZPAL CXVI/1192 (**L**), S_4 (hi) element ZPAL CXVI/1196 (**M**), S_2 element ZPAL CXVI/1194 (**N**), S_0 (tr) element ZPAL CXVI/1193 (**O**), S_2 (pl) element ZPAL CXVI/1195 (**P**), M element ZPAL CXVI/1197 (**Q**; holotype).

Kačak Shale of Bohemia classified by Chlupač and Turek (1983) as *A. holzapfeli* Wedekind, 1918. They co-occur there with more common ornate specimens attributed to *A. costulatus* Holzapfel, 1895, similarly as in their type horizon which is significantly younger than the Kačak Shale (see Wedekind 1918; House and Ziegler 1977: 76). The type horizon of *A. vanuxemi* (Hall, 1879), another species hardly distinguishable from the Śniadka specimen and morphologically variable, is older than the Kačak Shale (Becker and House 1994b: 110). Adult specimens of the European *Agoniatites* (Holzapfel 1895: pl. 5: 1) do not differ significantly from those of North America. The ecologically controlled world-wide expansion of the *Agoniatites–Holzapfeloceras* ammonoid association seems to be typical for the Kačak event (House 1978; Chlupač and Turek 1983; Becker and House 1994b; Belka et al. 1999). According to Becker and House (1994b) immediately before the end of the Kačak event first representatives of the *Maenioceras* lineage, typical for the Givetian, expanded virtually world-wide. The first forms had a rather simple suture.

Taghanic event.—In the Świętomarz–Śniadka section of the northern Łysogóry facies belt (Turnau and Racki 1999), Givetian goniatites are known since Sobolew (1909). These fossils have not been revised (the originals seem to be lost, as they can not be traced in the Tschernyschev Museum collection in St. Petersburg, Russia, where they were originally deposited) nor matched with the conodont record in the area because of the present lack of any fossiliferous exposures. Sobolew (1909) illustrated specimens from three Givetian horizons. His ammonoid sample from the Świętomarz exposure 1a include *Maenioceras terebratum* (Sandberger and Sandberger, 1856) (see Becker and House 1994b for illustration of types; Bensaïd 1974 illustrated complex mature suture line), *Agoniatites obliquus* (Whidborne, 1889), *Sobolewia* sp. and probably *Tornoceras* (or *Wedekindella*) sp. The sample 1c seems to be closely similar, if not identical in composition. Sobolew (1914) used juvenile *Agoniatites* specimen from this sample as the type of his *"Gomi-protomeroceras"* (a name suppressed by ICZN) *acutum* Sobolew, 1914; *Wedekindella* is documented there with specimens showing characteristic periodic constrictions occurring in *W. brilonensis* (Kayser, 1872).

Somewhat enigmatic is the composition of sample 5a$_2$ of Sobolew (1909). He listed ammonoids identical as in the previous assemblages but the illustrated specimens include *Sobolewia* identified by him with *S. nuciformis* (Whidborne, 1890), probable *Tornoceras* (see also Göddertz 1987), and most interestingly a 7 mm diameter evolute goniatite with the suture line of the *Pseudoprobeloceras* kind. This is the type of *P. polonicum* (Sobolew, 1914). Becker and House (1993: 116–117) interpreted *Pseudoprobeloceras* as related to the pharciceratids or the advanced anarcestid *Archoceras*. In fact, *Archoceras*, represented by relatively involute *A. tataense* Bensaïd, 1974 precedes slightly *Pseudoprobeloceras* in the Late Givetian of Morocco (Bensaïd 1974). The incursion of this Late Givetian fauna to the Holy Cross Mountains is likely to be related to the "pumilio Event" (Becker and House 1994b).

Subsequent evolution of the ammonoid fauna is marked by further complication of septal geometry in the maenioceratid lineage. This was also the epoch when the first gephuroceratid *Ponticeras* emerged (Kirchgasser 1975; House et al. 1985; Becker and House 1994b: 113). According to Korn (1999), *Ponticeras* originated from an agoniatitid and inherited after it the high whorl expansion rate and inner whorls with ventrolateral furrows, that makes the gephuroceratids distinct from the anarcestids, of low and stable whorl expansion rate. This first diversification of the gephuroceratids preceded the Givetian–Frasnian boundary. At the beginning of the Frasnian already three separate lineages were represented, those of *Ponticeras*, *Koenenites*, and *Acanthoclymenia* (Becker and House 1993). *Koenenites* may occur together with *Pharciceras* (Korn and Wunderlich 1982; Göddertz 1987). Also the tornoceratids started their diversification in the Givetian, including oxyconic *Epitornoceras* (House 1978). These transformations are not recorded in the Holy Cross Mountains.

The most abundant latest Givetian conodont assemblages in the Holy Cross Mountains are those found by Racki (1992: table 1) at Góra Zamkowa in the southern Chęciny facies region and in the Kostomłoty quarries in the northern Łysogóry facies region (Racki 1985; Racki et al. 1985). Among a few samples taken by myself at Góra Zamkowa, that from Racki's (1992: fig. 5) unit F appeared the most productive (almost exclusively *Polygnathus*; Fig. 2B–M). Belodellids are missing there but a piece of a prioniodinid element has been encountered (Fig. 2N), which suggests that the environment was a rather open sea. The largest *Polygnathus* P$_1$ (sp) elements (Fig. 2E) closely resemble the specimen identified as *P. webbi* Stauffer, 1938 by Racki (1992: fig. 31O), juvenile specimens from the same locality have been classified by him in another species of the *P. dubius* group. The remaining elements of the apparatus are gracile and virtually identical with those of *P. dubius* apparatus (Klapper and Philip 1971). The P$_1$ (sp) elements are slightly asymmetric in that the plane of their occlusion was oriented oblique to the plane of carina. This asymmetry, first identified by Klapper (1971), has been proposed to be the diagnostic character of *P. webbi* (Klapper and Lane 1985). However, the Chęciny P$_1$ elements are narrower and less prominently ornamented than the late Frasnian typical *P. webbi* at similar ontogenetic stages. Even the mature specimens from Góra Zamkowa and other localities, illustrated by Racki (1992: fig. 33G) as *Polygnathus* sp. A, with robust and somewhat lobate platform, are still far from the *P. webbi* morphology. Possibly, the late Givetian population from the Holy Cross Mountains is transitional between *P. dubius* and *P. aequalis* Klapper and Lane, 1985, both species being generalists with a wide geographic and ecological distribution.

At the southern slope of the Zamkowa hill in Chęciny the strata transitional to the Frasnian are exposed (Racki 1992) and an ammonoid specimen was found there (by Bogusław Waksmundzki, M.Sc.), which supports the conodont evidence (Fig. 50D). This marks the beginning of the biotic events which are the main topic of the present paper.

Sections of the Frasnian

Several sections in the Holy Cross Mountains have been sampled for this study (Fig. 4). In order to remove effects of punctuations in the record resulting from eustacy, sections from various facies have been selected. Those in the central Dyminy reef zone (Wietrznia) provide the record of high sea level stand episodes. These are rare intercalations in otherwise shallow-water, mostly peri-reefal sediments (Racki 1993). The sections from the Łysogóry facies region (Włochy) are generally developed in shaly facies, so conodonts are known there only from detrital carbonates deposited in low sea level stands. The real situation is not so simple but altogether almost complete Frasnian succession can be assembled in this way, with only a few gaps in the record. The most fossiliferous and complete are the sections in the Wietrznia I (Fig. 4A–C) and II (Fig. 4D) quarries (Racki 1993; Bultynck and Racki 1993; Szulczewski 1995). In fact, the studied sections have been already correlated by earlier workers (see Racki 1993).

The oldest parts of the Frasnian were sampled in a trench at Ściegnia near Bodzentyn (Wzdół Plebański of Kościelniakowska 1962), and in the Wietrznia I quarry exposure. In limestone intercalations within the shales at Ściegnia conodont frequencies are low and I failed to obtain reasonable number of elements from samples taken in the trench. However, a grey limestone block containing *Manticoceras* (almost certainly coming from an intercalation close to the top of the section) has yielded a few elements of *Mesotaxis* apparatus, among them fragmentary adult element suggestive of *M. asymmetrica* being there represented.

The gap between the sections A and B at the western end of Wietrznia I and section C in its central part is partially filled by the material from the trench dug at Włochy by Grzegorz Racki. Only two samples from Włochy have been studied. The older one (Wł-R/A1) yielded *A. nodosa* and *M. punctata*. In Wł-R/C1 specimens of *Ancyrodella lobata* with bifurcating lobe and *Mesotaxis bohemica* occur. Otherwise the samples do not differ significantly in composition, both containing also a *Mesotaxis* species similar to *M. falsiovalis* Sandberg et al., 1989.

The section C at Wietrznia covers most of the late Frasnian but is strongly condensed stratigraphically, with many gaps (Racki and Szulczewski 1996). A section of the succession corresponding to one of these gaps seems to be represented at section D of Wietrznia II (Fig. 1).

There are two maxima in total organic carbon contents in the Frasnian–Famennian boundary section at Kowala, about ten metres apart in the exposure (Joachimski et al. 2001). According to these authors, they resulted from a higher primary productivity and are time-equivalent to the Kellwasser horizons deposited in shallower water settings. Only proximities of the Upper Kellwasserkalk are conodont-rich. Near the top of the Frasnian radiolarians with preserved siliceous tests and sponge spicules are common, associated with chert bands (Racki 1999; Racki and Szulczewski 1996; Vishnevskaya et al. 2002). The palmatolepidid *Lagovilepis bogartensis* (Figs. 30, 41, 42) is represented in two horizon separated by an intercalation with dominant *Manticolepis winchelli*. The Kowala section is of special interest because of mass occurrence of silicified ammonoids together with conodonts.

The topmost strata of the stratigraphically uncondensed Frasnian have been recovered in several trenches dug at Płucki near Łagów (Racki et al. 2002; Olempska 2002). Two black cephalopod limestone beds are represented there. The upper one (sample Pł-391; Fig. 4) terminates the Frasnian and certainly corresponds to the German Upper Kellwasserkalk horizon. The lower bed's (sample Pł-22; Fig. 4) stratigraphic position is less certain and it may or may not represent the Lower Kellwasserkalk.

Most notably, in both the cephalopod limestone horizons at Płucki the palmatolepidids *Klapperilepis praetriangularis* and *Conditolepis*? *linguiformis* are represented (Fig. 35). This suggests that incursions of these lineages of cryptic origin (possible ancestor of the latter is "*Palmatolepis*" *ederi* Ziegler and Sandberg, 1990) are controlled mostly by environmental factors. They definitely originated significantly before the deposition of the lower cephalopod limestone and lived in time separating the horizons in an unknown region, but the Płucki area was relatively close to their habitat. Similarly to other late Frasnian palmatolepidids they can be used only to an ecostratigraphic correlation of local importance. It seems that correlations based on the evolution of *Ancyrodella* and *Ancyrognathus* are somewhat more reliable, as discussed below, although of a low resolution. Both this general evolutionary pattern and environmentally controlled incursions of conodont species have been used to correlate the studied sections (Fig. 4).

There are several other sections of the Frasnian in the Holy Cross Mountains which I sampled but have not used in this study because of low frequencies of conodont elements which does not allow complete apparatus reconstructions. Now, when apparatuses are more or less safely identified, it is possible to identify conodont species in apparatus terms even on the basis of a few elements, with precision of identification depending, of course, on how diagnostic are the elements at hand.

Taxonomic identity of the Frasnian conodonts from the Holy Cross Mountains

Belodellids.—At least four species of *Belodella* are represented in the Frasnian of the Holy Cross Mountains (Fig. 5A–Q; Tables 1 and 2). They differ from each other mostly in pattern of denticulation and species distictions are apparent. The differences are so deep that the genus may be polyphyletic; more evidence on the Middle Devonian belodellids is necessary to prove or disprove this.

Icriodontids.—The earliest Frasnian population of the icriodontids, probably conspecific with *Icriodus expansus* Branson and Mehl, 1938 (see Müller and Müller 1957), is rather generalised morphologically but does not seem to be directly related to the preceding Givetian species known from Chęciny (Fig. 2A). The icrion of the Frasnian form is more elongated (Fig. 6A, B). In the mid-Frasnian another species, probably conspecific with *I. symmetricus* Branson and Mehl, 1934, is represented in the Kielce facies region (Wietrznia; sample Wtr-13), resembling those from Włochy, but with an arched profile, the denticles of the main row in proximity of the cusp being much higher than the denticles lateral to them.

A species characterized by an extremely narrow icrion, partly owing to the alternation of the central row of denticles (Fig. 6I, J) occurs in sample Wtr-5. There seems to be a continuity between these extremely narrow icriodontids and the somewhat younger population from the lower cephalopod limestone at Płucki (Pł-22), possibly conspecific with *Icriodus elegantulus* Stauffer, 1938 from the coeval Olentangy Shale of Ohio (Stauffer 1938) (Fig. 6K–M,Q).

In the latest Frasnian Upper Kellwasserkalk population of *Icriodus* (sample Pł-391; Fig. 6N–P, R) the denticles tend to merge into transverse ridges close to the end of the carina. This may be *Icriodus iowaensis* Youngquist and Peterson, 1947 if all the specimens in the type sample from the Shef-

Fig. 10. The Frasnian prioniodinid *Pluckidina kielcensis* sp. nov. from the early Frasnian of Wietrznia (sample Wtr-9), Holy Cross Mountains, P_1 (sp) element ZPAL CXVI/1063 (**A**, holotype), P_2 (oz) element ZPAL CXVI/1064 (**B**), S_2 (pl) element ZPAL CXVI/1066 (**C**), S_0 (tr) element ZPAL CXVI/1065 (**D**), S_1 (lo) element ZPAL CXVI/1067 (**E**), S_3 (ke) element ZPAL CXVI/1068 (**F**), S_4 (hi) element ZPAL CXVI/1069 (**G**), and M (ne) element ZPAL CXVI/1070 (**H**).

field Formation of Iowa (various names for which were proposed by Youngquist and Peterson 1947) represent the same species. Large mature specimens at Płucki attain a fusiform shape of the icrion (Fig. 6N). A single specimen of *I. iowaensis* has been found in that sample together with more numerous *I. symmetricus*. This is the only case when a co-occurrence of sympatric *Icriodus* species can be proven in the Frasnian of the Holy Cross Mountains.

The population of the earliest Famennian (sample Pł-16; Fig. 6S–W) usually attributed to as *I. alternatus*, differs a little from that of the latest Frasnian *Icriodus iowaensis* population in a slightly wider icrion and somewhat stronger denticles of the medial row.

A complete lack of the icrion characterises the very rare *Pelekysgnathus planus* Sannemann, 1955 (Pł-391; Figs. 4, 6Y).

Prioniodinids.—In the oldest Frasnian strata at Wietrznia (samples Wtr-8 to Wtr-9; Fig. 4, Table 1) the prioniodinids are represented by highly variable species *Pluckidina kielcensis* gen. et sp. nov. (Fig. 10). Whether any other prioniodinid species occur in these strata is difficult to prove because of the wide population variability of the prioniodinids. Only a few specimens seem to be diagnostic enough to be distinct species (as indicated in Table 1). At least two other prioniodinid species are represented in somewhat higher strata. One of them is here referred to as *Dyminodina* gen. nov., the other may be conspecific with *Ligonodina pectinata* Bassler, 1925 (Figs. 7, 8).

Polygnathids without platform.—Non-platform polygnathids (*Mehlina*, *Tortodus* s.l., *Nicollidina*) are so generalised morphologically and their apparatuses are so poorly known that only tentative species attribution is possible.

Polygnathids with reduced platform.—Among polygnathids with an advanced apparatus structure, that is with

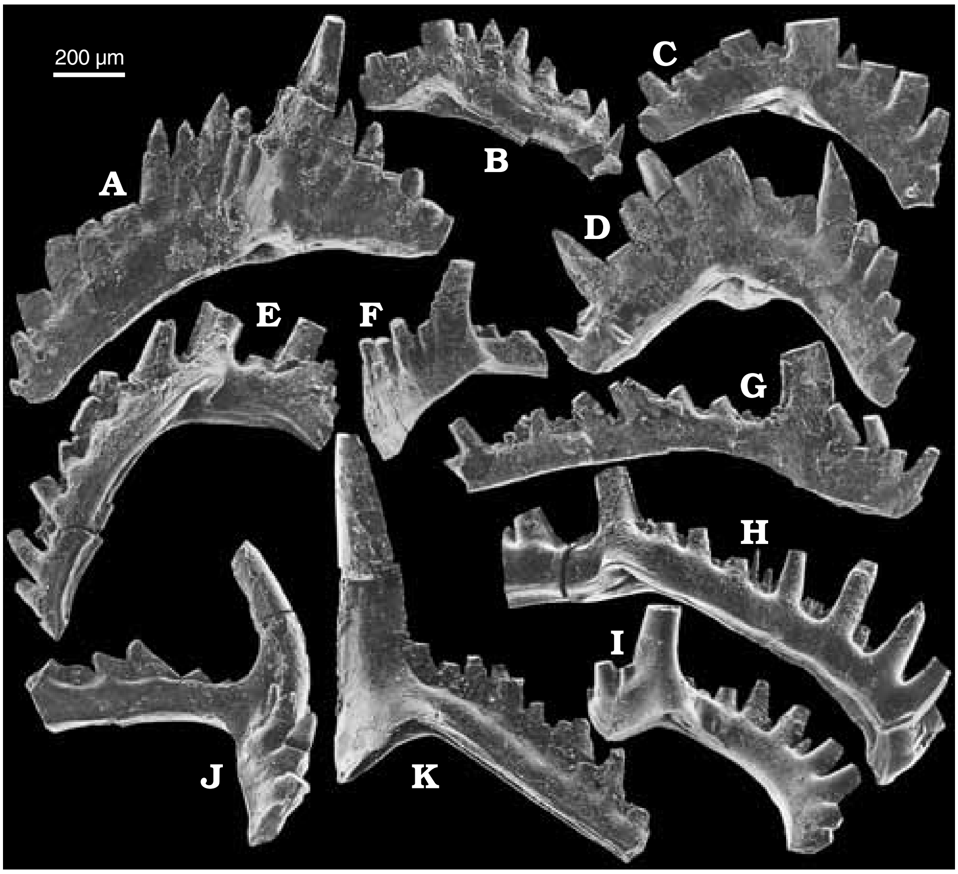


Fig. 11. The prioniodinid *Pluckidina slupiensis* sp. nov. from the early Frasnian of Włochy (sample Wł-R/A1) in the Holy Cross Mountains, P_1 (sp) elements ZPAL CXVI/871 and 874 (**A**, **B**), P_2 (oz) elements ZPAL CXVI/875 and 872 (**C**, **D**), S_1 (lo) elements ZPAL CXVI/879 and 876 (**E**, **F**), S_4 (hi) element ZPAL CXVI/880 (**G**), S_2 (pl) elements ZPAL CXVI/877 and 878 (**H**, **I**; **H** holotype), S_0 (tr) element ZPAL CXVI/873 (**J**), and M (ne) element ZPAL CXVI/881 (**K**).

long processes of the symmetry transition series elements and strongly angular arrangement of processes in the S_1 (lo) elements, there are forms either lacking platform at early ontogenetic stages of the P_1 (sp) elements or with the platform very short, restricted to the area immediately above the basal cone. This is probably not a primitive status but, instead, as already proposed by Weddige and Ziegler (1979), an offshoot of the Eifelian polygnathids with fully developed platform. The lineage, the generic name *Ctenopolygnathus* being available for it, is well represented in the Frasnian of the studied area. The platform shape shows an extremely wide population variability, which is also suggestive of this being a secondary reduction—an effect of a released selection pressure. This variability makes the P_1 (sp) elements morphology of little taxonomic use, especially when the sample size is small. Species identifications are thus tentative and require confirmation by studies on the apparatus structure in the type material. The two most prolific samples from the Płucki lower (Pł-22) and upper (Pł-391) cephalopod horizons show differences mostly in the shape of the $S_{3–4}$ (hi) elements. In those from the lower horizon, the elements are rather robustly denticulated and with a long, rather straight external process. In the upper horizon the process is bent at its tip and the alternating denticles are more numerous and rounded in cross section (Fig. 17).

The earliest Famennian population of *Ctenopolygnathus* (Pł-20) is different from that of the upper Kellwasserkalk horizon in more robust appearance of the symmetry transition series and M (ne) elements (Fig. 18H). This is not the morphology known from the Płucki lower cephalopod limestone (Pł-22), as the $S_{3–4}$ (ke-hi) elements show strongly bent process (Fig. 18).

Typical polygnathids.—Because of a very generalised apparatus structure and an extreme platform shape variability it is usually difficult to be sure of species identity of polygnathids with platform-bearing P_1 (sp) elements. Some comments on the taxonomic identification are thus necessary as an addition to the review of their distribution.

An asymmetry, expressed mostly in elevation of the platform margin in P_1 (sp) elements (Klapper 1971: 66), is typical of the *Polygnathus webbi* Stauffer, 1938 lineage. The rostral margin of the platform is raised in the right element and caudal in the left, which gives them a good fit at occlusion. An incipient asymmetry of this kind developed already in the Givetian, in forms attributable to *Polygnathus aequalis* Klapper and Lane, 1985 (Fig. 2B–M). In the early Frasnian populations of the lineage the platform of P_1 (sp) elements remains relatively narrow and robust, resembling the situation in the late Givetian. The range of variability, however, overlaps with morphologies typical of the late Frasnian. In the early Frasnian samples (Wtr-7, Wtr-8, and Wtr-11; Fig. 20A–F, Q) morphologies similar to those of the Givetian dominate. Somewhat above in the Wietrznia section (sam-

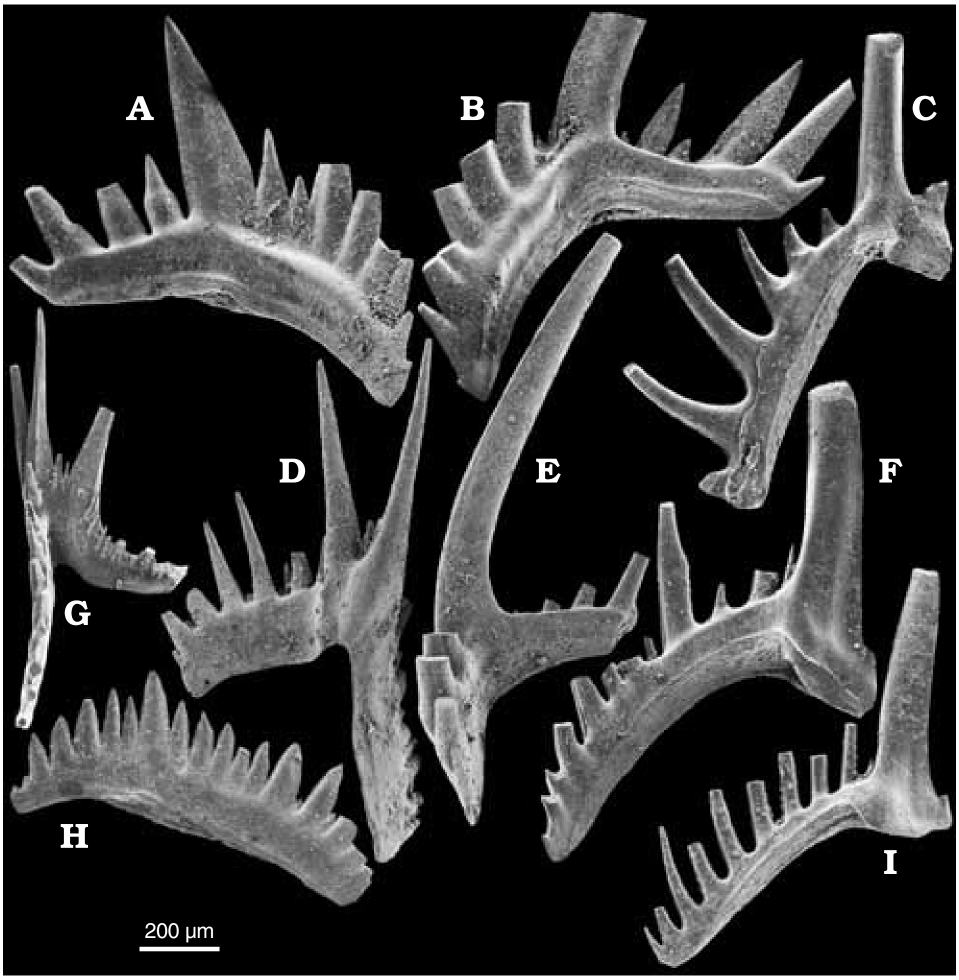


Fig. 12. The prioniodinid *Pluckidina* from the Frasnian of the Holy Cross Mountains. **A**–**F**. *Pluckidina robustipegmata* sp. nov. from the early Frasnian of Wietrznia (Sample Wtr-5), P_1 (sp) element ZPAL CXVI/701 (**A**, holotype), P_2 (oz) element ZPAL CXVI/702 (**B**), S_2 (pl) elements ZPAL CXVI/703 (**C**), S_1 (lo) element ZPAL CXVI/705 (**D**), S_4 (hi) element ZPAL CXVI/706 (**E**), and M (ne) element ZPAL CXVI/700 (**F**). **G**–**I**. *Pluckidina lipperti* (Bischoff, 1956) from the latest Frasnian Upper Kellwasserkalk at Płucki (sample Pł-391), S_1 (lo) element ZPAL CXVI/409 (**G**), P_1 elements ZPAL CXVI/420 (**H**), and M element ZPAL CXVI/389 (**I**).

ples Wtr-9, Wtr-10) adult specimens with fusiform outline and relatively wide platform became more common, which makes this population distinct from the earliest Frasnian one (Fig. 20G–P). Generally, the asymmetry of elements is rather weak and they are actually transitional between typical *P. webbi* and *P. aequalis* (in fact Klapper and Lane 1985 list these species as co-occurring sympatrically). Asymmetry and wide platform seem to develop late in the ontogeny and then spread in the evolution to earlier and earlier developmental stages.

The polygnathid with generalised P_1 (sp) elements and highly sophisticated S_0 (tr) elements, *Avignathus*, is well represented in the studied area at Włochy (sample Wł R/A1; Fig. 21A–M) by *A. decorosus* (Stauffer, 1938). The only difference in otherwise variable P_1 (sp) elements of this species in respect to *Polygnathus aequalis* and *P.* sp. nov. consists in a wider ventral (“anterior”) end of the platform. In *Avignathus* the platform gently narrows towards the dorsal tip and is slightly constricted at the level of the basal pit, with its free end expanded and with wide concave areas. The basal cone is generally larger than in most polygnathids.

Polygnathus pacificus is characterised by a smooth platform margin at least in its dorsal (“posterior”) part (Fig. 23A–J). The platform usually extends to the tip of the process, although rarely, in juvenile specimens, a short platformless process may extend at the tip. In ontogeny the platform of *P. pacificus* expands much faster than in *Avignathus*. In the late Frasnian samples of *Polygnathus webbi*, the asymmetry is apparent even at very early ontogenetic stages (Fig. 22). This makes the species easy to distinguish from associated *P. pacificus* or *P.* ex gr. *semicostatus*. Otherwise the platform shape and ornamentation of *P. webbi* is extremely variable (Fig. 23). Similarly variable are other elements of the apparatus which makes this species difficult to determination and of little correlative value. There are probably some differences between populations of different age but they are difficult to specify. In the early Frasnian populations from the Holy Cross Mountains the platform is ornamented mostly with transverse ribs, which change into tubercles in larger specimens. In the latest Frasnian they merge into a transverse anastomosing riblets, but specimens with tubercles are also common.

The advanced polygnathid *Ancyrodella*.—There is no convincing evidence for presence of more than one species of *Ancyrodella* per sample in the Holy Cross Mts. material. The species are here understood in population terms and their ranges are not necessarily consistent with the widely used ty-

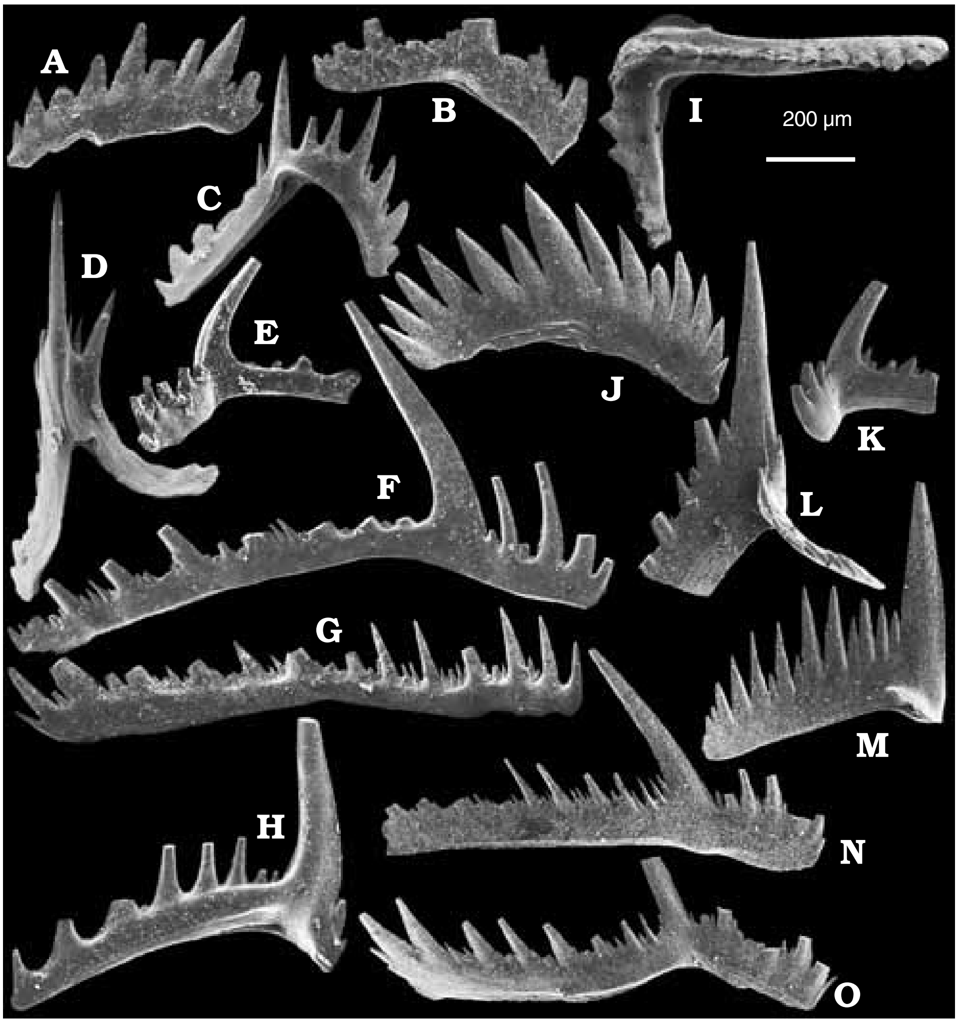


Fig. 13. The prioniodinid *Pluckidina* from the Frasnian of the Holy Cross Mountains. **A**–**H**. *Pluckidina lagoviensis* sp. nov. from late Frasnian lower cephalopod limestone at Płucki, sample Pł-22, P_1 (sp) element ZPAL CXVI/610 (**A**), P_2 (oz) element ZPAL CXVI/607 (**B**), S_2 (pl) element ZPAL CXVI/611 (**C**), S_1 (lo) element ZPAL CXVI/612 (**D**), S_0 (tr) element ZPAL CXVI/608 (**E**), S_4 (hi) element ZPAL CXVI/609 (**F**), S_3 (ke) element ZPAL CXVI/613 (**G**, holotype), and M (ne) element ZPAL CXVI/614 (**H**). **I**–**O**. *Pluckidina nonaginta* (Klapper et al., 1996) from mid-Frasnian sample Wtr-13 at Wietrznia, P_1 (sp) element ZPAL CXVI/833 (**I**), P_2 element ZPAL CXVI/834 (**J**), S_0 element ZPAL CXVI/835 (**K**), S_2 element ZPAL CXVI/836 (**L**), M element ZPAL CXVI/839 (**M**), S_4 element ZPAL CXVI/838 (**N**), and S_3 (ke) element ZPAL CXVI/837 (**O**).

pological definitions. Unfortunately, the non-platform elements in the apparatus of *Ancyrodella* are extremely variable within population and of little use in identification of species.

The taxonomy of early *Ancyrodella* has been partially clarified with biometrics by Racki and Bultynck (1993: fig. 3). It appeared that most of the allegedly primitive "species" are based on juvenile P_1 elements. In the oldest Wietrznia populations (Racki 1993) the modal robustness of tuberculation and the platform width in these elements corresponds to what Klapper (1985) classified as "*A. rotundiloba* early form". A question of the valid name for this species arises as both the holotype of *A. pristina* Khalymbadzha and Chernysheva, 1970 and *A. soluta* Sandberg et al., 1989 can easily be fit into the ontogenetic trajectories of several early Frasnian populations of *Ancyrodella*, as nicely shown by Racki (in Bultynck and Racki 1993: fig. 5). For some reason Racki and Bultynck (1993) did not draw conclusions from their results and continued to use artificial taxonomy. Perhaps *A. binodosa* Uyeno, 1967, originally based on juvenile specimens, is the appropriate name of this chronospecies, although population studies based on the earliest Frasnian populations are needed to prove this. This early species is definitely distinct from *A. rotundiloba* (Bryant, 1921) represented slightly above at Wietrznia.

The populations of *Ancyrodella* (Fig. 25A, B) co-occurring with *Mesotaxis falsiovalis* (sample Wtr-8 in Fig. 4; Table 1) differ from those associated with *M. asymmetrica* significantly enough in the ontogenetic development of tuberculation and the platform shape to consider them at least separate chronosubspecies (Fig. 26). Less easy is to name them. When both these diagnostic characters are considered, positions of the clusters on the plot are clearly different but the holotypes (or topotypes) of both *A. rotundiloba* and *A. rotundiloba alata* occupy marginal positions with respect to them, thus not substantiating any taxonomic distinction.

Much better taxonomic resolution is offered by the ontogenetic change in just a single character—the density of tuberculation. The trajectory of the ontogeny in sample Wtr-7 (Fig. 26) clearly encompasses the two Glenister and Klapper's (1966) type horizon specimens of *A. rotundiloba alata*, leaving the *A. rotundiloba* holotype much away (Bultynck and Racki 1993: fig. 5). The trajectory of sample Wtr-9 points to the holotype of *A. rotundiloba* whereas that of *A. rotundiloba alata* holotype is apart of the cluster.

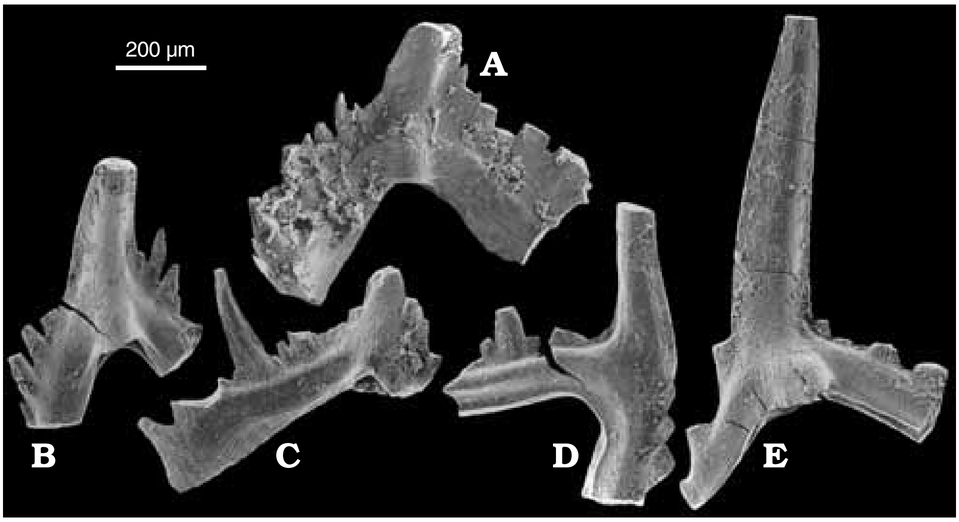


Fig. 14. Residual elements of unknown affinities from the early Frasnian of Włochy; samples Wł-R/C1 (**A**) and Wł-R/A1 (**B**–**E**); S_2 (pl) elements ZPAL CXVI/929 and 911 (**A**, **C**), S_1 (lo) element ZPAL CXVI/912 (**B**), S_4 (hi) element ZPAL CXVI/913 (**D**), and M (ne) element ZPAL CXVI/914 (**E**).

I fail to see any stable morphological distinctions which could substantiate the numerous species of the anchor-like *Ancyrodella* (Fig. 25D–J). Until this is convincingly documented I recommend use of the oldest available name, that of the type species of the genus, *A. nodosa* Ulrich and Bassler, 1926 (see Huddle 1968). The platform on both sides of the ridge may be very narrow in some specimens. Whether they truly represent the separate species *A. ioides* remains to be documented biometrically on large populations.

In sample Wł-R/A1 from Włochy almost all specimens show anchor-like contour, but in some the rostral lobe is slightly swollen and in one specimen it is bifurcated. The point of bifurcation is there rather distant from the basal pit which means that bifurcation developed at later ontogenetic stages than in the late Frasnian species of the *A. curvata* group. Rare specimens with branched lobe occur in sample Wtr-5 where the modal morphology is a rather narrow platform and extreme morphs are not far from the *A. ioides* morphology (Fig. 25F). All the specimens in Wł-R/A1 and Wtr-5 are classified as *Ancyrodella nodosa* Ulrich and Bassler, 1926.

Population variability and species demarcation in the latest Frasnian palmatolepidids.—The Upper Kellwasserkalk sample Pł-391 from Płucki is very productive in elements of the palmatolepidids. This offers an opportunity to make the meaning of species more precise and biologically meaningful with biometrics.

Lagovilepis bogartensis is there well represented (with 232 M elements; Fig. 42). Only two M (ne) elements of *Manticolepis* morphology have been found in the sample (Fig. 40O, P). They may belong as well to *M. rhenana* or *C.*? *linguiformis*, both present in the assemblage (Table 5; Fig. 35B, C). Even if *M. winchelli* is represented in the sample, its contribution is subordinate and one might expect some bimodality in at least one platform character distribution in the sample. In contrary to this expectation, among the P_1 (sp) elements in the sample several show morphology generally believed to be diagnostic to *M. winchelli*, that is relatively straight carina with straight lateral orientation of the rather robust platform lobe (Fig. 41E).

In an attempt to check this I measured eight dimensions in 740 specimens extracted from a part of the sample. These were standard measurements of the element length, width of the platform lobe, length of free carina and length of the dorsal ("posterior") process. To describe skewness of the platform and curvature of the carina the distance between element tips and the tip of the lobe, the distance between the beginning of the platform and the lobe tip, and the angle between the inner process and the platform lobe were measured. Not one of these characters shows any sign of bimodality in distribution, splitting of their routes in ontogeny, or any apparent clustering of specimens. Combination of characters yielded the same result. To check whether at later stages of the ontogeny some distinctions appear, 341 more specimens with length exceeding 1 mm were separated from the rest of the sample and measured for five characters (three measurements of the platform skewness have appeared to give the same results as the lobe proclination angle alone; Fig. 43). The distribution remained clearly unimodal in any checked combination. The proclination angle seems to control the shape of the element to a large degree but is extremely variable. It increases in early ontogeny, with more and more twisted appearance of elements, with the mean value for the first measured sample being 102° (standard deviation ± 61), whereas in large elements its mean value is 106° (standard deviation ±81). Among the large elements, those with morphologies considered diagnostic for *M. winchelli* by Klapper and Foster (1993) occupy marginal position in the scattergram (Fig. 43). If they cluster at all, this is very weakly expressed, with complete transition to morphologies attributed to *L. bogartensis*.

As any biometric separation of P_1 (sp) elements of *Lagovilepis* and *Manticolepis* failed in the Płucki material, this analysis was extended to sample Wtr-18 from Wietrznia in which 16 M (ne) elements of *Manticolepis* have been found (six belonging probably to *M. rhenana*, others to *M. gigas*)

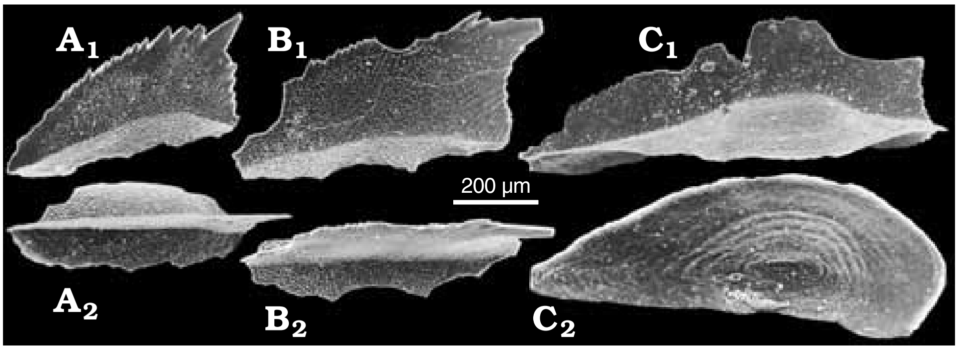


Fig. 15. *Playfordia primitiva* (Bischoff and Ziegler, 1957) from the early Frasnian of Wietrznia I quarry, sample Wtr-9; elements ZPAL CXVI/1061 (**A**), 1062 (**B**), and 1060 (**C**).

but not one of *Lagovilepis*. Elements of presumed *M. gigas* or *M. winchelli* were measured for their length and proclination angle, in the same way as those of *L. bogartensis* from Płucki. Results are equally disappointing (Fig. 43). The mean value for the proclination angle in this sample is 105° (standard deviation ±71), thus the elements are actually a little closer morphologically to those assumed to be characteristic for *L. bogartensis*, although no diagnostic M (ne) element was found and *L. bogartensis*, if present at all in this sample, must be subordinate in respect to *M. winchelli*. It appears thus that P_1 (sp) elements are of little use in identifying these fundamentally different apparatuses.

Results of this study are in contrast with the shape analysis by Klapper and Foster (1993) based on digitalised outline analysis of 15 specimens for each of the species. However, their specimens of *L. bogartensis* came from five separate samples collected at two European localities (Steinbruch Schmidt and Coumiac) whereas those of *M. winchelli* represent four samples from an American locality (Sweetland Creek). It is not clear how the specimens analysed by Klapper and Foster (1993) were selected from samples and whether this was meaningful in populational terms. To use the measuring method of Klapper and Foster (1993) or Renaud and Girard (1999) for samples numerous enough to show more reliably the population variability would be technically too complex and thus not practical. In the Płucki sample the only apparent bimodality in platform shape variation separates elements of the species *M. winchelli* and *L. bogartensis* taken together from those of "*Palmatolepis*" *praetriangularis*.

Restoration of the Frasnian conodont apparatuses

The classic works on the Late Devonian conodont apparatuses include those by Lange (1968), Klapper and Philip (1971, 1972), Boogaard and Kuhry (1979), Klapper and Foster (1993), Metzger (1994), and Schülke (1999). Below these literature data are supplemented with the new evidence from the Frasnian of the Holy Cross Mountains. The conodont species are listed in order, arranged from the least derived apparatuses with coniform elements to the most advanced, according to their classification in Sweet (1988) and Dzik (1991b).

Belodella tenuiserrata sp. nov. (Fig. 5A, B).—This is a rare species and its apparatus remains incompletely known, the only source of information on its composition being specimens from samples Wtr-11 and Wtr-5, each represented by only nine elements.

Belodella minutidentata sp. nov. (Fig. 5C–F).—Samples Wtr-4 and Wtr-5 from Wietrznia II quarry provide enough information to restore the apparatus. This is a typical *Belodella*, and locations are tentatively identified using terminology for the panderodontids (see Dzik 1991).

Belodella devonica (Stauffer, 1940) (Fig. 5G–N).—The species is common throughout the whole Frasnian, although usually in small numbers of elements. Wtr-11 and Wtr-9 are the samples with the apparatus components most completely represented. The cluster from the Upper Kellwasserkalk described by Lange (1968) seems to be incomplete, with the posteriormost undenticulated M (ne) elements pair missing.

Belodella robustidentata sp. nov. (Fig. 5O–Q).—Sample Wtr-9 provides the basic information on the apparatus composition, but possibly not all element types are identified.

Icriodus expansus Branson and Mehl, 1938 (Fig. 6A–D).—This oldest Frasnian *Icriodus*, well represented in sample Wtr-8, is characterised by a primitive tear-drop contour of the icrion, with sharply pointed dorsal end. It became less pointed in adult specimens, but even in robust large forms (common in samples Wtr-7 and Wtr-10) the tear-drop contour remains. In juvenile specimens denticles of the middle row are of virtually the same height as those of the side rows, later in the ontogeny the medial denticles fuse in the middle part of the element and rise above the rest of the icrion. Whether this population is truly conspecific or not with the type population of *I. expansus* from the Mineola Limestone of Missouri, requires population studies. Associated ramiform elements are of extremely simple morphology and it is hard to tell which of them are complete elements and which are disassociated denticles of processes with unmineralised bases.

