THE FAMENNIAN "GOLDEN AGE" OF CONODONTS AND AMMONOIDS IN THE POLISH PART OF THE VARISCAN SEA

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The stratigraphically complete and extremely fossiliferous geological sections in the Holy Cross Mountains and Sudetes, Poland, cover the whole history of the Famennian tropical high-diversity pelagic ecosystem. Apparatus reconstruction of 142 conodont species allowed paleobiological interpretation of the faunal succession. Three families, nine genera and 39 species are newly proposed. 76 species of goniatites, with one genus and five species new, and 70 species of clymenias were also identified. Like in all other equatorial localities, a significant (but not catastrophic) decline of diversity marks the beginning of the Famennian. The local pelagic fauna developed mostly as a result of successive reappearances of lineages earlier occurring in the area but temporally removed from it by environmental factors. During the whole Famennian, 101 immigrations of conodont lineages are documented. In 31 of the lineages persisting in the area a more or less complete record of their phyletic evolution is represented; they cover about half (46%) of the summarized ranges of all the lineages. About half of them are suitable for stratophenetic studies. The fossil record of the ammonoids is much more punctuated, but it is estimated that 110 lineages was represented there, only 14 of them possibly evolving phyletically in the area (single case was stratophenetically proven). At the transition between goniatites and clymenias, a succession within the plexus of closely related sympatric species is observed, but the exact phyletic change is not recorded and probably all the first clymenias are immigrants from the east. At least two profound rebuildings of the fauna within the Famennian are observed, but only the terminal Devonian Hangenberg event was of truly dramatic nature. The newly acquired evidence supports the earlier notion thate it is more difficult to trace evolution stratophenetically in the equatorial regions than in high latitudes.

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

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INTRODUCTION

The Famennian is among those epochs of the Earth history, which experienced the deepest transformation of the living world. Not only its boundaries are unusually clear-cut but revolutionary changes occurred repeatedly throughout its duration (Walliser 1996). The beginning of the Famennian corresponds to the world-wide collapse of reefal coral-stromatoporoid ecosystems and the following profound reduction of biological diversity at least in its part represented by the fossil record. Afterward, the diversity of fossil assemblages of pelagic organisms such as ammonoids and conodonts dramatically increased, to reach levels unprecedented in earlier or later history of these groups. The end of that acme of pelagic tropical faunas was similar to what happened at its beginning, resulting in a drastic reduction of diversity to just a few lineages of ammonoids and conodonts.

The events demarcating the Famennian are generally believed to be of a catastrophic nature and are listed among the greatest extinction events in the history of life (Walliser 1996; but see House 2002 and Bambach *et al*. 2004). Paradoxically, there are reasons to question not only the importance of these events but even the very possibility to prove their existence at the world-wide scale (Dzik 1995, 2005). One may thus ask: how is it possible that such extreme points of view emerge from examination of essentially the same fossil material? The answer is: all this is rooted in disparate methodologies of inference. The distinction between a literal reading of the fossil record as it stands and a humble recognition of its limits, with a long distance separating the raw data on fossils from the knowledge of actual transformations of ancient ecosystems. From the second point of view there is no correspondence between the observed appearance and disappearance of a lineage in rock sections and its evolution (Dzik 1995). Furthermore, there is no necessary connection between the speciation and evolution rates (Dzik 1999). If this point of view is accepted by the reader (however unlikely it is), the fossil record appears to represent a kind of Platonic shadow only roughly corresponding to the real succession of events. Fortunately for us, however subtle the correspondence is, it may be specific enough to allow reasonable inference. Coming to specific points, the drastic change in diversity observed in the Laurentian sections at the Frasnian–Famennian or Famennian–Tournaisian boundaries indicates just that the transformation of the environment in the equatorial regions of those times (McGhee 1996; Streel *et al*. 2000; Joachimski and Buggisch 2002; Joachimski *et al*. 2001, 2004; Bambach *et al*. 2004; Racki 2005) forced the organisms earlier living there to migrate elsewhere or to reduce dramatically their area of distribution.