Icriodus symmetricus Branson and Mehl, 1934 (Fig. 6E–H).—Mature elements from Włochy and Wietrznia show there

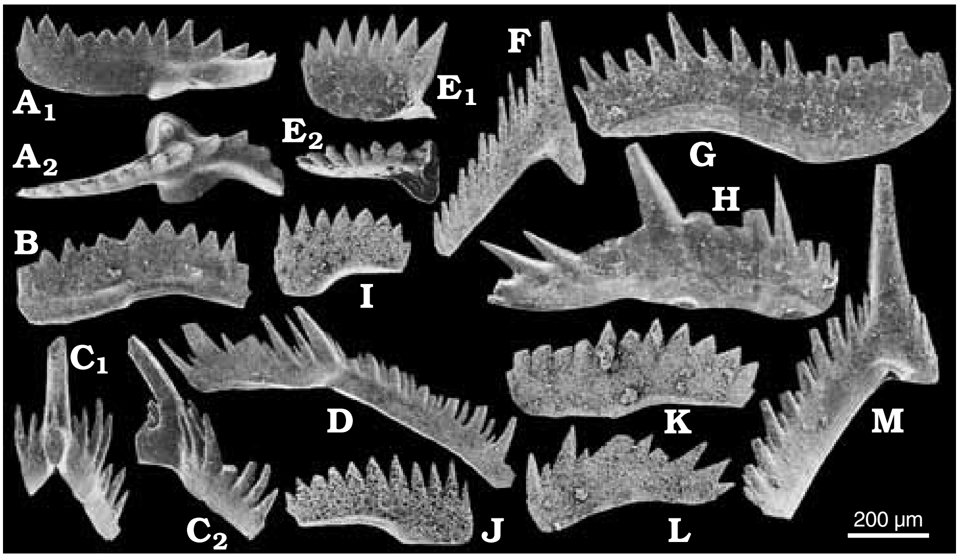


Fig. 16. Polygnathids without platform from the Frasnian of the Holy Cross Mountains. **A–D**, **F**, **M**. *Tortodus treptus* (Ziegler, 1958) from the early Frasnian of Wietrznia I quarry (**A–D**, **M**, sample Wtr-13; **F**, sample Wtr-20); P_1 (sp) element ZPAL CXVI/822 (**A**), P_2 (oz) element ZPAL CXVI/823 (**B**), S_0 (tr) element ZPAL CXVI/824 (**C**), S_2 (pl) element ZPAL CXVI/825 (**D**), M (ne) elements ZPAL CXVI/1177 (**F**) and 826 (**M**). **E**. *Nicollidina brevis* (Bischoff and Ziegler, 1957) from Wietrznia (sample Wtr-5); P_1 element ZPAL CXVI/730. **G**, **H**. *Mehlina irregularis* Youngquist, 1945 from the Upper Kellwasserkalk at Płucki (sample Pł-391); P_1 element ZPAL CXVI/ 397 (**G**) and P_2 element ZPAL CXVI/396 (**H**). **I–L**. *Tortodus*? sp. from the mid-Frasnian of Wietrznia I quarry (**I**, sample Wtr-31; **J–L**, sample Wtr-30), P_1 elements ZPAL CXVI/1097, 1095, and 1095 (**I–K**) and P_2 element ZPAL CXVI/1095 (**L**).

characteristic parallel sides of P_1 (sp) elements (Branson and Mehl 1938; Müller and Müller 1957). The apparatus does not seem to differ from that of other Frasnian *Icriodus*.

Icriodus kielcensis sp. nov. (Fig. 6I, J).—Except for a very narrow icrion of P_1 (sp) elements the apparatus does not seem to differ from other species of the genus. In robust gerontic elements the icrion became irregular in outline but particular denticles remain separate.

Icriodus elegantulus Stauffer, 1938 (Fig. 6K–M, Q).—This is a Płucki lower cephalopod limestone (Pł-22) species, one of several with the "alternatus" morphology of the icrion, with primitively erect cusp and separate denticles even in gerontic elements.

Icriodus iowensis Youngquist and Peterson, 1947 (Fig. 6N–P, R).—Clusters of coniform denticles have been found in the Upper Kellwasserkalk (Pł-391) at Płucki where the species occurs abundantly. The main difference in respect to earlier species is in the tendency of denticles in the icrion to form transverse ridges, especially in gerontic specimens. The cusp is slightly proclined.

Icriodus alternatus Branson and Mehl, 1934 (Fig. 6S–W).—This species from the base of the Famennian at Płucki is represented also by clusters with numerous denticles. Its species identification is uncertain, as there is not enough information on its type population (Branson and Mehl 1938; lectotype selected by Ziegler 1962: 51). From the preceding Upper Kellwasserkalk species it differs in lacking tendency to develop transverse ridges on the icrion and even more proclined cusp.

Pelekysgnathus planus Sannemann, 1955 (Fig. 6Y).—Only P_1 (sp) elements have been identified and it is unclear whether the remaining apparatus was the same as in *Icriodus*, or with robust denticles, as in the Famennian species of *Pelekysgnathus*.

Playfordias primitiva (Bischoff and Ziegler, 1957) (Fig. 15).—Elements of this enigmatic species are frequent enough in the early Frasnian of Wietrznia I quarry to make presence of other element types in the apparatus unlikely.

Ligonodina pectinata Bassler, 1925 (Figs. 7A, C, H, I, 8).—This is one of the Frasnian apparatuses most difficult to restore and identify. Its elements are extremely variable and, when associated with other prioniodinids, virtually indistinguishable at most locations in the apparatus. Much of the difficulties arise from the profound ontogenetic changes in the morphology of the apparatus. The proposed restoration is mostly based on samples from Włochy (Wł R/A1), where most elements of prioniodinids, although poorly preserved, are of similar ontogenetic age. Their association seems to be consistent with that from the species' type locality, that is the Rhinestreet Shale Member of the West Fall Formation in New York (Huddle 1968). The apparatus of *Ligonodina pectinata* is of a rather generalised and primitive appearance, except for the M (ne) element which is sharp-edged and wide ("*Prioniodus alatus*" in Huddle 1968). Such elements are usually represented in association with robust ramiform elements typical of *Ligonodina* in the Holy Cross Mountains samples. Sample Pł-22 seems to be crucial, as there is no other prioniodinid species there to which these elements could belong. Some uncertainty is introduced, however, by the content of sample Wtr-9 (and to less degree Wł-R/C1), where various elements of typical *Ligonodina* morphology are associated with M (ne) elements showing arched processes and a robust denticulation. Such elements are missing in other samples with characteristic S_1 (lo) and S_0 (tr) elements of *Ligonodina* but co-occur with late *Pluckidina* (Fig. 12F, I). Thus, either there are two different lineages of prioniodinid apparatuses differing only at the M (ne) location or the restoration of *L. pectinata* presented here is incorrect. The discussed species differs from *Delotaxis* sp. nov. A of Klapper and Philip (1971) in processes of the S_0 element being curved in a way similar to those of S_4 (hi) elements and from *Pluckidina*(?) *tortoides* (Sparling, 1981) in the lack of

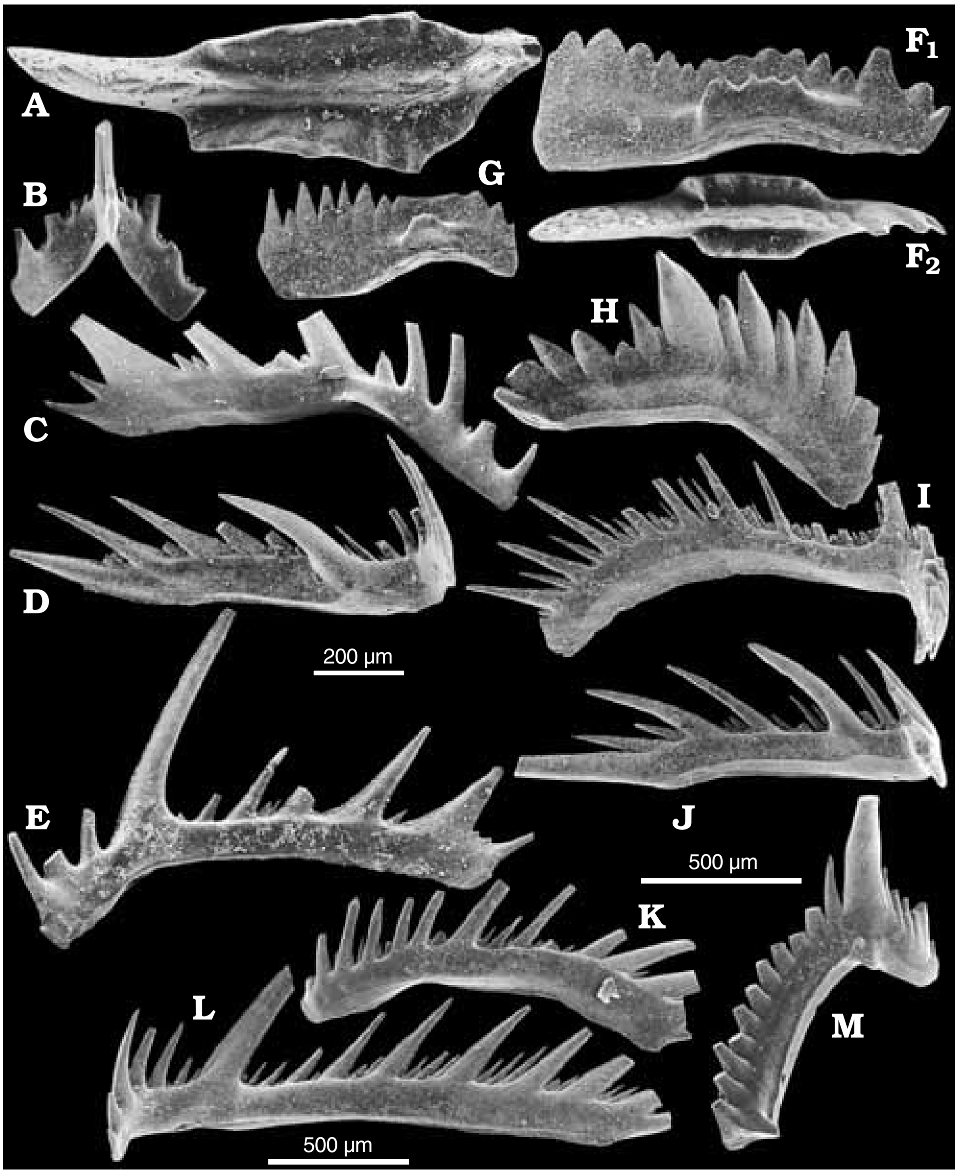


Fig. 17. *Ctenopolygnathus* from the Frasnian of the Holy Cross Mountains. **A**–**E**. *Ctenopolygnathus angustidiscus* (Youngquist, 1945) from the lower cephalopod limestone at Płucki (sample Pł-22); P_1 (sp) element ZPAL CXVI/564 (**A**), S_0 (tr) element ZPAL CXVI/549 (**B**), S_2 (pl) element ZPAL CXVI/550 (**C**), S_1 (lo) element ZPAL CXVI/551 (**D**) and $S_{3–4}$ (ke-hi) element ZPAL CXVI/553 (**E**). **F**–**M**. *Ctenopolygnathus* sp. A from the Upper Kellwasserkalk horizon at Płucki (sample Pł-391), P_1 elements ZPAL CXVI/431 and 433 (**F**, **G**), P_2 (oz) element ZPAL CXVI/434 (**H**), S_0 element ZPAL CXVI/436 (**I**), S_2 element ZPAL CXVI/437 (**J**), S_1 element ZPAL CXVI/435 (**K**), $S_{3–4}$ element ZPAL CXVI/438 (**L**), and M (ne) element ZPAL CXVI/439 (**M**). Magnifications shown by the bar scale in the centre, except for **H**–**K** and **L**, **M** with their own scales.

S_3 (ke) elements having processes long and almost in a single plane. Both these features characterise apparatuses classified here in *Pluckidina*.

Dyminodina planidentata sp. nov. (Fig. 9A–I, O–Q).—Elements of this species are abundant in the lower cephalopod limestone at Płucki (sample Pł-22) and the mid-Frasnian of Wietrznia II (Wtr-5). The apparatus structure is rather safely established. The elements share a similar coloration and relatively flat denticles which allow to disscriminate them from associated prioniodinid species.

Dyminodina anterodenticulata sp. nov. (Fig. 9H–J).—Although the species is generally rare, the Upper Kellwasserkalk at Płucki (sample Pł-391) has yielded enough material to enable complete apparatus restoration. Its weakest point is the identification of P_1 (sp) elements, which are rare and very variable.

Dyminodina kovalensis sp. nov. (Fig. 9K–Q).—Sample Ko-151at the Kowala Quarry offers a reasonable basis for the apparatus reconstruction. Except for the M (ne) elements, the apparatus seems not much different from the other species of the genus. Elements are easy to distinguish owing to their extreme flatness, unusual for a prioniodinid.

Pluckidina kielcensis sp. nov. (Fig. 10).—The most complete representation of this species is offered by sample Wtr-11 (see Dzik 1991: fig. 2, illustrated as *Prioniodina* sp.) where most of the elements are subadult. Their morphology changes rather substantially in ontogeny, becoming robust in late stages. Denticles in the platform series and the M (ne) elements tend to merge into a solid blade. A sample with elements of very different ontogenetic ages is Wtr-8; it may be that different species are represented. A gradation within this extreme variability is well illustrated in sample Wtr-7. It is especially impressive in the case of S_1 (lo) elements, which show a transition from strongly arched and twisted processes

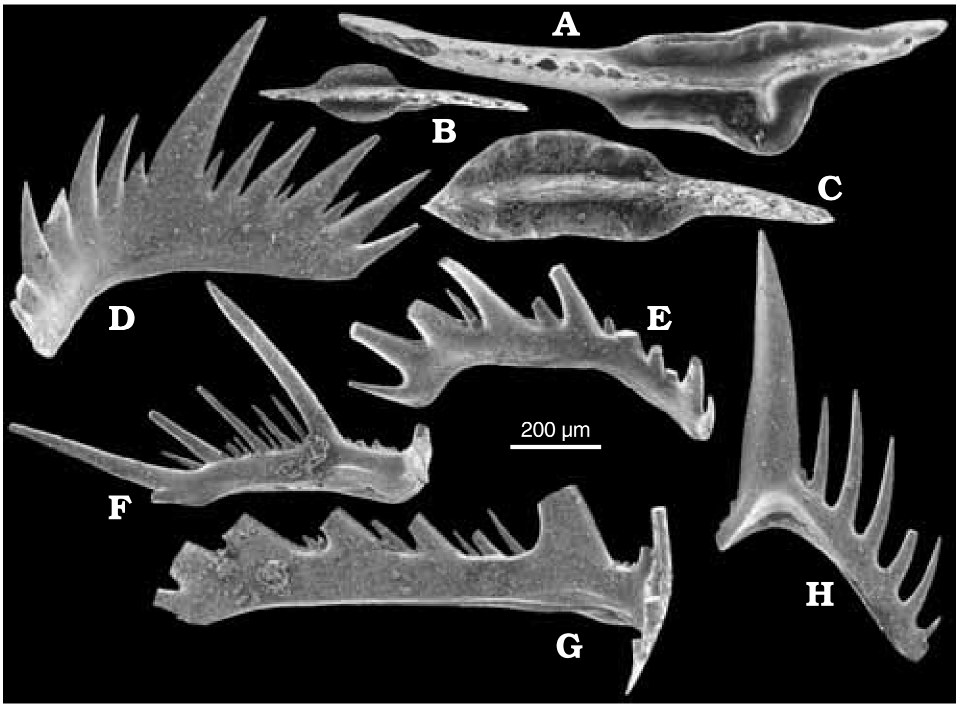


Fig. 18. *Ctenopolygnathus* sp. B from the earliest Famennian of Płucki in the Holy Cross Mountains; P_1 (sp) elements ZPAL CXVI/1008, 1010, and 1009 from sample Pł-20 (**A**, **B** juvenile, **C**), P_2 (oz) element ZPAL CXVI/1011, same sample (**D**), S_2 (pl) element ZPAL CXVI/1012, same sample (**E**), S_1 (lo) element ZPAL CXVI/1014 from sample Pł-16 (**F**), S_{3-4} (ke-hi) element ZPAL CXVI/1015, same sample (**G**), and M (ne) element ZPAL CXVI/1013, same sample (**H**).

(a morphology typical rather of the late Frasnian *P. lipperti*) to much less derived morphs with processes arranged at a wide angle. Also P_1 (sp) elements are variable, some showing an incipient platform and a regular arrangement of denticles, other are laterally sinuous with an irregular denticulation. In the somewhat geologically younger sample Wtr-9 elements are of a rather robust appearance.

Pluckidina slupiensis sp. nov. (Fig. 11).—This species well represented in the early Frasnian of Włochy (sample Wł-R/A1) is to some degree morphologically transitional between *Pluckidina* and *Dyminodina* in that its symmetry transition series elements bear long processes. Otherwise it is similar to *P. kielcensis* which makes the apparatus restoration rather easy, despite the poor preservation, by homologising elements.

Pluckidina robustipegmata sp. nov. (Fig. 12A–F).—The species is rather well represented in sample Wtr-5 from the early Frasnian of Wietrznia. It is difficult to separate some of its robust elements from associated *Ligonodina*, especially S_2 (pl) elements.

Pluckidina lipperti (Bischoff, 1956) (Fig. 12G–I).—Philip and McDonald (1975) included the symmetry transition series elements of this and related species into their restoration of apparatuses of various species of *Mesotaxis*. They put such S_1 (lo) elements also in the apparatus of *Manticolepis winchelli* (their *Palmatodella hassi*)

Pluckidina lagoviensis sp. nov. (Fig. 13A–H).—It is a not especially numerous Płucki lower cephalopod limestone species (sample Pł-22) with unusually long processes of the symmetry transition series elements which make apparatus identification rather easy.

Pluckidina nonaginta (Klapper et al., 1996) (Fig. 13I–O).—Numerous specimens from sample Wtr-13 at Wietrznia enable the apparatus restoration. Its weak point is the identification of P_1 (sp) and P_2 (oz) elements—they may appear reversed, as P_2, not P_1 elements are laterally bent in related species.

Gen et sp. indet. (Fig. 14).—Rare elements of an apparatus with some prioniodinid aspects but with regular appearance of denticulation and flat processes resembling rather *Ancyrognathus* occur sparsely in some samples. The material is too incomplete to enable taxonomic placement.

Tortodus treptus (Ziegler, 1958) (Fig. 16A–D, F, M).—The characteristically sinuous P_1 (sp) elements of the species (Klapper 1988; Klapper et al. 1996), seem to belong to a platform-less relative of the Eifelian type species of *Tortodus*, *T. kockelianus* (Bischoff and Ziegler, 1957). Co-occurring elements with a straight blade may represent the P_2 (oz) location (Fig. 16B). Rare possible other elements of the apparatus are of primitively polygnathid appearance. Unfortunately, the apparatus structure remains unknown in true *Tortodus*.

Tortodus? sp. (Fig. 16I–L).—These are even more simplified elements without any torting but with a somewhat radiating arrangement of the denticles, resembling that of *T. treptus*. The associated P_2 (oz) element is only tentatively attributed to the same apparatus.

Nicollidina brevis (Bischoff and Ziegler, 1957) (Fig. 16E).—This is probably a secondarily simplified polygnathid. The apparatus was restored by Nicoll (1985) and the rare non-P_1 (sp) elements fit his reconstruction.

Mehlina irregularis Youngquist, 1945 (Fig. 16G, H).—This

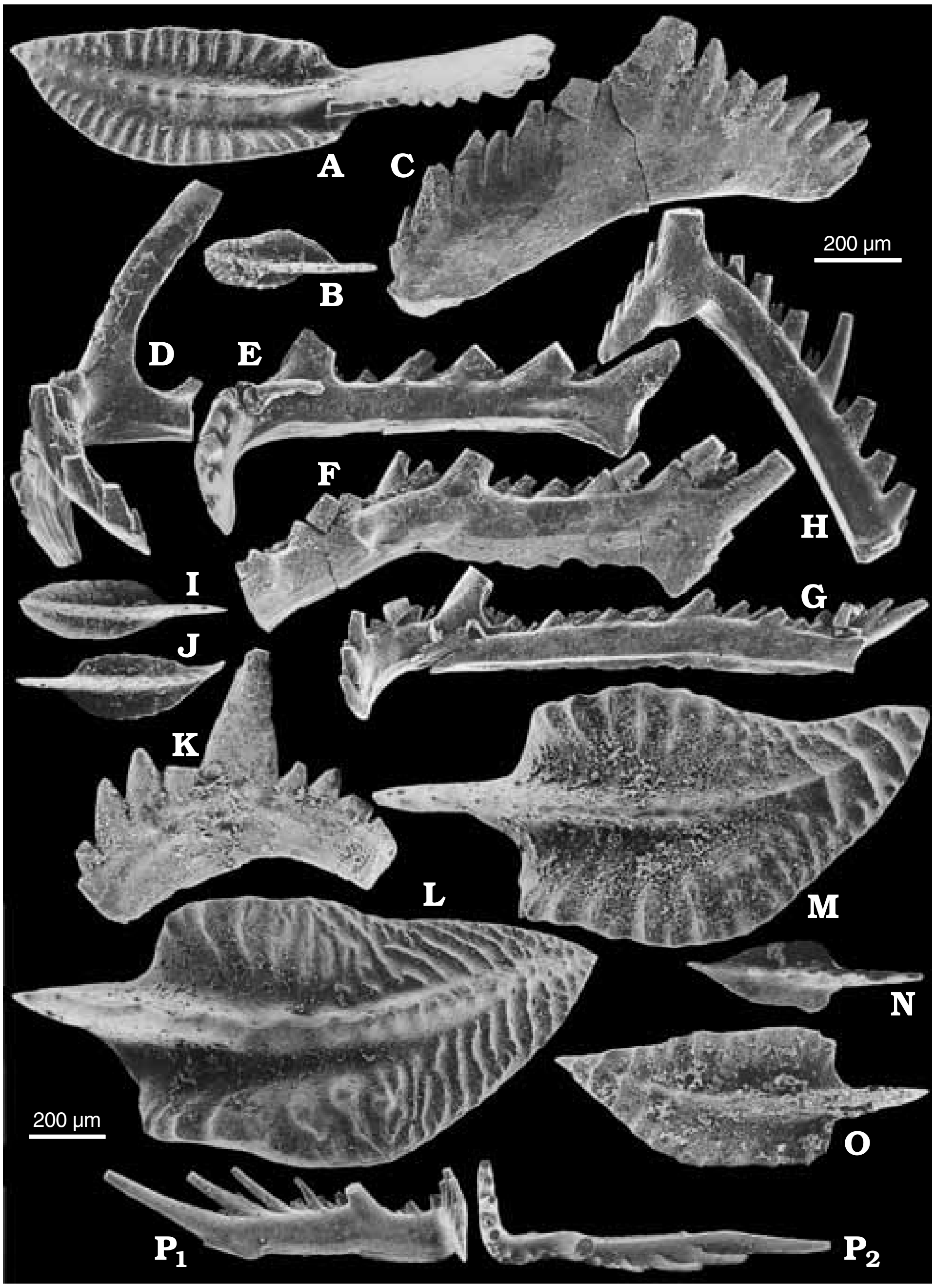


Fig. 19. Robust polygnathids from the Frasnian of the Holy Cross Mountains. **A**–**F**. *Polygnathus aequalis* Klapper and Lane, 1985 from the early Frasnian of Włochy (sample Wł-T/A1); P_1 (sp) elements ZPAL CXVI/882, 883 (**A**, **B**), P_2 (oz) element ZPAL CXVI/884 (**C**), S_0 (tr) element ZPAL CXVI/885 (**D**), S_1 (lo) element ZPAL CXVI/886 (**E**), S_2 (pl) element ZPAL CXVI/887 (**F**), S_{3-4} (ke-hi) element ZPAL CXVI/888 (**G**), and M (ne) element ZPAL CXVI/889 (**H**). **I**–**P**. *Parapolygnathus brevis* (Miller and Youngquist, 1947) from the lower cephalopod limestone at Płucki (sample Pł-22; **I**, **J**, **L**, **O**) and mid-Frasnian of Wietrznia II quarry (sample Wtr-5; **K**, **M**, **N**, **P**); P_1 elements ZPAL CXVI/556, 675, 673, 728, 729, and 674 (**I**, **J**, **L**–**O**), possible P_2 element ZPAL CXVI/728 (**K**), and S_2 element ZPAL CXVI/723 (**P**). Magnifications shown by the scale bar in the upper right corner, except for **L** with its own scale.

is the only Frasnian polygnathid with probably originally non-platform P_1 (sp) elements and a generalised apparatus inherited after the Early Devonian *Pandorinellina*. The co-occurring holotype of *M. gradatus* Youngquist, 1945 is conspecific with it, as already pointed out by Müller and Müller (1957).

Ctenopolygnathus? sp. cf. "*Polygnathus*" *gracilis* Klapper and Lane, 1985.—In the early Frasnian of Wietrznia and somewhat higher horizons at Włochy a species occurs with P_1 (sp) elements developing a sharp and marginally crenulated platform at late ontogenetic stages. Juveniles look like *Mehlina*. The basal cavity is rather wide, especially in the Włochy sample. The available material is very limited and the lack of adult specimens with the platform of so wide extent as in the type population of "*P.*" *gracilis* (see Klapper and Lane 1985) may be due to this. No other element can be convincingly associated with these P_1 elements and their affinities to *Ctenopolygnathus* are questionable.

Ctenopolygnathus angustidiscus (Youngquist, 1945) (Fig. 17A–E).—Only in the lower cephalopod limestone at Płucki (sample Pł-22) this species is represented well enough to allow the apparatus restoration. It is rather generalised, with short processes of S_1 (lo) and S_2 (pl) elements, which supports its proximity to the early *Parapolygnathus*. The platform of P_1 (sp) elements is extremely variable, probably an effect of its secondary reduction with no stabilising selection acting.

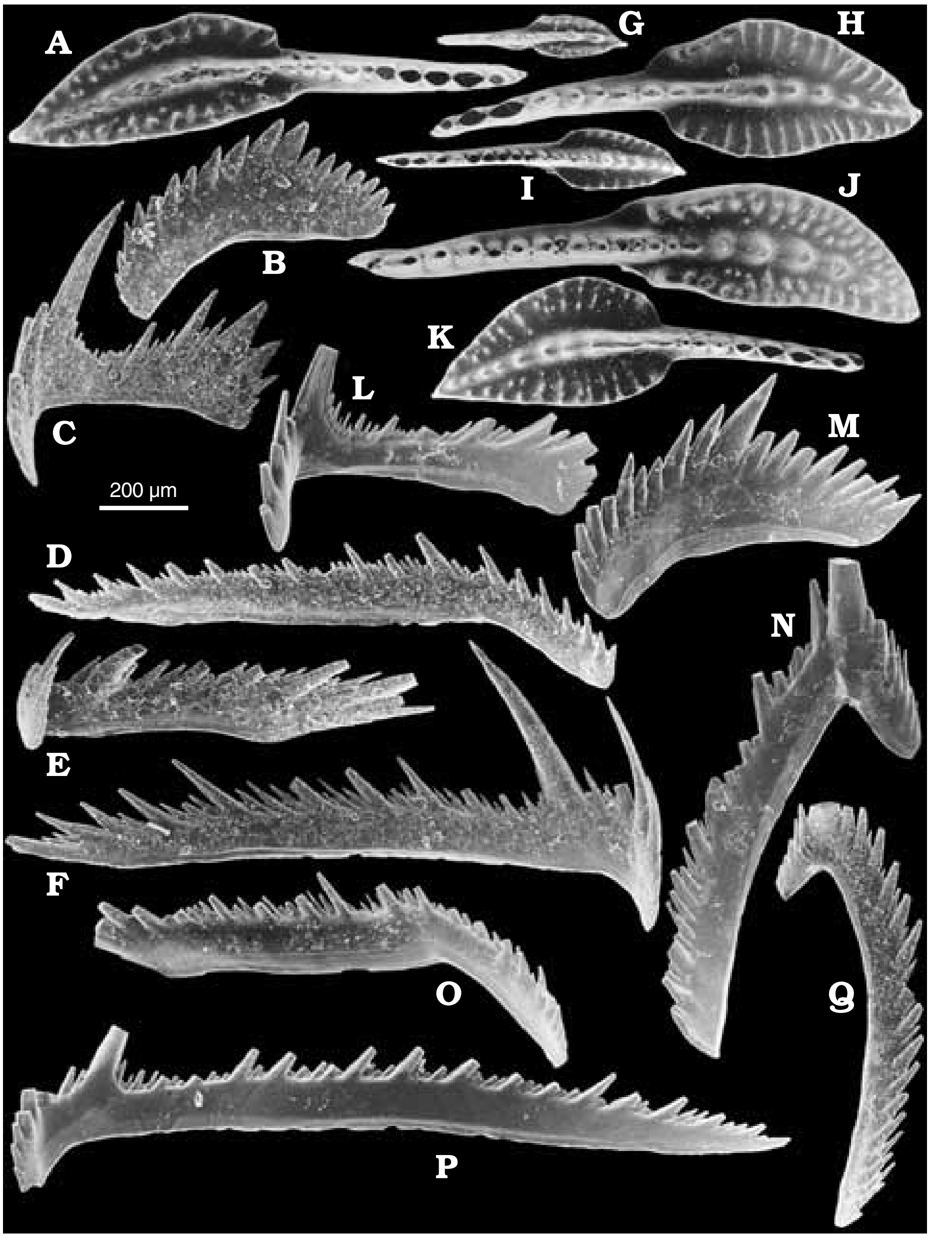


Fig. 20. *Polygnathus* sp. nov. from the early Frasnian of the Wietrznia I quarry, early form from sample Wtr-11 (**A**–**F**, **Q**) and late form from Wtr-9 (**G**–**P**), P_1 (sp) elements ZPAL CXVI/1047 (**A**), 1073, 1075, 1072, 1071, 1074 (**G**–**K**), P_2 (oz) element ZPAL CXVI/1048 and 1076 (**B**, **M**), S_0 (tr) elements ZPAL CXVI/1049 and 1077 (**C**, **L**), S_2 (pl) elements ZPAL CXVI/1050 and 1078 (**D**, **O**), S_1 (lo) element ZPAL CXVI/1051 (**E**), S_{3-4} (ke-hi) elements ZPAL CXVI/1052 and 1079 (**F**, **P**), and M (ne) elements ZPAL CXVI/1080 and 1053 (**N**, **Q**).

Ctenopolygnathus sp. A (Fig. 17F–M).—In this species from the Upper Kellwasserkalk horizon at Płucki (sample Pł-391), the platform of P_1 (sp) elements is even weaker but it remains unclear whether they are specifically distinct or not.

Ctenopolygnathus sp. B (Fig. 18).—The same comment applies to the population from the earliest Famennian of Płucki in the Holy Cross Mountains. These conodonts are too variable to decide whether there was a continuity between the Frasnian and Famennian populations of the lineage or not.

Polygnathus aequalis Klapper and Lane, 1985 (Fig. 19A–F).—In both studied Włochy samples, P_1 (sp) elements dominate which are strongly asymmetric and with an arched profile. In the sample Wł-R/C1 this is less apparent, but they seem to be connected by transitional morphologies with forms typical for the probably younger sample Wł-R/A1. The apparatus is rather heavily built. The most characteristic feature of the species seems to be the early ontogeny of P_1 (sp) elements. The platform initially developed as strongly concave and very wide in its ventral end. Later it became only slightly swollen and separated from the rest of the platform by an insignificant constriction (Fig. 19B). In this respect the elements show some similarity to those of the probably related *Avignathus* lineage but differ from *P. webbi*, in which the platform margin is at the beginning of its development parallel to the carina, with no separation of the ventral part and with the dorsal tip of the element platformless.

Parapolygnathus brevis (Miller and Youngquist, 1947) (Fig. 19I–P).—The P_1 (sp) elements of the species are rather characteristic and easy to distinguish (Szulczewski 1973; Klapper and Lane 1985). Its ontogeny is rather characteristic, at early stages making it closely similar to *Polygnathus aequalis* (see Fig. 19B, I). Some poorly preserved P_2 (oz) and other elements may belong to the same apparatus, but their frequencies are too low to make this well founded.

Polygnathus sp. nov. (Fig. 20).—This early Frasnian species predates *Avignathus*, the only difference in otherwise variable P_1 (sp) elements being the platform wider at the ventral ("anterior") end. Among the associated S_0 (tr) elements all are triramous, with the middle process of a medium size (Fig. 20C, L) which places it still at the *Polygnathus* grade.

Avignathus decorosus (Stauffer, 1938) (Fig. 21A–M).—The apparatus of this species was restored by Boogaard (1983). From the presumably ancestral *Polygnathus* sp. nov. it can be distinguished by the generically diagnostic S_0 (tr) elements and by the platform of P_1 (sp) elements which gently narrows towards its dorsal tip and is slightly constricted at the level of the basal pit, with its free end expanded and with wide concave areas. The basal cone is generally larger than in most polygnathids. The holotype of *Avignathus beckmanni* Lys et al., 1957 comes from the late Frasnian pink limestone with *Manticoceras*, Coumiac quarry, Montagne Noire (Lys and Serre 1957: fig. 2a, b), thus from strata roughly coeval with the type horizon of *Polygnathus decorosus* Stauffer, 1938, that is the Olentangy Shale of Ohio (Stauffer, 1938).

Avignathus bifurcatus sp. nov. (Fig. 21N–S).—Except for the peculiar appearance of the symmetrical element, the rest of the apparatus is identical with *A. decorosus*.

Polygnathus webbi Stauffer, 1938 (= *Polygnathus normalis* Miller and Youngquist, 1947; see Klapper and Lane 1985) (Fig. 22).—The main distinction of the species, which is otherwise difficult to determine because of a generalised morphology and great population variability, is the ontogeny of P_1 (sp) elements. Unlike somewhat similar *P. aequalis*, they do not show any separation of the two platform regions. The platform develops on sides of the element as a rather simple blade and only at later stages the profound asymmetry of the element sides developes. In this respect there is a close similarity to *P. pacificus*. The apparatus of *P. webbi* is well known owing to clusters from the Upper Kellwasserkalk (Lange 1968; Schülke 1999), found also at Płucki at several levels.

Polygnathus pacificus Savage and Funai, 1980 (Fig. 23A–J).—The species occurs abundantly only in some restricted horizons, the most prolific being that of sample Wtr-13 at Wietrznia and the lower cephalopod limestone at Płucki (Pł-22; also Janczyce: Matyja and Narkiewicz 1995). The elements did not reach sizes comparable with mature elements of *P. webbi* and the remaining part of the apparatus is more gracile. In many cases, however, separation of ramiform elements of these species is difficult and has been done somewhat arbitrarily.

Polygnathus sp. (aff. *P. nodocostatus* Branson and Mehl, 1934) (Fig. 23K–P).—The P_1 (sp) elements of this species from the lower cephalopod limestone (sample Pł-22) at Płucki are robust despite relatively small mature size. The P_2 (oz) elements matched with them are of a regular shape and with uniformly distributed denticles. Other elements of the apparatus are rather robust and with relatively short processes.

Polygnathus semicostatus Branson and Mehl, 1934 (Fig. 24).—This is the only polygnathid occurring in the earliest Famennian at Płucki. Identification of the apparatus elements is thus relatively safe, supported also by clusters of elements.

Ancyrodella rotundiloba (Bryant, 1921) (Fig. 25A, B).—The apparatus was restored by Klapper and Philip (1972). In samples from the lower part of the Wietrznia I section robust P_2 (oz) elements are rather safely identifiable and only juvenile specimens can be misidentified with those of other polygnathids. The symmetry transition series specimens attributable to *Ancyrodella* bear relatively short processes. The dorsal process is usually bent basally. A characteristic feature is the hooked terminal end of the ventral process. However, the ramiform elements are highly variable and there is a continuous morphologic transition to the co-occurring robust polygnathids. Juvenile elements and some of adults can be only arbitrarily attributed taxonomically. This refers also to M (ne) elements.

Ancyrodella alata Glenister and Klapper, 1966.—Robust non-platform elements in sample Wtr-9 which may belong to the species are extremely variable and do not seem different from those from older samples containing the previous species.

Ancyrodella rugosa Branson and Mehl, 1934 (Fig. 25C).—Rare robust ramiform elements associated with the P_1 (sp) elements attributed to this species in sample Wtr-13 do not seem to differ from those of the older species of *Ancyrodella*.

Ancyrodella nodosa Ulrich and Bassler, 1926 (Fig. 25D–J).—Although numerous robust ramiform elements are associated with P_1 (sp) elements of *Ancyrodella* in sample Wł-R/A1, I failed to offer any convincing apparatus reconstruction. There seems to be a gradation towards associated robust polygnathids. Especially controversial is the morphology of S_2 (pl) and S_1 (lo) elements. Along with forms resembling those of *Polygnathus*, there are specimens with very short processes. I am not able to decide which of those truly belong to *Ancyrodella*.

Ancyrodella lobata Branson and Mehl, 1934 (Fig. 27A–F, K).—A very few ramiform elements have been identified in sample Wł-R/C1 as possibly belonging to this species which is characterised by a wide and frequently bifurcating rostral lobe. Sample Pł-22 from the lower cephalopod limestone at Płucki yielded unnumerous robust ramiform elements which may belong to the species but they show a very wide variability and the differences from associated polygnathids are not clear.

Ancyrodella curvata Branson and Mehl, 1934 (Fig. 27G–J, L, M).—Non-platform elements from the Upper Kellwasserkalk at Płucki (Pł-391) are similar to those referred to this species by Schülke (1997), but the S_2 (pl) elements identified by him belong rather to *Dyminodina*, whereas the M (ne) element may represent *Pluckidina*.

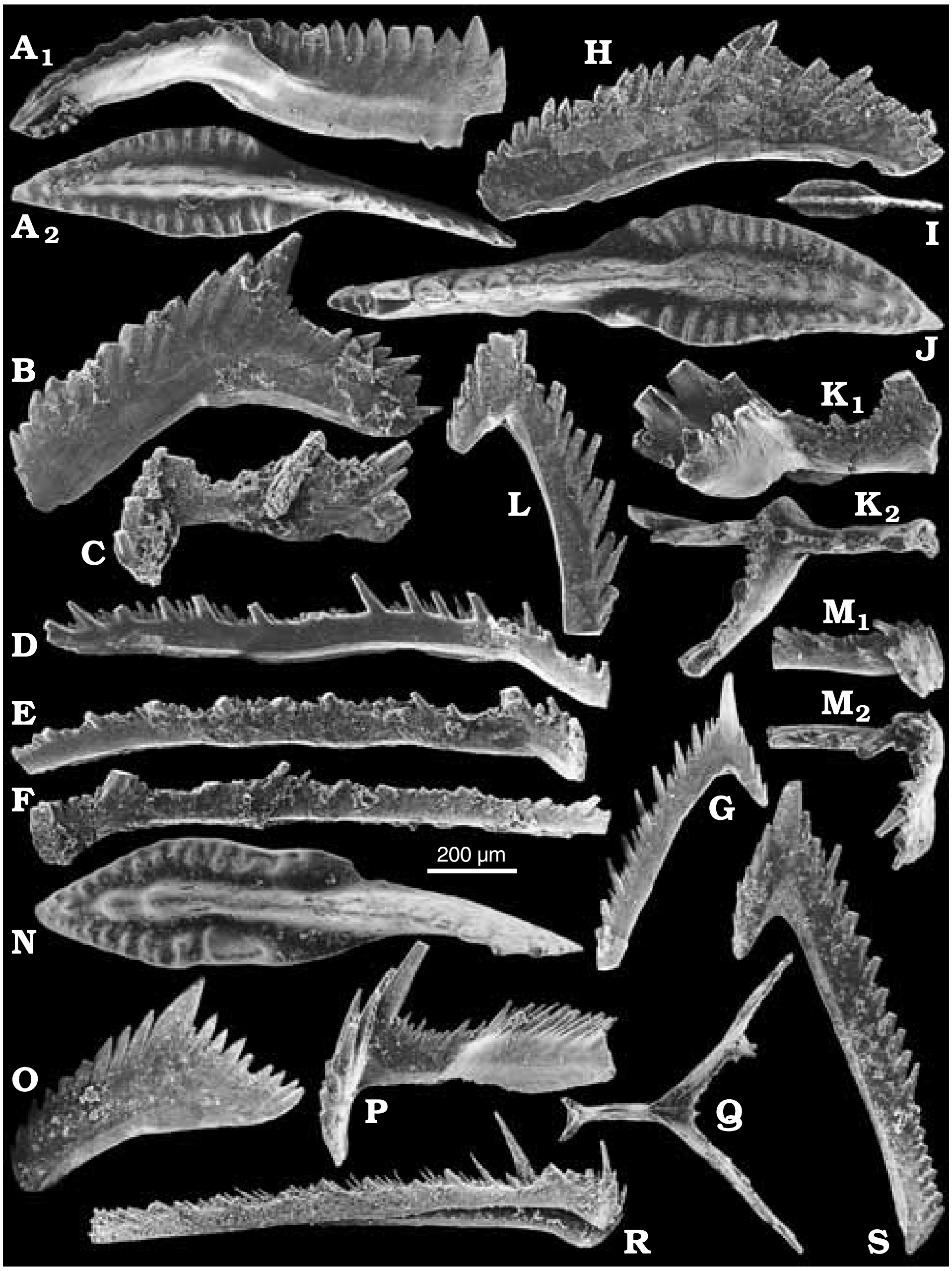


Fig. 21. Polygnathids with ramified symmetrical elements from the Frasnian of the Holy Cross Mountains. **A**–**M**. *Avignathus decorosus* (Stauffer, 1938) from the mid-Frasnian of Włochy, sample Wł-R/C1 (**A**–**G**) and WL-R/A1 (**H**–**M**), P_1 (sp) elements ZPAL CXVI/933 (A), 892, and 891 (**I**, **J**), P_2 (oz) elements ZPAL CXVI/934 and 893 (**B**, **H**), S_0 (tr) elements ZPAL CXVI/935 and 890 (**C**, **K**), S_2 (pl) elements ZPAL CXVI/937 (**D**), $S_{3–4}$ (ke-hi) elements ZPAL CXVI/940 (**E** × 95) and 939 (**F** × 90), S_1 (lo) element ZPAL CXVI/895 (**M**), and M (ne) elements ZPAL CXVI/941 and 897 (**G**, **L**). **N**–**S**. *Avignathus bifurcatus* sp. nov. from the late Frasnian lower cephalopod limestone at Płucki, sample Pł-22 (**N**–**Q**, **S**) and Pł-110 (**R**); P_1 element ZPAL CXVI/677 (**N**), P_2 elements ZPAL CXVI/545 (**O**), S_0 elements ZPAL CXVI/562 (P) and 1145 (**Q**; holotype in basal view), cluster of S_3 and S_4 elements ZPAL CXVI/1146 (**R**) and M element ZPAL CXVI/679 (**S**).

Ancyrognathus triangularis Youngquist, 1945 (Fig. 28. K, M-P, ?L, ?J).—Klapper (1990) identified the P_2 (oz) elements which are also represented in my material. Some other elements of the apparatus seem to be identifiable in samples from Wietrznia but they are never numerous enough to allow reliable complete apparatus reconstruction.

Ancyrognathus asymmetricus (Ulrich and Bassler, 1926) (Fig. 28F–I, M, ?L).—Robust P_2 (oz) elements are well represented in the lower cephalopod limestone at Płucki (Pł-22) and in sample Wtr-23 at Wietrznia (Table 3) but relatively few ramiform elements provisionally attributed to the species have been found. They allow rather reliable restoration of the apparatus, as among associated platform elements no other conodont species can be reasonably arranged with them in the same apparatus.

Ancyrognathus ubiquitus Sandberg et al., 1988 (Fig. 28A–D, ?B, C, E).—Along with the platform series elements a few non-platform elements possibly belonging to this species have been found at Kowala sample Ko-149 and in the Upper Kellwaserkalk at Płucki (sample Pł-391).

Klapperina sp. (Fig. 29A–E).—From Wietrznia sample Wtr-9 come two P_2 (oz) elements and single S_2 (pl) element, which differ from those of associated *Mesotaxis* in lacking any platform and a more generalised appearance. They may belong to the apparatus.