Whether the removal of populations from particular regions was connected with their total extinction or not, cannot be inferred from the available evidence. The numerous cases of Lazarus taxa show that this was not the case on many occasions. I hardly see any intellectual or practical profit from the assumption that a discontinuity in distribution of fossil species in a section marks the extinction of its lineage. It is more profitable to consider this to be just a phenomenon of lateral shift in distribution of ecosystems, a local (although widespread) replacing of one environment (together with its organisms) by another. This gives a chance to search for the place (or refugium) where the process of evolution possibly continued instead of taking the risk of circular reasoning resulting from basing correlation on the alleged extinction event.

My main goal is thus to separate evolution from ecologically controlled shifts in occurrence. This is not an easy task (Dzik 2005) and even if I am succesful in doing this, the whole evidence presented here represents only a small area of the late Devonian world. To trace lineages with reasonable confidence not only in time but also in geographical space, several similarly designed works have to be completed in other regions of the World with similar faunas. One has to hope that we will not wait too long.

In fact, the Famennian is especially suitable for these kind of studies. It was an epoch of relatively high sea level and pelagic faunas of that age are relatively widespread and well sampled. The exposures of the Devonian along margins of the Variscan orogenic belt in central Europe (Fig. 1) are by no means unique in this respect. Their special value is only in that these are the classic regions of the paleontological and biostratigraphical research on fossils of pelagic Famennian organisms. The Sudetes are among the first recognized localities of Devonian ammonoids in the world (von Buch 1839 and numerous publications by other authors referred to in the ammonoid part of this work). Even in the Holy Cross Mountains, located on the distant eastern tip of the belt, the first Devonian conodonts were identified already by Gürich (1901). Monographic descriptions of the Famennian conodonts from Poland started with Wolska (1967), then with subsequent work by Szulczewski (1971), supplemented by Nehring (1967), Narkiewicz (1978; Narkiewicz and Narkiewicz 1992), Baliński (1979), and Matyja and Narkiewicz (1995). The ammonoids from the Holy