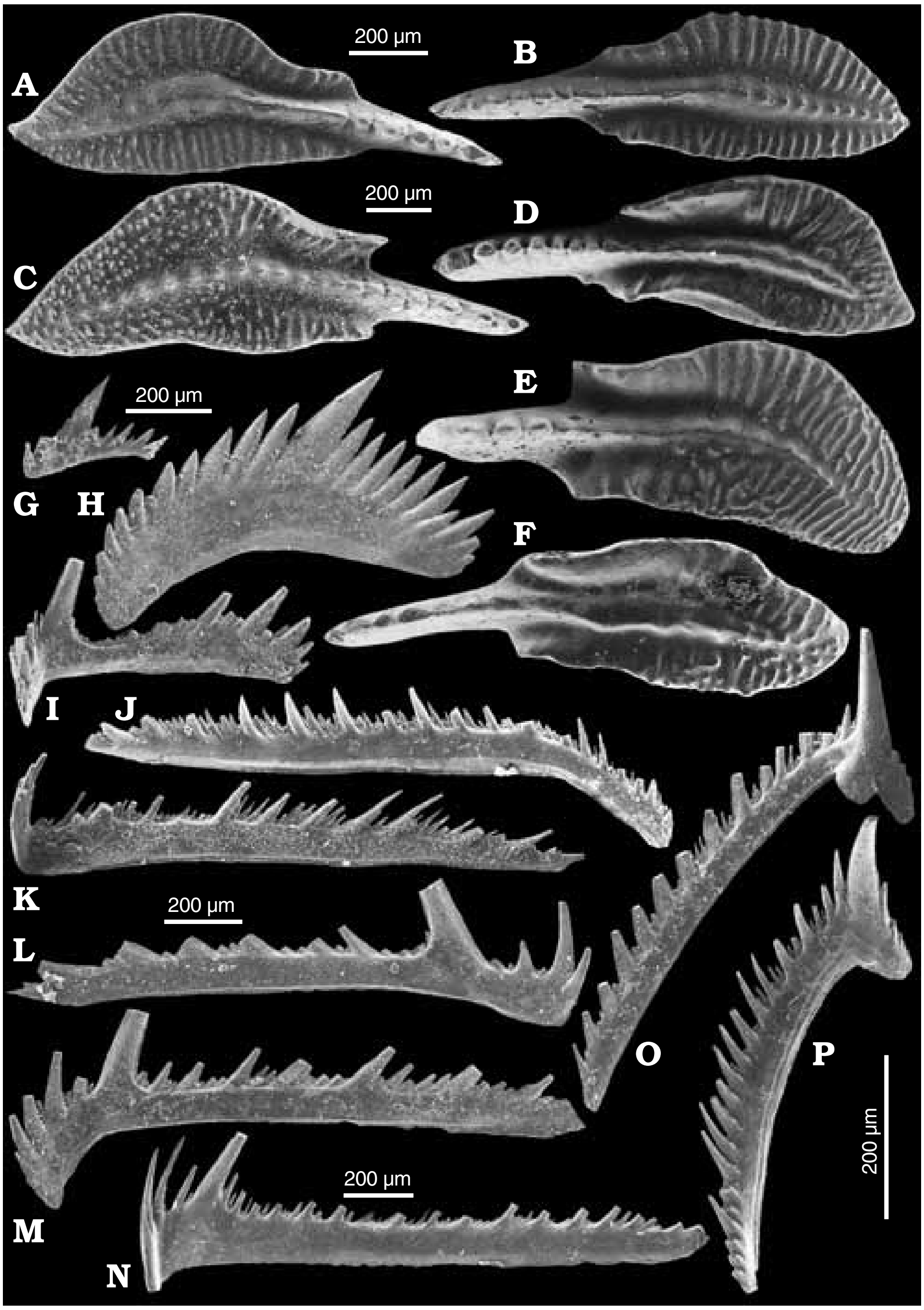


Fig. 22. *Polygnathus webbi* Stauffer, 1938 from the mid-Frasnian of Wietrznia (sample Wtr-13; **A**, **B**), late Frasnian of Wietrznia II quarry (sample Wtr-5; **H**), lower cephalopod limestone at Płucki (sample Pł-22; **C**, **G**, **J**–**O**), latest Frasnian of Kowala (sample Ko-149; **F**, **I**) and Upper Kellwasserkalk at Płucki (sample Pł-391; **D**, **E**, **P**), Holy Cross Mountains, P_1 (sp) elements ZPAL CXVI/843 and 842 (**A**, **B**), 536, 1179, 1183, 502 (**C**–**F**), P_2 (oz) elements ZPAL CXVI/547 and 720 (**G**, **H**), S_0 (tr) element ZPAL CXVI/507 (**I**), S_2 (pl) element ZPAL CXVI/559 (**J**), S_1 (lo) element ZPAL CXVI/560 (**K**), S_{3-4} (ke-hi) elements ZPAL CXVI/575, 571 and 572 (**L**, **M**), and M (ne) elements ZPAL CXVI/561 and 388 (**O**, **P**). Magnifications shown by the bar scale at the top, except for **C**, **G**, **J**–**L**, **M**, **O**, and **P** with their own scales.

Mesotaxis falsiovalis Sandberg et al., 1989 (Fig. 30A–K).—Sample Wtr-11 from Wietrznia is the most productive, allowing identification of the whole set of elements, despite their fragility and small size (Dzik 1991b). Most importantly, there are nine triramous S_0 (tr) elements in the sample, all with a relatively long medial process, although showing signs of a size reduction. The platform of P_1 (sp) elements is variable both in the ontogeny and population, but they are always elongated and virtually symmetrical. A weak platform develops also in P_2 (oz) elements but only at adult stages. The remaining elements of the apparatus are very small and gracile which resulted in their poor representation in samples.

Mesotaxis asymmetrica (Bischoff and Ziegler, 1957) (Fig. 30L–T).—The apparatus was restored by Klapper and Philip (1971). Sample Wtr-9 from Wietrznia is the only one with the complete set of non-platform elements represented. They are similar to those of *M. falsiovalis* but much more robust, with a tendency to irregular distribution and orientation of denticles, which makes them superficially similar to those of *Palmatolepis* (see Dzik 1999b).

Mesotaxis? *punctata* (Hinde, 1879) (Fig. 31A–H).—Klapper and Foster (1993) identified P_2 (oz) element of this species. The species is represented by relatively numerous P_1 (sp) ele-

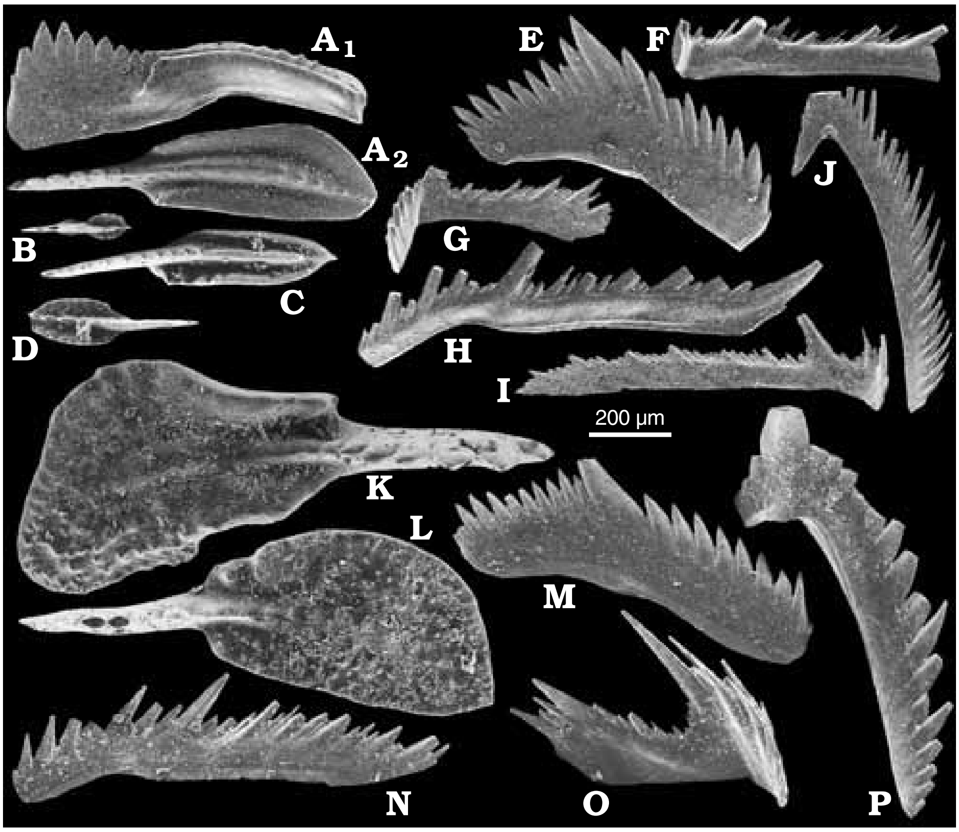


Fig. 23. Subordinate Frasnian *Polygnathus* species from the Holy Cross Mountains. **A–J**. *Polygnathus pacificus* Savage and Funai, 1980 from the mid-Frasnian of Wietrznia, sample Wtr-13; P_2 (oz) element ZPAL CXVI/844 (**E**), S_1 (lo) element ZPAL CXVI/846 (**F**), S_0 (tr) element ZPAL CXVI/852 (**G**), S_2 (pl) element ZPAL CXVI/847 (**H**), $S_{3–4}$ (ke-hi) element ZPAL CXVI/848 (**I**), M (ne) element ZPAL CXVI/849 (**J**). **K–P**. *Polygnathus* sp. (aff. *P. nodocostatus* Branson and Mehl, 1934) from the lower cephalopod limestone at Płucki, sample Pł-22, P_1 (sp) elements ZPAL CXVI/554 and 555 (**K**, **L**), P_2 element ZPAL CXVI/557 (**M**), S_1 element ZPAL CXVI/570 (**N**), S_0 element ZPAL CXVI/566 (**O**), and M element ZPAL CXVI/569 (**P**).

ments in sample Wł-R/A1, associated with ramiform elements of *Mesotaxis* morphology. Unfortunately, no S_0 (tr) element has been found. Based on the transitional position between non-lobate *Mesotaxis* species and *M. bohemica*, it is predicted that the medial process was still present in it.

Mesotaxis bohemica (Klapper and Foster, 1993) (Fig. 31I–R).—The species is best represented in sample Wł-R/C1 from Włochy. The platform of P_1 (sp) elements is variable in outline; some large elements resemble *M. proversa* in the lateral lobe being obliquely oriented and with a furrow, but it does not reach the length typical of that species. The carina of P_2 (oz) elements is high, with denticles tending to merge and form a smooth wall, which resembles the situation in homologous elements from sample Wtr-13, rather arbitrarily attributed to *M. proversa* (Fig. 32B). Whether this reflects a relationship or not, has to be clarified with a better material. Only two S_0 (tr) elements have been found, both with a rudimentary medial process (Fig. 31K, L). If properly attributed to the apparatus (a poor alternative is *M. asymmetrica* represented by disproportionally rare, possibly reworked, P_1 elements), the species belongs to *Mesotaxis*.

Mesotaxis? *domanicensis* (Ovnatanova, 1976) (Fig. 32D–L).—The advanced morphology of the P_2 (oz) elements in samples Wtr-15 and Wtr-30 from Wietrznia introduces some uncertainty to the proposed apparatus interpretation. With their angular profile they resemble rather the homologous elements of *Manticolepis rhenana* than the generalised P_2 elements attributed to *M. domanicensis* by Klapper and Foster (1993).

Mesotaxis? *simpla* (Ziegler and Sandberg, 1990) (Fig. 32M–U).—Ramiform elements associated in sample Wtr-31 with the platform ones are of a rather robust appearance and somewhat resemble those of *M.*? *domanicensis*, but no generically diagnostic symmetrical element has been found.

Mesotaxis? *proversa* (Ziegler, 1958) (Fig. 32A, B).—The material from Wietrznia, sample Wtr-13, is too poor to enable any apparatus restoration. The possible match with P_2 (oz) elements is rather arbitrarily chosen, although it is not inconsistent with their identification by Boogaard and Kuhry (1979) and Klapper and Foster (1993). Note, however, that the morphology of P_2 elements in early palmatolepidids is rather generalised and not less variable than in other members of the family. Because of a morphological similarity to the species from Włochy identified here as *Mesotaxis bohemica*, attribution to the same genus seems likely.

Kielcelepis ljashenkoae (Ovnatanova, 1976) (Fig. 33A–H).—This is the oldest palmatolepidid with documented loss of the medial process in S_0 (tr) element, represented at Wietrznia in samples Wtr-15 and Wtr-16. Unfortunately the species is invariably associated with other, more advanced palmatolepidids which makes identification of the elements uncertain.

Kielcelepis? (or *Lagovilepis*) *jamieae* (Ziegler and Sandberg, 1990) (Fig. 34A–P).—In sample Wtr-20 from the late Frasnian of Wietrznia, S_0 (tr) elements with the *Kielcelepis* morphology (Fig. 34F) co-occur with those showing an incipient bifurcation of processes (Fig. 34G). This is interpreted here

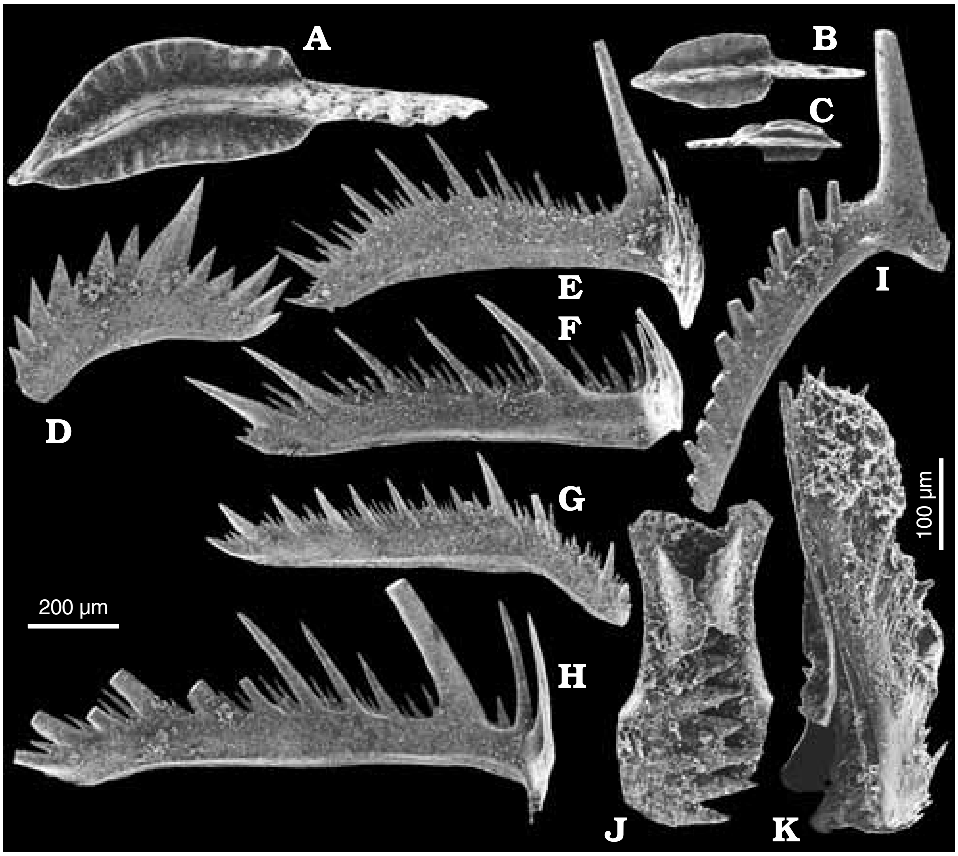


Fig. 24. Earliest Famennian *Polygnathus semicostatus* Branson and Mehl, 1934 from Płucki, sample Pł-16, P_1 (sp) elements ZPAL CXVI/1016, 1020, and 1017 (**A**–**C**) and cluster ZPAL CXVI/1019 of two juvenile elements in occlusion (**J**), P_2 (oz) element ZPAL CXVI/1021 (**D**), S_0 (tr) element ZPAL CXVI/1022 (**E**), S_1 (lo) element ZPAL CXVI/1023 (**F**), S_2 (pl) element ZPAL CXVI/1024 (**G**), S_{3-4} (ke-hi) element ZPAL CXVI/1026 (**H**), M (ne) element ZPAL CXVI/1018 (**I**). Cluster ZPAL CXVI/457 of juvenile elements probably belonging to *Polygnathus webbi* Stauffer, 1938 from the latest Frasnian (Upper Kellwasserkalk; sample Pł-391) of Płucki (**K**) shows the spatial arrangement of elements S_1 (lo), S_2 (pl) and two S_3 (hi). Magnifications shown by the bar scale on left, except for **J**, **K** with their own scale.

as an expression of the transitional position of the species. The primitive appearance of M (ne) elements places the species between the *Kielcelepis* and *Lagovilepis* grades. The concept of *K.*? *jamiae* is controversial (Klapper and Becker 1999: 343). Only a complete apparatus reconstruction based on the type population, which comes from the bed of the Adorf Limestone 1.2 m below the base of the Lower Kellwasserkalk at the Steinbruch Schmidt, Braunau near Bad Wildungen, Germany, may resolve it.

Kielcelepis hassi (Müller and Müller, 1957) (Fig. 33I–S).—I matched surprisingly advanced (as for their occurrence at Wietrznia together with *Kielcelepis*) P_1 (sp) elements with P_2 (oz) elements virtually lacking platform, S_0 (tr) element from sample Wtr-16 lacking the medial process (Fig. 33M), and M (ne) elements with a wide angle between processes. In the last character it resembles *Manticolepis*. The remaining elements of the apparatus are not so derived, being relatively robust if compared with the late Frasnian members of the same clade. Possible relationship to later species of *Manticolepis* is thus not certain. The P_2 (oz) element included in the apparatus by Klapper and Foster (1993) is somewhat different.

Manticolepis gigas (Miller and Youngquist, 1947) (Figs. 36A–N, 37A–M, 38A–H).—Very rich sample Wtr-5 from the mid-Frasnian of Wietrznia II quarry enabled a rather reliable apparatus reconstruction which is supported by sample Wtr-23. Distinctions from *Manticolepis muelleri* (Klapper and Foster, 1986) are weak. The profile of P_2 (oz) elements is less arched, with gently decreasing height of the carina towards the dorsal process end. The elements show some variability, the ventral process being generally straight but in some specimens bent in a way resembling *M. muelleri*. A bifurcation of processes in S_0 (tr) elements occurs almost invariably (but see Figs. 36H, 37G) but is generally much weaker than in the latest Frasnian populations *of M. winchelli* (however, such weakly bifurcating elements have been found also in sample Wtr-18 which may represent a relic population). The specimens from sample Wtr-5 show an extensive variability in the platform shape of P_1 (sp) elements, which are of rather generalised morphology. Possibly, the population is transitional between the *M. winchelli* lineage and that leading to *M. muelleri* and *M. rhenana*. The type population from the Sweetland Creek Shale of Iowa (see comments in Klapper and Foster 1993) is associated with *Ancyrognathus symmetricus* Branson and Mehl, 1934 (which proves a rather late Frasnian age) but also *Ancyrodella gigas* Youngquist, 1947, which makes it slightly older that the transition to *A. curvata*.

Manticolepis rhenana (Ziegler, 1958) (Fig. 40A–F, G–M).—Boogaard and Kuhry (1979) correlated (as *Palmatolepis gigas*) a P_2 (oz) element typical of this species with P_1 (sp) element which is closely similar to those of *M. rhenana* with its characteristic angular profile. They may represent an early population of *M. rhenana*. Klapper and Foster (1993) identi-

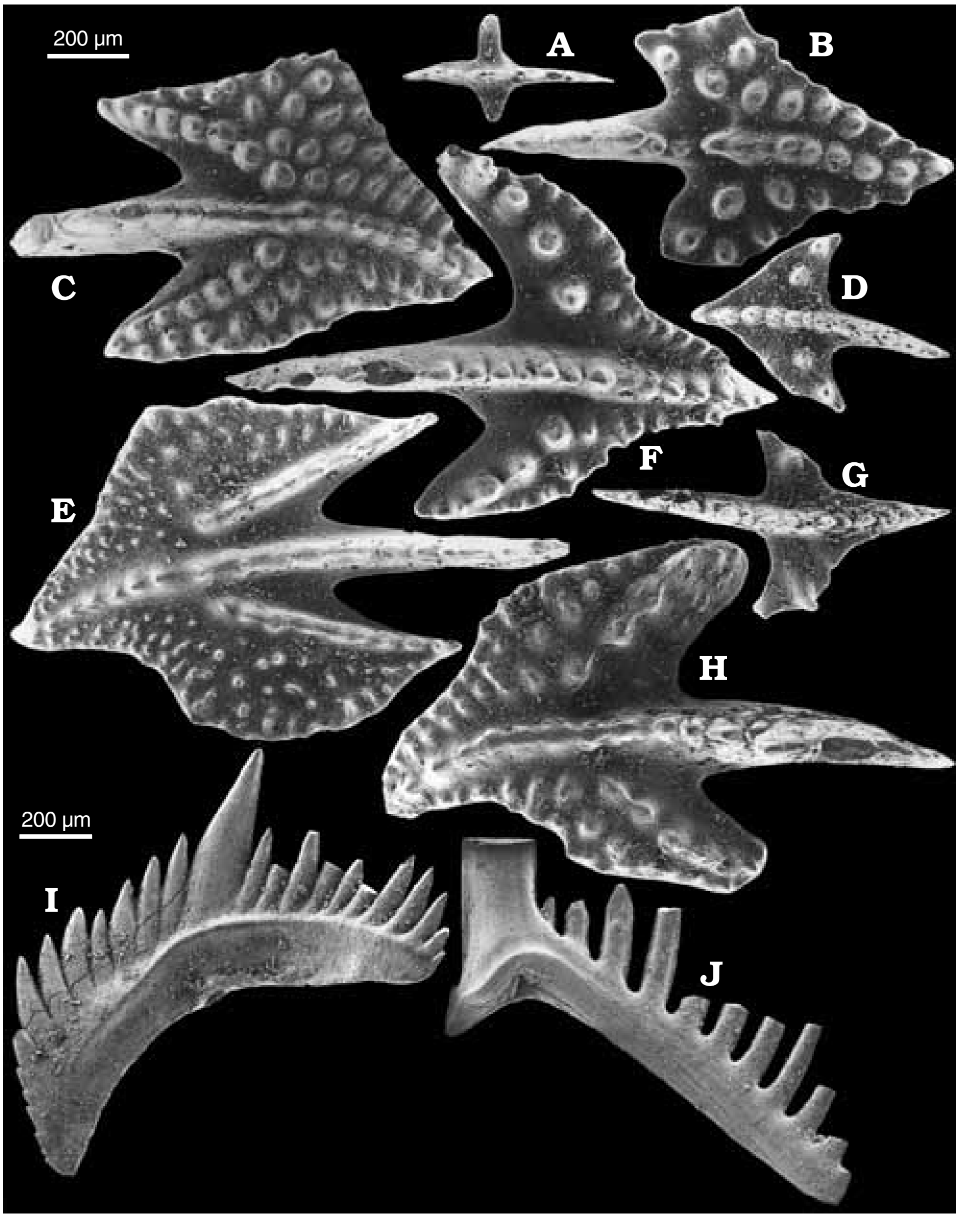


Fig. 25. Early *Ancyrodella* from the early Frasnian of Wietrznia I and mid-Frasnian of Wietrznia II quarries. **A**, **B**. *Ancyrodella rotundiloba* (Bryant, 1921) from sample Wtr-11, P_1 (sp) elements ZPAL CXVI/1054 and 1055. **C**. *Ancyrodella rugosa* Branson and Mehl, 1934 from sample Wtr-13, P_1 element ZPAL CXVI/854. **D**–**J**. *Ancyrodella nodosa* Ulrich and Bassler, 1926 from samples Wtr-4a (**D**) and Wtr-5, P_1 elements ZPAL CXVI/788, 739, 732, 733, and 731 (**D**–**H**), P_2 (oz) element ZPAL CXVI/734 (**I**), and M (ne) element ZPAL CXVI/707 (**J**). Magnifications shown by the bar scale in the upper left corner, except for **F** and **H**–**J** with their own scale.

fied P_2 (oz) element of the apparatus in the typical form of the species. Its shape differs somewhat from the Polish specimens. The non-platform elements of the apparatus are robust and easily identifiable, although rare in the studied samples. The apparatus is very advanced evolutionarily, which is expressed in a very early ontogenetically bifurcation of processes in the symmetrical element (Fig. 40B, H) and fan-like arranged inner denticles of the M (ne) elements (Fig. 40G, J). When associated with other species of *Manticolepis*, P_1 (sp) elements of *M. rhenana* are easily identifiable owing to a characteristic convexity, which especially concerns the rostral field of the platform. They are usually finely tuberculated. There seems to be a gradual transition from *M. muelleri* and some populations may be difficult to classify.

Manticolepis winchelli (Stauffer, 1938) (Fig. 39A–Q).—This is a well-known species. The first incomplete restoration of the apparatus (as *Palmatodella hassi*) was proposed by Philip and McDonald (1975: fig. 5), based on a sample from the classic German locality Steinbruch Schmidt, 0.43 m below the Lower Kellwasserkalk. They did not identify the actual P_2 (oz) elements and included S_1 (lo) elements of *Pluckidina* in it. The apparatus was completely reconstructed (as *Palmatolepis subrecta*) by Boogaard and Kuhry (1979) and then by Klapper and Foster (1993). Note however, that the P_1 (sp) element illustrated by by Boogaard and Kuhry (1979) corresponds closer to the morphology considered to be diagnostic for *Lagovilepis bogartensis* by Klapper and Foster (1993; as well as Schülke 1998). This is an expression of the tremendous population variability of the platform elements, which make them of little use in species identification, as shown above in the discussion on population variability and species demarcation in the latest Frasnian palmato-

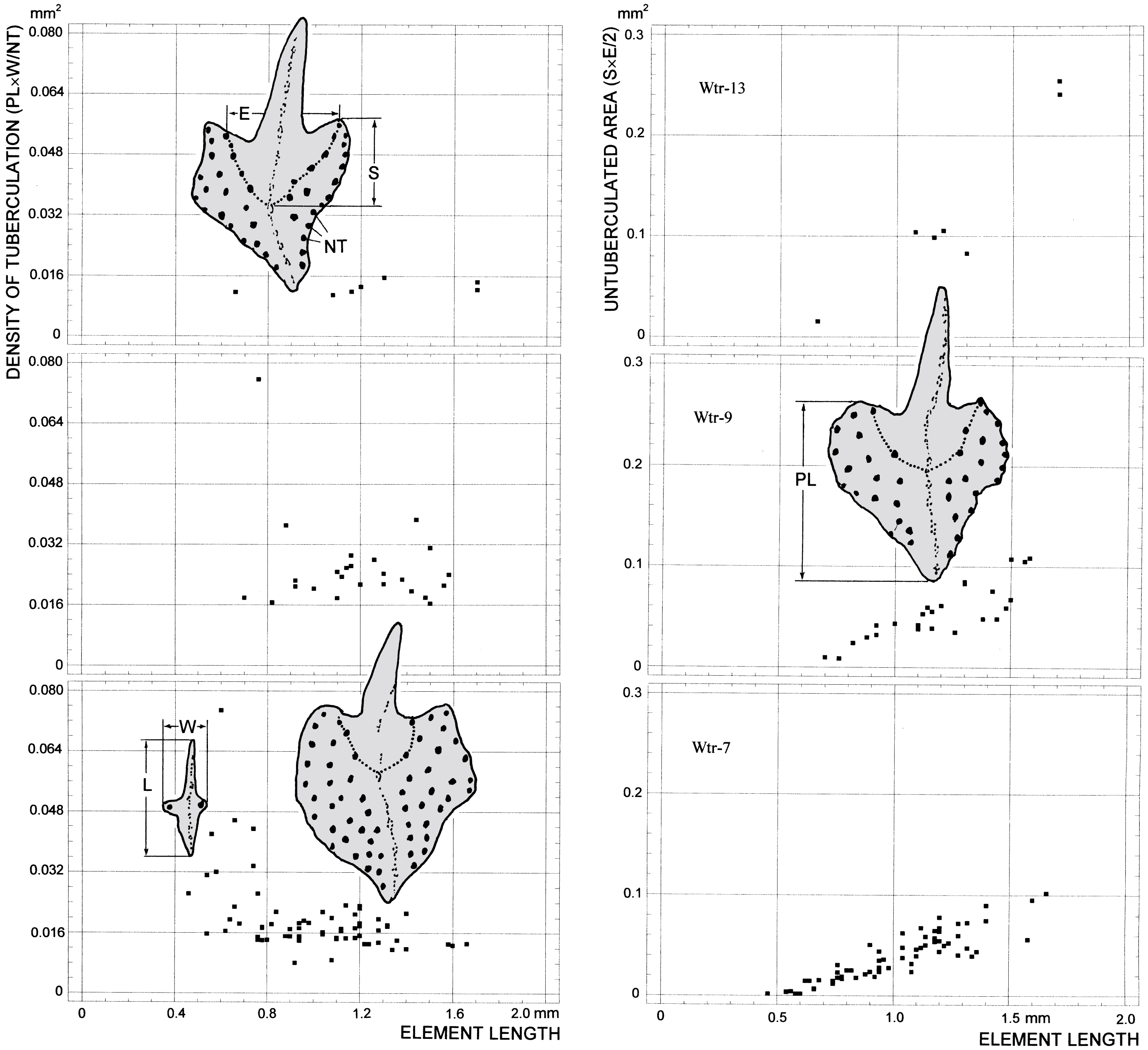


Fig. 26. Variability and species distinctions of P_1 (sp) elements in early *Ancyrodella*. Scattergrams of density of tuberculation quantified as a ratio of approximated platform area (platform length PL multiplied by its width W) to the number of denticles (except those of carina) and approximated area of the smooth surface on the ventral end of the platform (length of this area S multiplied by its lateral extend E) against element length which serves as an approximation of ontogenetic stage. Three successive samples from Wietrznia are represented by pairs of these scattergrams. That of sample Wtr-7 is *A. rotundiloba* (Bryant, 1921), sample Wtr-9 represents *A. alata* (Glenister and Klapper, 1966), and sample Wtr-13 *A. rugosa* Branson and Mehl, 1934.

lepidids. The type population of *M. winchelli* occurs in the Upper Olentangy Shale. It may be roughly coeval with the lower cephalopod limestone population from sample Pł-22 at Płucki. The *Ancyrodella* co-occurring with the type is represented by P_1 (sp) specimens with both unbranched and branched processes (Over and Rhodes 2000) thus seems to be close to transition from *A. gigas* (?= *A. buckeyensis*) to *A. curvata*. The phylogenetically most sensitive symmetrical element of the apparatus in the Płucki population shows generally good development of lateral processes. They are weak only in juvenile elements (Fig. 39E).

Lagovilepis bogartensis (Stauffer, 1938) (Figs. 41A–O, 42A–N, 43).—This apparatus is the best known among the Frasnian palmatolepidids. Its statistical reconstruction (Klapper and Foster 1993) is well supported by numerous clusters from the European Upper Kellwasserkalk (Lange 1968; Schülke 1997) and by the new material from sample Pł-391 at Płucki.

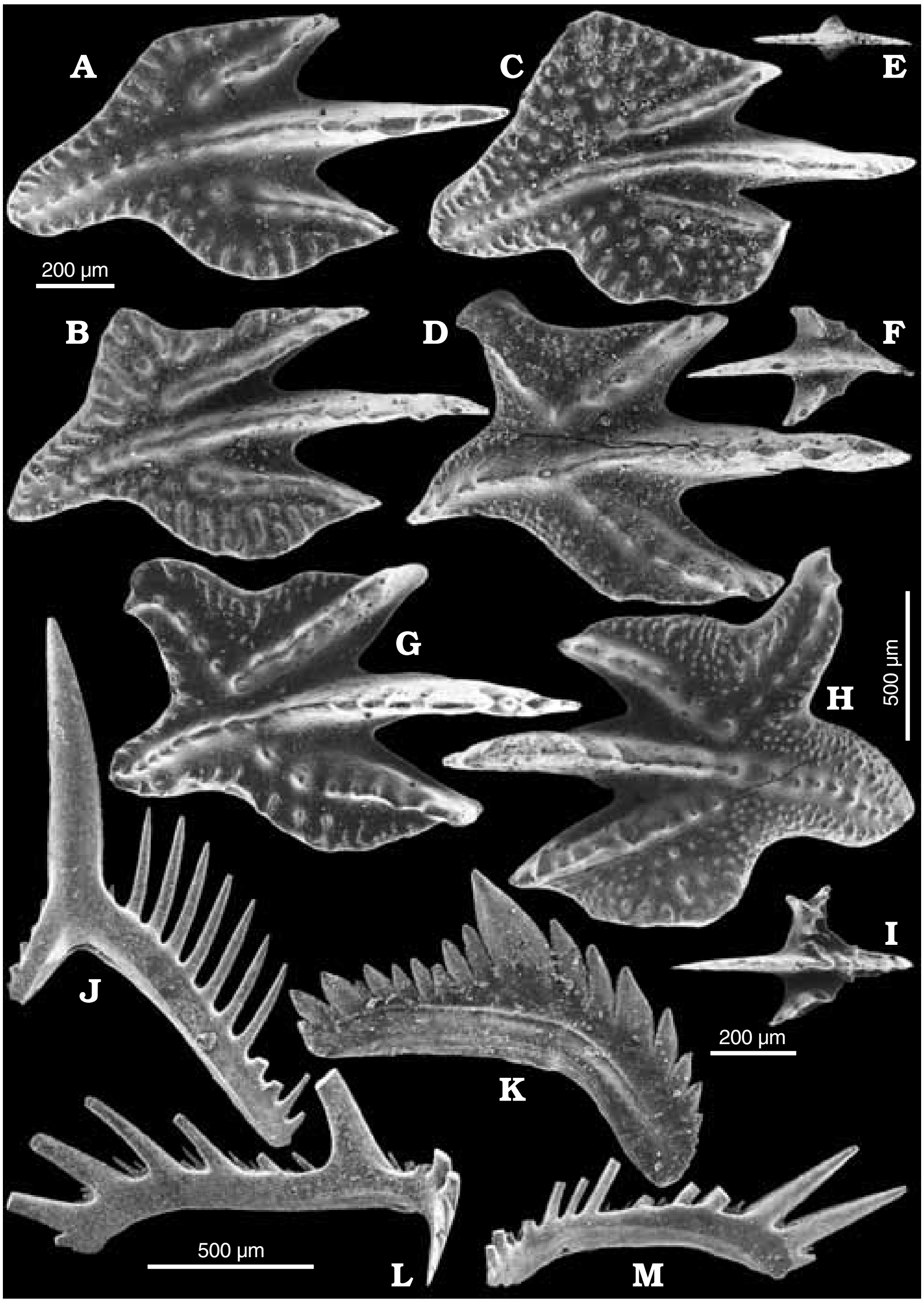


Fig. 27. Late *Ancyrodella* from the late Frasnian of Płucki. **A**–**F**, **K**. *Ancyrodella lobata* Branson and Mehl, 1934 from the lower cephalopod limestone, sample Pł-22, P_1 (sp) elements ZPAL CXVI/627, 625, 626, 624, 630, and 629 (**A**–**F**), and P_2 (oz) element ZPAL CXVI/632 (**K**). **G**–**J**, **L**, **M**. *Ancyrodella curvata* Branson and Mehl, 1934 from the Upper Kellwasserkalk, sample Pł-391, P_1 elements ZPAL CXVI/483, 1184, 484, 490, 632, 489, and 487 (**G**–**I**), M (ne) element ZPAL CXVI/490 (**J**), S_{3-4} (ke-hi) element ZPAL CXVI/489 (**L**), and S_2 (pl) element ZPAL CXVI/487 (**M**). Magnifications shown by the bar scale in the upper left corner, except for **G**, **J**, **L**, **M**, and **H** with their own scales.

Klapperilepis praetriangularis (Ziegler and Sandberg, 1988) (Figs. 44–46).—Both in the lower (sample Pł-22; Fig. 44) and upper (sample Pł-391; Fig. 45) cephalopod limestones at Płucki complete sets of the apparatus elements were identified. The late form of the species from the earliest Famennian at Płucki (samples Pł-20 and Pł-16) is documented with clusters of elements (Fig. 46K, Q), some representing significant portions of the apparatus. Schülke (1999) restored apparatuses of related early Famennian forms of the genus.

Conditolepis? aff. *linguiformis* (Müller, 1956) (Fig. 35B, C).—The apparatus of *C.*? *linguiformis* remains unknown. The only sample in my disposal in which this species dominates among the palmatolepidids is that from the Olentangy Shale, taken at Lazarus Camp, Ohio. *C.*? *linguiformis* co-occurs there with *M. winchelli* and *Avignathus*, but also with an early *Ancyrodella* without bifurcation of lobes (Fig. 35E–J). According to Over and Rhodes (2000), the Frasnian–Famennian boundary is within the green Upper Olentangy Shale containing a mixed latest Frasnian (e.g., *Lagovilepis bogartensis*, *C.*? *linguiformis*) and earliest Famennian (e.g., *K. triangularis*, *K. delicatula*, *P. subperlobata*) conodont fauna but this does not seem the case in the studied sample. Boogaard and Kuhry (1979) identified the P_2 (oz) element in a sample from Steinbruch Schmidt as having a wide platform and sinuous course of the carina. It is not unlike the P_2 (oz) element from Olentangy Shale illustrated here (Fig. 35D, G). Those authors pointed out the similarity in both platform elements to those of *Conditolepis crepida* (Sannemann, 1955), but the rest of the apparatus as identified here does not support such affinity.

Diagnoses of new and emended conodont taxa

Class Conodonta Eichenberg, 1930
Order Panderodontida Sweet, 1988
Family Belodellidae Khodalevich and Chernich, 1973

Remark.—In the Late Devonian species, S_0 (tr) elements shape is the most diagnostic, with their external surface flat in *B. resima* (Philip, 1965), very strongly concave in *B.*? *tenuiserrata* sp. nov. and raised in *B. robustidentata* sp. nov. The new species introduced below differ from each other also in orientation of denticles, proclined in *B.*? *tenuiserrata* sp. nov. and perpendicular in *Belodella minutidentata* sp. nov.

Genus *Belodella* Ethington, 1959

Type species: *Belodus devonicus* Stauffer, 1940.

Belodella? *tenuiserrata* sp. nov.

Holotype: ZPAL CXVI/692; S_0 (tr) element (Fig. 5B).

Type horizon and locality: Sample Wtr-5, Wietrznia II quarry near Kielce, mid-Frasnian.

Derivation of the name: Referring to extremely fine denticulation of elements.

Diagnosis.—Except for the M (ne) location, the edge of elements serrated with very small, proclined denticles.

Distribution.—Mid-Frasnian of Wietrznia in the Holy Cross Mountains, Poland (see Table 1 and Fig. 4).

Belodella minutidentata sp. nov.

Holotype: ZPAL CXVI/692; S_0 (tr) element (Fig. 5D).

Type horizon and locality: Sample Wtr-5, Wietrznia II quarry near Kielce, mid-Frasnian.

Derivation of the name: Referring to fine denticulation.

Diagnosis.—Except for the M (ne) location, the edge of elements serrated with minute sharp, perpendicularly arranged denticles.

Distribution.—Early to mid-Frasnian of Wietrznia in the Holy Cross Mountains, Poland (see Table 1 and Fig. 4).

Belodella robustidentata sp. nov.

Holotype: ZPAL CXVI/686; S_0 (tr) element (Fig. 5Q).

Type horizon and locality: Sample Wtr-5, Wietrznia II quarry near Kielce, late Frasnian.

Derivation of the name: Referring to robust denticulation.

Diagnosis.—Only a few robust denticles arm the edge of elements.

Distribution.—Early to mid-Frasnian of Wietrznia in the Holy Cross Mountains, Poland (see Table 1 and Fig. 4).

Order Prioniodontida Dzik, 1976
Family Icriodontidae Müller and Müller, 1957
Genus *Icriodus* Branson and Mehl, 1934

Type species: *I. expansus* Branson and Mehl, 1934.

Icriodus kielcensis sp. nov.

Holotype: ZPAL CXVI/714 (Fig. 6I).

Type horizon and locality: Sample Wtr-5, Wietrznia II quarry in Kielce, late Frasnian.

Derivation of the name: Referring to the location of its type locality in Kielce.

Diagnosis.—Very narrow icrion with the middle row of denticles asymmetrically disposed, tending to disappear at some distance from the cusp; one of the lateral rows in more or less well expressed continuity with the cusp.

Distribution.—Only the mid-Frasnian of Wietrznia (see Table 2 and Fig. 4).

Incertae ordinis
Family Playfordiidae nov.

Diagnosis.—Elements of the apparatus with very thin, finely denticulated blades and very wide basal cavity; little shape differentiation within the apparatus.

Remark.—Despite its originally suggested icriodontid affinities, the apparatus of *Playfordia primitiva* (Bischoff and Ziegler, 1957) is basically different from those of the icriodontids in not showing distinction between the platform series and the symmetry transition series elements, as discussed above (Fig. 15). Some remote similarities to the Early Carboniferous *Eotaphrus* can be traced, but there is too long time hiatus separating these genera. Symmetrical elements of *Playfordia* resemble superficially *Ancyrognathus ancyrognathoideus* (Ziegler, 1958) (see Wang 1994: pl. 10: 1) but to make them homologous would require to assume that the basal cone of *Playfordia* is an extremely thin platform derived from that of *Ancyrognathus*. They also differ in surface ornamentation (see Figs. 15B and 28), which in the ancyrognathids, as well as in *Dinodus*, is covered with cell imprints and not finely tuberculated. Moreover, the stratigraphic occurrence of *Playfordia* makes it derivation from *Ancyrognathus* unlikely.

Genera included.—Only *Playfordia* Glenister and Klapper, 1966.

Order Ozarkodinida Dzik, 1976
Family Prioniodinidae Bassler, 1925
Genus *Ligonodina* Bassler, 1925

Type species: *L. pectinata* Bassler, 1925.

Emended diagnosis.—The anteriormost element of the apparatus (ne) with a wide and flat cusp.

Nomenclatorial comment.—No doubt that *Ligonodina*, *Lonchodina*, and *Hibbardella* are closely related. Jeppson

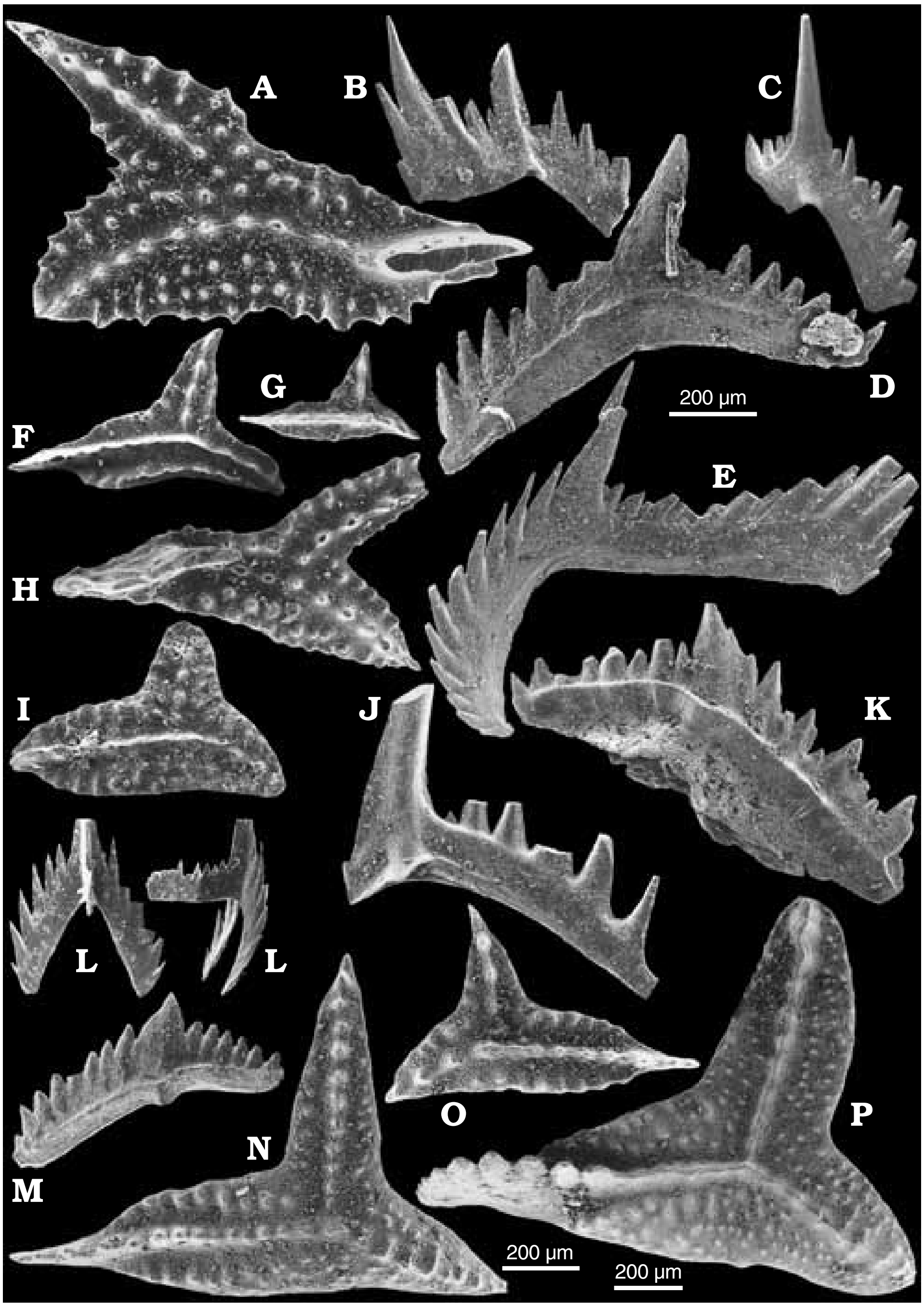


Fig. 28. *Ancyrognathus* from the Frasnian of the Holy Cross Mountains. **A**–**D**, ?**B**, **C**, **E**. *Ancyrognathus ubiquitus* Sandberg et al., 1988 from the Upper Kellwasserkalk at Płucki, sample Pł-391, P_1 (sp) element ZPAL CXVI/410 (**A**), P_2 (oz) element ZPAL CXVI/411 (**D**), possibly belonging to this genus S_2 (pl) element ZPAL CXVI/398 (**B**), S_1 (lo) element ZPAL CXVI/404 (**C**), and $S_{3–4}$ (ke-hi) element ZPAL CXVI/403 (**E**). **F**–**I**, **M**, ?**L**. *Ancyrognathus asymmetricus* (Ulrich and Bassler, 1926) from the lower cephalopod limestone at Płucki, sample Pl-22, P_1 element ZPAL CXVI/636, 634, 639, and 637 (**F**–**I**), P_2 element ZPAL CXVI/641 (**M**) and possibly belonging to this genus S_0 (tr) element ZPAL CXVI/642 (**L**). **K**, **M**–**P**, ?**L**, ?**J**. *Ancyrognathus triangularis* Youngquist, 1945 from the late Frasnian of Wietrznia II quarry, sample Wtr-5, P_2 (oz) element ZPAL CXVI/743 (**K**), P_1 elements ZPAL CXVI/741, 742, and 740 (**N**–**P**), possibly belonging to this genus M (ne) element ZPAL CXVI/747 (**J**), and S_0 (tr) element ZPAL CXVI/642 (**L**). Magnifications shown by the bar scale in the upper right corner, except for **N** and **P** with their own scales.