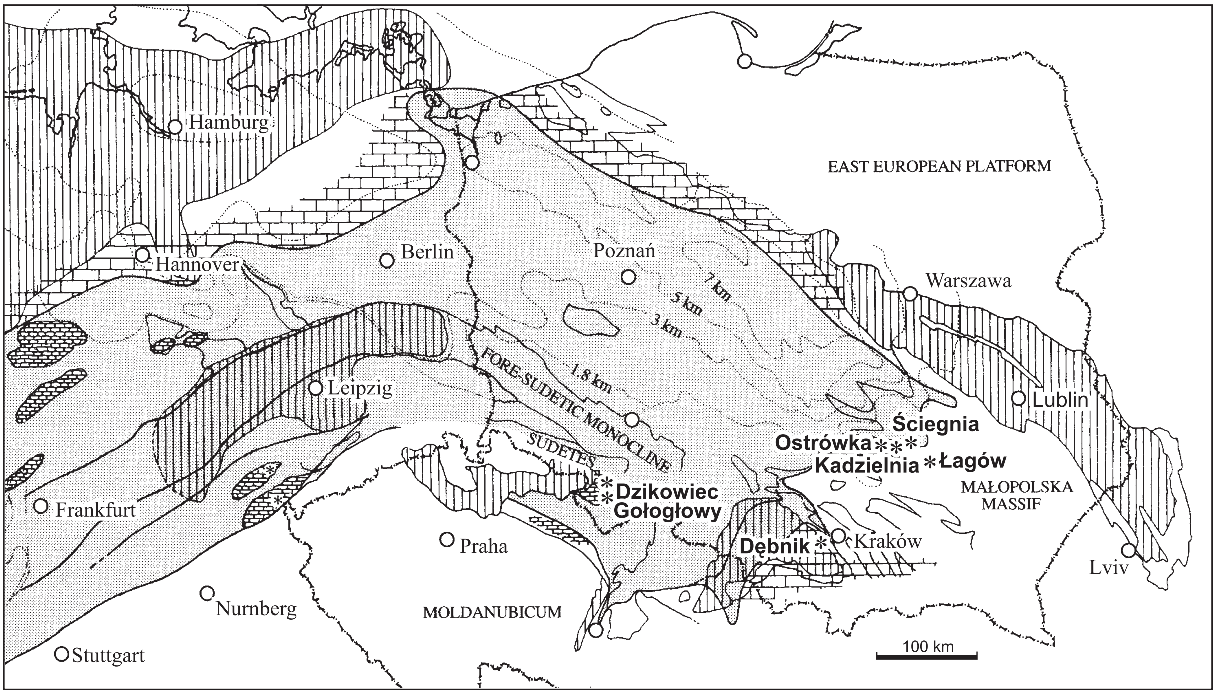

Fig. 1. Non-palinspastic palaeogeographic map of central Europe in the Famennian (for sources see Dzik 1997, fig. 1). Known extent of the latest Devonian to earliest Carboniferous limestone facies shown by brick pattern, cephalopod limestone as fine shallower facies as coarser; areas of intense subsidence, where coal basins developed in the Carboniferous, vertically hatchured; extent of deeper-water (mainly fine clastic) sedimentation shown as grey.

Cross Mountains were monographed by Sobolew (1914a; supplemented by Dybczyński 1913 and Makowski 1991) and Czarnocki (1989; Pajchlowa et al. 2003). The present paper is intended to be an overview of the evolution and dynamics of pelagic faunas in the area.

Illustrated specimens are housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (abbreviated ZPAL), State Geological Institute in Warsaw (IG), Museum of Natural History of the Humboldt University in Berlin (MB), Geological Museum of the Wrocław University (UW), the Natural History Museum of the Ukrainian Academy of Sciences in Lvov (former Dzieduszyckis' Museum; MD), and Museum of the Institute of Geology and Paleontology of the Tübingen University (UTü).

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SAMPLED GEOLOGICAL SECTIONS

There are only three areas in Poland where the Devonian rocks can be sampled in exposures: the Holy Cross Mountains in central Poland about 200 km south of Warsaw, a small area in southern Poland west of Kraków, and the Sudetes on the southwestern tip of the country. Those exposures (Fig. 2, 3) are briefly re-

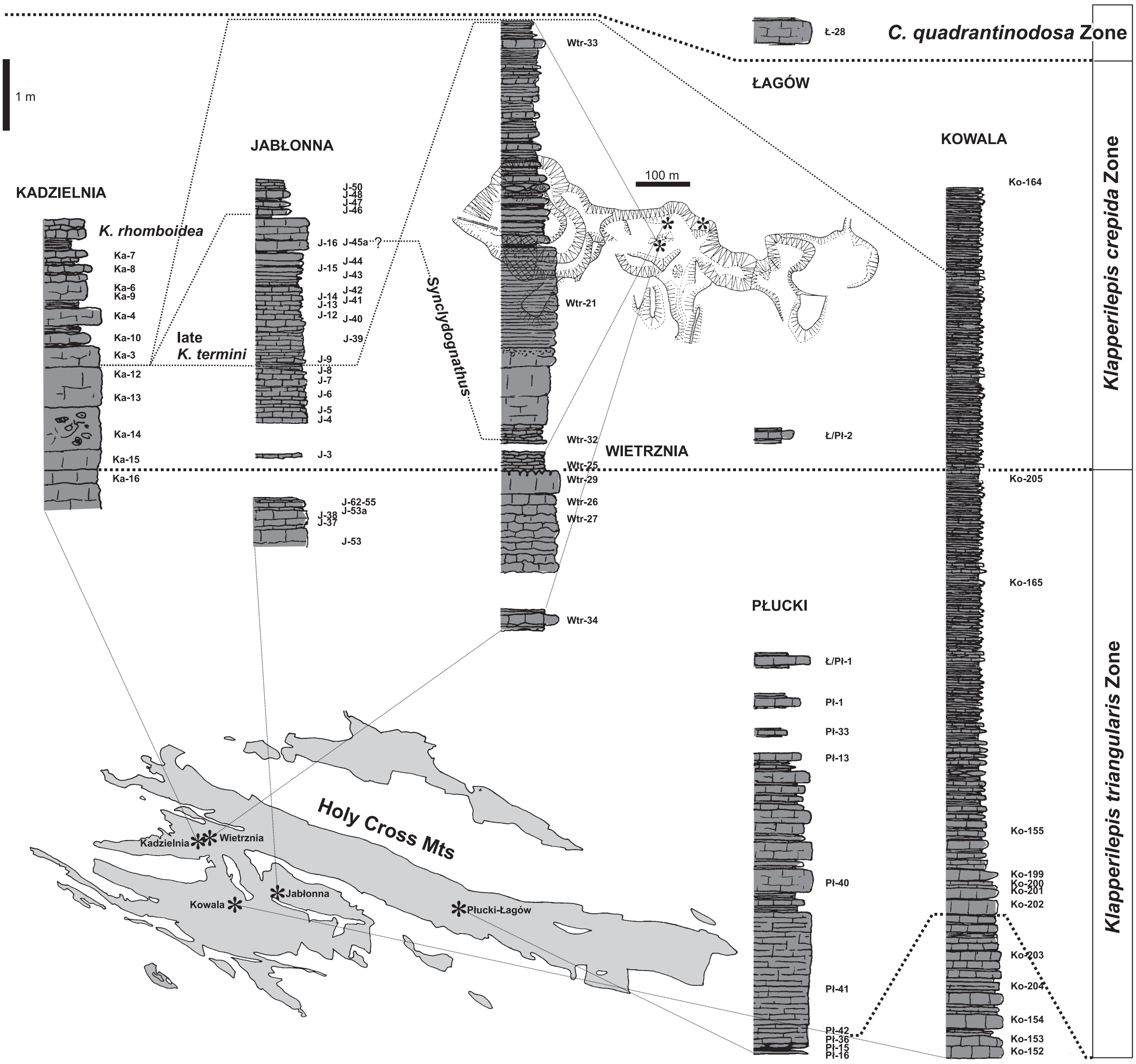


Fig. 2. The sampled sections of the early Famennian in the Holy Cross Mountains, with their relative position shown on a diagrammatic map of the extent of exposures of the Devonian. Position of zonal boundaries and their correlation indicated by broken lines. Composite section of Wietrznia is assembled from tectonically disjunct exposures; their location indicated on a map of the quarry.

viewed below starting with those of the Sudetes, near the southwestern shore of the Variscan sea, on the opposite side of it in respect to other regions studied.

GOŁOGŁOWY

The section at Gołogłowy near Kłodzko in the Sudetes is located about 1 km north of the village on the right side and above the abandoned quarry, 40 m upslope the forest road. It was described and illustrated by Haydukiewicz (1981), who reported early Tournaisian conodonts from a calcareous mudstone near the top of the section. I sampled the well-bedded Famennian part of the succesion. Most of samples contained rare and strongly tectonically deformed conodonts. They apparently represent a transgressive succesion from a shallow-water fauna dominated by *Polygnathus znepolensis* and *P. extralobatus* in the nodular limestone below (sample Goł-11) to an assemblage rich in *Palmatolepis rugosa* and *Tripodellus gracilis* near the top of the Devonian bedded muddy limestone (sample Goł-3). A similar, but more complete succession is represented in the same area, 25 km northward, at Dzikowiec.