(1969), while proposing the first apparatus restoration of a prioniodinid, made choice of *Ligonodina* as the generic name and this has to be followed, contrary to later choices of *Hibbardella* (Clark et al. 1981) and *Prioniodina* (Sparling 1981). *Delotaxis* Klapper and Philip, 1971 should not be used for Devonian species because its type species, the Silurian *D. elegans* (Walliser, 1964) is of a very primitive aspect. Its biramous S_0 (tr) element, weakly asymmetric S_2 (pl) elements, and M (ne) elements with short processes and a slightly basally bent cusp resemble rather the Ordovician *Oulodus* Branson and Mehl, 1933. *Oulodus* differs from *Delotaxis* only in having even more primitive M (ne) elements with radiating denticles, not parallel to the cusp as is the case in virtually all the post-Ordovician ozarkodinids.

Genus *Dyminodina* nov.

Type species: *Dyminodina planidentata* sp. nov.

Derivation of the name: From the Dyminy reef structure in the Holy Cross Moutains.

Diagnosis.—Generally flat and sharp-edged denticulation of elements; M (ne) element with short, transversely oriented inner process.

Species included.—The type species, *D. anterodenticulata* sp. nov., and *D. kovalensis* sp. nov.

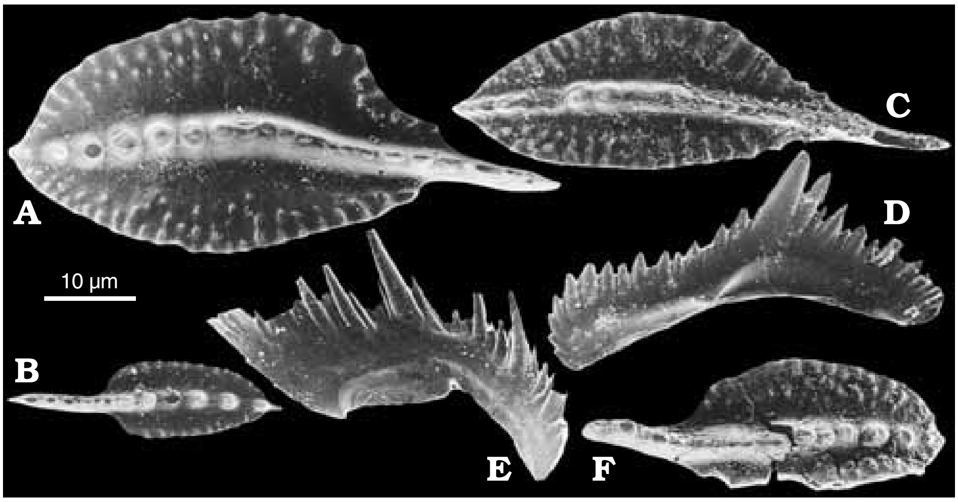


Fig. 29. *Klapperina* from the early Frasnian of the Holy Cross Mountains. **A**–**E**. *Klapperina* sp. from Wietrznia, sample Wtr-9, P_1 (sp) elements ZPAL CXVI/1083, 1082, and 1081 (**A**–**C**), P_2 (oz) element ZPAL CXVI/1093 (**D**), and S_2 (pl) element ZPAL CXVI/1084 (**E**). **F**. *Klapperina* sp. indet. from Włochy, sample Wł-R/A1, P_1 (sp) element ZPAL CXVI/916.

Dyminodina planidentata sp. nov.

Fig. 9A–G.

Holotype: M (ne) element ZPAL CXVI/606 (Fig. 9G).

Type horizon and locality: Sample Pł-22 from the lower cephalopod limestone at Płucki in the Holy Cross Mountains, Poland, late Frasnian.

Derivation of the name: Referring to the flat denticulation of elements.

Diagnosis.—Generally albid denticles, M (ne) element with gentle, parabolic outline of the smooth outer process and short inner process with fan-like arrangement of denticles (“cyrtoniodus” morphology).

Distribution.—Late Frasnian (see Table 2 and Fig. 4).

Dyminodina anterodenticulata sp. nov.

Fig. 9H–J.

Holotype: M (ne) element ZPAL CXVI/390 (Fig. 9I).

Type horizon and locality: upper Kellwasserkalk at Płucki, sample Pł-391, Holy Cross Mountains, Poland, latest Frasnian.

Derivation of the name: Referring to denticulated ventral (conventionally “anterior”) process of the diagnostic element.

Diagnosis.—Usually the M (ne) element with two minute denticles on the outer process, otherwise similar to the type species of the genus.

Distribution.—Latest Frasnian and earliest Famennian of Płucki and Kowala in the Holy Cross Mountains, Poland (see Table 2 and Fig. 4).

Dyminodina kovalensis sp. nov.

Fig. 9K–Q.

Holotype: M (ne) element ZPAL CXVI/1197 (Fig. 9Q).

Type horizon and locality: Topmost Frasnian horizon at the Kowala Quarry (set H-3 of Racki and Baliński 1998), sample Ko-151, Holy Cross Mountains, Poland, latest Frasnian.

Derivation of the name: From the type locality.

Diagnosis.—Elongated ventral (“anterior”) process of the M (ne) element, remaining elements with flat denticulation.

Distribution.—Latest Frasnian and early Famennian of the Holy Cross Mountains (see Table 6 and Fig. 4).

Genus *Pluckidina* nov.

Type species: *Pluckidina lagoviensis* sp. nov.

Derivation of the name: From the village Płucki.

Diagnosis.—Elements of the apparatus with a tendency to angular lateral bending, S_3 (ke) and S_4 (hi) elements morphologically distinct, with long and straight outer processes.

Species included.—Type species, *P. tortoides* (Sparling, 1981), *P. kielcensis* sp. nov., and *P. nonaginta* (Klapper et al., 1996), *P. lipperti* (Bischoff, 1956).

Pluckidina kielcensis sp. nov.

Fig. 10.

Holotype: P_1 (sp) element ZPAL CXVI/1063 (Fig. 10A).

Type horizon and locality: Wietrznia I quarry in Kielce, sample Wtr-9; early Frasnian—associated with *Ancyrodella rotundilobata* and *Mesotaxis asymmetrica*.

Derivation of the name: From Kielce, the capital city of the region.

Diagnosis.—External process of the S_3 (ke) elements with gently curved, M (ne) elements with relatively long inner process and acute outer ones.

Remark.—The apparatus of *Pluckidina kielcensis* sp. nov. has been already illustrated (as *Prioniodina* sp.) in Dzik (1991b). Both elements M (ne) and S_2 (pl) in this species are of a generalised appearance, which make it different from *P. slupiensis* sp. nov. *Prioniodina tortoides* Sparling, 1981 seems to be closely related and may be ancestral to *P. kielcensis* sp. nov.

Distribution.—Early Frasnian of Wietrznia in the Holy Cross Mountains, Poland (see Table 1 and Fig. 4).

Pluckidina slupiensis sp. nov.

Fig. 11.

Holotype: S_2 (pl) elements ZPAL CXVI/877 (Fig. 11H).

Type horizon and locality: Early Frasnian sample Wł-R/A1from Włochy near Nowa Słupia, Holy Cross Mountains.

Derivation of the name: From Nowa Słupia, a nearby historical village.

Diagnosis.—Strongly twisted S_2 (pl) elements with elongated processes.

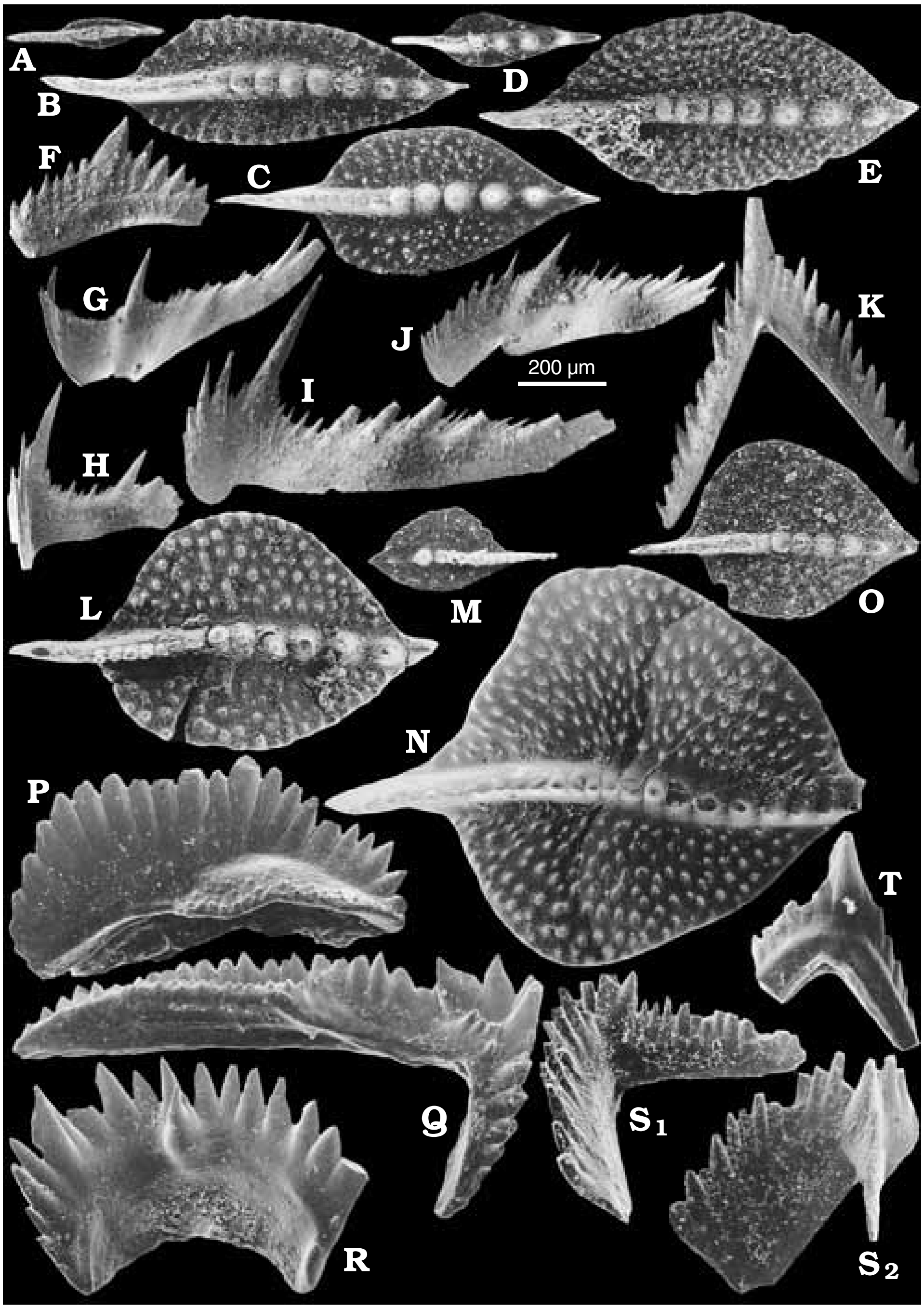


Fig. 30. Early *Mesotaxis* from the early Frasnian of Wietrznia I quarry and Włochy. **A**–**K**. *Mesotaxis falsiovalis* Sandberg et al., 1989 from sample Wtr-11 (see also Dzik 1991b), P_1 (sp) elements ZPAL CXVI/1045, 1041, 1043, 1040, and 1042 (**A**–**E**), P_2 (oz) element ZPAL CXVI/1213 (**F**), S_1 (lo) element ZPAL CXVI/1214 (**G**), S_0 (tr) element ZPAL CXVI/1215 (**H**), $S_{3–4}$ (ke-hi) element ZPAL CXVI/1216 (**I**), S_2 (pl) element ZPAL CXVI/1217 (**J**), and M (ne) element ZPAL CXVI/1218 (**K**). **L**–**T**. *Mesotaxis asymmetrica* (Bischoff and Ziegler, 1957) from Włochy, sample Wł-R/A1, P_1 element ZPAL CXVI/915 (**L**) and from Wietrznia, sample Wtr-9 (**M**–**T**), P_1 elements ZPAL CXVI/1085, 1087, and 1086 (**M**–**O**), P_2 element ZPAL CXVI/1088 (**P**), $S_{3–4}$ element ZPAL CXVI/1089 (**Q**), S_1 elements ZPAL CXVI/1090 (**R**), S_0 element ZPAL CXVI/1091 (**S**), and M element ZPAL CXVI/1092 (**T**).

Distribution.—Early Frasnian of Włochy in the Holy Cross Mountains, Poland (see Table 1 and Fig. 4).

Pluckidina robustipegmata sp. nov.

Fig. 12A–F.

Holotype: P_1 (sp) element ZPAL CXVI/701 (Fig. 12A).

Type horizon and locality: Mid-Frasnian sample Wtr-5 from Wietrznia II quarry in Kielce.

Derivation of the name: Referring to the robust appearance of the incipient platform that makes a kind of connection (Greek *pegma*) between the element processes.

Diagnosis.—Mature P_1 (sp) and P_2 (oz) elements tending to develop a narrow platform, M (ne) elements with relatively long inner process.

Remark.—The available material is too small to be sure whether two types of the $S_{3–4}$ (ke-hi) series elements are represented or not. Generic attribution is based on the presence of the S_1 (lo) element with strongly bent processes and general morphology of the platform series elements—despite *Ligonodina*-like morphology of the M (ne) elements, the P_1 (sp) elements are not sinuous.

Distribution.—Mid- and late Frasnian of Wietrznia in the Holy Cross Mountains, Poland (see Table 2 and Fig. 4).

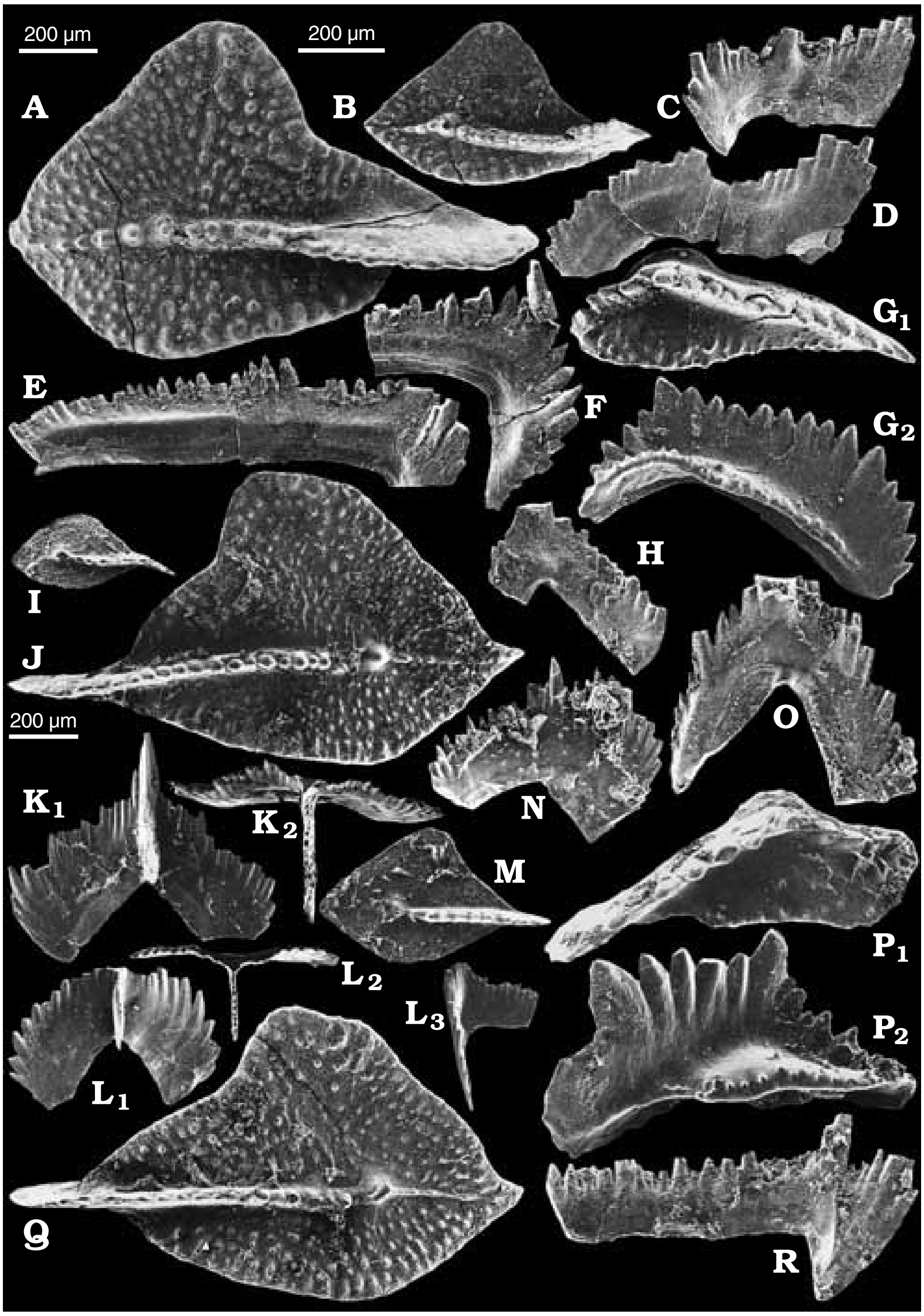


Fig. 31. Late Frasnian *Mesotaxis* from Włochy. **A**–**H**. *Mesotaxis punctata* (Hinde, 1879) from sample Wł-R/A1, P_1 (sp) elements ZPAL CXVI/898 and 899 (**A**, **B**), S_1 (lo) element ZPAL CXVI/901 (**C**), S_2 (pl) element ZPAL CXVI/902 (**D**), $S_{3–4}$ (ke-hi) elements ZPAL CXVI/903 and 904 (**E**, **F**), P_2 (oz) element ZPAL CXVI/900 (**G**), and M (ne) elements ZPAL CXVI/905 (**H**). **I**–**R**. *Mesotaxis bohemica* (Klapper and Foster, 1993) from sample Wł-R/C1, P_1 elements ZPAL CXVI/921, 918, 920 and 919 (**I**, **J**, **M**, **Q**), S_0 (tr) elements ZPAL CXVI/924 and 924 (**K**, **L**), S_2 element ZPAL CXVI/925 (**N**), M element ZPAL CXVI/927 (**O**), P_2 element ZPAL CXVI/922 (**P**), and $S_{3–4}$ element ZPAL CXVI/926 (**R**). Magnifications shown by the bar scale in the upper left corner, except for **B** and **J** with their own scales.

Pluckidina lagoviensis sp. nov.

Fig. 13A–H.

Holotype: S_3 (ke) element ZPAL CXVI/613 (Fig. 13G).

Type horizon and locality: Płucki near Łagów, sample Pł-22, late Frasnian.

Derivation of the name: From Łagów, a town near the type locality.

Diagnosis.—Albid denticles, P_1 (sp) element weakly bent, S_3 (ke) element with linearly arranged long processes.

Distribution.—Lower cephalopod limestone at Płucki in the Holy Cross Mountains, Poland (see Table 4 and Fig. 4).

Family Polygnathidae Bassler, 1925

Genus *Nicollidina* nov.

Type species: *Spathognathodus brevis* Bischoff and Ziegler, 1957.

Derivation of the name: In honour of Robert S. Nicoll, who restored the apparatus of the type species.

Diagnosis.—Minute elements with reduced medial process in S_0 (tr) element and shortened processes in S_1 (lo) and S_2 (pl) elements which still preserved linear arrangement.

Remarks.—Species included here in this new genus were previously classified in *Ozarkodina* Branson and Mehl,

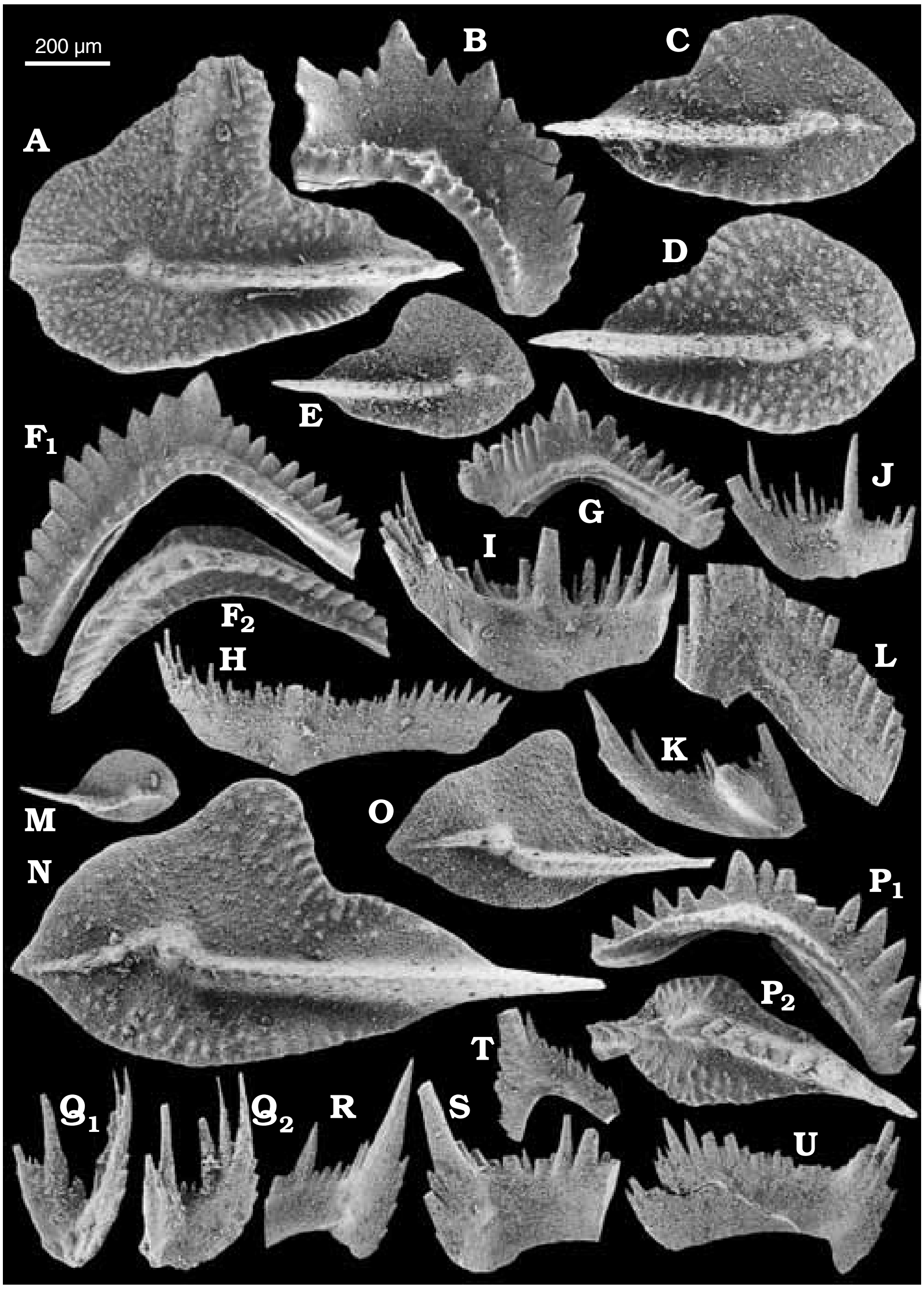


Fig. 32. Early palmatolepidids from the mid-Frasnian of Wietrznia. **A**, **B**. *Mesotaxis*? *proversa* (Ziegler, 1958) from Wietrznia, sample Wtr-13; P_1 (sp) element ZPAL CXVI/858 (**A**) and P_2 (oz) elements ZPAL CXVI/859 (**B**). **C**–**L**. *Mesotaxis*? *domanicensis* (Ovnatanova, 1976) from Wietrznia, sample Wtr-30 (**C**, **G**–**I**), Wtr-15 (**D**–**F**, **J**, **K**), and Wtr-16 (**I**, **L**); P_1 elements ZPAL CXVI/1115, 1106 and 1107 (**C**–**E**), P_2 element ZPAL CXVI/1121 and 1134 (**F**, **G**), S_2 (pl) elements ZPAL CXVI/1116, 1113, and 1111 (**H**–**J**), S_1 (lo) elements ZPAL CXVI/1112 (**K**), and M (ne) element ZPAL CXVI/1104 (**L**). **M**–**U**. *Mesotaxis*? *simpla* (Ziegler and Sandberg, 1990) from sample Wtr-31 and Wtr-16 (**Q**, **T**); P_1 elements ZPAL CXVI/1139, 1137, and 1138 (**M**–**O**), P_2 element ZPAL CXVI/1140 (**P**), S_2 elements ZPAL CXVI/1105 (**Q**), S_{3-4} (ke-hi) elements ZPAL CXVI/1136, 1141, and 1142 (**R**, **S**, **T**), and S_1 element ZPAL CXVI/1114 (**U**).

1933, the type species of which is a Silurian primitive ozarkodinid with biramous S_0 (tr) elements. Its lineage probably survived to the late Palaeozoic (Dzik 1991b) being represented there by species of *Hindeodus* Rexroad and Furnish, 1964 and *Synclydagnathus* Rexroad and Varker, 1992 (misspelled *Syncladognathus* in Dzik 1997). They all show angular profiles of bases of S_0 (tr), S_1 (lo) and S_2 (pl) elements, unlike *N. brevis*. In the latter, the ramiform elements of the apparatus look rather like early juvenile elements of typical polygnathids. Most likely, evolutionary diminution in size resulted in a secondary reduction of the medial process of the S_0 element. *Nicollidina* gen. nov. is thus a secondarily simplified member of the Polygnathidae, not the Spathognathodontidae sensu Dzik 1991b. This is not a unique case. Similar evolutionary transformations took probably place in the evolution of the early Carboniferous *Siphonodella* (Dzik 1997).

Species included.—Along with type species also *N. raaschi* (Klapper and Barrick, 1983) and *N. postera* (Klapper and Lane, 1985).

Distribution.—Eifelian to Frasnian (Klapper and Barrick 1983; Nicoll 1985; Klapper and Lane 1985; Racki 1992).

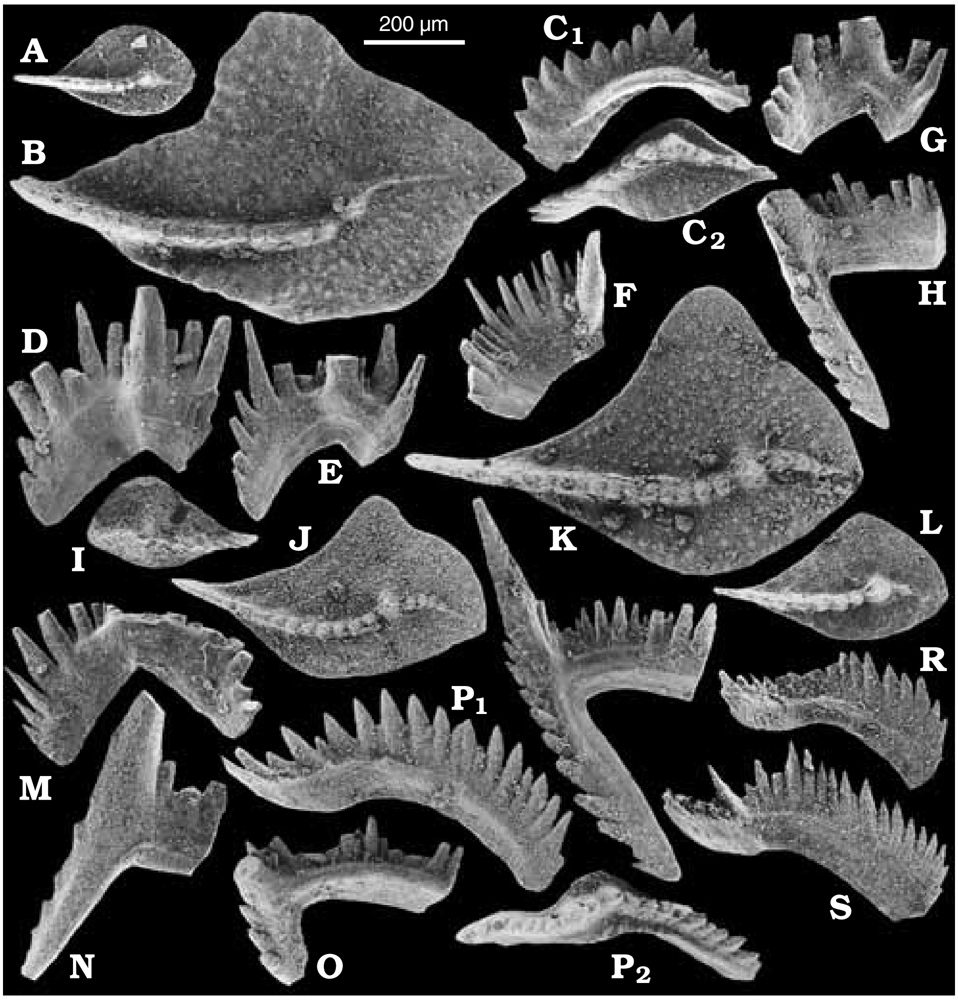


Fig. 33. Palmatolepidids from the mid-Frasnian of Wietrznia. **A**–**H**. *Kielcelepis ljashenkoae* (Ovnatanova, 1976) from Wietrznia, sample Wtr-15; P_1 (sp) elements ZPAL CXVI/1108 and 1120 (**A**, **B**), P_2 (oz) element ZPAL CXVI/1109 (**C**), S_0 (tr) element ZPAL CXVI/1122 (**D**), S_1 (lo) element ZPAL CXVI /1110 (**F**), S_2 (pl) elements ZPAL CXVI/1123 and 1102 (**E**–**G**), and S_{3-4} (ke-hi) element ZPAL CXVI/1124 (**N**). **I**–**S**. *Kielcelepis hassi* (Müller and Müller, 1957) from sample Wtr-16 (**M**, **O**, **S**) and Wtr-30 (**I**–**L**, **N**, **P**–**R**); S_0 element ZPAL CXVI/ 1125 (M), P_1 (sp) elements ZPAL CXVI/ 1130, 1128, 1127, and 1129 (**I**–**L**), M (ne) element ZPAL CXVI/1133 (**N**), S_{3-4} elements ZPAL CXVI/1126 and 1132 (**O**, **Q**), and P_2 elements ZPAL CXVI/1135, 1131, and 1103 (**P**, **R**, **S**).

Genus *Parapolygnathus* Klapper and Philip, 1971

Type species: *Polygnathus angusticostatus* Wittekindt, 1966.

Emended diagnosis.—Polygnathids with gently curved processes of S_1 (lo) elements, robust platform of P_1 (sp) elements, and relatively weakly reclined processes of M (ne) elements.

Remarks.—The genus was originally established by Klapper and Philip (1971) in result of a misidentification of the apparatus. The type species belongs to one of the two main Middle Devonian branches of the polygnathids with robust platforms, the other comprising *P. linguiformis* (see Weddige and Ziegler 1979). They both differ from the type lineage of *Polygnathus* not only in the elaborate platform of the P_1 (sp) elements, but also in a more robust morphology of the M (ne) elements and a less angular appearance of the S_1 (lo) elements (Chatterton 1974; Sparling 1981). There is a need to split the too widely interpreted and species-rich genus *Polygnathus* into more narrowly defined genera and I propose to redefine the genus *Parapolygnathus* for this purpose.

Genus *Ctenopolygnathus* Müller and Müller, 1957

Type species: *Polygnathus angustidiscus* Youngquist, 1945 (?= *Polygnathus brevilamina* Branson and Mehl, 1934).

Emended diagnosis.—Polygnathids with platform that does not reach the dorsal (“posterior”) tip in most of the P_1 (sp) elements even at late ontogenetic stages.

Genus *Avignathus* Lys and Serre, 1957

Type species: *Avignathus beckmanni* Lys and Serre, 1957 in Lys et al. 1957 (?= *Polygnathus decorosus* Stauffer, 1938).

Emended diagnosis.—Symmetrical element with the medial process bearing two additional lateral rami.

Remark.—In the Polish early Frasnian P_1 (sp) elements occur closely similar to those of *A. decorosus* but without any *Avignathus*-type symmetrical elements in the apparatus. Despite similar P_1 (sp) elements they should be classified in different genera and species.

Species included.—*A. decorosus* and *A. bifurcatus* sp. nov.

Avignathus bifurcatus sp. nov.

Fig. 21N–S.

Holotype: S_0 (tr) element ZPAL CXVI/1145 (Fig. 21Q).

Type horizon and locality: Lower cephalopod limestone at Płucki sample Pł-22, Holy Cross Mountains, Poland, late Frasnian.

Derivation of the name: Referring to the bifid appearance of the medial process of symmetrical elements.

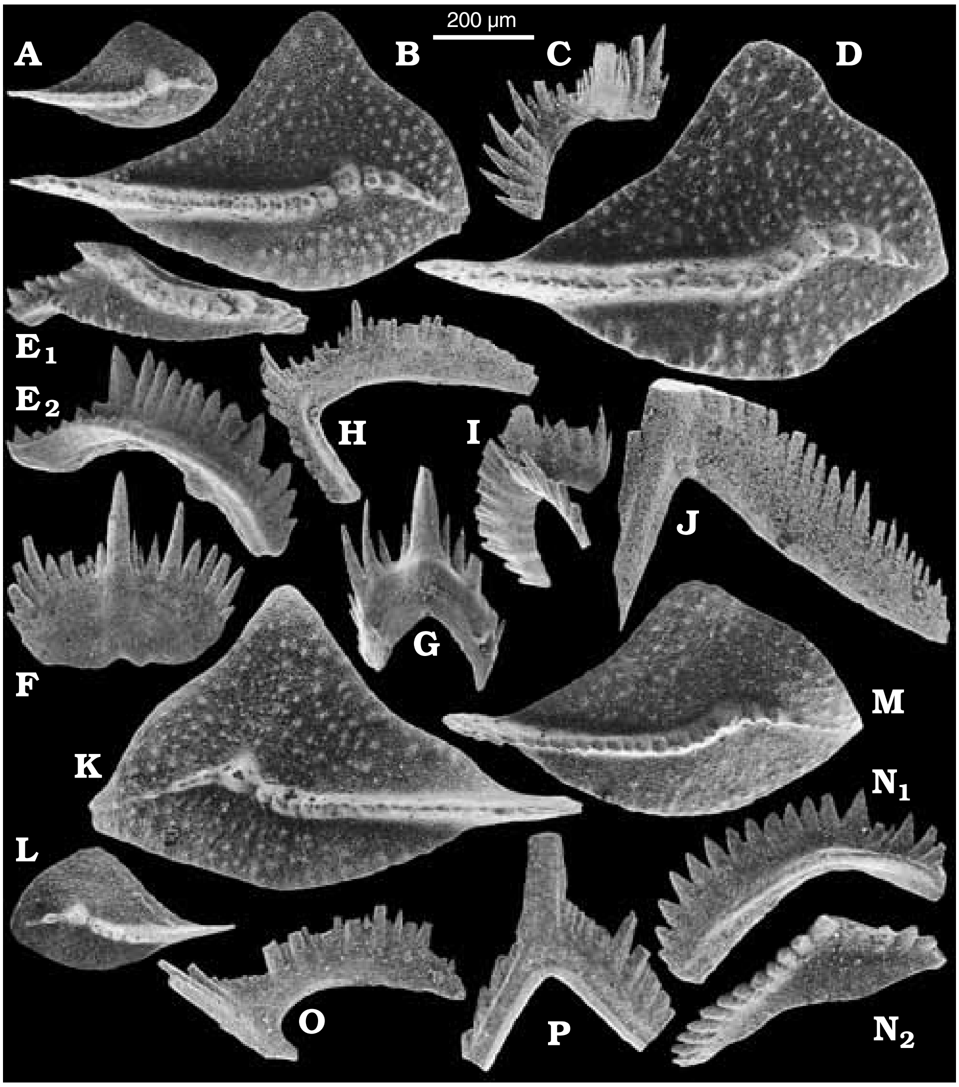


Fig. 34. Palmatolepidid *Kielcelepis*? (or *Lagovilepis*) *jamieae* (Ziegler and Sandberg, 1990). **A**–**H**, **J**. Early form from the late Frasnian of Wietrznia, sample Wtr-20; P_1 (sp) elements ZPAL CXVI/1170, 1169, and 1168 (**A**, **B**, **D**), S_2 (pl) elements ZPAL CXVI/1174 (**C**), P_2 (oz) element ZPAL CXVI/1173 (**E**), S_0 (tr) elements ZPAL CXVI/1171 and 1172 (**F**, **G**), S_{3-4} (ke-hi) element ZPAL CXVI/ 1175 (**H**), and M (ne) element ZPAL CXVI/ 1176 (**J**). **I**, **K**–**P**. Late form, sample Wtr-24; S_1 (lo) element ZPAL CXVI/1165 (**I**), P_1 elements ZPAL CXVI/1161, 1163, and 1162 (**K**–**M**), P_2 element ZPAL CXVI/1164 (**N**), S_{3-4} element ZPAL CXVI/1166 (**O**), and M element ZPAL CXVI/1167 (**P**).

Diagnosis.—The medial process of the symmetrical process of the apparatus almost completely reduced distally of the base of dorsal (“posterior”) lateral processes.

Distribution.—Late Frasnian of the Holy Cross Mountains (see Table 4 and Fig. 4).

Family Palmatolepididae Sweet, 1988

Emended diagnosis.—Apparatus with M (ne) element having straight processes and S_0 (tr) element with more or less reduced medial process; usually platform-bearing P_1 (sp) and P_2 (oz) elements.

Genera included.—*Mesotaxis* Klapper and Philip, 1972, *Kielcelepis* gen. nov., *Manticolepis* Müller, 1956, *Lagovilepis* gen. nov., *Klapperilepis* gen. nov., *Tripodellus* Sannemann, 1955, *Palmatolepis* Ulrich and Bassler, 1926, *Panderolepis* Helms, 1963, and *Conditolepis* van den Boogard and Kuhry, 1979.

Genus *Mesotaxis* Klapper and Philip, 1972

Type species: *Polygnathus asymmetricus* Bischoff and Ziegler, 1957.

Emended diagnosis.—Symmetrical S_0 (tr) elements triramous, non-lobate or weakly lobate platform of the P_1 (sp) element, A-shaped M (ne) elements.

Genus *Kielcelepis* nov.

Type species: *Palmatolepis ljashenkoae* Ovnatanova, 1976.

Diagnosis.—Palmatolepidids with primitively biramous symmetrical elements of the apparatus bearing almost straight processes; M (ne) elements with narrow angle between processes, basally bent dorsal process of the P_1 (sp) element.

Remarks.—The medial process of symmetrical elements gradually disappeared in the course of evolution from *Mesotaxis* to *Kielcelepis* gen. nov. and bifurcated at transition to *Manticolepis* and *Lagovilepis* gen. nov. In populations of transitional species a significant variability of these characters can be expected. Still, the observed range of variability of the ramiform elements and its overlap with related species is much lower than in platform elements. Both generic and species identification is generally not possible in

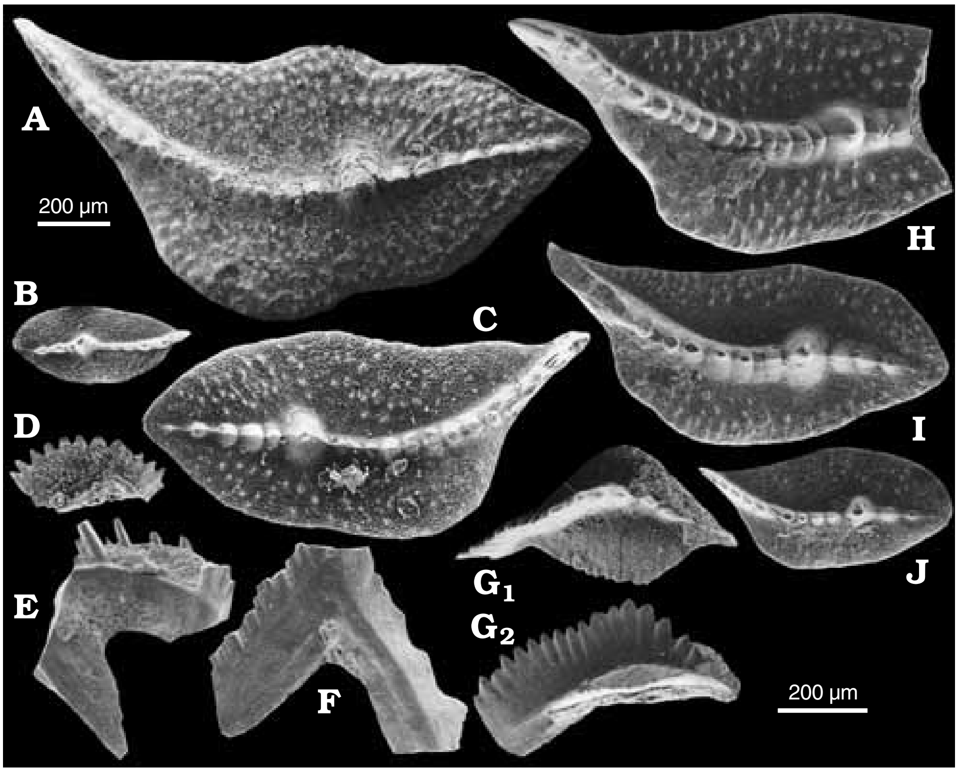


Fig. 35. Late Frasnian palmatolepidids lacking the platform lobe. **A**. *Conditolepis*? aff. *linguiformis* (Müller, 1956) from the lower cephalopod limestone at Płucki, sample Pł-22, P_1 (sp) element ZPAL CXVI/672. **B**–**J**. *Conditolepis*? *linguiformis* (Müller, 1956) from the Upper Kellwasserkalk at Plucki, sample Pł-391 (**B**, **C**), juvenile element possibly belonging to the species from sample Pł-43 (**D**), and probable apparatus element association from the Upper Olentangy Shale at Lazarus Camp, Ohio (**E**–**J**); P_1 elements ZPAL CXVI/987, 407, 1185, 1186, and 1187 (**B**, **C**, **H**–**J**), P_2 (oz) elements ZPAL CXVI/1206 and 1188 (**D**, **G**), S_{3-4} (ke-hi) element ZPAL CXVI/1189 (**E**), and M (ne) element ZPAL CXVI/1190 (**F**). Magnifications shown by the bar scale in the lower right corner, except for **A** with its own scale.

Frasnian palmatolepidids without consulting the apparatus structure.

Species included.—The type species, *K. hassi* (Müller and Müller, 1957), and *K.*? *jamieae* (Ziegler and Sandberg, 1990).

Genus *Manticolepis* Müller, 1956

Type species: *Palmatolepis subrecta* Miller and Youngquist, 1947 = *Palmatolepis winchelli* (Stauffer, 1938) (Klapper and Foster 1993).

Emended diagnosis.—Palmatolepidids with P_1 (sp) elements of generalised shape and typically Frasnian basal bending of the dorsal process and M (ne) elements with wide angle between processes.

Remarks.—Other names are available for this genus: *Ligonodinoides* Stauffer, 1938, with the type species *Ligonodinoides ohioensis* Stauffer, 1938 based on M (ne) element of *L. winchelli* (Stauffer, 1938), and *Gnamptognathus* Ziegler, 1958, with type species *Gnamptognathus walliseri* Ziegler, 1958 being S_1 (lo) element probably of *M. rhenana* (Ziegler, 1958) or *M. winchelli* (*Palmatolepis unicornis* in Ziegler 1958: pl. 6: 11).

Species included.—The type species *Manticolepis gigas* (Miller and Youngquist, 1947) and *Manticolepis rhenana* (Ziegler, 1958).

Genus *Lagovilepis* nov.

Type species: *Palmatolepis bogartensis* (Stauffer, 1938).

Derivation of the name: From Łagów, a town near Płucki, where the type species is well documented.

Diagnosis.—Palmatolepidids with P_1 (sp) elements of generalised shape and typically Frasnian basal bending of the dorsal process, and A-shaped M (ne) elements with primitively narrow angle between elongated processes.

Remarks.—The type species of the genus has a symmetrical element in the apparatus with processes which do not bifurcate. This seems to be a reversal to the state typical of *Kielcelepis* rather than an inherited character.

Species included.—Only the type species.

Genus *Klapperilepis* nov.

Type species: *Palmatolepis triangularis* Sannemann, 1955.

Derivation of the name: To recognise Gilbert Klapper's contribution to understanding Devonian conodont apparatuses.

Diagnosis.—Palmatolepidids with P_1 (sp) elements with rised tip of the dorsal process and generalised appearance of the remaining elements of the apparatus.

Comparison.—The new genus differs from its Frasnian predecessors in raised platform tip of the P_1 (sp) elements, from the mid-Famennian *Palmatolepis* Ulrich and Bassler, 1926 in a regular distribution of denticles and dominant cusp in ramiform elements of the apparatus, from *Conditolepis* van den Boogard and Kuhry, 1979 in a non-derived shape of the platform, from *Panderolepis* Helms, 1963 in high arched M (ne) elements, and from *Tripodellus* Sannemann, 1955 in biramous P_2 (oz) elements of a generalised appearance.

Species included.—The type species, *K. praetriangularis* (Ziegler and Sandberg, 1988), *K. quadrantinodosolobata* (Sannemann, 1955), *K. abnormis* (Branson and Mehl, 1934), and *K. sandbergi* (Ji and Ziegler, 1993).

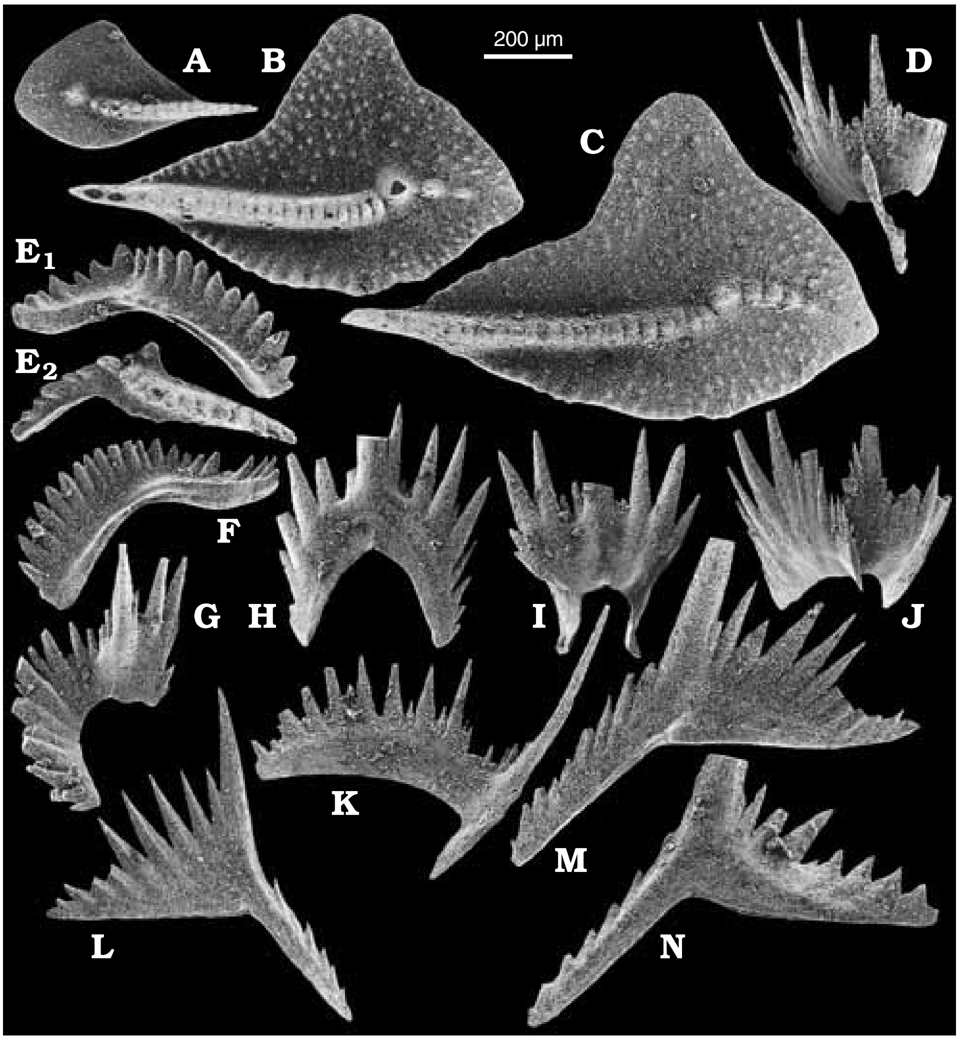


Fig. 36. Late Frasnian palmatolepidid *Manticolepis gigas* (Miller and Youngquist, 1947) from Wietrznia, sample Wtr-23; P_1 (sp) elements ZPAL CXVI/1149, 1148 and 1147 (**A**–**C**), S_1 (lo) elements ZPAL CXVI/1154 and 1155 (**D**, **J**), P_2 (oz) elements ZPAL CXVI/1151 and 1150 (**E**, **F**), S_2 (pl) element ZPAL CXVI/1156 (**G**), S_0 (tr) elements ZPAL CXVI/1152 and 1153 (**H**, **I**), S_{3-4} (ke-hi) element ZPAL CXVI/1157 (**K**), and M (ne) elements ZPAL CXVI/1158, 1159, and 1160 (**L**–**N**).

Klapperilepis praetriangularis (Ziegler and Sandberg, 1988)

Holotype: SMF 38 572, Ziegler and Sandberg 1988: pl. 1: 1a, b.

Type horizon and locality: Latest Frasnian cephalopod limestone SW Hamar Laghdad near Erfoud, Morocco.

Emended diagnosis.—Relatively wide and short platform of P_1 (sp) elements, generalised appearance of M (ne) elements.

Remarks.—The species was originally defined typologically on the basis of a flat (instead of curved downward, as in the Frasnian species of *Manticolepis*, or raised, as in the Famennian *P. triangularis*) dorsal part of the P_1 (sp) elements. In result, it is reported to occur as late as in the mid-*P. triangularis* Zone (Wang 1994). Actually, this character is rather variable within both the late Frasnian and earliest Famennian samples. The main difference in respect to the type population of *K. triangularis* consists in less derived platform shape and apparatus structure.

Klapperilepis triangularis (Sannemann, 1955)

Holotype: Sannemann (1955: pl. 24: 3).

Emended diagnosis.—Relatively elongated P_1 (sp) elements of otherwise generalised appearance, M (ne) elements with narrower angle between processes than in ancestral *K. praetriangularis*.

Genus *Tripodellus* Sannemann, 1955

Type species: *Tripodellus flexuosus* Sannemann 1955 = *T. minutus flexuosus* (Sannemann, 1955).

Emended diagnosis.—Apparatus with triramous P_2 (oz) elements.

Genus *Palmatolepis* Ulrich and Bassler, 1926

Type species: *Palmatolepis perlobata* Ulrich and Bassler, 1926.

Emended diagnosis.—Apparatus with the symmetry transition series elements with weakly developed cusps and irregular arrangement of denticles, M (ne) element processes following one line, and P_1 (sp) elements with lobate platform.

Genus *Panderolepis* Helms, 1963

Type species: *Palmatolepis glabra* Ulrich and Bassler, 1926.

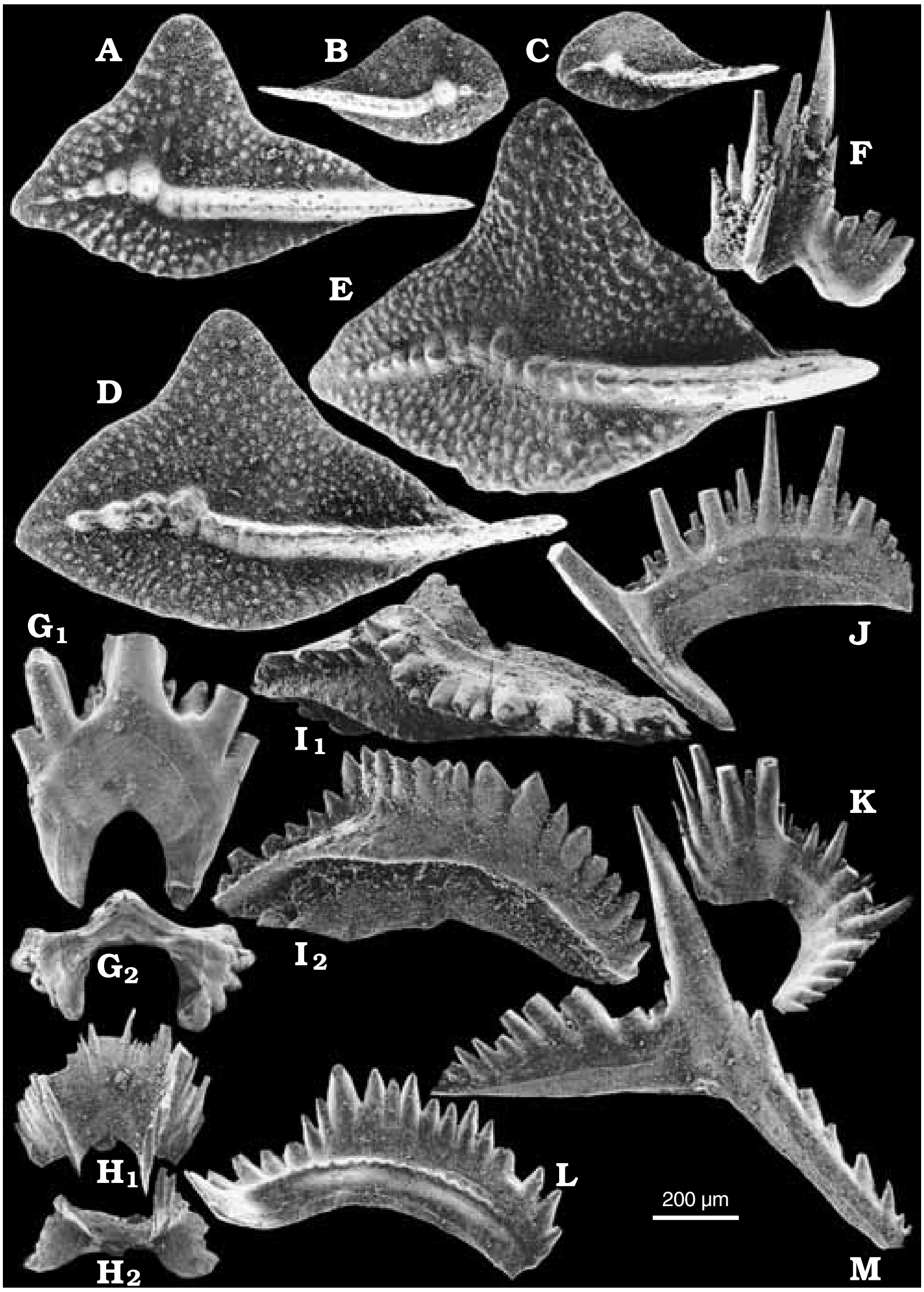


Fig. 37. Palmatolepidid *Manticolepis gigas* (Miller and Youngquist, 1947) from the mid-Frasnian of Wietrznia II quarry, sample Wtr-5; P_1 (sp) elements ZPAL CXVI/752, 753, 754, 751, and 750 (**A**–**E**), S_1 (lo) element ZPAL CXVI/758 (**F**), S_0 (tr) elements ZPAL CXVI/761 and 760 (**G**, **H**), P_2 (oz) element ZPAL CXVI/755 and 762 (**I**, **L**), S_{3-4} (ke-hi) element ZPAL CXVI/759 (**J**), S_2 (pl) element ZPAL CXVI/757 (**K**), and M (ne) element ZPAL CXVI/756 (**M**).

Emended diagnosis.—Apparatus with laterally sinuous P_2 (oz) elements, M (ne) element having linearly arranged processes and weakly lobate platform of P_1 (sp) elements.

Conditolepis van den Boogard and Kuhry, 1979

Type species: *Palmatolepis marginifera* Helms, 1959.

Emended diagnosis.—Apparatus with non-lobate P_1 (sp) elements, wide platform in P_2 (oz) elements and radiating denticles of M (ne) elements with short linearly arranged processes.

Ecological succession of the Frasnian conodonts in the Holy Cross Mountains

Because of low frequencies of conodonts in the transitional strata in the Holy Cross Mountains, I am not able to trace changes in apparatus-based conodont assemblages composition across the Givetian–Frasnian boundary.

The oldest prolific Frasnian samples come from the unit C at the Wietrznia I quarry (see Racki 1992; my sample Wtr-9

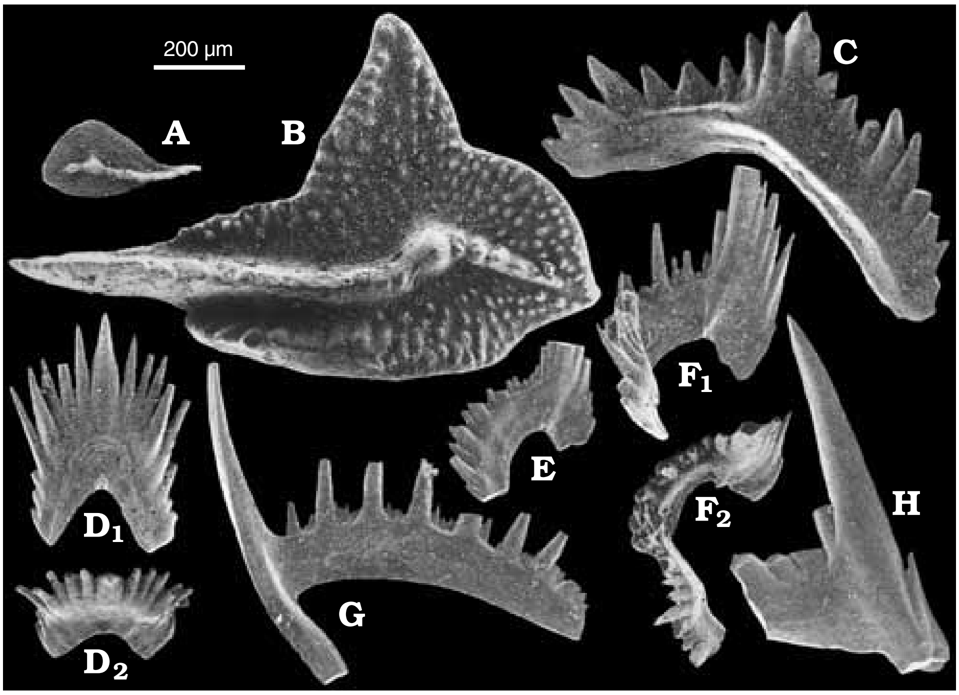


Fig. 38. Possible relic population of *Manticolepis gigas* (Miller and Youngquist, 1947) from the latest Frasnian of Wietrznia, sample Wtr-18; P_1 (sp) elements ZPAL CXVI/1037 and 1044 (**A**, **B**), P_2 (oz) element ZPAL CXVI/1043 (**C**), S_0 (tr) element ZPAL CXVI/1042 (**D**), S_2 (pl) element ZPAL CXVI/1040 (**E**), S_1 (lo) element ZPAL CXVI/1041 (**F**), $S_{3–4}$ (ke-hi) element ZPAL CXVI/1039 (**G**), and M (ne) element ZPAL CXVI/1038 (**H**).

was collected immediately above his bed 14, but the most productive were samples Wtr-8 and Wtr-7 collected 7 m below; Fig. 4). The conodonts there represent the same assemblage which is associated with ammonoids at Ściegnia and Laskowa. It contains successors of all the species represented in the Givetian Chęciny sample reviewed above, but enriched in several lineages earlier unknown. *Polygnathus webbi* is the dominant species, but it is followed by deeper-water species of *Ancyrodella*, *Mesotaxis*, and *Dyminodina* gen. nov. (see Table 1). The latter new genus is a prioniodinid, the diversity of which in the Frasnian of the Holy Cross Mountains is a surprise. The prioniodinid species are almost completely neglected in the stratigraphic literature because their identification requires apparatus studies; nonetheless, they frequently dominate the assemblages. It appears thus that any ecological or biogeographic analysis based only on platform conodont elements must be fundamentally biased.

Below, the distribution of particular taxonomic groups of conodonts in the Frasnian of the Holy Cross Mountains is reviewed. Of course, the supraspecific units are by definition of phylogenetic, not ecological, nature. An unavoidable consequence is that the pattern of spatial distribution of conodonts in respect to a carbonate platform can hardly be observed on above-species level (Belka and Wendt 1992; cf. Racki and Bultynck 1993). However, many taxa seem to preserve some ecological coherency.

Belodellids.—These are perhaps the most environmentally sensitive conodonts of the Frasnian (Fig. 5A–Q; Table 1). They occur throughout the Frasnian with variable but always very low frequencies, except for the reef environment. The distribution of the belodellids does not show any stratigraphically useful pattern and seems to be controlled only by the water depth or proximity to a reef. Unlike *Icriodus*, the contribution of *Belodella* to the assemblages does not increase towards the shore. One may speculate that *Belodella* did not tolerate clay suspended in the water or even a slight decrease in salinity (in fact, even the generally shallow-water *Icriodus*, like all other conodonts, did not occur in brackish waters). In sample Wtr 12 taken at Wietrznia (Fig. 4, below sections B and C) from the limestone with *Receptaculites neptuni* and *Alveolites*, *Belodella resima* (Philip, 1965) is the dominant species, being associated only with a generalised *Polygnathus* represented by juvenile specimens (probably *P. webbi*).

Icriodontids.—Like the belodellids, the icriodontid species show a complex distribution in the Holy Cross Mountains, related not so much to the geological time but rather to subtle environmental factors. The earliest Frasnian population (Fig. 6A, B), probably conspecific with *Icriodus expansus* Branson and Mehl, 1938 (see Müller and Müller 1957) does not seem to be directly related to the preceding Givetian species known from Chęciny (Fig. 2A). In the Łysogóry facies region (Ściegnia and Włochy) this species continued to the mid-Frasnian.

In strata of the same mid-Frasnian age in the Kielce facies region (Wietrznia; sample Wtr-13) another lineage is represented, *I. symmetricus*. It continued its occurrence throughout the middle Frasnian high water stand.

Interestingly, when conodonts reappeared at Wietrznia after a reefal facies episode, a completely different icriodontid was represented (sample Wtr-5; Fig. 6I, J). There seems to be a continuity between these icriodontids and the somewhat younger population of *Icriodus elegantulus* from the lower cephalopod limestone at Płucki (Pł-22) (Fig. 6K–M, Q).

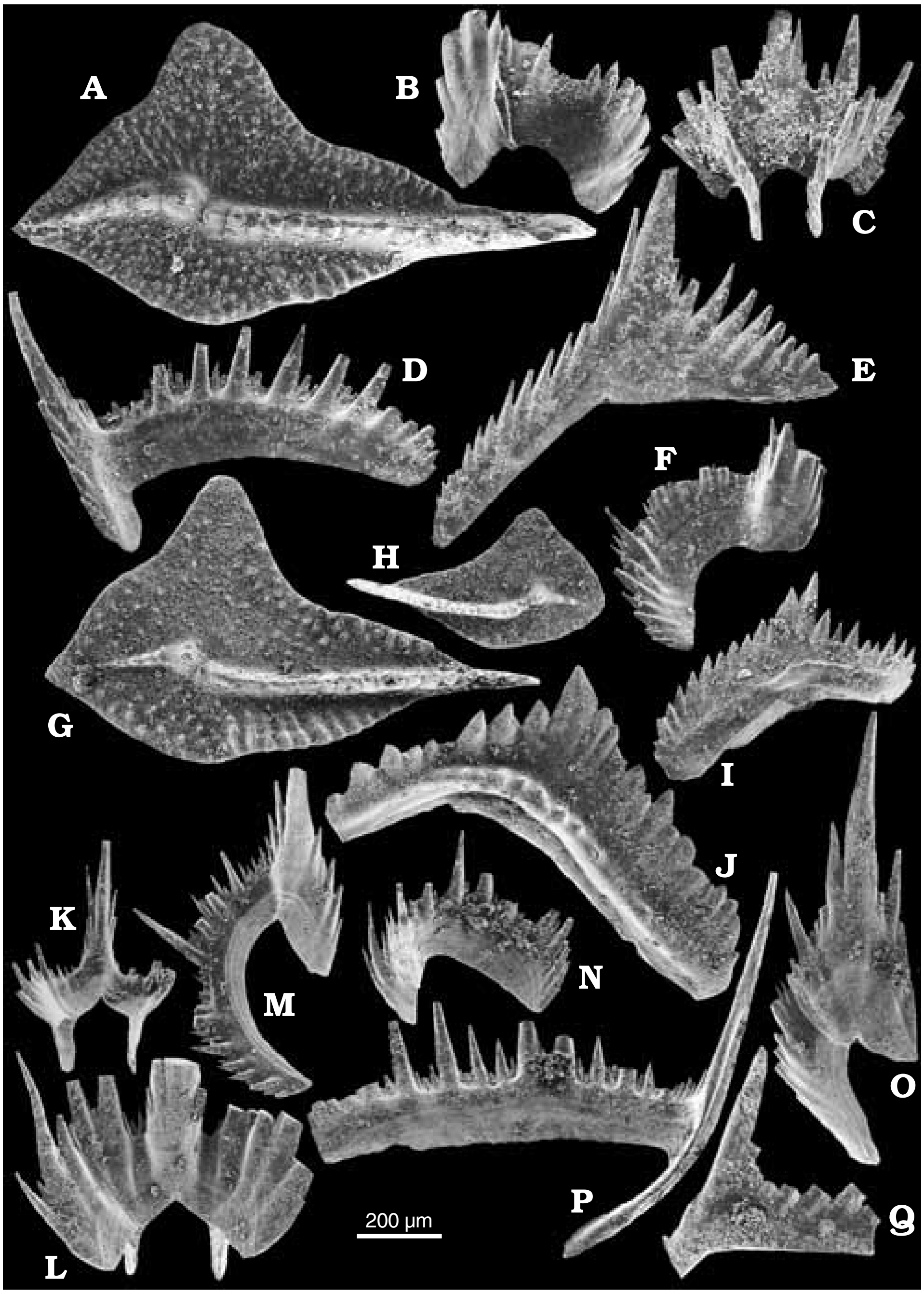


Fig. 39. Palmatolepidid *Manticolepis winchelli* (Stauffer, 1938). **A**–**F**. Early population from the lower cephalopod limestone at Płucki, sample Pł-22; P_1 (sp) element ZPAL CXVI/664 (**A**), S_1 (lo) element ZPAL CXVI/660 (**B**), S_0 (tr) element ZPAL CXVI/659 (**C**), S_{3-4} (ke-hi) element ZPAL CXVI/653 (**D**), M (ne) element ZPAL CXVI/654 (**E**), and S_2 (pl) element ZPAL CXVI/669 (**F**). **G**–**Q**. Late population from Kowala, samples Ko-149 (**G**, **H**, **J**) and Ko-151 (**I**, **K**, **M**, **N**); P_1 (sp) element ZPAL CXVI/494 and 495 (**G**, **H**), P_2 (oz) element ZPAL CXVI/1200 and 496 (I, J), S_0 element ZPAL CXVI/1201 and 497 (**K**, **L**), S_1 element ZPAL CXVI/1203 (**M**), S_1 (lo) element ZPAL CXVI/1202 and 498 (**N**, **O**), S_{3-4} element ZPAL CXVI/500 (**P**) and M element ZPAL CXVI/493 (**Q**).

A good example of ecologically controlled changes in the frequency of the icriodontids is the latest Frasnian Kowala succession (Szulczewski 1989; Racki and Szulczewski 1996). Four peaks in their abundance (up to 50%; samples Ko-146, Ko-135, and Ko-149; see Figs. 4 and 48) are interfingered with peaks of a high contribution of the palmatolepidids. A eustatic cause of this phenomenon is clear. It starts from a relatively high contribution of *Pelekysgnathus* in the oldest productive sample Ko–144, wiped out with the first incursion of the open-sea *Manticolepis*. Most interestingly, the same change from *Pelekysgnathus* to *Icriodus* took place immediately below the Upper Kellwasserkalk at Płucki (samples Pł-38 to Pł-21 on Fig. 48).

The *Icriodus iowaensis* population, typical for the latest Frasnian Upper Kellwasserkalk (sample Pł-391; Fig. 6N–P, R) seems to be a continuation of that which immigrated to Płucki (the lower cephalopod bed; sample Pł-22), together with a pelagic assemblage of other conodonts. These forms disappeared immediately after this eustatic event when shallow-water polygnathids (*P. pacificus*) appeared in association with benthic organisms (sample Pł-25). The *I. iowaensis* lineage seems confined to open-sea environments. Interestingly, in the near-reef Wietrznia

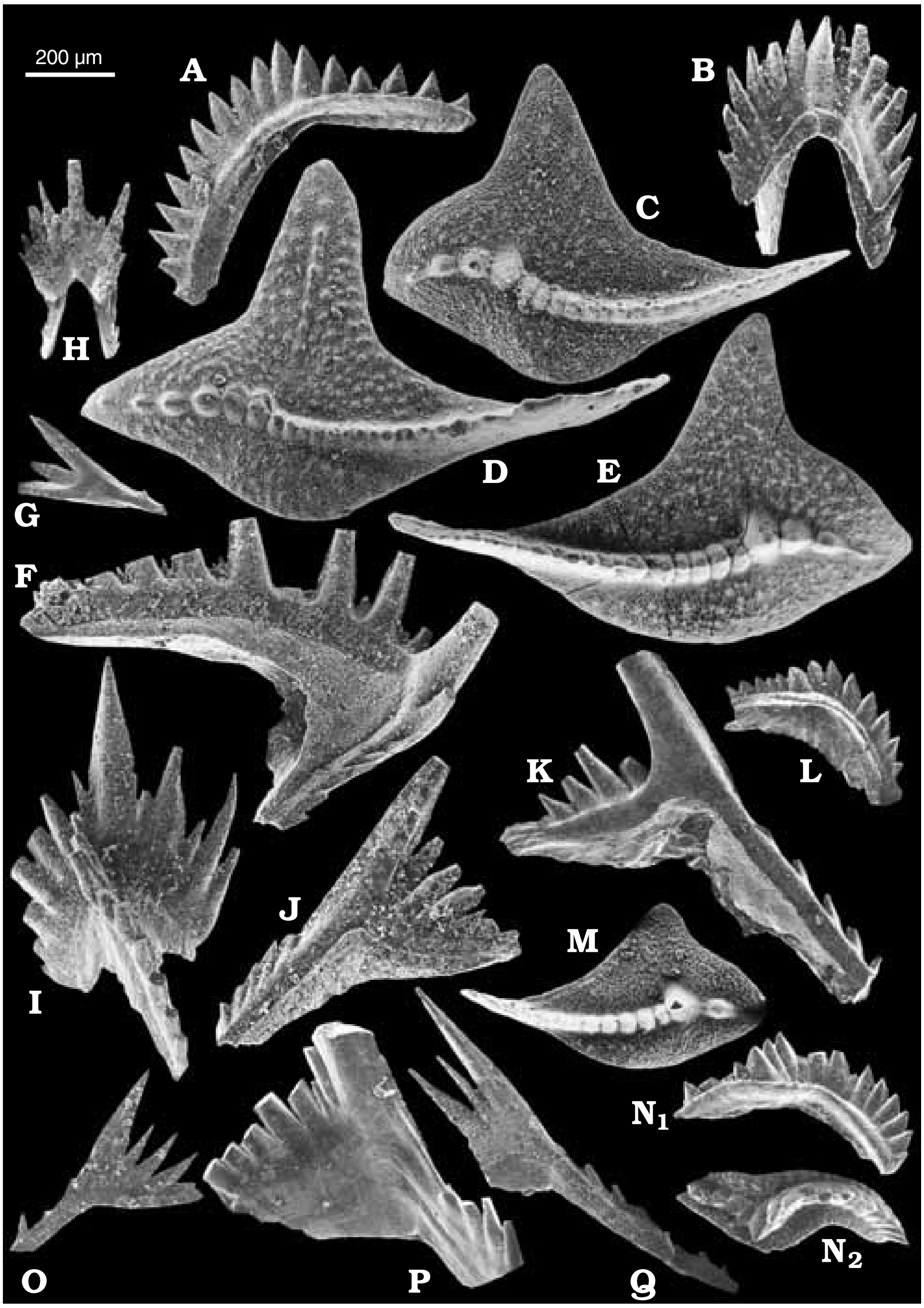


Fig. 40. Palmatolepidid *Manticolepis* species from the mid-Frasnian of Wietrznia I quarry and Płucki, samples Wtr-18 (**A**–**D**), Pł-391 (**E**, **G**, **K**–**M**), and Pł-82 (**F**, **I**, **J**). **A**–**F**, **G**–**M**. *Manticolepis rhenana* (Ziegler, 1958); P_2 (oz) elements ZPAL CXVI/804 and 984 (**A**, **L**), S_0 (tr) element ZPAL CXVI/805 (**B**), P_1 (sp) elements ZPAL CXVI/803, 802, 977, and 978 (**C**–**E**, **M**), S_1 (lo) element ZPAL CXVI/799 (**I**), $S_{3–4}$ (ke-hi) element ZPAL CXVI/800 (**F**), and M (ne) element ZPAL CXVI/979, 801, and 980 (**G**, **J**, **K**). **H**, **N**–**Q**. *M. rhenana* or *Manticolepis winchelli* (Stauffer, 1938) ramiform elements from the Upper Kelwasserkalk at Płucki, sample Pł-391; S_0 element ZPAL CXVI/452 (**H**), P_2 element ZPAL CXVI/414 (**N**), and M elements ZPAL CXVI/456, 985, and 986 (**O**–**Q**).

succession, 50 cm below the top of the Frasnian (sample Wtr-22), an *Icriodus* population of *I. alternatus* morphology occurs. This stratum is close in age to the lower cephalopod limestone at Płucki (Pł-22).

The population of the earliest Famennian (sample Pł-16; Fig. 6S–W) usually attributed to as *I. alternatus*, differs a little from that of the latest Frasnian *Icriodus iowaensis* population, being closer to the Płucki lower cephalopod limestone icriodontids. However, a continuity between the latest Frasnian and earliest Famennian populations cannot be excluded.

The very rare *Pelekysgnathus planus* Sannemann, 1955 appears in the Holy Cross Mountains in the latest Frasnian (Pł-391, Figs. 4, 6Y). It continued to occur to the early Famennian, when it became more common, similarly as elsewhere (Ji 1989a).

Prioniodinids.—In the oldest Frasnian strata at Wietrznia (samples Wtr-8 to Wtr-9; Fig. 4, Table 1) the prioniodinids are represented by highly variable species *Pluckidina kielcensis* gen. et sp. nov. (Fig. 10). Slightly later at least two separate lineages of *Ligonodina* and *Dyminodina* gen. nov. emerged, among them *L. pectinata* (Figs. 7, 8) appearing and disappearing several times in the studied sections.

Polygnathids without platform.—From some reason non-

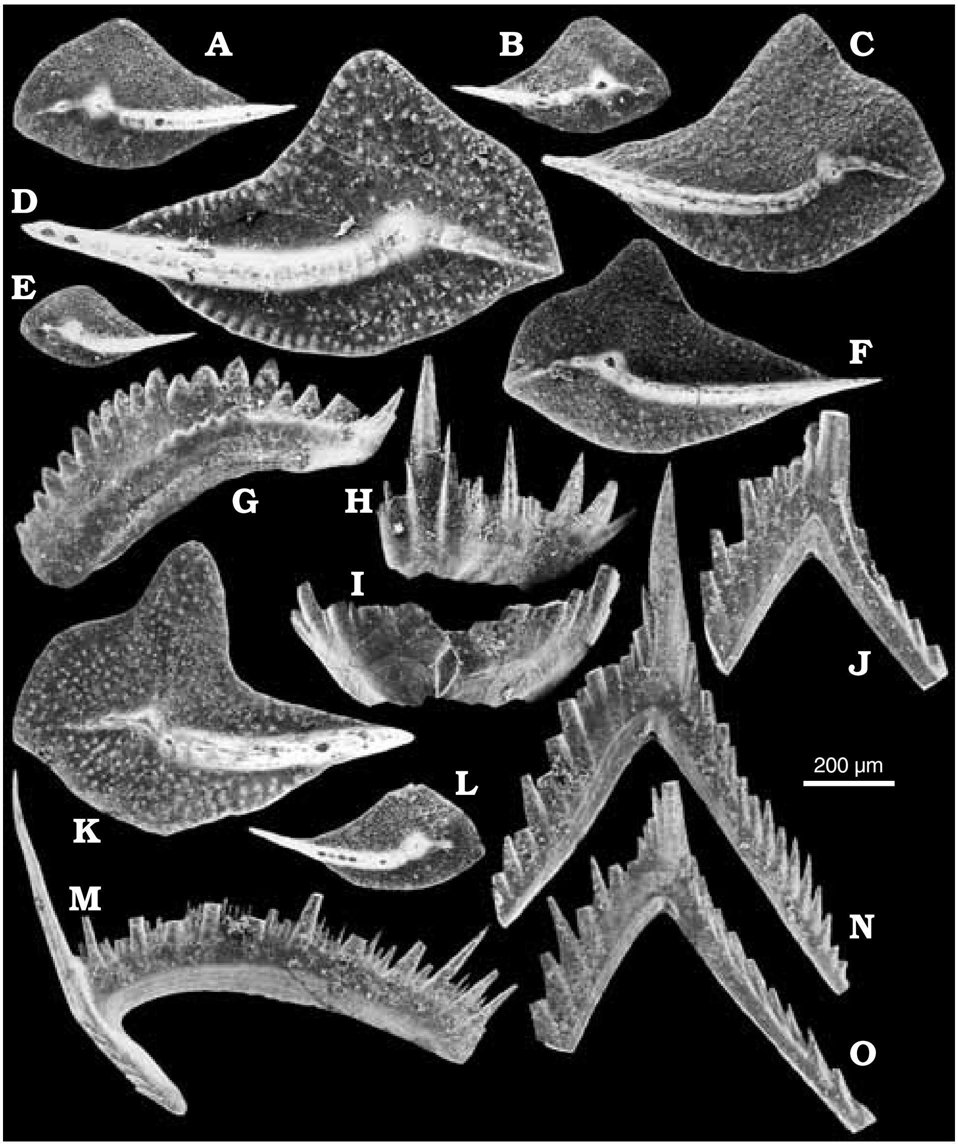


Fig. 41. Palmatolepidid *Lagovilepis bogartensis* (Stauffer, 1938). **A**–**J**. Early population from the lower cephalopod limestone at Płucki, sample Pł-22; P_1 (sp) elements ZPAL CXVI/656, 665, 1209, 657, 655, 1208 (**A**–**F**), P_2 (oz) element ZPAL CXVI/658 (**G**), S_0 (tr) element ZPAL CXVI/667 (**H**), S_1 (lo) element ZPAL CXVI/668 (**I**), and M (ne) element ZPAL CXVI/663 (**J**). **K**–**O**. Late population from Kowala, samples Ko-149 (**K**, **L**, **O**) and Ko-151 (**M**, **N**); P_1 (sp) elements ZPAL CXVI/491 and 492 (**K**, **L**), S_{3-4} (ke-hi) element ZPAL CXVI/1204 (**M**), and M (ne) elements ZPAL CXVI/1205 and 501 (**N**, **O**).

platform polygnathids (*Mehlina*, *Tortodus* s.l., *Nicollidina*) are very rare in the Frasnian of the Holy Cross Mountains and there seems to be no regularity in their distribution.

Polygnathids with reduced platform.—The lineage of *Ctenopolygnathus* is well represented in the Frasnian of the studied area, crossing also the Frasnian–Famennian boundary. As the earliest Famennian population (Pł-20; Fig. 18H) is slightly different from that of the Upper Kellwasserkalk, it remains uncertain whether there was a complete continuity across the boundary or rather a foreign population immigrated to the area to replace that of the latest Frasnian.

Typical polygnathids.—Polygnathids with platform-bearing P_1 (sp) elements are usually facies-sensitive and in the Holy Cross Mountains sections most species show short ranges. The *Polygnathus webbi* lineage, well represented in the early Frasnian, was later replaced by other *Polygnathus* species and reappeared after some time of their domination (Fig. 22).

The derived polygnathid *Avignathus* seems to be characteristic of open-sea environments and invaded the studied area at high sea level stands episodes. With the sea shallowings (at Wietrznia sample Wtr-30), *Avignathus* tended to be replaced by another polygnathid, *P. pacificus* (Fig. 23A–J).

The advanced polygnathid *Ancyrodella*.—Populations of the lineage immigrated to Europe together with the basal Frasnian transgression (e.g., Bultynck 1974; Racki 1992) being initially subordinate to shallow water conodont species in low biological productivity communities. It supplemented the *Polygnathus–Icriodus–Belodella* low diversity assemblage which continued from the Givetian (Bultynck and Racki 1993: table 1). There is no convincing evidence for presence of more than one species of *Ancyrodella* per sample in the Holy Cross Mts. material. The lineage occurred continuously in pelagic environments of the area until the end of the Frasnian.

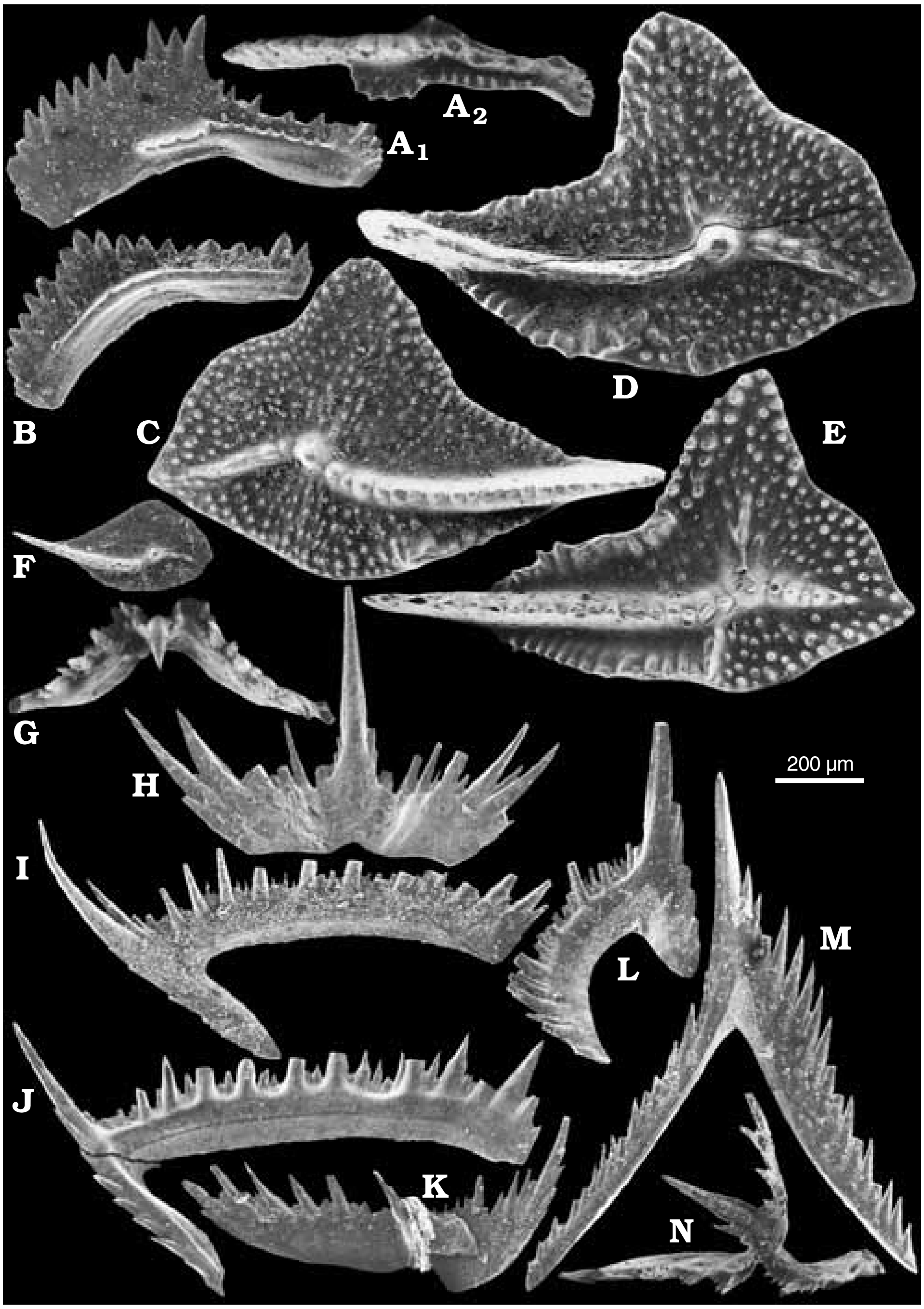


Fig. 42. Palmatolepidid *Lagovilepis bogartensis* (Stauffer, 1938) from the latest Frasnian Upper Kellwasserkalk at Płucki, sample Pł-391; P_2 (oz) elements ZPAL CXVI/442 and 448 (**A**, **B**), P_1 (sp) elements ZPAL CXVI/440 (**C**, modal morphology), 989 (**D**, extreme morphology), 981 (**E**, possibly *Manticolepis winchelli*), and 441 (**F**), S_0 (tr) elements ZPAL CXVI/443 and 990 (**G**, **H**), $S_{3–4}$ (ke-hi) elements ZPAL CXVI/446 and 992 (**I**, **J**), S_1 (lo) element ZPAL CXVI/991 (**K**), S_2 (pl) elements ZPAL CXVI/445 and 444 (**L**, **N**), and M (ne) element ZPAL CXVI/447 (**M**).

The possible palmatolepidid *Ancyrognathus*.—These conodonts are relatively rare in the studied sections, which apparently were located in marginal areas of the *Ancyrognathus* habitat.

Palmatolepidids.—In the Wietrznia succession *Mesotaxis falsiovalis* increases its contribution to almost 60% in sample Wtr-11 (Fig. 4B; Table 1), where *Ancyrodella* is rare, to be replaced by *Icriodus* higher up. It seems that this incursion of *Mesotaxis* took place during a brief prominent sea level rise. The second such sea rise (sample Wtr-9) brought *M. asymmetrica* to the area but its contribution was low (less than 5%) and prioniodinids replaced *Icriodus* that time.

In the mid-Frasnian succession at Wietrznia (Fig. 4C) section palmatolepidids initially (sample Wtr-13) were rare and their contribution increased together with *Icriodus*, which then was replaced with *Avignathus*. An interesting feature of the assemblage is relatively high contribution of *Polygnathus pacificus*. A similar succession of different species of the same genera characterises the late Frasnian Wietrznia II succession (Fig. 4D). In both cases this is probably caused by gradual sea-level rise.