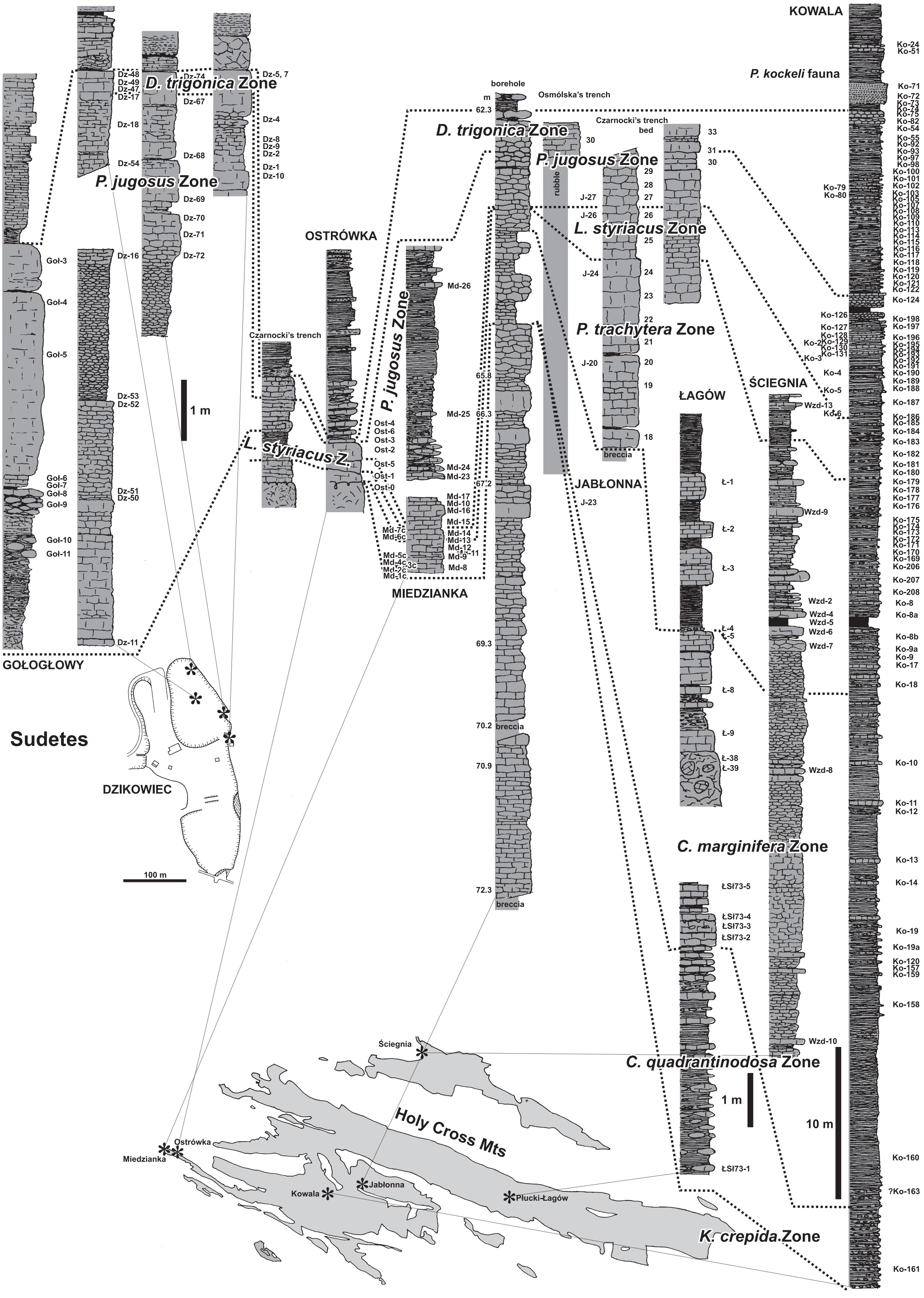


Fig. 3. The sampled sections of the late Famennian in the Sudetes and the Holy Cross Mountains, relative position of the latter shown on a diagrammatic map of the extent of exposures of the Devonian. Position of zonal boundaries and their correlation indicated by broken lines. Location of sections in the Wapnica quarry in Dzikowiec shown on a map.