The late Frasnian part of the Wietrznia I section (Fig. 4C)

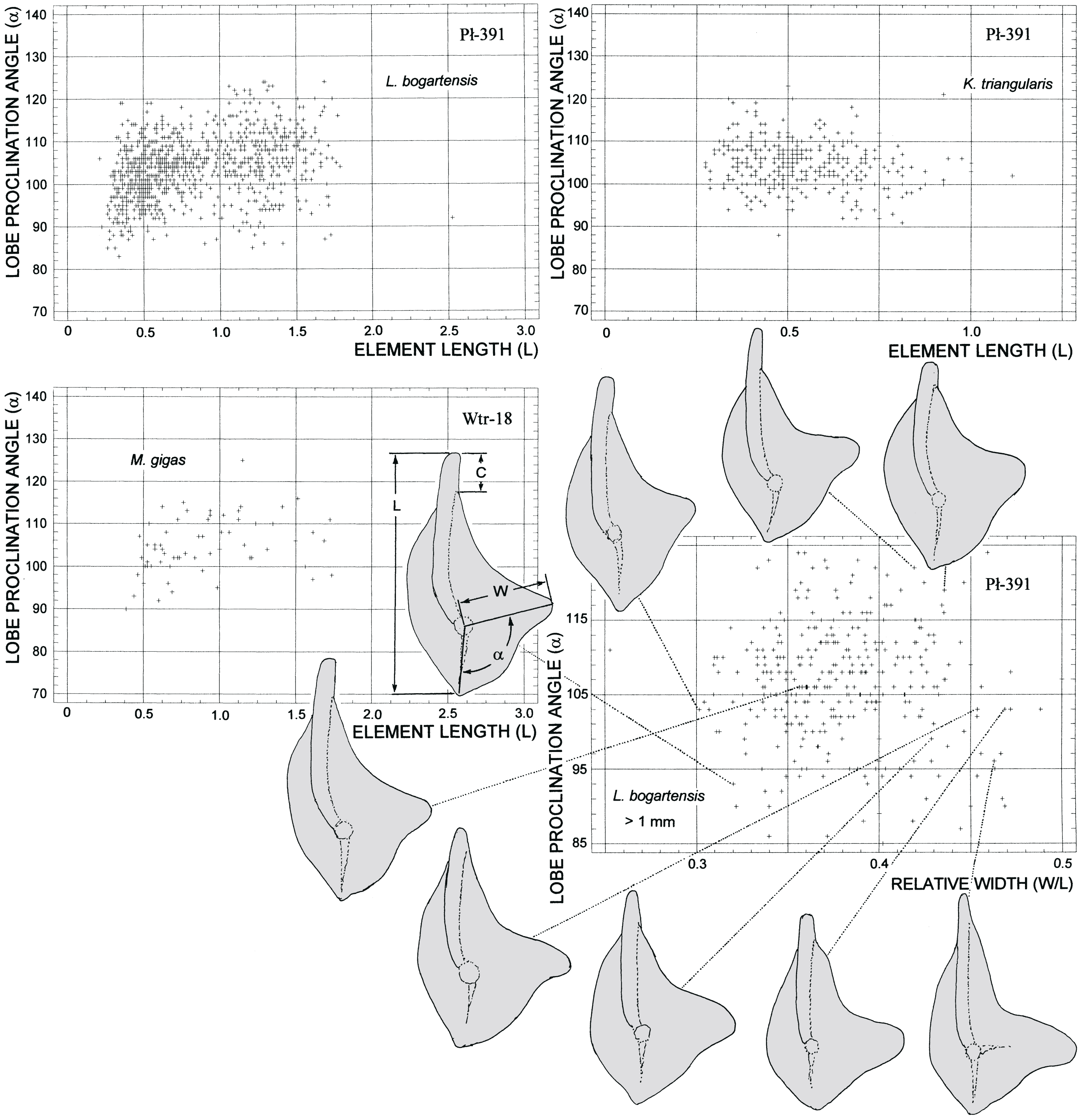


Fig. 43. Variability of P_1 (sp) elements of the latest Frasnian palmatolepidids. Scattergrams show ontogenetic changes of the angle between the dorsal process and the posterior lobe of the platform in sample Pł-391 from the Upper Kellwasserkalk at Płucki (Fig. 42) overdominated by *Lagovilepis bogartensis* (with rare *Manticolepis winchelli* documented with its M elements), associated *Klapperilepis triangularis* and sample Wtr-18 from Wietrznia where only M elements of *Manticolepis* (probably a relic population of *M. gigas*) have been found (Fig. 38A–H). The Pł-391 population variability is separately shown for adult elements (longer than 1 mm) with contours of extreme and modal morphologies added. Note that there is no apparent difference in the course of ontogeny and morphologic variability of platform shape between *L. bogartensis* and *M. winchelli* or *M. gigas* (despite fundamental differences in the apparatus organisation) whereas *K. triangularis* is different in all these respects (plus the dorsal process bending).

shows a reversal of this trend. *Avignathus* present but rare in sample Wtr-20 disappears immediately above, then the same happens with *Ancyrodella* which gives way to a not especially common *Icriodus*. Immediately below the top of the section (sample Wtr-18) *Polygnathus webbi* is the dominant species (Table 3). With each of these rebuildings of the as-

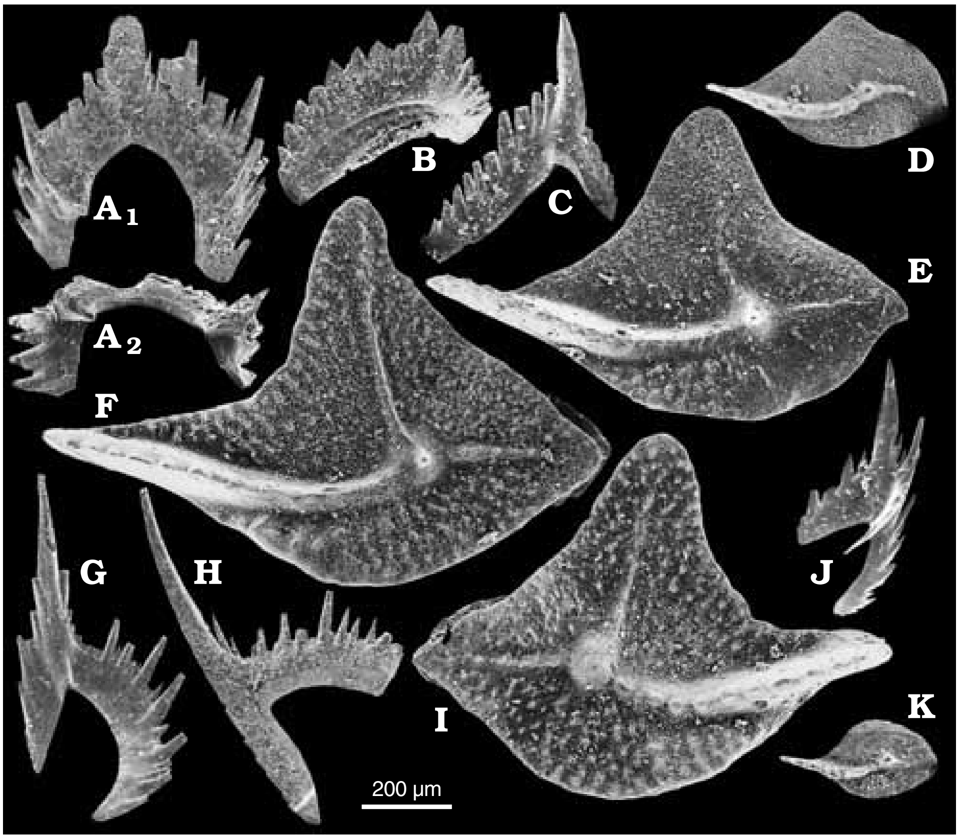


Fig. 44. Palmatolepidid *Klapperilepis praetriangularis* (Ziegler and Sandberg, 1988) from the lower cephalopod limestone at Płucki, sample Pł-22; S_0 (tr) element ZPAL CXVI/650 (**A**), P_2 (oz) element ZPAL CXVI/649 (**B**), M (ne) element ZPAL CXVI/671 (**C**), P_1 (sp) elements ZPAL CXVI/647, 644, 646, 645, and 648 (**D**–**F**, **I**, **K**), S_2 (pl) element ZPAL CXVI/652 (**G**), S_{3-4} (ke-hi) element ZPAL CXVI/662 (**H**), and S_1 (lo) element ZPAL CXVI/651 (**J**).

semblage, particular lineages of the palmatolepidids replace each other. A more specific pattern of this replacement is identifiable at Kowala, where these seems to be a succession from *Manticolepis rhenana* to *M. winchelli*, then to *Lagovilepis bogartensis*, and finally *Conditolepis*? *linguiformis*. *Klapperilepis praetriangularis* is not represented in the Frasnian of Kowala, although it has been encountered as rare (not more than 2%) in the lower cephalopod limestone at Płucki (Pł-22; Figs. 44 and 48) and in the Upper Kellwasserkalk (Pł-391) its contribution is significant (about 10%). It seems that this was the most open-sea species of all occurring in the late Frasnian of the Holy Cross Mountains. The localities are only 35 kilometres apart.

Another interesting aspect of the Płucki succession, which is the most complete of all in the Holy Cross Mountains is the ecologically gradual nature of the faunal shift around the Frasnian–Famennian boundary. The environmentally sensitive species of *Icriodus*, *Klapperilepis* and *Polygnathus* (*P. semicostatus*) gradually change their contribution but the Frasnian species of *Lagovilepis*, *Manticolepis* and *Polygnathus* (*P. webbi*) were suddenly eliminated within this gradient. This looks as if a certain threshold conditions were reached which triggered a local environmental catastrophe.

All this makes it virtually impossible to trace details of the palmatolepidid evolution in the Holy Cross Mountains material. Only a very general picture can be drawn.

Evolutionary transformations of the Frasnian conodonts in the Holy Cross Mountains

The pelagic conodonts *Ancyrodella*, *Ancyrognathus*, and the Palmatolepididae are more likely to offer a good record of their phyletic evolution than the more spatially restricted forms. Still, their stratigraphic distribution is mostly controlled by the environment and only rarely truly convincing evolutionary change can be documented in strata deposited in the tropical Palaeozoic environments (Dzik 1983).

Evolution of *Icriodus*.—According to Sandberg and Dreesen (1984), *I. symmetricus*, *I. alternatus*, and *I. iowensis* are parts of a single evolutionary lineage constantly confined to the same kind of environment. This is not confirmed by the data from the Holy Cross Mountains. These were allopatric lineages. *I. symmetricus* and *I. alternatus* were coeval, but they met occasionally only in some transitional environments (sample Pł-25 at Płucki).

The only case of an apparent evolutionary transition is that recorded at the Wietrznia II quarry section from forms of the *I. alternatus* appearance (with three distinct rows of denticles, the medial being slightly weaker) to populations in which the icrion is extremely narrow and the medial row of denticles is almost completely reduced (*I. kielcensis* of sam-

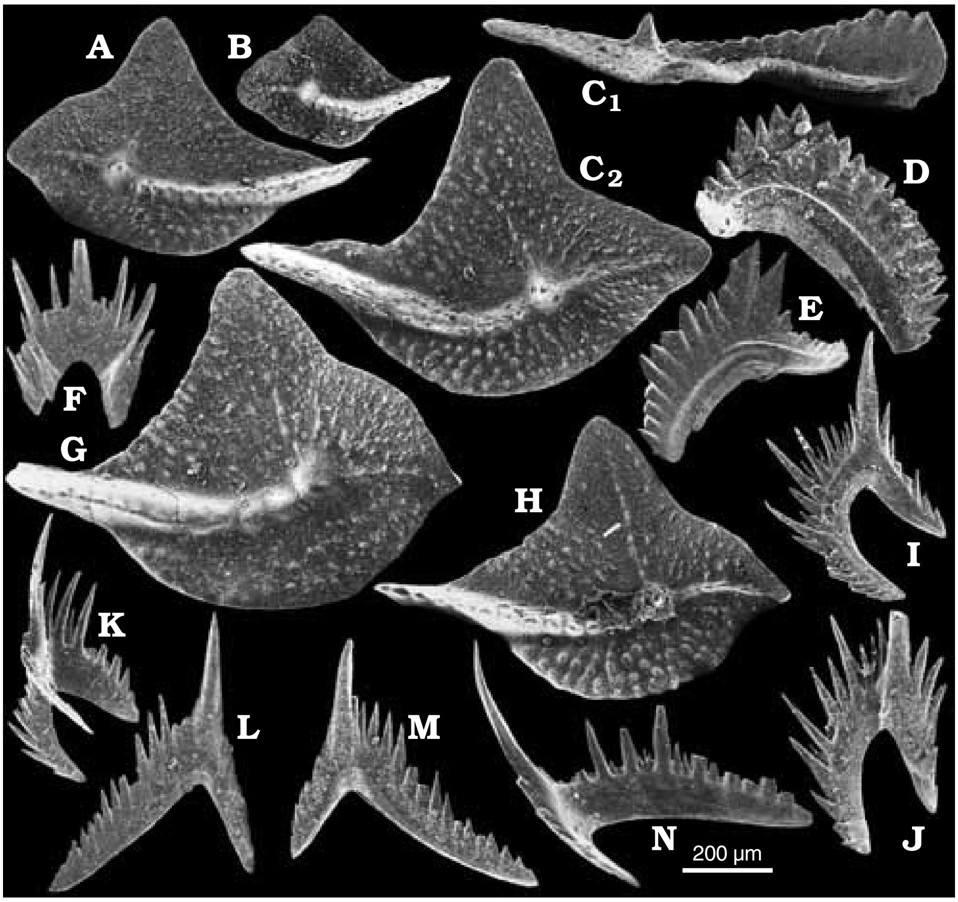


Fig. 45. Palmatolepidid *Klapperilepis praetriangularis* (Ziegler and Sandberg, 1988) from the Upper Kellwasserkalk at Płucki, sample Pł-391; P_1 (sp) elements ZPAL CXVI/998, 450, 995, 449, and 1000 (**A**–**C**, **G**, **H**), P_2 (oz) elements ZPAL CXVI/451 and 996 (**D**, **E**), S_0 (tr) element ZPAL CXVI/997 (**F**), S_2 (pl) elements ZPAL CXVI/393 and 400 (**I**, **J**), S_1 (lo) element ZPAL CXVI/453 (**K**), M (ne) elements ZPAL CXVI/999 and 391 (**L**, **M**), and $S_{3–4}$ (ke-hi) element ZPAL CXVI/455 (**N**).

ple Wtr-5). The icrion becomes somewhat wider in the later population from the lower cephalopod limestone at Płucki (sample Pł-22) and larger specimens tend to develop a strong asymmetry in the icrion organisation, one of the denticle row merging with the cusp while the other disappears at distance from the cusp. In even wider specimens from the upper Kelwasserkalk at Płucki (sample Pł-391), classified as *I. iowensis*, this asymmetry is rarely expressed, in mature elements icrion tending to widen in proximity to the cusp.

According to Sandberg and Dreesen (1984) the disappearance and appearance of the icrion was repeated in the evolution of the Late Devonian icriodontids, but there seems to be a continuity between the late Frasnian and earliest Famennian *Pelekysgnathus* populations.

Evolution of *Polygnathus* and *Avignathus*.—In the Holy Cross Mountains, the *Polygnathus webbi* lineage seems to evolve towards a partial reduction of asymmetry. Earlier populations of probable *Polygnathus aequalis* (Fig. 20A–F, Q) at Wietrznia, co-occurring with *Mesotaxis falsiovalis* (samples Wtr-7 or Wtr-8), still show morphology of P_1 (sp) elements similar to those of the Givetian, with a rather narrow platform. Asymmetry, if developed, is expressed in a different elevation of its ventral ends on the rostral and caudal sides. In later populations (samples Wtr-9 or Wtr-10; Fig. 20G–P), associated with *Mesotaxis asymmetrica*, P_1 (sp) elements may still develop some asymmetry but, unlike *P. webbi*, the middle part of the platform tends to be elevated on one side, not on its ventral end. Among S_0 (tr) elements associated with *P. aequalis* all are primitively triramous, with a medium–size middle process (Fig. 20C, L).

It is likely that a continuation of this lineage is *Avignathus*, which shows a unique additional processes on both sides of the middle process of the S_0 (tr) element. The similarity of *Polygnathus pacificus* and *Avignathus decorosus* at early ontogenetic stages suggests that they share a common ancestry. Possibly the *P. xylus* lineage may be ancestral to *P. pacificus*, although the apparatus of *P. xylus*, restored on the basis of numerous element clusters by Nicoll (1985), is a rather generalised and primitive in its elements morphology.

The late Frasnian *Avignathus* shows an almost completely reduced medial process distally of the point of emergence of lateral processes which gives an appearance of bifurcation (Fig. 21Q). All the seven S_0 (tr) specimens collected from the lower cephalopod limestone at Płucki show this bifurcation, so the character is rather stable. Somewhat surprisingly, in a sample taken from immediately above (Pł-25), the typical *A. decorosus* occurs as a member of a shallow-water conodont assemblage.

Evolution of *Ancyrodella*.—As it follows from the preceding discussion on the succession of *Ancyrodella* species, its

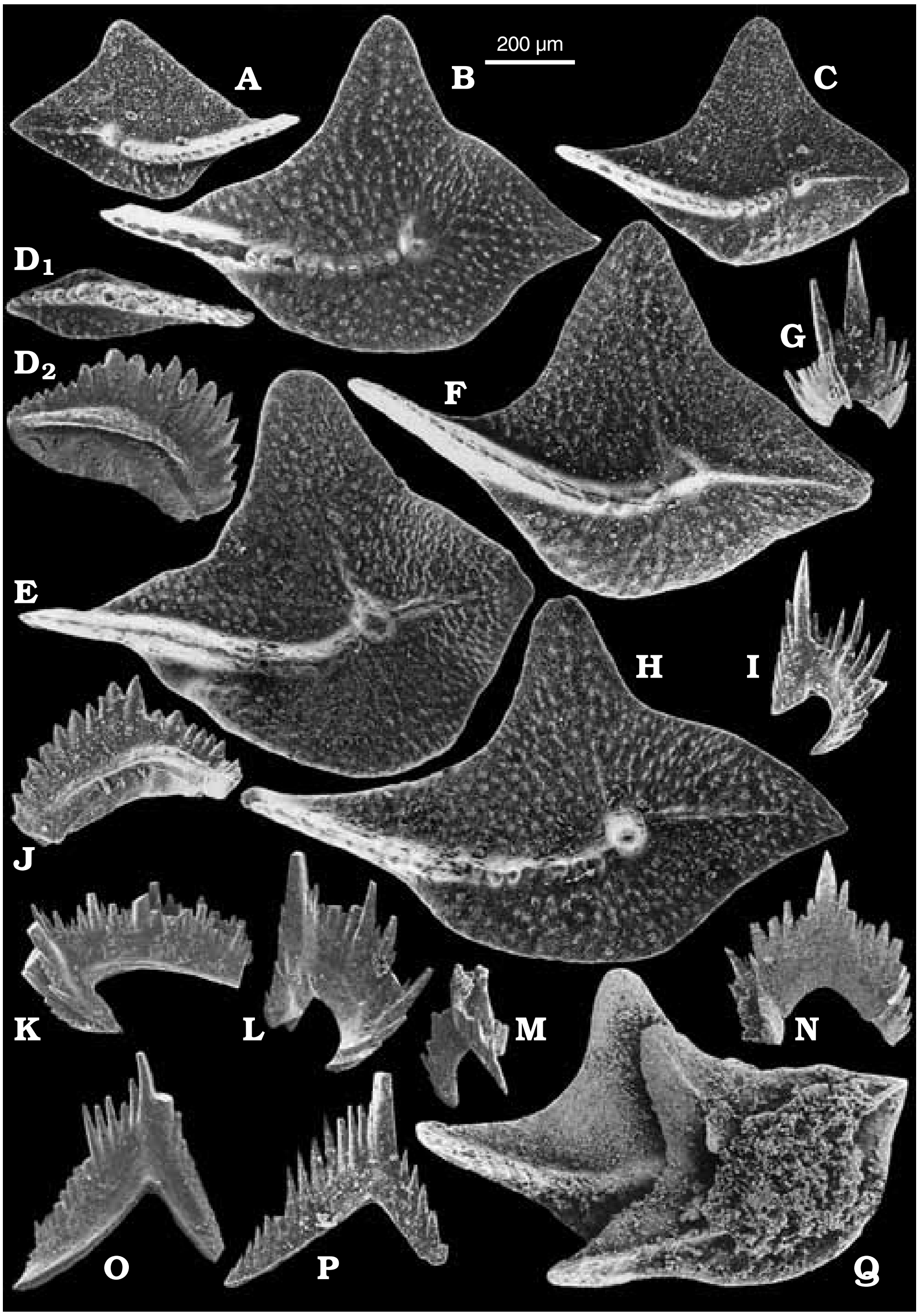


Fig. 46. Palmatolepidid *Klapperilepis praetriangularis* (Ziegler and Sandberg, 1988) late form from the earliest Famennian at Płucki, samples Pł-20 (**A**, **C**, **F**, **G**, **I**, **J**, **P**) and Pł-16 (**B**, **D**, **E**, **H**, **K**–**O**, **Q**); P_1 (sp) elements ZPAL CXVI/793, 1030, 794, 1028, 792, 1029, and 1027 (**A**–**C**, **E**, **F**, **H**, **Q**), P_2 (oz) elements ZPAL CXVI/1031 and 795 (**D**, **J**), S_1 (lo) elements ZPAL CXVI/796 and 1033 (**G**, **M**), S_2 (pl) elements ZPAL CXVI/797 and 1034 (**I**, **L**), S_0 (tr) element ZPAL CXVI/1032(N), and M (ne) elements ZPAL CXVI/1035 and 798 (**O**, **P**). Note that specimens ZPAL CXVI/1036 (**K**) and 1027 (**Q**) are clusters of two elements each, showing different curvature of successive $S_{3–4}$ (ke-hi) elements in the apparatus and strictly mirror image symmetry of P_1 (sp) elements.

distribution is strongly controlled by rarely developing appropriate ecological conditions and this makes its fossil record in the Holy Cross Mountains strongly punctuated. Still, it seems likely that the lineage underwent gradual phyletic evolution and its incursions to the area represent discontinuous record of a continuous evolutionary change.

The evolution of *Ancyrodella* is generally accepted as a useful tool of age correlation in the early Frasnian (Vandelaer et al. 1989). Unfortunately, the platform shape is very variable within populations of early *Ancyrodella* species and changes dramatically during its ontogeny. Most authors discussing the correlative value of the *Ancyrodella* lineage species (Klapper 1985; Garcia-López 1986, 1987; Sandberg et al. 1989; Kirchgasser 1994; Kralick 1994; Weary and Harris 1994; Gouwy and Bultynck 2000) use the vertical (typological) species concept which is highly inappropriate for such a variable and ontogenetically sensitive characters as these conodonts' platform shape. The general pattern of the evolution of the earliest *Ancyrodella* is relatively clear. As typical for the polygnathid conodonts, the inversion of the basal cavity of the P_1 (sp) elements occurs at certain stage in development of the platform. In the course of evolution, this change from conical to inverted or flat basal cavity became earlier and earlier in the ontogeny, to stabilise and be of little taxonomic value in later chronospecies of *Ancyrodella*. In its early species also the platform tuberculation was gradually smaller and smaller (Klapper 1985), and then lateral extensions of the platform developed, which finally bifurcated on one side (Garcia-López 1986). The lobes formation and the moment of their bifurcation also moved backward in the ontogeny to reach the point of inversion of the basal cavity. Basal ridges developed along the bifurcating lobe. All this is highly variable within population of transitional chronospecies to be finally stabilised. Problems may thus arise if the ontogenetic advancement of compared specimens is not strictly considered and within-sample variability neglected.

Ancyrodella species are generally very variable and the status of the majority of them is questionable. The difficulties in separating the ontogenetic from evolutionary changes in the fossil record of *Ancyrodella* also hamper identification of its ancestry. The apparatus of the oldest well-known species, *A. rotundiloba*, as restored by Klapper and Philip (1972) is similar to that of *Parapolygnathus* except for a more widely disposed processes of the M (ne) elements (see Sparling 1981). Perhaps some species with a tuberculate platform and widened basal cavity, classified in *Schmidtognathus*, were ancestral to *Ancyrodella*. Unfortunately, no information on their apparatus structure is available. Moreover, this is just opposite to earlier expectations that forms without platform gave rise to *Ancyrodella*. *Pandorinellina insita* (Stauffer, 1940) and *A. binodosa* Uyeno, 1967 are believed to be the connecting links (Bultynck 1983). The *P. insita* apparatus does not show any resemblance to that of *A. rotundiloba* (see Klapper and Philip 1971). No data on the apparatus structure of *A. binodosa* are available to test this ancestor-descendant relationship hypothesis.

The earliest *Ancyrodella* species tend to be represented only by juveniles, prone to misidentification as truly primitive forms (e.g., Ji 1989b: fig. 2). Supposed co-occurrence of primitive species together with morphologically much more advanced is rather an expression of the range of population variability than evolution (see Sandberg et al. 1989: pl. 1 and Racki and Bultynck 1993: fig. 3). *A. soluta* from the base of the Frasnian sequence at Wietrznia (Racki 1993) is distinct from *A. rotundiloba* (Bryant, 1921) represented slightly above at Wietrznia in both the size of basal cone in the P_1 elements and density of tuberculation of its platform. The specimens from the topmost strata exposed at Wietrznia II quarry are even more advanced in density of their tuberculation, approaching *A. rugosa* Branson and Mehl, 1934 (Fig. 26).

The stratigraphic distribution of some easily measurable characters, such as the density of tuberculation, is not consistent with their expected directional change. It appears thus that although the tubercles were more and more numerous on the platform, which significantly widened (as expected) in the succession of *A. soluta*, the density decreased between samples Wtr-7 and Wtr-9. This was an evolutionary reversal of this particular trait. Distinctions between these populations are significant enough to warrant taxonomic separation (Fig. 26). A significant overlap of the population variability makes a genetic continuity between these populations of different age likely. There is some difficulty, however, with choosing appropriate name for it. The holotype of *A. rotundiloba* was found as reworked; it can only be assumed that its morphology is modal for the type population. The modal density of tuberculation in the older Wietrznia population (sample Wtr-7; Fig. 26) is closer to the Australian type population of *A. rotundiloba alata* rather than to the American type population of *A. rotundiloba*. However, to not introduce confusion I follow the traditional naming of chronospecies and classify the sample Wtr-7 population in *A. rotundiloba*.

A trend was initiated in this succession of the *Ancyrodella* populations to widen the triangular smooth area on the ventral end of the platform. This was a prelude to develop an arched row of strong tubercles separating it, which gave the late Frasnian species of the genus their anchor-like appearance. This is actually the main character which enables separation of the populations represented in the basal part of the Wietrznia section from those from its middle. Some differences in this respect can be even identified between samples Wtr-7 and Wtr-9, but Wtr-13 departs very much from the ontogenetic trajectory of the triangular area size. It starts from the same point but overlaps only in juvenile specimens of different populations, being completely separate above 1.5 mm length of the elements (Fig. 26). Klapper (1985) proposed to classify the stage in the evolution of *Ancyrodella* corresponding to sample Wtr-13 as *A. alata* late form, but in the development of the triangular area they are so distinct that the species-rank distinction seems reasonable. Perhaps *A. rugosa* type is conspecific with populations of sample Wtr-13 (Figs. 25C, 26). The end of this evolutionary tendency is a robust ridge separating the untuberculated area from the rest of the platform.

In the stratigraphically condensed Wietrznia succession, 1 m below the top of the Frasnian (sample Wtr-23) specimens of the anchor-like *Ancyrodella* with the sharp ridge delimiting the tuberculated from untuberculated parts of the platform are associated with an ancestral *Manticolepis*. Perhaps this was the peak in platform reduction, which subsequently increased again by its bifurcation.

The development of the external lobe bifurcation is another apparent trend requiring populational studies. Müller and Müller (1957) believed that the bifurcation is a character of high taxonomic value and proposed separate genera for bifurcated and nonbifurcated ancyrodellids. This seems unlikely and the presence or lack of bifurcation (as well as corresponding ridges) is rather a matter of population variability at least at early stages of evolutionary development of this character, represented in the Włochy section by *Ancyrodella nodosa*. In sample Wł-R/A1 almost all specimens show anchor-like outline, but in some the rostral lobe is slightly swollen and in one specimen it is bifurcated. The point of bifurcation is there rather distant from the basal pit which means that

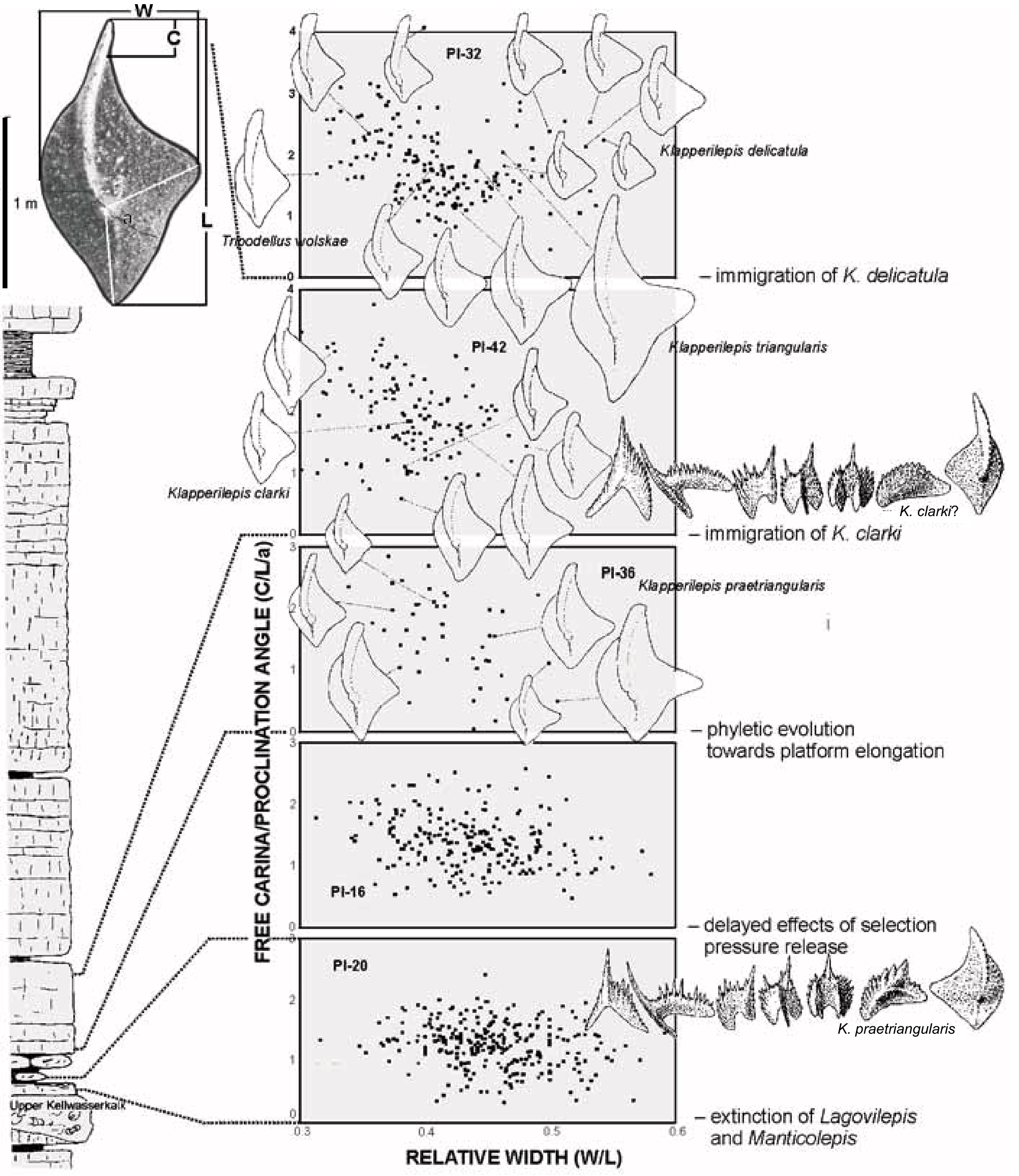


Fig. 47. Succession of the earliest Famennian *Klapperilepis* gen. nov. populations at Płucki (see also Fig. 46). A ratio of the relative extent of the free carina (C/L) to the caudal lobe proclination angle is plotted for P_1 (sp) elements. All measurable palmatolepidid platform elements from each sample are included (shape of the platform alone does not allow to discriminate species; they differ also in their more or less flat appearance). The number of species changes from one (Pł-20 and Pł-16) to two (Pł-42) to three (Pł-32). The pattern of variability of *K. praetriangularis* in the first Famennian sample Pł-20 (where it occurs alone as the only palmatolepidid) is indistinguishable from that in the latest Frasnian. Note increase of variability in sample Pł-16 which may be an effect of released competition from other palmatolepidids and character displacement in Pł-42, where the lineage of *K. clarki* appears, documented both by the diagnostic M (ne) elements and bimodal frequency distribution of P_1 elements morphs. Subsequent changes resulted from a combination of immigration events and a phyletic evolution at the site.

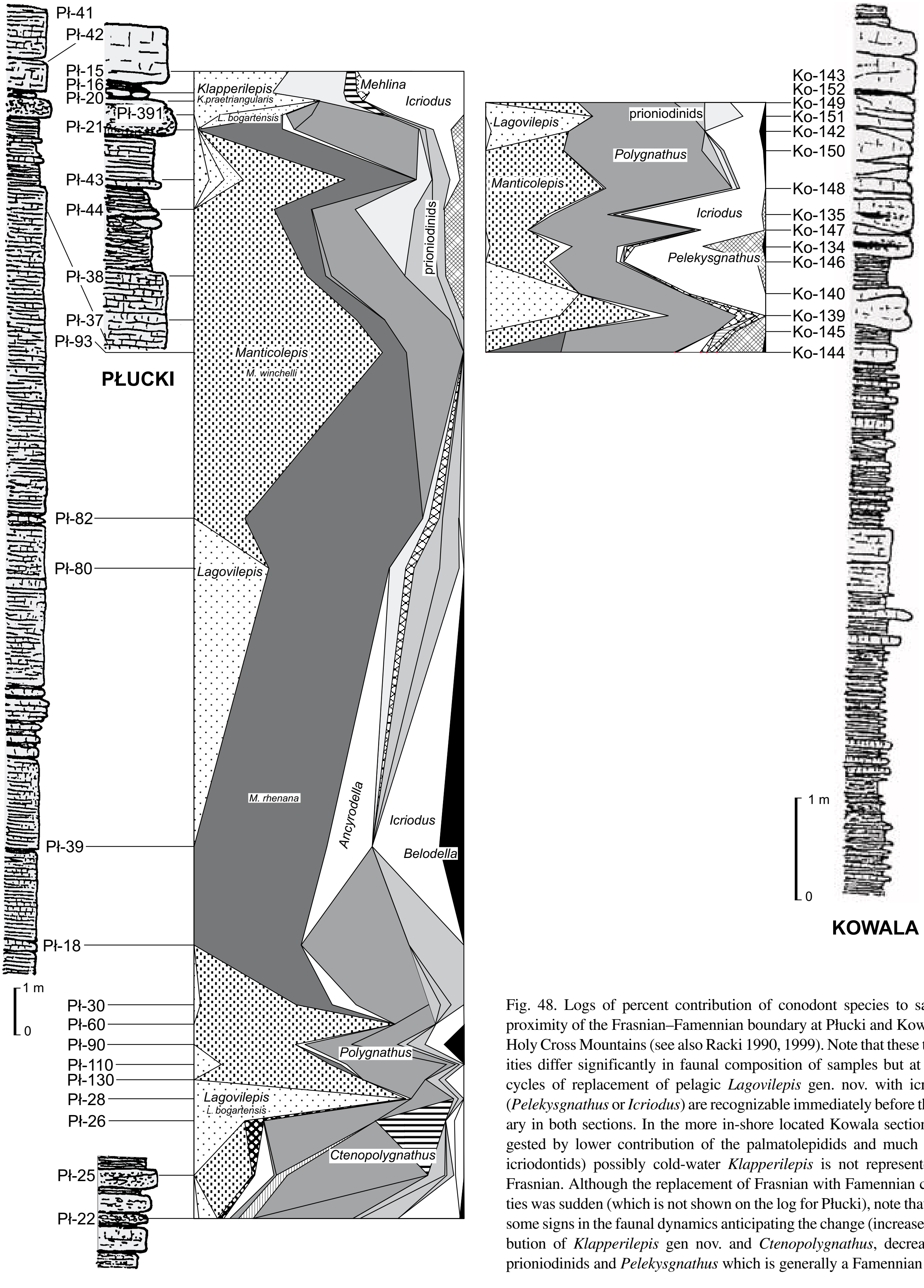


Fig. 48. Logs of percent contribution of conodont species to samples in proximity of the Frasnian–Famennian boundary at Płucki and Kowala in the Holy Cross Mountains (see also Racki 1990, 1999). Note that these two localities differ significantly in faunal composition of samples but at least two cycles of replacement of pelagic *Lagovilepis* gen. nov. with icriodontids (*Pelekysgnathus* or *Icriodus*) are recognizable immediately before the boundary in both sections. In the more in-shore located Kowala section (as suggested by lower contribution of the palmatolepidids and much higher of icriodontids) possibly cold-water *Klapperilepis* is not represented in the Frasnian. Although the replacement of Frasnian with Famennian communities was sudden (which is not shown on the log for Płucki), note that there are some signs in the faunal dynamics anticipating the change (increase in contribution of *Klapperilepis* gen nov. and *Ctenopolygnathus*, decrease of the prioniodinids and *Pelekysgnathus* which is generally a Famennian lineage).

bifurcation developed at later ontogenetic stages than in the late Frasnian species of the *A. curvata* group. Rare specimens with branched lobe occur in sample Wtr-5 where the modal morphology is a rather narrow platform and extreme morphs are not far from the *A. ioides* morphology (Fig. 25F).

In the late Frasnian section at Płucki the earliest rich assemblage of *Ancyrodella* of the lower cephalopod horizon (sample Pł-22) contains mostly P_1 (sp) element specimens with the caudal ("lateral") process bearing a lobe and the basal cavity underneath unbranched. In some specimens branching of this process took place and there is a complete gradation between branched and unbranched morphotypes, clearly showing that this is a single homogenous population (Fig. 27A–F, K). The lobe branching is frequent also in the mid-Frasnian *Ancyrodella lobata* from sample Wł-R/C1, where the majority of its P_1 (sp) elements show a subquadrate contour of the rostral lobe and bifurcation of the basal cavity below.

Starting from sample Pł-28, located a few meters above the lower cephalopod limestone at Płucki (Pł-22), only specimens with the branching have been found. As high as in sample Pł-39 (15 m below the Upper Kellwasserkalk) two specimens without bifurcation have still been encountered. Fifty cm below the top of the Wietrznia Frasnian succession (sample Wtr-22) non-bifurcated elements of *A. ioides* morphology co-occur with those typical of *A. curvata*. Available samples are too small to establish the exact nature of variation and the evolutionary transition. All 116 specimens of *A. curvata* from the Upper Kellwasserkalk horizon (sample Pł-391) show bifurcated caudal process.

Although the evolution of *Ancyrodella* is rather superficially known, it seems much more reliable as the basis for time correlation than the evolution of the palmatolepidids, widely used for this purpose. A provisional *Ancyrodella*-based scheme of chronozonation is used here. It can be further developed to serve as the evolutionary reference standard for the Frasnian.

***Ancyrognathus* lineage**.—As many as 15 species of *Ancyrognathus* have been distinguished in the most recent taxonomic revision of the lineage (Klapper 1990), with up to five coeval lineages being represented in some time slices. Unfortunately, no population study has followed, although the platform shape is extremely variable within samples of these conodonts. The actual number of lineages remains thus to be convincingly documented.

The apparatus structure, known in the geologically younger species of *Ancyrognathus*, shows some similarity to *Mesotaxis*, which suggests an evolutionary relationship (Fig. 28). It is generally accepted that the ancestral species of the branch is *Ancyrognathus ancyrognathoideus* (Ziegler, 1958) with the polymorphic platform appearance, usually resembling early *Mesotaxis* but in some specimens bearing a prominent lateral process, with transitional specimens occurring within the same samples (Ziegler 1958; Klapper 1990). In somewhat younger populations the platform surface became ornate, with the process orientation variable, but usually projecting transversely to the blade; such forms are traditionally classified as *A. triangularis*. It was thus of some surprise to find at Wietrznia (sample Wtr-7; Table 1) in association with *Mesotaxis falsiovalis*, a single minute specimen of *Ancyrognathus* with crenulated margins of otherwise smooth, very thin platform. Unless this is a contamination (unlikely) or the specimen is pathologic, the roots of *Ancyrognathus* may be slightly deeper in time than previously documented, although early *Mesotaxis* remains its plausible closest relative.

In even younger late Frasnian populations, the lateral process was more and more alike the dorsal ("posterior") part of the blade, and this part of the specimen received a bifid appearance, with a wide platform unifying the processes. Many morphologically transitional specimens occur in horizons transitional in age, so there seems to be a continuity in the evolution within a single lineage. The result of this process was *A. asymmetricus* (Fig. 28F–I). The latest Frasnian populations abound in almost symmetrically bifurcated elements (Fig. 28A–D) and perhaps it is reasonable to classify them as a separate temporal unit, as suggested by Sandberg et al. (1988), although the species rank seems to be too high for them.

According to Schülke (1996), *A. asymmetricus* continued into the earliest Famennian, gradually losing its lateral process.

Origin and apparatus diversification of the palmatolepidids.—The most unusual feature of the typical palmatolepidids is the high-arched shape of their M (ne) elements with straight processes and the lack of the medial process in the S_0 (tr) element. Phylogenetic meaning of these features remained uncertain for a long time.

The most primitive member of the family with known apparatus composition is *Mesotaxis falsiovalis* from the basal part of the Wietrznia section (sample Wtr-8; Table 1; Dzik 1991b). Its M (ne) elements (Fig. 30K) are already of the palmatolepidid appearance, with both processes strongly denticulate and arranged into an A-shape. As there are no data on the corresponding parts of the apparatuses of possible ancestors of *Mesotaxis*, that is in *Klapperina* (but see Fig. 29) and *Schmidtognathus*, it remains uncertain whether this M (ne) element shape originated within the lineage or was inherited after an unknown ancestor.

Although the fossil record of *Mesotaxis* is punctuated in the Holy Cross Mountains, a continuity between the populations of *Mesotaxis* from two deeper-water horizons at Wietrznia (Wtr-11 and 9), distant 5 m from each other (Figs. 4, 30), is likely. Although still hypothetical, the *M. falsiovalis–M. asymmetrica* transition may thus provide a convenient datum to age correlation. The ancestral lineage of *Klapperina* seem also to continue up to the upper Wietrznia horizon (Wtr-9; Fig. 29) which means that only some of its populations allopatrically transformed into *Mesotaxis*.

In *Mesotaxis* the S_0 (tr) element is triramous, of a typical polygnathid appearance, although the medial process is relatively short (Fig. 30H, S; Klapper and Philip 1971; Dzik 1991b). The Wietrznia and Włochy material offer some evidence concerning the subsequent evolution of the palmatolepidids. In the earliest palmatolepidids with lobate platform, *Mesotaxis*? *punctata* and *M. bohemica* apparatuses, the S_0 (tr) element medial process continues to be present, although even shorter (Fig. 31K, L). This trend towards the process shortening suggests that the primitive appearance of other elements of the symmetry transition series was an effect of secondary simplification, not of any direct relationship to the spathognathodontid lineage. The medial process subsequently disappeared, and this seems to be a much better point to demarcate the boundary between *Mesotaxis* and its palmatolepidid successors then the platform shape.

The oldest palmatolepidids S_0 (tr) elements with loss of the medial process have been found at Wietrznia in samples Wtr-15 and Wtr-16 (Fig. 33D, M). Unfortunately, the conodont assemblage there is of a high diversity, with three palmatolepidid species represented. Based on their occurrences in other samples such elements are tentatively attributed to the apparatuses classified in a new genus of *Kielcelepis* as *K. ljashenkoae* and not to co-occurring *Mesotaxis*? *domanicensis* (Ovnatanova, 1976) which according to Klapper and Foster (1993) is the end member of the *M. punctata* → *M. bohemica* lineage, based on morphology of its P_1 (sp) and P_2 (oz) elements. They also proposed that *K. ljashenkoae* is ancestral to *M. proversa*, but at Wietrznia the latter occurs in an older stratum (Wtr-13) together with *Mesotaxis punctata*. As high above as in Wtr-31, a possibly late member of the *Mesotaxis* lineage, *M. simpla* has been encountered (Fig. 32M–U). Perhaps the characteristic strong proclination of the platform lobe is a fluctuating character and these forms truly represent the same lineage. The third ancient Wietrznia palmatolepidid species, *Kielcelepis hassi* (samples Wtr-15 and 16), seems to represent the central lineage for the later evolution of the palmatolepidids.

In even younger sample Wtr-20 at Wietrznia, palmatolepidid S_0 (tr) elements occur having no medial process but sometimes with incipient bifurcation of lateral processes (Fig. 34F, G). They represent thus a transitional stage between *Kielcelepis* and a more advanced apparatus. The associated platform elements (Fig. 34B, D) suggest that this is *Kielcelepis*? (or *Lagovilepis*) *jamieae*. Such a palmatolepidid was probably ancestral to the three main lineages of the late Frasnian palmatolepidids: the most primitive *Lagovilepis* gen. nov. with not bifurcated processes of the symmetrical element in the apparatus, *Manticolepis* with an almost linear arrangement of processes in the anteriormost element of the apparatus, and *Klapperilepis* gen. nov. with raised tip of the platform in the posteriormost element.

Symmetrical S_0 (tr) elements of the palmatolepidids are too infrequent in the available mid-Frasnian material to allow reliable apparatus reconstructions and tracing precisely the phylogeny. It thus remains unknown whether the lack of lateral processes bifurcations (Figs. 41H, 42H) in the late Frasnian *Lagovilepis bogartensis* is a result of secondary simplification or was inherited after *Kielcelepis*. The wavy course of processes suggests that the S_0 (tr) element of *L. bogartensis* is derived, but the high angular profile of the M (ne) element (Fig. 42M) supports its direct connection with the earliest palmatolepidids. The incipient bifurcation of processes in sample Wtr-20 indicates early invention of the S_0 (tr) element morphology which is typical for most of the palmatolepidids. In early *Manticolepis* from samples Wtr-5 and Wtr-23, classified here tentatively as *M. gigas* bifurcation of the S_0 (tr) element processes is highly variable (Figs. 36H, I, 37G, H; Klapper and Foster 1993 synonymised *Palmatolepis gigas* with *P. winchelli*; alternatively, these populations could be classified as early *P. winchelli*).

In somewhat younger populations of typical *Manticolepis winchelli* the bifurcation is a stable character (Fig. 39K, L) but the point of bifurcation distant from the cusp indicates its late ontogenetic development. Some inconsistency to this picture is introduced by the weak bifurcation of the S_0 (tr) element processes in the latest Frasnian sample Wtr-18 (Fig. 37D). Perhaps *P. gigas* survived somewhere allopatrically and replaced *M. winchelli* after its brief occurrence at Wietrznia.

The point of bifurcation is much closer to the cusp and all the four terminal processes are prominent in the lineage of *Manticolepis rhenana* (Fig. 40B, H). The high-arched P_2 (oz) element of *M. rhenana* was perhaps inherited after *M. muelleri*, which otherwise is closely similar to *M. winchelli* (Foster and Klapper 1993)

Palmatolepidids at the Frasnian–Famennian transition.—Together with *Lagovilepis* and *Manticolepis* yet another palmatolepidid lineage is represented in the Upper Kellwasserkalk, characterised by a different profile of its P_1 (sp) elements (raised, instead of bent, tip of the platform) but also with a different apparatus structure. In the apparatus, the primitive (plesiomorphic) high angular profile of the M (ne) elements is associated with clearly tetraramous S_0 element (Figs. 44–46). It is proposed thus to separate these conodonts generically as *Klapperilepis* gen. nov. This lineage has been identified at Płucki already by Wolska (1967) as *P. triangularis* but Frasnian populations are now usually classified in *K. praetriangularis*. It had a virtually world-wide distribution in the latest Frasnian (e.g., Ji 1989a).

There is no problem with distinguishing P_1 (sp) elements of *Klapperilepis praetriangularis* from associated *L. bogartensis* and *M. winchelli* in the Upper Kellwasserkalk samples (Fig. 43). Their morphology is basically different in that the dorsal process is not bent basally and the platform is much wider. The proclination angle is similar, however, which may mean that this kind of the platform geometry is primitive (plesiomorphic) for the palmatolepidids.

According to Schülke (1999: p. 54) the lineage of *Klapperilepis* ("*P. triangularis*") originated during the Upper Kellwaserkalk event from *M. winchelli*. This was definitely not the case. First, the oldest *K. praetriangularis* population occurs in the lower cephalopod limestone at Płucki (Pł-22; Fig. 44), second, its M (ne) element is much less derived in respect to early palmatolepidids than that of *M. winchelli*. Probably *Klapperilepis* is a "sister" lineage of *Manticolepis*

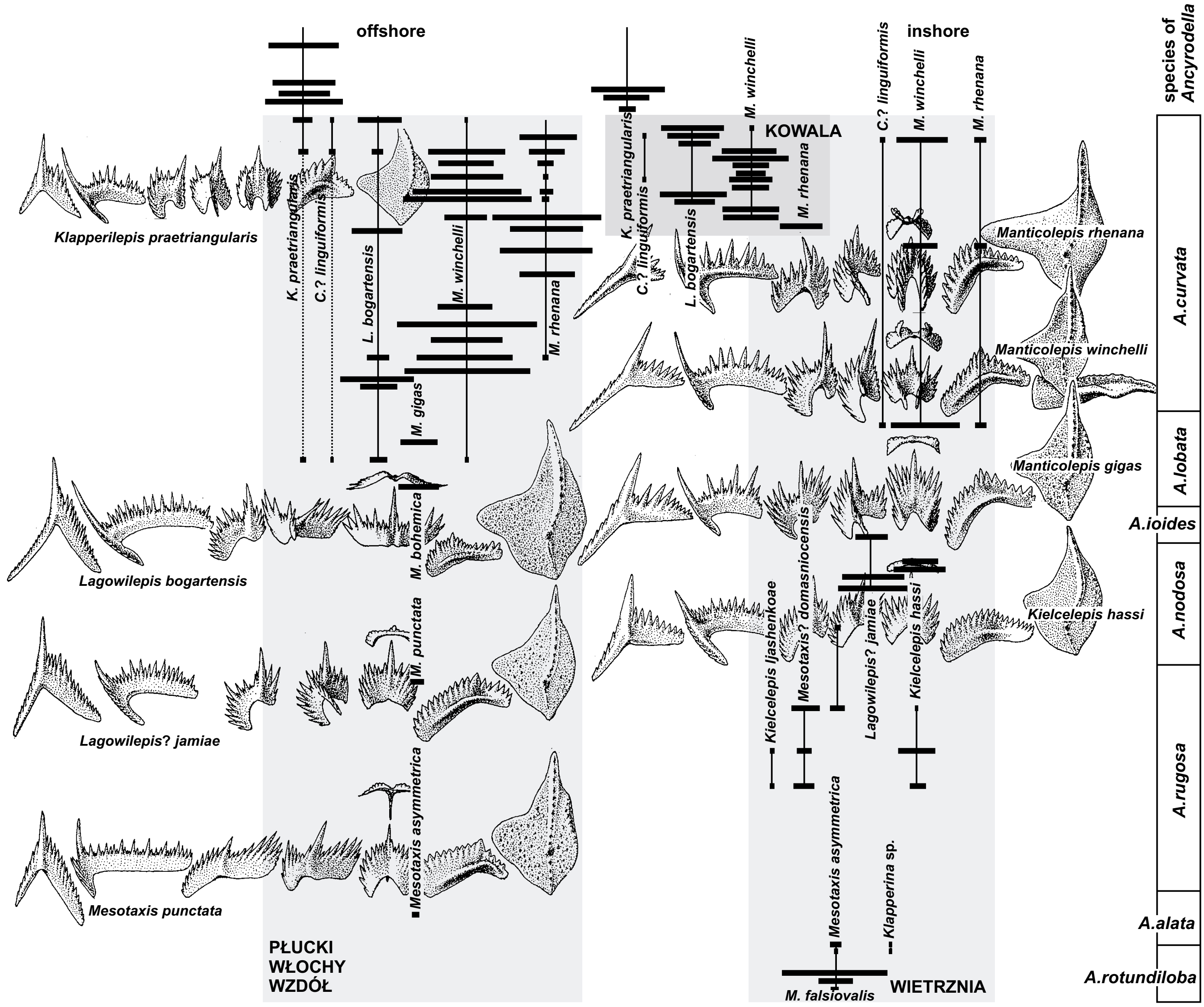


Fig. 49. Succession of palmatolepidid species in sections of the Frasnian and earliest Famennian representing probably relatively deeper (Płucki, Włochy) and shallower (Wietrznia) areas in the Holy Cross Mountains. Approximate percent contribution to samples shown by horizontal bars; provisional *Ancyrodella*-based zonation used to correlate sections (each lower zonal boundary defined on the evolutionary origin of its nominal species – they remain to be documented biometrically). Note that *Klapperilepis triangularis* and *Conditolepis*? *linguiformis* first appear in offshore areas and then expand to shallower environments. Also *Lagovilepis bogartensis* may be an open-sea species. Only *K. praetriangularis* survives the Frasnian–Famennian boundary event, probably being a relatively cold-water species. The record is too incomplete and punctuated to allow precise evolutionary studies but a general pattern of the evolution is shown with diagrammatic presentation of apparatuses.

and originated together with *Lagovilepis* from *Kielcelepis* after the bifurcation of the S_0 (tr) element processes developed. The *K. praetriangularis* population from sample Pł-20 (Fig. 46) differs from that in the immediately underlying Upper Kellwasserkalk horizon (sample Pł-391; Fig. 45) only in that it occurs alone, without any other palmatolepidids. From this point enhanced evolution and diversification of *Klapperilepis* began. Sample Pł-20 comes from a limestone layer covering the cephalopod limestone with a diverse Frasnian conodont assemblage. Immediately above, a black clay with limestone concretions follows. It appears thus that the change was coeval with, or slightly preceded, a significant change in sedimentary regime. Although the facies of sample Pł-16 is rather unusual for the Płucki section (Fig. 4), otherwise rather monotonous succession of laminated marly shales and thin-bedded marly limestone, by no means was the change dramatic. The *Klapperilepis* population from sample Pł-16 differs somewhat from that of sample Pł-20 in a skewed distribution of the platform lobe proclination angle.

The difference between samples Pł-20 and Pł-16 is expressed only in a small increase in contribution of specimens with more transversely oriented lobe. There is no apparent bimodality in distribution. This may possibly be an effect of relief from competitive influence of other palmatolepidid species, which disappeared a little earlier (in the Upper Kellwasserkalk, *K. praetriangularis* shows much narrower variability range than associated *L. bogartensis*; Fig. 43).

In successive samples above the Frasnian–Famennian boundary in the Płucki section the skewed distribution of the platform lobe proclination angle becomes more and more apparent in *Klapperilepis*. Although the mean value of the proclination does not changes significantly (the dominant morphologies are more or less similar) its variance increases significantly (for Pł-391 it counts 29, Pł-20–34, Pł-16–39, Pł-36–48, Pł-42–48, Pł-41–78, and Pł-32–35). The most likely explanation for this change in variability is that the samples higher in section are heterogenous as another species of *Klapperilepis* migrated to the area. The alternative, that sympatric speciation took place is not supported by the evidence.

In sample Pł-36 representing return of the micritic limestone sedimentation in the area (set C-2 of Racki et al. 2002), morphologies of P_1 (sp) elements traditionally classified in various species are there represented, but all show transitions within a very variable population. Despite extensive additional sampling only a single set of morphologies of ramiform elements of the apparatus has been documented, which does not differ from that of older *K. praetriangularis*.

The occurrence of additional species of *Klapperilepis* is recognisable for the first time in sample Pł-42 above the Frasnian–Famennian boundary. Specimens with a relatively narrow platform and transverse orientation of the angular (in contour) platform lobe seem to form a separate cluster (Fig. 47). The modal morphology for *K. praetriangularis* is represented there only by a fraction of the sample. Specimens with a very wide platform disappeared. The associated M (ne) elements are of two kinds, one of them of *K. praetriangularis* morphology, the other shows a fan-like arrangement of denticles on the external process, similar to those attributed to "*P.*" *arcuata* Schülke, 1995 by Schülke (1999; note that the type population of the species is of much younger age; perhaps *P. clarki* Ziegler, 1962 is conspecific with the Płucki population). Other ramiform elements are variable, but there is no apparent multimodality in their frequency distribution, perhaps except the S_0 (tr), with two kinds different in ontogenetically earlier or later bifurcation of processes.

The likely explanation for the decrease in population variability of the *K. praetriangularis* P_1 (sp) elements in sample Pł-42 is the ecological phenomenon of character displacement, already invoked to interpret profound changes in population variability of Carboniferous conodonts (Dzik 1997: 70). Possibly the lineage of *K. arcuata* originated allopatrically from *K. praetriangularis* somewhere else and immigrated to the area. This forced the local population of *K. praetriangularis* to accommodate to new conditions of partially overlapping ecological niches (and competition for resources between the physiologically closest specimens). In sample Pł-32, located significantly higher in the section, the empty field of wide platforms is filled again by the *K. delicatula* (Branson and Mehl, 1934) lineage (Fig. 47; see Schülke 1995, 1999).

It seems that in the course of evolution of *Klapperilepis* close to the Frasnian–Famennian boundary the platform elements became gradually narrower and the P_2 (oz) elements develop stronger platform. Populations from the type horizon of *K. triangularis* (Sannemann, 1955) show more derived apparatus structure than those from immediately below and above the boundary. Whatever would be the diagnosis of *K. triangularis*, the only possibility to define morphologically its origin from *K. praetriangularis* is well after the disappearance of *Lagovilepis* and *Manticolepis*. There is hardly any possibility to match the definition of the Frasnian/Famennian boundary based on environmentally controlled faunal changes (Klapper et al. 1994) with the phyletic evolution of the *Klapperilepis* lineage.

Post-Frasnian evolution of the palmatolepidids.—The earliest Famennian palmatolepidid faunas, as shown by their apparatuses reconstructed by Schülke (1999), were of a rather low morphologic diversity. Some lineages, for instance that of *Klapperilepis quadrantinodosolobata* (Sannemann, 1955) preserved the same apparatus structure for relatively long time (Metzger 1994). The first derived form which significantly modified the ancestral *Klapperilepis* ground plan of the apparatus was *K. clarki* (or *K. arcuata* as discussed above).

The Famennian palmatolepidid lineage which deviates the most from the Frasnian apparatus ground-plan was that of *Tripodellus*. Initially its P_2 (oz) elements further developed the lateral bent of processes, the trait occurring already in *K. praetriangularis*. In populations transitional to *Tripodellus* some forms developed additional third process in elements at this location (Schülke 1999: pl. 9: 25). This took place after the palmatolepidid faunas restored already their diversity. In *Tripodellus minutus* (Branson and Mehl, 1934) the process was fully developed (Metzger 1994) which persisted in the late Famennian species of the lineage (Dzik 1991b).

In the Famennian lineages of *Palmatolepis* and *Panderolepis* the processes of M (ne) elements acquired a position closely similar to that in the Frasnian *Manticolepis*. Schülke (1999) documented a succession from *Klapperilepis abnormis* (Branson and Mehl, 1934) through *Klapperilepis sandbergi* (Ji and Ziegler, 1993) to *Palmatolepis tenuipunctata* Sannemann, 1955—a good case of convergence (homoplasy). The latter species is close to *Panderolepis unca* Sannemann, 1955 and other species of the genus which developed and subsequently lost the originally wide platform in their sinuous P_2 (oz) element (Dzik 1991b; Metzger 1994; Schülke 1999). Also species of *Conditolepis* share a wide smooth platform of P_2 (oz) elements and radial arrangement of denticles in M (ne) elements with early *Panderolepis*, despite a rather different morphology of their P_1 (sp) elements, lacking lateral lobe and thus resembling the Frasnian *C.*? *linguiformis*. Typical species of *Palmatolepis* show a robust irregular denticulation of ramiform elements in the apparatus (Dzik 1991b; Metzger 1994).

This general pattern of the Famennian evolution of the palmatolepidids, understood as a diversification of the ancestral *Klapperilepis* apparatus plan, is consistent with the available evidence. Nevertheless, it has to be documented stratophenetically before the possibility of independent lineages crossing the Frasnian–Famennian boundary (Schülke 1995, 1999; Donoghue 2001) is excluded. *C.*? *linguiformis* and *M. winchelli* are also plausible candidates to the ancestry of some of the mid-Famennian lineages.

Ecological succession of Frasnian ammonoids in the Holy Cross Mountains

Ammonoids occur only in a few horizons within the Frasnian succession of the Holy Cross Mountains. The early Frasnian ammonoid localities are known only in the northern and southern marginal parts of the area. Virtually nothing can be inferred from the data about the course of their evolution because ecologically controlled punctuated distribution. The review below thus refers only to separate events of immigration of groups whose phyletic evolution can be traced elsewhere.

Frasne event fauna.—The first early Frasnian ammonoids were found in shales at Ściegnia by Kościelniakowska (1962), who initially identified them as clymeniids, to change her mind to gephuroceratids after identification of Frasnian conodonts there (Kościelniakowska 1967).

Virtually the same ammonoid fauna is known from a dark shale intercalation within thin bedded limestone and marls at the Kostomłoty II quarry (Racki 1985; collected by J. Malec). Pyritized small ammonoid conchs steinkerns of *Koenenites lamellosus* (Sandberger and Sandberger, 1856) (see House 1978: 48) occur there in a few centimetres thick dark shale intercalation within a horizon with pyrite marking the top of the Szydłówek Beds (Racki and Bultynck 1993). Much larger pyritic nuclei and a specimens of *K. lamellosus* with body chamber preserved in limestone (Fig. 50A–C, E) have been found at Ściegnia. A single crushed specimen (Fig. 50D) of this species comes from the scree at Zamkowa Góra in Chęciny at the southern slope of the hill, not far above the conodont-based Givetian–Frasnian boundary (Racki 1992). The appearance of an ammonoid fauna with *K. lamellosus* in the Holy Cross Mountains seems to be coeval with similar assemblage entry in the Western European part of the Variscan sea (House et al. 1985) in relation to the Genundewa–Frasne eustatic pulse (Becker et al. 1993).

Acanthoclymenia, characterized by a tabulate venter and a evolute whorl almost from the beginning of its ontogeny (Fig. 50F–I), invaded North America and Europe with the first Frasnian eustatic rise. There is a morphologic and probably stratigraphic transition to it from *Ponticeras* (House and Ziegler 1977: 80). Its first relatively well known species is *A. genundewa* (Clarke, 1898) with its type from the Genundewa Limestone of New York (Kirchgasser 1975; House 1978; Becker and House 1993). Subsequent evolution of *Acanthoclymenia*, well documented by Kirchgasser (1977), concerns mostly septal geometry, with lobes becoming more acute. Early *Acanthoclymenia* (Fig. 50F–I) is well represented in the ammonoid-bearing shale at Ściegnia (see Kościelniakowska 1967) and at Kostomłoty (Laskowa Quarry; Racki et al. 1985). Noteworthy, the Ściegnia population differs from that of Kostomłoty and the Genundewa Limestone in much less acute lateral saddle; in this respect resembling rather the ancestral *Ponticeras* species. This suggests a somewhat older age of the Kostomłoty ammonoid horizon, which is supported by co-occurrence of *Epitornoceras*, most probably represented by *E. mithracoides* (Frech, 1887) (Fig. 50N, O), a rare species at Laskowa, the only one with acute venter at adult stages. Its type horizon is the Late Givetian *Stenopharciceras lunulicosta* Zone at Oberscheld in Germany (House 1978: 60), thus the lineage has rather deep evolutionary roots.

A generalized tornoceratid occurring at Laskowa and Ściegnia (Fig. 50K–M) is similar to the coeval poorly known North American *Linguatornoceras compressum* (Clarke 1899) (see House 1965). Specimens from the late Frasnian of Timan identified as *Linguatornoceras clausum* (Glenister, 1958) by Becker et al. (2000) may be related, too (but not those approximately coeval to the Polish population, classified as *L.* aff. *clausum*, which show narrower lobes).

Among specimens of Kościelniakowska (1967: pl. 3: 9) are some with periodic constrictions showing narrow ventrolateral lappets at the aperture. They are too poorly preserved to be sure to which of the lappeted umbilicate tornoceratids known from younger strata are related (see House and Price 1985).

Lower Płucki cephalopod limestone fauna.—In the German late Frasnian succession there are two horizons of black Kellwasser limestone generally believed to correspond to brief sea level maxima (e. g., Johnson et al. 1985; Sandberg et al. 1988; Racki 1990; Wendt and Belka 1991; Morrow 2000). They seem to be widely correlatable but there are some inconsistencies in the meaning of the term "Kellwasserkalk events" and its expression in facies. For instance, while referring to the Moroccan succession, Belka and Wendt (1992) extended the "lower Kellwasser member" as far back as the earliest Frasnian black limestone horizon. In this respect the distribution of facies in Morocco resembles more that of Timan (e.g., Becker et al. 2000) than of the central Europe.

At Płucki there is a black limestone horizon located some thirty metres below the similar bed terminating the Frasnian (Pł-22; Fig. 4; Racki et al. 2002). At present I am not able to correlate it with the Steinbruch Schmidt section precisely enough to be sure of its correspondence to the Lower Kellwasserkalk. This may be a local, accidental sudden accumulation of pelagic sediment with cephalopod shells. Cephalopod conchs in the lower cephalopod limestone at Płucki are numerous but almost invariably crushed. Only few specimens represent phragmocones with suture lines preserved. Therefore species identification is rarely possible and the real diversity may be higher. In any case, this is an assemblage of low diversity, dominated with two forms of discoidal gephuroceratids conventionally classified as *Manticoceras intumescens* (Beyrich, 1837) and *Manticoceras lamed* (Sandberger and Sandberger, 1850) (Fig. 51E–J; see House and Ziegler 1977) and the tornoceratid *Linguatornoceras* sp. (Fig. 51A–C). Only two small conch fragments of *Aulatornoceras*, possibly *A. auris* (Quenstedt, 1846), supplement this species list. In a few juvenile specimens of *Manticoceras* protoconch was exposed; it does not differ in size and shape from those of the Laskowa gephuroceratids.

While the Płucki lower cephalopod limestone assemblage is represented by juvenile specimens with only fragmentary larger specimens (Fig. 51G) the only Frasnian ammonoid horizon at Wietrznia (bed of sample Wtr-17; Fig. 4) contains only large manticoceratid conchs (Fig. 51K, L). They are usually incomplete and difficult to extract from the rock but a few more or less complete specimens show that there is some variety in conch robustness, despite closely similar umbilicus size and suture. In this respect the Wietrznia gephuroceratids resemble those from the lower cephalopod limestone at Płucki. Whether this is a population variability or two distinct species are represented in both cases, requires more evidence.

There are also two unconfirmed reports on occurrences of beloceratids in the Holy Cross Mountains (a lineage which continues the trend initiated by *Acanthoclymenia genundewa*). Dybczyński (1913) illustrated two juvenile pyritized specimens found in a reworked material at now abandoned Sieklucki's brickpit in Kielce (Quaternary clays containing fossils from eroded Late Devonian strata, mostly Famennian) which are unfortunately not represented in the Muzeum Dzieduszyckich (now Natural History Museum of the Ukrainian Academy of Sciences) in Lvov. *Beloceras acutodorsatum* Dybczyński, 1913 shows prominent ribs on the shell surface and, as shown on a very diagrammatic drawing by Dybczyński (1913: pl. 1: 15) and strongly compressed conch with numerous acute lobes, both characters consistent with affiliation to *Beloceras*. Undescribed beloceratids (Henryk Makowski personal communication) occur in the *Manticoceras* limestone at the Kadzielnia Quarry in Kielce (see Szulczewski 1971). In the Canning Basin of Australia, where the most complete succession of beloceratids is documented, they occur to the equivalent of the Lower Kellwasserkalk (Becker et al. 1993), elsewhere ranging even up to the end of the Frasnian (Becker and House 1994a). A similar age is plausible for the Holy Cross Mountains occurrences.

In strata between the lower and upper cephalopod limestones at Płucki only a single juvenile *Manticoceras* about 30 m NW of the main trench (sample Pł-28) and a *Linguatornoceras* coming probably from somewhat below the upper cephalopod horizon have been found.

A cephalopod limestone with discoidal *Manticoceras* has been reported by Miłaczewski (1972) from the borehole Opole Lubelskie IG 1, located about 50 km NE of the Holy Cross Mountains area.

Upper Kellwasserkalk fauna.—Belka and Wendt (1992) included the German Lower and Upper Kellwaserkalk horizons in a single event covering their Upper Kellwasser member, extending to the middle of the Famennian (in fact, the dark-coloured rocks extend as high also in the Łagów area of the Holy Cross Mountains). The Upper Kellwasserkalk goniatite horizon has been identified at Płucki by Makowski (1971) and in the Kowala succession by Racki (Racki and Baliński 1998: fig. 8). They contain similar ammonoid assemblages, although there are some differences in their composition from bed to bed. Remarkably, whereas in the lower cephalopod horizon at Płucki and in the silica-rich horizons at Kowala the fossil assemblages seem completely homogenised (Fig. 53C), in Płucki frequently conchs of the same species are found in the same piece of the rock (Fig. 53A, B). This does not seem to be a random distribution and there remain a possibility that monospecific shoals appeared periodically, producing monospecific fossil assemblages that subsequently were more or less homogenised within the sediment. This may explain apparently random variation in composition of ammonoid faunas in the succession. Apparently, this phenomenon makes assemblage zone concept, as well as the graphic correlation method, highly unreliable.

The Kowala Quarry section contains in its latest Frasnian part several horizons with silicified macrofossils (Racki and Baliński 1998; Racki 1999). Although details of conch ornamentation and suture lines are rarely shown by specimens preserved in this way (Figs. 53, 56), they can be easily ex-

Fig. 50. Early Frasnian goniatites from the northern part of the Holy Cross Mountains. **A–E**. *Koenenites lamellosus* (Sandberger and Sandberger, 1856), specimens from Racki's trench at Ściegnia (**A, B**), from goniatite shale intercalation at Laskowa quarry in Kostomłoty (**C, E**; also Racki et al. 1985: pl. 8: 4), and from the southern slope of the Zamkowa Hill at Chęciny (**D**), preserved in a limestone intercalation (**A** × 1.5), as pyritized nuclei (**B** × 3, **C** × 5, **E** × 20), and crushed in marly limestone (**D** × 1), ZPAL AmVII/1683, 1687, 970, 1947, and 1663. **F–I**. *Acanthoclymenia genundewa* (Clarke, 1898), crushed specimens from trenches dug at Ściegnia by Racki (**F**) and Kościelniakowska (**G** × 5) and pyritized from Laskowa (**H, I**; probably an older population) (**F–H** × 5; **I** × 20), ZPAL AmVII/1686, unnumbered specimen of Kościelniakowska (1967: pl. 2: 6), and ZPAL AmVII/969 (also Racki et al. 1985: pl. 7: 3a, b) and ZPAL AmVII/1664. **J**. *Aulatornoceras*? sp., unnumbered specimen from Kościelniakowska's trench at Ściegnia, × 10. **K–M**. *Linguatornoceras compressum* (Clarke 1899), unnumbered crushed specimen of Kościelniakowska (1967: pl. 3: 5) from Ściegnia (**K** × 5) and pyritized nuclei from Laskowa (**L** × 5; also Racki et al. 1985: pl. 7: 6) and Racki's trench at Ściegnia (**M**, × 20), ZPAL AmVII/976 and 1709. **N, O**. *Epitornoceras mithracoides* (Frech, 1887) pyritized specimens from Laskowa (**N** × 5; also Racki et al. 1985: pl. 7: 4; **O** × 20), ZPAL AmVII/978 and 1665. Pictures of Kościelniakowska's (1967) originals of unknown place of deposition were taken from her negatives.

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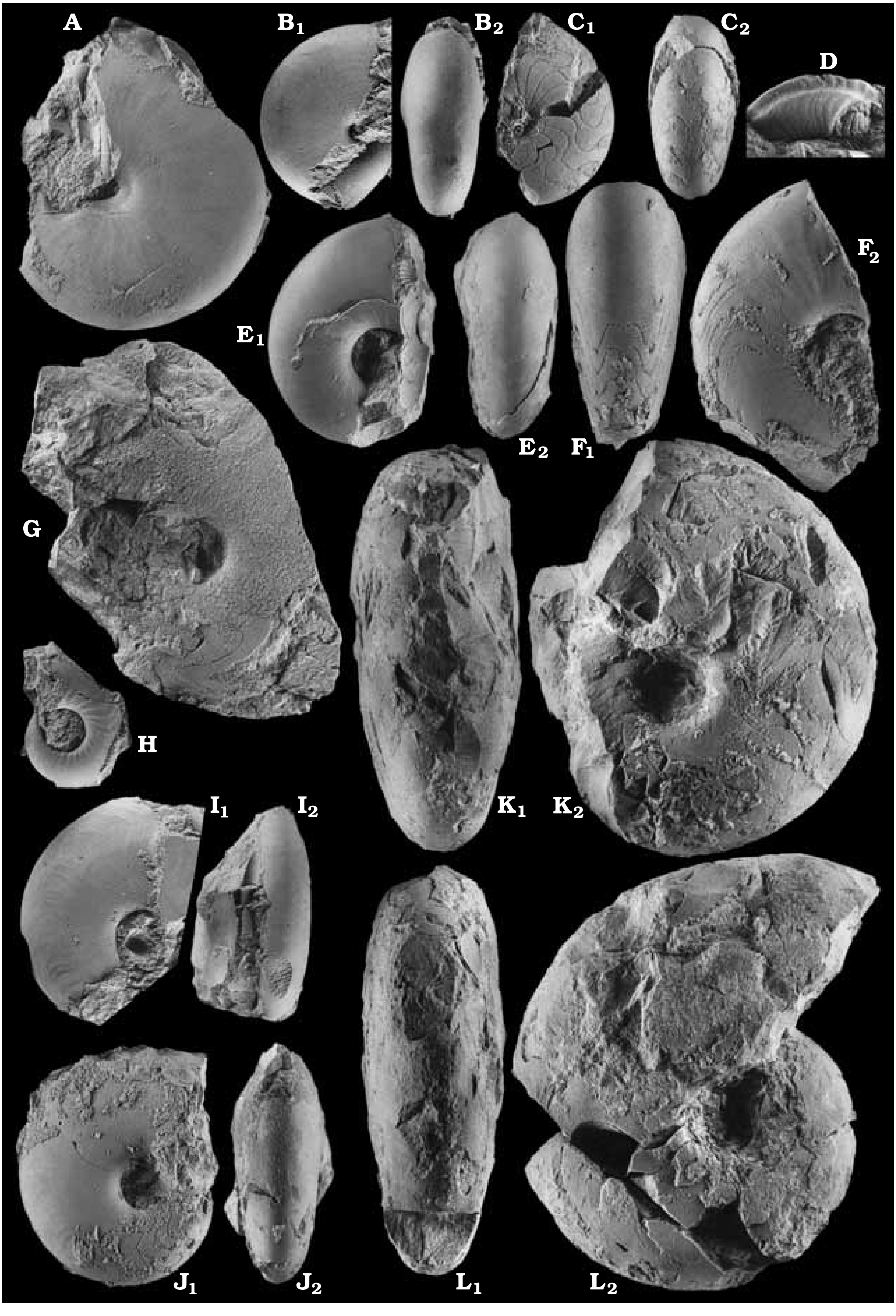
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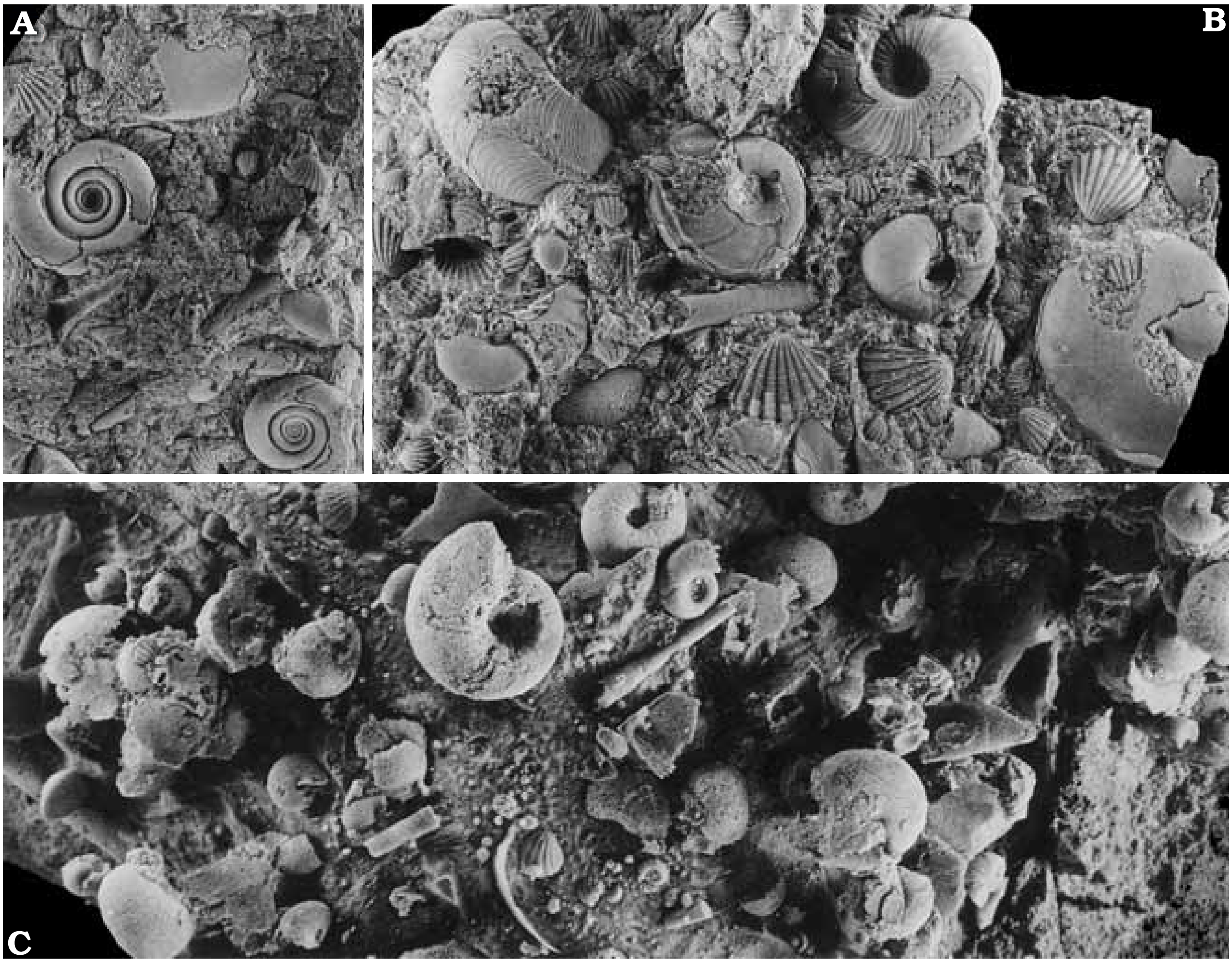


Fig. 52. Accumulations of goniatite conchs and other fossils in the latest Frasnian strata of the Holy Cross Mountais. **A**. Conchs of *Archoceras varicosum* (Drevermann, 1901) in a piece of the Upper Kellwasserkalk from Płucki (Pł-391). **B**. Conchs of *Aulatornoceras belgicum* (Matern, 1931) in association with *Linguatornoceras* sp. from the same bed. **C**. Acid etched sample Ko-142 from Kowala with similar but more homogenized association.

tracted from the rock in great numbers and identified by analogy with other occurrences. Most impressive is the variation in contribution to the assemblages of those species which are extremely conservative and pass the Frasnian–Famennian boundary reappearing as Lazarus taxa (*Archoceras*, *Aulatornoceras*, and *Linguatornoceras*) and those which are confined to the late Frasnian (*Manticoceras* and *Crickites*).

It is not completely clear whether the Frasnian–Famennian boundary is represented at Kowala. Probably the latest Frasnian ammonoid fauna in the Holy Cross Mountains is that at Płucki (Pł-391). The most common (and best preserved) goniatite specimens at Płucki belong to the relic anarcestid *Archoceras varicosum* (Drevermann, 1901) (Fig. 54A–H). Makowski (1971) followed Wedekind (1918) in classifying it among gephuroceratids under the name *Manticoceras bickense*. The *Archoceras* lineage was extremely conservative, with punctuated stratigraphic distribution. Apparently, it had restricted environmental preferences to conditions which were continuously available in time span from the Late Givetian to early Famennian. The Płucki species conchs show extensive variability in whorl cross section, development of varices, and ornamentation (Fig. 54A–H).

The second in number is the very long ranging and morphologically variable tornoceratid *Linguatornoceras* sp. (Fig. 54N–S) characterized by a deep lateral suture lobe. It shows a great variability in conch morphology, which refers both to the whorl cross section but also prominency of ornamentation, with always acute lappets sometimes forming shallow ventrolateral furrows (Fig. 54N). There is thus hardly a need to separate such forms in a separate genus (or even subgenus) *Truyolsoceras*.

◄ Fig. 51. Goniatites from the lower cephalopod horizon at Płucki (**A**–**J**) and from sample Wtr-17 bed at Wietrznia (**K**, **L**). **A**–**C**. *Linguatornoceras* sp., specimens ZPAL AmVII/1622, 1554, and 1627 (**A** and **B** × 1.4; **C** × 1.9). **D**. *Aulatornoceras* cf. *auris* (Quenstedt, 1946), specimen ZPAL AmVII/1577, × 1.9. **E**, **F**, **K**. *Manticoceras intumescens* (Beyrich, 1837), specimens ZPAL AmVII/1626, 1625, and 1662 (**E** × 1.9; **F** × 1.4; **K** × 0.9). **G**–**J**, **L**. *Manticoceras lamed* (Sandberger and Sandberger, 1850), specimens ZPAL AmVII/1556, 1555, 1553, 1558, and 1661 (**G** × 0.9; **H** × 2.8; **I**, **J** × 1.4; **L** × 0.9).

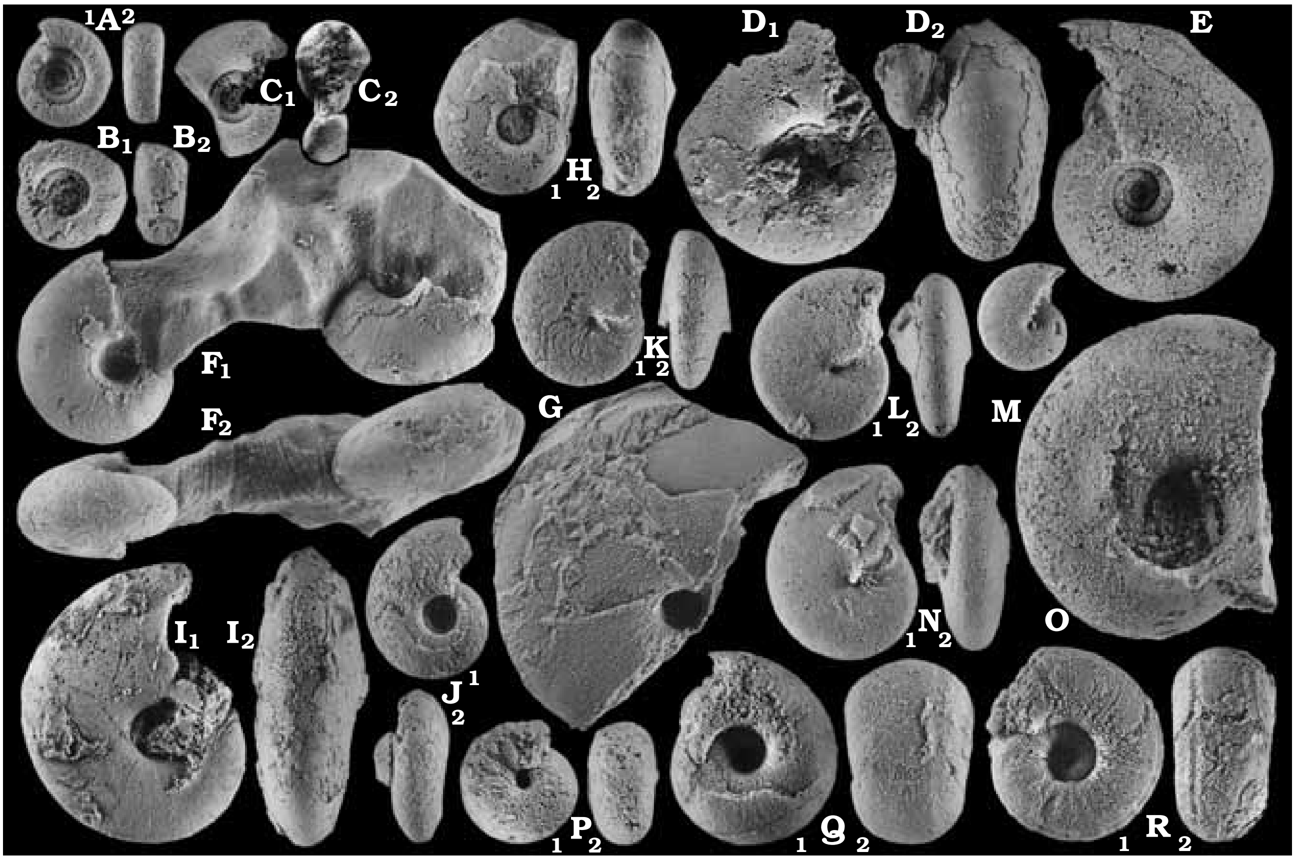


Fig. 53. Silicified goniatites from the topmost Frasnian strata at Kowala Quarry. Specimens rarely preserve suture, species identification is thus in many cases based on pressumed conspecifity with better preserved specimens from nearby coeval cephalopod limestone of Płucki; all × 2. **A**. *Archoceras varicosum* (Drevermann, 1901), sample Ko-134, specimen ZPAL AmVII/1667. **B**–**E**. *Manticoceras adorfense* (Wedekind, 1913), samples Ko-134 (**B**) Ko-142 (**C**, **D**) and Ko-159 (**E**), specimens ZPAL AmVII/1610, 1717, 1713, and 963. **F**–**H**. Involute *Manticoceras*? sp. sample Ko-159, specimens ZPAL AmVII/964, 962, and 960. **I**, **J**. *Manticoceras drevermanni* (Wedekind, 1913), sample Ko-142 (**I**) and Ko-134, specimens ZPAL AmVII/1714 and 1675. **K**–**N**. *Linguatornoceras* sp. aff *L. clausum* (Glenister, 1958), samples Ko-142 (**K**, **M**, **N**) and Ko-134 (**L**), specimens ZPAL AmVII/1716, 1671, 1715, and 1718. **O**. *Crickites holzapfeli* Wedekind, 1913 (or perhaps *Sphaeromanticoceras* sp.), sample Ko-159, specimen ZPAL AmVII/958. **P**–**R**. *Aulatornoceras belgicum* (Matern, 1931), samples Ko-142 (**P**, **R**) and Ko-134 (**Q**), specimens ZPAL AmVII/1719, 1668, and 1714.

Discoidal conchs of *Manticoceras drevermanni* (Wedekind, 1913) dominate among larger goniatites (Fig. 55A–C). Co-occurring there *Manticoceras adorfense* (Wedekind, 1913) (Fig. 55D–I) and *Crickites holzapfeli* Wedekind, 1913 (Fig. 55J–M) are also variable in the conch whorl cross section and only the specimens with well preserved growth lines can be classified with confidence (apertural lappets are missing in *Crickites*). Unfortunately, only a fraction of specimens from Płucki show conch wall preserved well enough to show this crucial feature. This makes also a little uncertain whether there is only one robust *Manticoceras* species at Płucki, with adult specimens showing a somewhat subquadrate whorl cross section (Fig. 55I). Makowski (1963) reported occurrence of gephuroceratid specimens reaching 205 mm in diameter, which is consistent with similar occurrence of giant gephuroceratids with weakly convex or biconvex growth lines in coeval strata of Canning Basin, included in *Sphaeromanticoceras* by Becker et al. (1993). Makowski (1963) identified the Płucki gephuroceratids as *Manticoceras ammon* (Keyserling, 1844) (the smaller form reaching 71 mm in diameter) and *M. intumescens*. The type populations of both species are rather not similar morphologically (see House and Ziegler 1977, and Becker et al. 2000) and are unlikely to occur in such a young stratum. Even less likely is that they represent a dimorphic pair, as suggested by Makowski (1963) because they fundamentally differ in the shape of aperture virtually from the beginning of their ontogeny (cf. Fig. 55G and J).

Among well preserved conchs those of an open umbilicate tornoceratid are the most impressive (Fig. 54I–M), showing great variability in ornamentation and whorl cross section. The latter is even better documented by silicified material from Kowala. The conch shows unusually profound, as for Frasnian ammonoids, ontogenetic transformations, their umbilicus initially being very narrow and whorls wide, while mature specimens are evolute. This Płucki population seems to be a late member of the lineage of *Aulatornoceras auris*, known from pyritized juvenile specimens from the mid-Frasnian Büdesheim shales (House and Price 1985) and presumably occurring also in the lower

Fig. 54. Non-gephuroceratid goniatites from the Upper Kellwasserkalk at Płucki. **A**–**H**. *Archoceras varicosum* (Drevermann, 1901), specimens ZPAL AmVII/1471, 626, 1478, 1477, 1479, 1473, 617, and unnumbered SEM picture. **I**–**M**. *Aulatornoceras belgicum* (Matern, 1931), specimens ZPAL AmVII/616, 1510, 1505, 1506, and 628; note variation in conch proportions and ontogenetic changes in conch evoluteness. **N**–**S**. *Linguatornoceras* sp., specimens ZPAL AmVII/1380, 1727, 1725, 1374, 1376, and 1403; note variation in relative conch width. All × 2, except for **H** which is × 20 and **P** which is × 1.5.

cephalopod limestone at Płucki. The Upper Kellwaseerkalk species seems to be identical with *Crassotornoceras belgicum* (Matern, 1931) occurring in coeval strata of Belgium (House and Price 1985; separate generic names for these chronospecies may appear superfluous). *A. auris* differ from related and apparently ancestral species of *Linguatornoceras*, including *Truyolsoceras undulatum* (Sandberger and Sandberger, 1856), in its open umbilicus and more robust ornamentation, including periodic internal thickenings of the conch.

Makowski (1971) diagrammatically illustrated an allegedly oxyconic gephuroceratid from the Płucki Upper Kellwasserkalk, identified as *Manticoceras inversum* Wedekind, 1913 (the type of which comes from an older horizon of the

Frasnian; Wedekind 1918). If correctly identified, this would be another anomalously late occurrence. The original specimens could not be traced in the Department of Geology of the University of Warsaw collection, which would make plausible a possibility that this was a crushed specimen of *M. drevermanni*.

The distribution of typically Frasnian goniatite species and those which survived to the Famennian is highly irregular in the latest Frasnian strata in the Holy Cross Mountains sections (Fig. 57). At Płucki in the Upper Kellwasserkalk horizon (Pł-391) the three gephuroceratid species together contribute about one third to the assemblage. In the most completely sampled Kowala succession samples Ko-150 (25 specimens) and Ko-142 (29 goniatite specimens), both located near its top, manticoceratids are missing and only the "Famennian" lineages of *Linguatornoceras*, *Aulatornoceras*, and *Archoceras* are represented. The picture is complicated by the assemblage from sample Ko-149 (located within a few centimetres proximity to the bed of Ko-142 but taken at distance of a dozen of metres which makes any precise correlation uncertain). This is the only Kowala sample (56 specimens) in which gephuroceratids dominate, with not a single specimen of *Aulatornoceras*, but the species of *Manticoceras* represented there are distinct from those in other samples and from other latest Frasnian assemblages in the area (Fig. 53E–G). The largest sample of 2285 specimens (Ko-142) supports the feeling that the contribution of gephuroceratids was generally low in the latest Frasnian of Kowala.

Apparently, no single gephuroceratid passed the Frasnian–Famennian boundary (Becker et al. 1993) but at Kowala they were not represented in several faunas before the end of the Frasnian. Moreover, it has to be kept in mind that not a single ammonoid has been found in the earliest Famennian of the Holy Cross Mountains, although rich latest Frasnian faunas are known from the same sections. Several late Frasnian lineages (*Archoceras*, *Aulatornoceras*, *Tornoceras* s. l.) returned later, when environmental conditions similar to those of the latest Frasnian re-established. It was just a disappearance from the record in subtropical regions of the Late Devonian world and this is all what can be directly inferred from the fossil evidence.

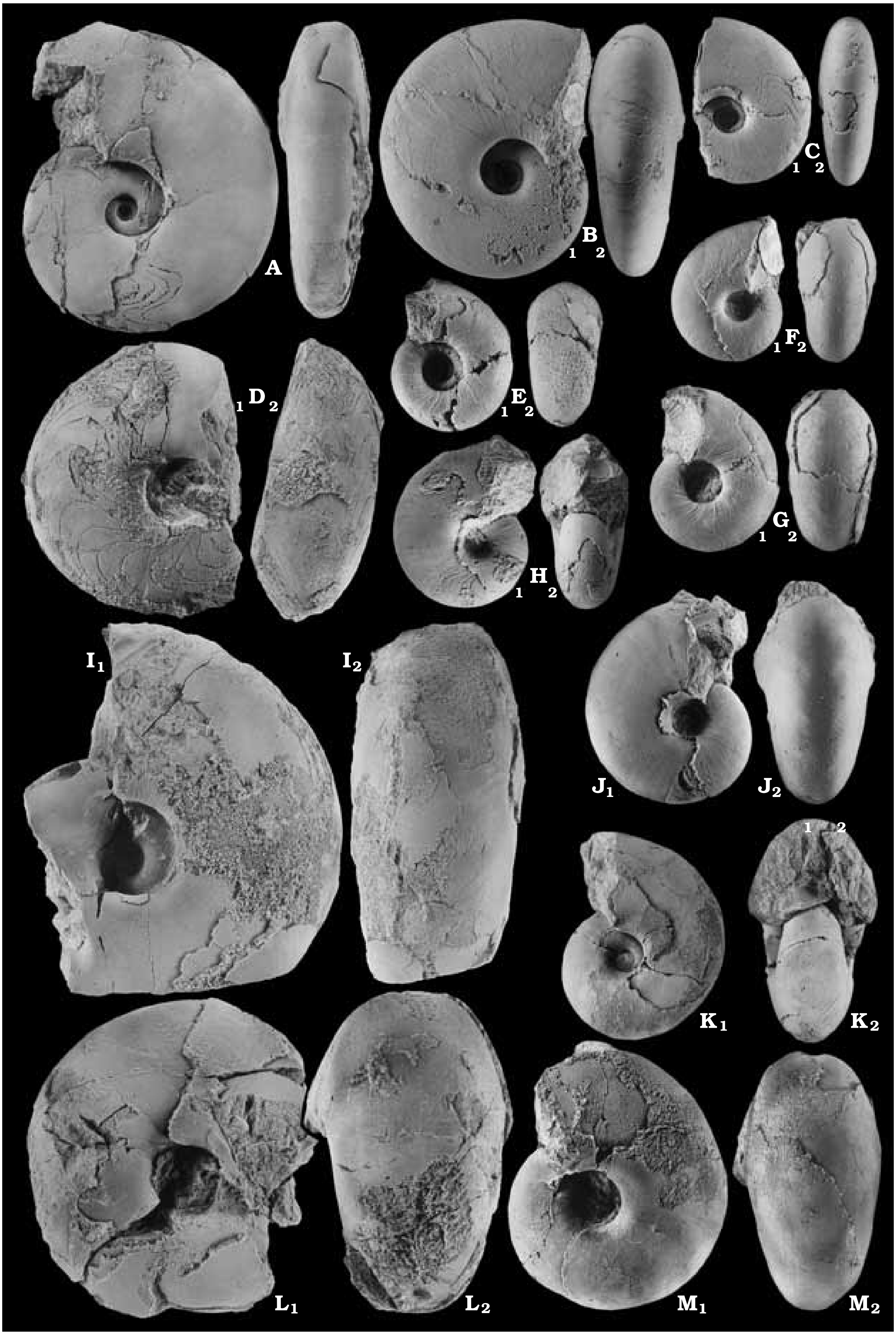
Generally, the tornoceratids represented a whole branch of ammonoids which did not care about the allegedly global extinction at the Frasnian Famennian boundary. Virtually all of its numerous lineages passed the boundary (House and Price 1985) although they dissapear completely from the record for some time.

The nature of the Frasnian–Famennian transition

The facies succession at the Frasnian–Famennian transition is similar over the world. No doubt thus that it was controlled by a global change of sea level, oceanic circulation, and climate (e.g., Becker and House 1994a; Hallam and Wignall 1999). The differences between particular areas depend rather on local bathymetry and sediment supply. The similarities in general pattern are truly astonishing, ranging from carbonate platform succession of South China (Ji 1989a, b) where nodular limestone sedimentation marks the beginning of the Famennian to the generally clastic successions such as that in Iran (Yazdi 1999) where limestone sedimentation was confined to the latest Frasnian (*P. linguiformis* Zone) and late Famennian, limy intercalations starting from the *P. crepida* Zone. This is generally interpreted as a latest Frasnian and mid-Famennian flooding and a brief drop in sea-level at the beginning of the Famennian (Johnson et al. 1985; Ji 1989a; Racki and Baliński 1998). Generally, the strata of that age were deposited in higher energy environments that those of the latest Frasnian (tsunamite of Sandberg et al. 1988; Wang 1994). The lack of shallow water corals in the early Famennian of most of the world has been explained by Poty (1999) as a result of cool climatic conditions. According to Streel et al. (2000), the palynological evidence shows a rather hot climate culminating during the latest Frasnian. The equatorial conditions expanded by that time, while during the early and mid-Famennian the scarcity of miospores in high latitudes suggests a very cold climate. This implies climatic control of the eustatic events, possibly connected with polar ice caps development (Streel et al. 2000).

The changes in sedimentation at the Frasnian–Famennian boundary were followed by transformations in fossil assemblages (e.g., Becker and House 1994a; Girard and Feist 1997; Casier et al. 2000; Streel et al. 2000). An almost world-wide increase in contribution of *Icriodus* elements to samples is reported at the beginning of the Famennian (Sandberg et al. 1988; Ji 1989a; Racki 1999; Morrow 2000). Although the picture of a revolutionary change in the environment, leading to the destruction of the extensive reefal ecosystems that thrived since the Late Ordovician, is generally agreed upon, details of the succession, the cause of the event and its evolutionary implications are a matter of controversy. For instance, according to Bratton et al. (1999) the Kellwasserkalk anoxia was not directly connected with the Frasnian/Famennian faunal turnover. In the North American Central Great Basin a decrease in organic diversity preceded the sea level lowering. Also the pattern of change among benthic organisms at the boundary, as exemplified by ostracods (contrary to interpretation by Casier et al. 1999; see their table 1), does not seem to differ especially from the preceding Frasnian faunal succession. Pelagic tentaculites range well within the Famennian (You 2000). It is thus not completely clear whether the term "mass extinction" adequately describe this event (see

Fig. 55. Gephuroceratid goniatites from the Upper Kellwasserkalk at Płucki. **A**–**C**. *Manticoceras drevermanni* (Wedekind, 1913), specimens ZPAL AmVII/1724, 1428, 1470. **D**–**I**. *Manticoceras adorfense* (Wedekind, 1913), specimens ZPAL AmVII/1722, 954, 1542, 618, and 1721. **J**–**M**. *Crickites holzapfeli* Wedekind, 1913, specimens ZPAL AmVII/1529, 604, 1726, and IG 175.11.41. **A**, **D**, **I**, **K**, **M** × 0.9; **B**, **L** × 1.4; **C**, **F**, **J** × 1.8; **E**, **G** × 2.7. ➛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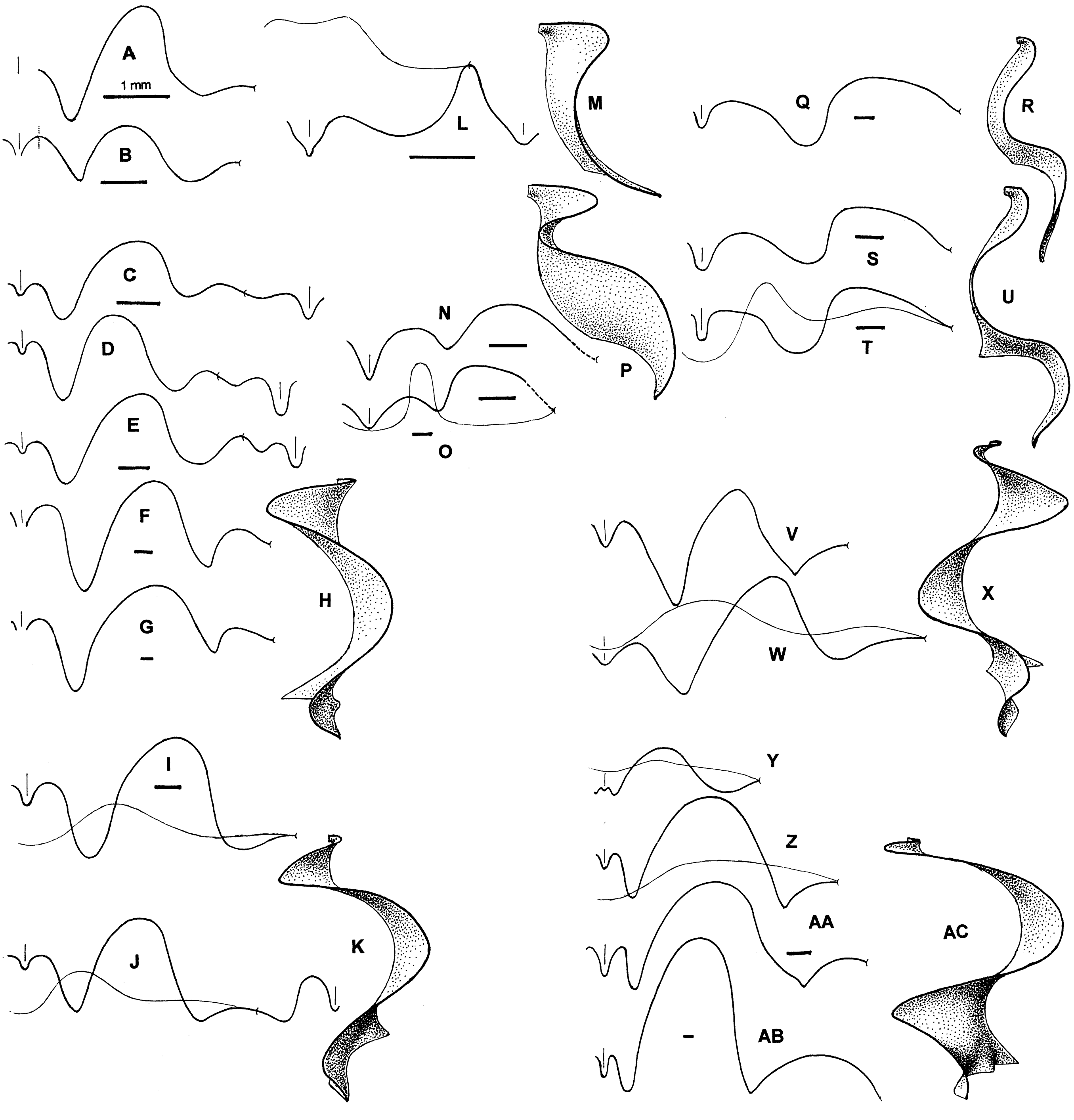

Fig. 56. Suture and growth lines and septal geometry of Frasnian goniatites from the Holy Cross Mountains. **A**, **B**. *Acanthoclymenia genundewa* (Clarke, 1898), suture lines of specimens ZPAL AmVII/1686 from Ściegnia and ZPAL AmVII/969 from Laskowa Góra (Kostomłoty). **C**–**H**. *Koenenites lamellosus* (Sandberger and Sandberger, 1856), suture lines and septum in lateral view of specimens ZPAL AmVII/1685 (also septal geometry, **H**) and 1687 from Ściegnia, ZPAL AmVII/970 from Laskowa, 1683 from Ściegnia, and ZPAL AmVII/1947 from Zamkowa Góra at Chęciny. **I**. *Manticoceras lamed* (Sandberger and Sandberger, 1850), specimen ZPAL AmVII/1558 from the lower cephalopod horizon at Płucki. **J**, **K**. *Manticoceras adorfense* (Wedekind, 1913) from the Upper Kellwasserkalk at Płucki, suture line and septal geometry of specimen ZPAL AmVII/1561 and growth line of ZPAL AmVII/1530. **L**, **M**. *Archoceras varicosum* (Drevermann, 1901) from the Upper Kellwasserkalk at Płucki, suture, growth line, and septal geometry of specimen ZPAL AmVII/1484. **N**–**P**. *Aulatornoceras belgicum* (Matern, 1931) from the Upper Kellwasserkalk at Płucki, suture, growth line, and septal geometry of specimens ZPAL AmVII/1504, 1512, and 1505. **Q**, **R**. *Linguatornoceras* sp. from the lower cephalopod horizon at Płucki, suture, growth line, and septal geometry of specimens ZPAL AmVII/1504, 1512, and 1505. **S**–**U**. *Linguatornoceras* sp. from the Upper Kellwasserkalk at Płucki, suture, growth lines and septal geometry of specimens ZPAL AmVII/1377, 1382, 1383, and 1523. **V**, **X**. *Manticoceras drevermanni* (Wedekind, 1913) from the Upper Kellwasserkalk at Płucki, suture, growth line, and septal geometry of specimens ZPAL AmVII/1429, 610, and 1520. **Y**–**AC**. *Crickites holzapfeli* Wedekind, 1913 from the Upper Kellwasserkalk at Płucki, suture and growth lines of specimens ZPAL AmVII/1520, 1527, 606, and 1531 (also septal geometry). Scale given when suture was traced from single more or less complete septum, composite drawings out of scale.

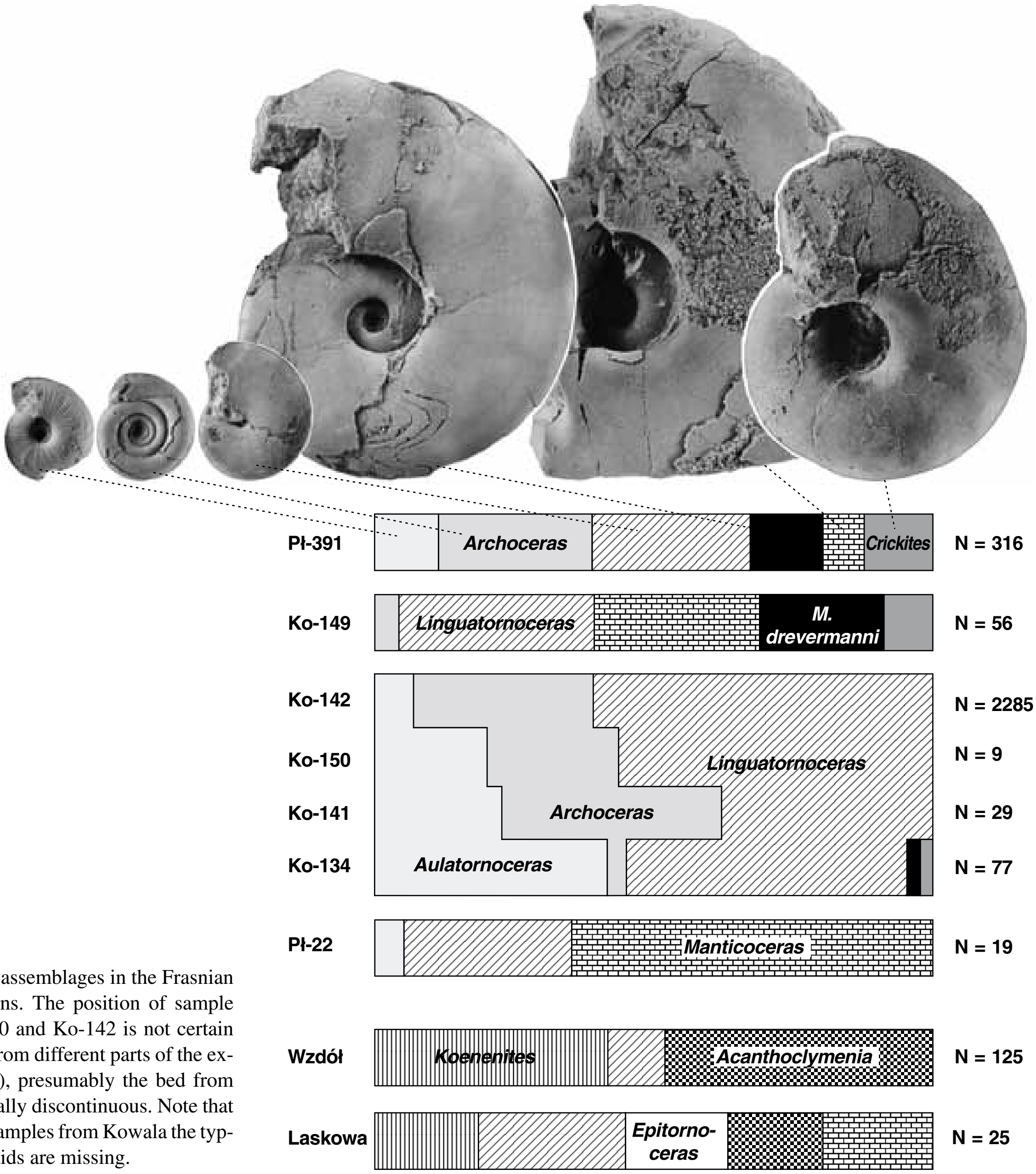

Fig. 57. Spectra of goniatite assemblages in the Frasnian of the Holy Cross Mountains. The position of sample Ko-149 in respect to Ko-150 and Ko-142 is not certain (sampled at different times from different parts of the exposure in a working quarry), presumably the bed from which it was taken was laterally discontinuous. Note that in most of the late Frasnian samples from Kowala the typically Frasnian gephuroceratids are missing.

House 2002; Bambach 2001). It is not easy to separate facts from speculations in such hotly disputed topics as the "end-Frasnian extinction" but apparently the main deficiency of the available geological record of the Frasnian–Famennian boundary events is its punctuation and incompleteness. As is usual with such sharp-cut boundaries, this one is usually represented in stratigraphically condensed or even reduced sections. Some of the Holy Cross Mountains sections may offer some useful data in this respect.

The Frasnian–Famennian boundary is best recorded in the Holy Cross Mountains at Płucki and Kowala (Fig. 4; see also Racki 1990, 1999). Other sections in Poland do not seem to be complete (Narkiewicz 1990; Matyja and Narkiewicz 1992; Matyja 1993). Paradoxically, in both Polish sections the beginning of the Famennian (as defined on the faunal change from *Manticolepis*-dominated high-diversity to *Klapperilepis*-dominated low-diversity conodont assemblage) does not coincide with any radical change in lithology. It seems rather to precede somewhat the ecological event marked by the appearance of dark shale. The changes in frequency distribution of conodont species at Płucki seem to parellel those of the planktonic entomozoacean ostracods (Olempska 2002), with a rather profound rebuilding of the assemblage at the Upper Kellwasser horizon.

The Kowala section, with its lower contribution of the palmatolepidid conodonts and much higher of icriodontids, probably represents relatively shallow-water environment (Figs. 47–49). Immediately before the end of Frasnian, there are some trends in the faunal dynamics preceding the change, even if generally it is sudden. Signs of anticipation of the fundamental faunal replacement are visible in the apparent step-wise increase in contribution of *Klapperilepis* and *Ctenopolygnathus*, whereas the prioniodinids and *Pelekysgnathus* (which is generally a Famennian lineage) reduce their abundance. Paradoxically enough, both an allegedly off-shore palmatolepidid and near-shore icriodontids became thus more and more important members of the fauna. This seemingly contradictory processes of faunal replacement would be understandable if *Klapperilepis* and the icriodontids were relatively cold-water species. This would also explain the apparent increase in biological productivity (black shale, and abundance of the prasinophycean *Tasmanites* and organisms with siliceus skeletons; Racki 1999) immediately before the boundary event and the tremendous reduction in biodiversity after it. The Kowala and Płucki successions support thus the idea that the Frasnian–Famennian boundary event was of climatic nature, possibly controlled by a Gondwanan glaciation (e.g., Streel et al. 2000).

It has to be stressed that there is no identifiable evolutionary change at the Frasnian–Famennian boundary but, instead, an apparent geographic shift in distribution of conodont species (Figs. 48, 49). Taxa not represented earlier in the area just immigrated into it. If this change is truly synchronous over the whole world, then the Frasnian–Famennian boundary is properly defined. *K. praetriangularis* occurs throughout the Płucki late Frasnian and it changes to *K. triangularis* well within the Famennian. Both species are useless as index fossils. To define the base of the "*P.*" *triangularis* zone and the Famennian stage on "mass appearance" of a species, as proposed for this case by Schülke (1999), may result in an unreliable time correlation.

Conclusions

The fastest evolving anteriormost M, and the medial, symmetric S_0 elements of the apparatus in the Frasnian palmatolepidids are the better index fossils in this part of the geological time scale, than the platform P elements. Platform shape is of importance in species identification only in the morphologically most derived species. The shape of the M elements is not only highly diagnostic but also relatively stable within populations and evolution which makes them reliable for discrimination of genera. The evolutionary transformations of S_0 element are even more profound in the early and mid-Frasnian but its great population variability makes taxonomic identifications difficult. The *Ancyrodella* succession seems to have much correlative value in the early Frasnian, where its resolution potential seems much higher than that of the palmatolepidids.

The Frasnian–Famennian boundary does not correspond to any major evolutionary event. Instead, this is a one more case when an environmental change did not stimulate any evolution but rather blocked it (Dzik 1999).

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Table 1. Distribution of conodont elements in samples from Śniadka (Sn), Chęciny (492), Wietrznia (Wtr), and Włochy (Wł) (see Fig. 1A, 4 and text for locations).

		Sn-1	Sn-2	492F-1	Wtr-8	Wtr-7	Wtr-11	Wtr-10	Wtr-9	Wtr-12	Wł-RC/1	Wł-R/A1
Belodella tenuiserrata	P_1–S_4		4				6					
	M						3					
B. minutidentata	S_{1-2}				1	2	2		1			
	S_{3-4}					2	4					
	M					1	3					
B. devonica	P_1						3	2	3			
	P_2				2	9	16		10			
	S_0				3		17		7	3		
	S_{1-2}				1		21	6	13	3	2	2
	S_{3-4}				2		13		8	1		
	M						7	3	4	5	1	
B. robustidentata	S_{1-2}								7			
	S_{1-2}								3			
	M								1			
Icriodus brevis	P_1	96	8									
I. subterminus	P_1			5								
I. expansus	P_1				112	224	1107	147	108			
I. symmetricus	P_1										18	55
Icriodus sp. sp.	P_2-M		1		1	5	67	8	15		3	4
Gen. indet.	S_1										1	1
	S_2										1	1
	S_{3-4}											1
	M											1
Ligonodina pectinata	P_1								?8		10	16
	P_2								18		7	29
	S_0								4		15	25
	S_1	1				3?			10		2	11
	S_2	1				2?						24
	S_{3-4}	1				2?					45	54
	M					1?			7		4	19
Pluckidina kielcensis	P_1				8	15	57		118		19	103
	P_2				10	9	75		68		42	98
	S_0				9	19	43		32		21	32
	S_1				1	15	19		29		23	18
	S_2				2	12	45		45		14	14
	S_{3-4}				28	56	193		25+8746		51	107
	M				20	38	78				12	83
Mehlina irregularis	P_1				4				8			
	P_2				4				22			
	S_0								2			
	S_2								?			
Bipennatus bipennatus	P_1	20										
	P_2	1										
	S_1	1										
	S_{3-4}	2										
Nicollidina brevis	P_1			2					1			
Playfordia prymitiva							3	4	6			
Parapolygnathus linguiformis	P_1	4	31									
	P_2	2	10									
	S_0		1									
	S_1	1										
	S_2		3									
	S_{3-4}		4									
	M		2									
Polygnathus timorensis	P_1	5	24									
P. aequalis	P_1			154	240	990	604	91	389	11		
P. webbi	P_1										39	90
Polygnathus sp. sp.	P_2	1	4	32	48	280	209	8	38	3	4	6
	S_0			8	8	38	58	2	12	2	13	16
	S_1		1	9	7	35	39		4	1	2	
	S_2			29	27	95	93	1	13	3	7	26
	S_{3-4}	2	1	39	32	271	293	7	28	3	12	21
	M		1	16	17	150	111	4	35	1	2	30
Avignathus decorosus	P_1										222	772
	P_2										36	153
	S_0										6	27
	S_1										11	21
	S_2										45	77
	S_{3-4}										81	66
	M										39	52

Table 1 (continued).

		Sn-1	Sn-2	492F-1	Wtr-8	Wtr-7	Wtr-11	Wtr-10	Wtr-9	Wł-R/A1	Wł-RC/1
Ctenopolygnathus C.? gracilis?	P_1	1	14			9	12	2		18	3
	P_2	4	3								
	S_1		1								
	M		1								
Ancyrodella rotundiloba	P_1				24	112	33	20	39		
A. lobata	P_1										10
A. nodosa	P_1									58	
Ancyrodella sp. sp.	P_2				18	81	32	22	46	42	7
	S_0				5	10	13	1	3	1	1
	S_1				3	17	7	2	7	2	
	S_2				10	25	31	3	2	8	1
	S_{3-4}				15	38	49	19	9	4	5
	M				7	34	37	15	9	1	1
Ancyrognathus triangularis	P_1					1					
	P_2					2?					
Klapperina sp.	P_1							7	7	3	
	P_2								2		
	S_1								1		
Mesotaxis falsiovalis	P_1				104	429	1222			23	5
	P_2				10	27	147				1
M. asymmetrica	P_1							6	46		
M. punctata	P_1									80	
M. bohemica	P_1										127
Mesotaxis sp. sp.	P_2								17	80	75
	S_0					1	9		1		2
	S_1				2	1	13			2	5
	S_2				3	5	10		2	4	6
	S_{3-4}				3	17	101		8	10	6
	M					28	2356		3	5	3

Table 2. Distribution of conodont elements in samples from Wietrznia block D and Wietrznia II (see Fig. 4C, D).

		Wtr-13	Wtr-14	Wtr-15	Wtr-16	Wtr-30	Wtr-31	Wtr-1	Wtr-2	Wtr-3	Wtr-4	Wtr-5	Wtr-6	Wtr-28
Belodella tenuiserrata	P_1-S_4											5		
	M							1		1	4	4		
B. minutidentata	P_1										1	5		
	P_2										1	3		
	S_0											3		
	S_{1-2}	8	2				10			1	11	27	1	1
	S_{3-4}							1			3	9	1	
	M								1		2	15	1	
B. devonica	P_1											2		
	P_2										1	4		
	S_0									1	1	2		
	S_{1-2}		1			1				1	3	2		
	S_{3-4}										1	7		
	M		1			1					1	2		
B. robustidentata	S_{1-2}				1			1				13		1
	S_{3-4}							1						
	M				1						1			
Pelekysgnathus planus	P_1	4												
Icriodus symmetricus	P_1	79	3	73	40	2	11							
I. alternatus	P_1							93	80	3				
I. kielcensis	P_1										63	1168	5	1
Icriodus sp. sp.	P_2-M	13	1	4	2			5	2	1	5	38		
Gen. indet.	S_1											1		
	S_2	1												
Ligonodina pectinata	P_1	4		2		1	2	1?				65		
	P_2	11	2	4	1	3	1	2	1	3	5?	65	1	1
	S_0	4		2	1	1	1			3	2	35		
	S_1	4					1					27		
	S_2	13	2	5		1	1	1	1	3	5	45	2	
	S_{3-4}	12	1	1		3	5		2	2	12	141	4	1
	M	3				1	4			5	5	3	2	

Table 2 (continued).

		Wtr-13	Wtr-14	Wtr-15	Wtr-16	Wtr-30	Wtr-31	Wtr-1	Wtr-2	Wtr-3	Wtr-4	Wtr-5	Wtr-6	Wtr-28
Dyminodina planidentata	P_1					2				1	1?	28		
	P_2					1		1		1	1?	18	1	
	S_0					1		1			1	1		
	S_1					9	2			5	5	42		
	S_2						1	4		7	4	41	2	
	S_{3-4}					1	1	9	1		6	19	2	
	M							7			2	42	4	
Pluckidina nonaginta	P_1	111	19											
	P_2	53	7											
	S_0	6	2											
	S_1	18	3	3										
	S_2	16		1										
	S_{3-4}	80	10											
	M	59	8											
P. robustipegmata	P_1	9										33		
	P_2											22		
	S_0	6										2		
	S_1	6										36		1
	S_2													
	S_{3-4}	3										18		
	M	6										21		
Mehlina irregularis	P_1			1	2	15	1	1						
	P_2			1	2	1								
	S_0				1									
	S_1			1										
	S_2				2									
	S_{3-4}			2										
	M				2	1								
Nicollidina brevis	P_1											2		
Tortodus treptus	P_1	5												
	P_2	1	1											
	S_0	1	1											
	S_2	1	1											
	M	1	1?											
Polygnathus sp. and *P. webbi*	P_1	325	24	28	25	18	24	182	37	33	86	1373	13	3
	P_2	?		5	2	14	3	19	4	26	35	303	2	2
	S_0		2	5	2	4	2	3	1	4	5	101		
	S_1	7	1	1	1	4	4	2			6	46		
	S_2	5	3	2	2	6	8	4	1	8	9	109		
	S_{3-4}	8	5	8	1	9	2	4	1	18	39	313	7	1
	M	5	4	1	2	11	2	5	1	7	22	155	1?	
Polygnathus sp.	P_1				6									
P. pacificus	P_1	201	22	35		117	134							
	P_2	69	11			7	10							
	S_0	9				5	2							
	S_1	6				8	1							
	S_2	19				8	10							
	S_{3-4}	35				17	8							
	M	20				7	5							
Avignathus decorosus	P_1					19	8			1		25		5
	P_2					10	10					1		9
	S_0					3	6							4
	S_1					1						1		1
	S_2													7
	S_{3-4}					8	12							6
	M					4								5
Parapolygnathus brevis	P_1			1	1					1		25		
	S_1											1		
Ancyrodella rugosa	P_1	46												
A. nodosa	P_1			7	4	15	10	1	6	23	22	462	4	
Ancyrodella sp. sp.	P_2	21	2	4		6	10		2	5	4	116	4	
	S_0					2	1			1				
	S_1													
	S_2					6	2			2	4		1	
	S_{3-4}	1				6	8			4	7	2		
	M	6	1			4	6		2		2	43	1	
Ancyrognathus triangularis	P_1		1					13			1	10		
	P_2		1					10				9		
	S_2							1				1?		
	S_{3-4}							1	1?	1?		1?		
	M					1		2			1?	1?		

Table 2 (continued).

		Wtr-13	Wtr-14	Wtr-15	Wtr-16	Wtr-30	Wtr-31	Wtr-1	Wtr-2	Wtr-3	Wtr-4	Wtr-5	Wtr-6	Wtr-28
Mesotaxis? sp.	P_1										8?			
	M													
M.? *simpla*	P_1						86							
M. punctata?	P_1	18				43								
Mesotaxis sp. sp.	P_2	3	1			7	9					1		
	S_0						1							
	S_1	1					1							
	S_2	3					2							
	S_{3-4}					3								
	M					1								
Mesotaxis? *domanicensis*	P_1			24	8	64								
	P_2			10	2	3								
	S_0													
	S_1			4	1	2								
	S_2			3	1	2								
	S_{3-4}					1								
	M				1	2?								
Kielcelepis ljashenkoae	P_1			6										
	P_2			2	1									
	S_0			2										
	S_1			2										
K. proversa	P_1	10												
	P_2	3												
K. hassi	P_1			20	22									
	P_2			6	3									
	M			1	2									
Manticolepis gigas	P_1							204	79	73	172	1348	25	2
	P_2							27	7	22	29	132	2	
	S_0							3		1	1	12		
	S_1							4	1	2	7	11		
	S_2								1		5	10		
	S_{3-4}							5	2	3	19	36		1
	M							9	6	4	16	49		1
Lagovilepis sp.	M											1		

Table 3. Distribution of conodont elements in samples from Wietrznia 1d–e (see Fig. 4A, B).

		Wtr-20	Wtr-24	Wtr-23	Wtr-22	Wtr-18	Wtr-17
Belodella devonica	S_3	1	2	18	2	1	1
B. robustidentata	S_3		5	7	1		
Pelekysgnathus planus	P_1				3		5
Icriodus alternatus	P_1	10	16	629	5		1
	P_2-M		1	135			
Ligonodina pectinata	P_1		3	1	1	1	
	P_2		7	2	2	2	
	S_0		1	5	1		1
	S_1		3	2	3	1	1
	S_2				1	1	
	S_{3-4}		14	11		2	
	M		3				
Dyminodina planidentata	P_1		3	9		1	
	P_2		1	8		2	
	S_0		7	8	2	2	
	S_1		2	11	5	3	
	S_2		3	5		1	
	S_{3-4}		9	26	2	3	
	M			30		5	
Pluckidina lipperti	P_1	1					
	P_2	3					
	S_0	2					
	S_1	3					
	S_2	3	2				
	S_{3-4}	11					
	M	2	2				
Mehlina sp.	P_1		4				1
	P_2		1				

Table 3 (continued).

		Wtr-20	Wtr-24	Wtr-23	Wtr-22	Wtr-18	Wtr-17
Nicollidina brevis	P_1	1			2	2	2
Ctenopolygnathus sp.	P_1				1		
Polygnathus webbi	P_1	85	170	127	9	572	13
	P_2	11	44	72	3	98	
	S_0	2	5	12		11	
	S_1	4	5	14		5	
	S_2	3	6	21	3	19	
	S_{3-4}	11	15	35	3	46	
	M	10		32	2	33	
P. pacificus	P_1		105	3004	39		
	P_2		3	258	3		
	S_0		3	5			
	S_1			6			
	S_2			15	1		
	S_{3-4}			58			
	M			37	1		
P. aff. *semicostatus*	P_1						53
	P_2						15
	S_0						2
	S_1						1
	S_2						1
	S_{3-4}						7
	M						4
Avignathus decorosus	P_1	6	148		17		
	P_2		48		1		
	S_0		4				
	S_1		6				
	S_2		15				
	S_{3-4}		16				
	M		15		1		
Ancyrodella nodosa and *A. curvata*	P_1	8	29	19	6	23	2
	P_2	10	30	3	2	1	1
	S_0	1	4				
	S_1		3				
	S_2		11			1	
	S_{3-4}	4	21		2	2	1
	M	2	34				
Ancyrognathus asymmetricus	P_1		2	238		9	1
	P_2		1	130		3	
	S_0			8		2	
	S_2			19		1	
	S_{3-4}		1	36			
	M		2	22		1	
Kielcelepis jamieae	P_1	87	202				
	P_2	23	59				
	S_0	3					
	S_1	3	4				
	S_2		1				
	S_{3-4}	5	9				
	M	6	8				
Manticolepis winchelli	P_1				88	106	79
	P_2				32	24	6
	S_0				4	4	
	S_1				9	6	
	S_2				8	1	2
	S_{3-4}				16	8	2
	M				10	10	
M. muelleri and *M. rhenana*	P_1			905	3	16	3
	P_2			366		25	2
	S_0			22		2	
	S_1			38	1	3	1
	S_2			26			
	S_{3-4}			95			1
	M			73		6	2
C.? linguiformis	P_1				1		2

Table 4. Distribution of conodont elements in samples from Płucki (see Fig. 4).

		Pł-22	Pł-25	Pł-26	Pł-28	Pł-130	Pł-110	Pł-90	Pł-60	Pł-30	Pł-18	Pł-39	Pł-80	Pł-82
Belodella devonica	P_{1-2}	34												
	S_{0-4}	23						2				1		
	M	148												
Icriodus symmetricus	P_1		8	1										1
I. iowensis	P_1	3439	1	1										
	P_2-M	221	1											
I. alternatus	P_1					3		1				1	1	
	P_2-M							1	2			2		
Ligonodina pectinata	P_1	14			1						1		1	
	P_2	8	2										2	
	S_0	15	2											1
	S_1	8								1				
	S_2	10	2				1			1			1	
	S_{3-4}	48	3			1	1	2					2	4
	M	4					1						2	2
Dyminodina planidentata	P_1	172												
	P_2	296												
	S_0	165												
	S_1	182						1						
	S_2	143								1				
	S_{3-4}	858	2											
	M	464	1							1				
Pluckidina lagoviensis	P_1	7				1								
	P_2	12	1				2			1			2	
	S_0	6	6											
	S_1	62	3										1	
	S_2	40	3							1			4	1
	S_{3-4}	95	7		1	1							1	
	M	37	2				2						2	
Mehlina irregularis	P_1												3	1
	P_2													1
	S_0													1
	S_{3-4}													1
Nicollidina brevis	P_1	1												
Ctenopolygnathus sp.	P_1	18		1										
	P_2	38		1										
	S_0	6		1										
	S_1	12												
	S_2	15												
	S_{3-4}	12		2										
	M	21		1										
Polygnathus semicostatus	P_1												2	2
	P_2												1	
	S_1												1	
	S_{3-4}												2	
P. pacificus	P_1	2748			3		8	2	1					
	P_2	602			3									
	S_0	68						1	1					
	S_1	134												
	S_2	501			1									
	S_{3-4}	1219			1			2	1					
	M	364			1									
Avignathus bifurcatus	P_1	305	49											
	P_2		19											
	S_0	7	2											
	S_1		17											
	S_2		17											
	S_{3-4}		43											
	M		18											
Polygnathus webbi	P_1	413	11			2	45	2		5	1			
	P_2	127	5			1	19			4	1			
	S_0	50	3			2	3							
	S_1						4							
	S_2		1				5							
	S_{3-4}	161	3			3	11	2		4				
	M	169	5			1	10	1						
P. tuberculatus	P_1	175		6										
	P_2	42		1										
	S_0	29		1										
	S_1	31		1										
	S_2	23												
	S_{3-4}	160		3										
	M	40		1										

Table 4 (continued).

		Pł-22	Pł-25	Pł-26	Pł-28	Pł-130	Pł-110	Pł-90	Pł-60	Pł-30	Pł-18	Pł-39	Pł-80	Pł-82
Parapolygnathus brevis	P_1	31	2											
Ancyrodella curvata	P_1				1		6	1		3		2		
A. nodosa	P_1	147	15											
	P_2	134	8											
	S_2	3												
	$S_{3\text{-}4}$	16	2											
	M	8	2							1				
Ancyrognathus asymmetricus	P_1	77	2	1			1							
	P_2	43												
	S_0	2		1										
	M	1												
Manticolepis rhenana	P_1	88					5			7	1	2	26	41
	P_2	10					2				1	1	8	7
	S_0	2												1
	S_1	7										1	2	8
	S_2	13											1	
	$S_{3\text{-}4}$	54					1					1	8	9
	M	61										1	3	4
M. winchelli	P_1		49			18	81	9	11	10				20
	P_2		12			5	13	1	1	1				
	S_0		4			1	1							
	S_1		3			1	1			1				
	S_2		1			2	4							
	$S_{3\text{-}4}$		2			2	10		2	3				
	M		1			1	4	1	1	1				
Lagovilepis bogartensis	P_1	792		6?	35		19						23	
	P_2	261			4		6						3	
	S_0	3			1									
	S_1	24											1	
	S_2	10			2									
	$S_{3\text{-}4}$	21			3								2	
	M	14					3						1	
Klapperilepis praetriangularis	P_1	246												
	P_2	8												
	S_0	4												
	$S_{3\text{-}4}$	1												
	M	1												
Conditolepis? *linguiformis*	P_1	1								1				

Table 5. Distribution of conodont elements in samples from Płucki (see Fig. 4).

		Pł-93	Pł-37	Pł-38	Pł-44	Pł-43	Pł-21	Pł-391	Pł-20	Pł-16	Pł-15
Pelekysgnathus planus	P_1			4	4	1	12	5	2	1	
Icriodus iowensis	P_1					1	14	2597	227	199	113
	P_2-M					3	2	2105	82	92	68
Ligonodina pectinata	P_1		1					10		1	1
	P_2				1	3	1	35			
	S_0					1	2	24			
	S_1					1		14		1	
	S_2			2			2	20			
	$S_{3\text{-}4}$		1		2	2		93			
	M						2	30			
Dyminodina anterodenticulata	P_1							8			
	P_2		1	1				14			
	S_0							7			
	S_1			1				8			1
	S_2			3	1			11			
	$S_{3\text{-}4}$			2	1			47			
	M			1	2			28			
Pluckidina lagoviensis	P_1							3			
	P_2						1	5			
	S_0							1			
	S_1						2	29		1	
	S_2						3	1			
	$S_{3\text{-}4}$							13			
	M							2			
Mehlina sp.	P_1							28	2	6	
	P_2							12		2	
	S_1									4	
	S_2									2	
	$S_{3\text{-}4}$									19	
	M									5	

Table 5 (continued).

		Pł-93	Pł-37	Pł-38	Pł-44	Pł-43	Pł-21	Pł-391	Pł-20	Pł-16	Pł-15
Ctenopolygnathus sp.	P_1							214	12	17	4
	P_2							49	20	6	2
	S_0							15	1	1	1
	S_1							25	5	2	2
	S_2							32	4	4	1
	$S_{3\text{-}4}$							64	7	9	3
	M							48	5	2	2
Polygnathus semicostatus	P_1				9	6			26	110	42
	P_2								22	29	12
	S_0				1				3	7	4
	S_1								6	13	4
	S_2				1				23	13	7
	$S_{3\text{-}4}$				2				15	37	21
	M									21	10
P. webbi	P_1	5	7	8	7		52	2353			
	P_2		2	2			18	535			
	S_0		1	3	1		9	129			
	S_1			2			3	143			
	S_2		1		1		10	234			
	$S_{3\text{-}4}$		4	3	1		18	579			
	M						8	369			
P. tuberculatus	P_1							1554			
	P_2							90			
	S_0							6			
	S_1							7			
	S_2							4			
	$S_{3\text{-}4}$							4			
	M							6			
P. brevis	P_1			1							
Ancyrodella curvata	P_1						9	116			
	P_2							46			
	S_0										
	S_1							13			
	S_2							27			
	$S_{3\text{-}4}$							27			
	M							81			
Ancyrognathus ubiquitus	P_1							19			
Manticolepis rhenana	P_1	2	5	4	5	20	63	6			
	P_2		1		1	3	5				
	S_0					1					
	S_1			1		1	2				
	S_2										
	$S_{3\text{-}4}$		1		1	1	4				
	M				1	2	8				
M. winchelli	P_1	16	25	18	14	23		85			
	P_2		3	4	1	6		6			
	S_0		2			2					
	S_1		1		1	1					
	S_2		3	1	1	3					
	$S_{3\text{-}4}$		2	2	1	2					
	M	1	2	2		5		2			
Lagovilepis bogartensis	P_1					5		2811			
	P_2					?		402			
	S_0							57			
	S_1							54			
	S_2							218			
	$S_{3\text{-}4}$							272			
	M					1		232			
Klapperilepis praetriangularis	P_1					3		1560	357	187	139
	P_2					3		109	39	37	18
	S_0							6		2	
	S_1							9	3	3	2
	S_2							4	4	5	1
	$S_{3\text{-}4}$							4	1	11	3
	M							6	3	4	1
Conditolepis? linguiformis	P_1					3	2	16			
	P_2					2					
	M					1		2?			

Table 6. Distribution of conodont elements in samples from Kowala (see Fig. 4).

		Ko-144	Ko-145	Ko-139	Ko-140	Ko-146	Ko-134	Ko-147	Ko-135	Ko-148	Ko-150	Ko-149	Ko-142	Ko-151
Belodella devonica	P_{1-2}													1
	S_{0-4}	1						1			7	1	2	3
	M						1					1		2
Pelekysgnathus planus	P_1	14	8			2	22		2					
Icriodus iowensis	P_1		1		22	35	24	46	85	11	6	792	9	31
	P_2-M				3	5	2	19	7		17	250	6	15
Ligonodina pectinata	P_2	1		1										
	S_0													
	S_1	1					1							2
	S_2	1					1		1	1				
	S_{3-4}		1		1		1				1			
	M				1						1			1
Dyminodina kovalensis	P_1		1									4		13
	P_2										1	3		10
	S_0								2	1	1	1		3
	S_1		1									4		9
	S_2		1									6		5
	S_{3-4}								1	1	1	27		23
	M						1					7		14
Pluckidina lipperti	P_1											1		
	P_2								1			13		6
	S_0	1									1	14		2
	S_1			1				1	1		2	8		2
	S_2	1				1					3	12		7
	S_{3-4}										2	27		11
	M			1					1			9		1
Mehlina sp.	P_1				1							3	1	
	P_2				1							1		
	M											1		
Nicollidina brevis	P_1	3				1	2	1			1			
	P_2	1						1						
	S_2							1						
	S_{3-4}	1					1							
	M	2						1						
Polygnathus sp.	P_1											10		
Tortodus sp.	P_1	1							1					
Polygnathus webbi	P_1	27	21		9	10	2	149	26	22	34	423	19	47
	P_2	1	6		4	3	2	7	4	6	9	113	1	25
	S_0		3				3			3	3	38		7
	S_1			1	2	1		1	1	2	2	26	2	14
	S_2	1	3	1	2	2	4	4	1	6	14	58	1	36
	S_{3-4}	5	6	4	14	4	3	11	2	17	19	116	10	69
	M	1	2	1	4		3	4	2		8	82	3	27
Ancyrodella curvata	P_1			1		2	5		2	1		53		3
	P_2			1										1
	S_2													
	S_{3-4}													1
	M							1	1					1
Ancyrognathus ubiquitus	P_1								1			7		1
	P_2											1		2
	S_2											5		
	S_{3-4}											2		
	M											7		
Manticolepis rhenana	P_1	21												
	M	2												
M. winchelli	P_1		14	5		12	25	17	38	44	20	55?	?	?
	P_2		1	2				21		6	9	?		
	S_0										1	5	1	3
	S_1		2			2					3			
	S_2						1	1			1			
	S_{3-4}		2	1			1	1	2	1	10			
	M		3	1		3		3		3	1	3		
Lagovilepis bogartensis	P_1			7	24							366	13	120
	P_2				4							110	5	30
	S_0													
	S_1											4	1	4
	S_2				2							10		13
	S_{3-4}				1							26		26
	M			1	1							19	1	19
Conditolepis linguiformis	P_1						2						1	

Table 7. Distribution of conodont elements in samples from the Famennian at Płucki (see Fig. 4).

		Pł-42	Pł-41	Ko-152	Ko-143	Ko-153	Ko-154	Wtr-19
Pelekysgnathus planus	P_1	1	2					179
	P_2-M							30
Icriodus alternatus	P_1	105	9	163	31	78	85	
	P_2-M	89	6	26		35	57	
Ligonodina sp.	P_2				21			1
Pluckidina sp.	P_1	1?		2		2	7	
	P_2	3				6	4	
	S_0					1	5	
	S_1	1?					5	
	S_2	2					13	
	S_{3-4}	5					8	
	M							
Mehlina? sp.	P_1	10	4				1	
	P_2	10						
	S_0		1				1	
	S_2	3						
	S_{3-4}	5	2				3	
	M		1				2	
Nicollidina brevis	P_1	1						
Polygnathus semicostatus	P_1	28	3	9	30	13	65	13
	P_2	10	5	2	13		24	3
	S_0	1	1	2	1	1	9	
	S_1	3			4	2	3	
	S_2	3		1	4	7	9	1
	S_{3-4}	27	9	6	40	10	29	2
	M	9	1	6	11	9	10	8
Ancyrognathus sinelamina	P_1							2
	P_2							2
	S_2							1
	S_{3-4}							2
	M							1
Klapperilepis triangularis	P_1		4	26	78	54	266	18
	P_2		5		3	2	27	
	S_0						1	
	S_1		3			1		
	S_2							
	S_{3-4}		4	1		1	4	
	M		2			1	2	
K. delicatula	P_1		1					
K. protorhomboidea?								1
K. circularis	P_1	20						7
K. tenuipunctata	P_1	27						4
	P_2							4
	S_0							2
	S_2							2
	M							2
Klapperilepis sp.	P_1							4
Tripodellus minutus	P_1	90						18
	P_2	26						
	S_0	2						
	S_1	6						
	S_2	4						
	S_{3-4}	7						
	M	4						