DZIKOWIEC

The geology of the Devonian at Dzikowiec has been recently reviewed in Berkowski (2002) and the Carboniferous by myself (Dzik 1997). The succession starts there with a conglomerate, composed of large blocks of gabbro with a limestone crust of probably algal origin, a detrital limestone with crystalline and metamorphic rock pebbles higher up, and the cephalopod *Wocklumeria* and *Gattendorfia* Stufen limestones near the top. In the dark grey organodetrital limestone, rich in calcareous tests of foraminifers and algal detritus, colonies of various tabulate (*Syringopora*) and rugose corals occur representing a rare case of the Famennian refugium with reefal organisms (Berkowski 2002). The only conodont species encountered in the middle part of this unit is *Polygnathus znepolensis* (sample Dz-11, 50) supplemented upwards by a prioniodinid (sample Dz-51) and a few more species (Dz-52), including *Dasbergina micropunctata*, *Mehlina*, *Branmehla*, and *Tripodellus gracilis*. In a sample taken from the base of the upper, nodular part of the main limestone (Dz-53), a few elements of the *Polygnathus extralobatus* apparatus have been found, which makes this part of the succession similar to that at Gołogłowy. The dark grey nodular limestone becomes more platy upwards and contains (Dz-16, Dz-62) the shallow-water species *P. znepolensis* associated with rare *T. gracilis*, *Palmatolepis rugosa*, and non-platform conodonts. Samples from the transitional strata between the dark grey and red cephalopod limestone (Dz-69, Dz-72) yielded a more diverse palmatolepidid fauna. The transition from *Dasbergina marburgensis* to *D. trigonica* takes place 0.4 m below the top of the red cephalopod limestone of the *Wocklumeria* Stufe.

The Famenian was sampled for conodonts near the northern tip of the quarry (Berkowski's locality 3), where the *Gattendorfia* Limestone succession is the most complete (Dzik 1997) but the base of the *Wocklumeria* Limestone and the top of the dark grey nodular limestone are there truncated by a fault. A continuity between these units can be traced in a rock in the western wall of the northern part of the quarry (Berkowski's locality 3). Samples were taken also from a rock immediately south of the steps leading outside the quarry (at the fence of the shooting field used for training by local hunters).

A bed-by-bed collecting of ammonoids was performed by Lewowicki (1959) who described in detail their distribution. *Wocklumeria sphaeroides* has not yet been found there. Of special interest is the occurrence of *Kamptoclymenia endogona* in the topmost layer of the Famennian, and *Kalloclymenia* throughout the exposed cephalopod limestone up to about 0.5 m below its top. *Glatziella* ranges from 1.2 to about 0.2 m below the top. Korn *et al*. (2005) identified *Soliclymenia* in the red limestone 0.4–0.8 below the top of the succession and suggested that a significant part of the latest Famennian is not represented there. I attempted also to collect ammonoids from these exposures but results were not especially exciting and most specimens come from the scree. A nice fauna with *Balvia* was collected from the scree near the exploitation chambers at the southern end of the quarry. Most of the Famennian is there hard to access in the vertical rock wall, but among loose blocks a highly fossiliferous dark grey relatively pure limestone with numerous bivalves is represented, yielding the latest Famennian *Protognathodus* fauna, otherwise unknown from the quarry.

KARCZÓWKA

In the collection of Dymitr Sobolew housed at the Museum of Natural History in Kharkov, Ukraine, blocks of cephalopod limestone from the Karczówka hill south of Kielce are represented. Evidently this is the same material as that reported by Sobolew (1911). I was allowed to process for conodonts a small piece of this limestone which yields an assemblage of a rather unusual composition for the early Famennian of the Holy Cross Mountains, with ornate simple cones of *Mitrellataxis*. Probably this was a shallow-water environment above the top of a stromatoporoid-coral Frasnian buildup. Such palaeocological context is typical also for other sections of the Famennian in the area.

MIEDZIANKA

A few metres-wide belt of exposures of the Famennian extends along the southern slope of the hill Miedzianka near Chęciny (Fig. 4). Apparently, the somewhat marly and thin bedded rocks of this unit were more prone of dislocation than the massive mudmound and lagoonal deposits of the underlying Frasnian and Givetian. The copper ore mineralization within the faults was the reason for intense quarrying since the 18th century. The complex tectonics makes stratigraphy there difficult to establish and only two sections in this

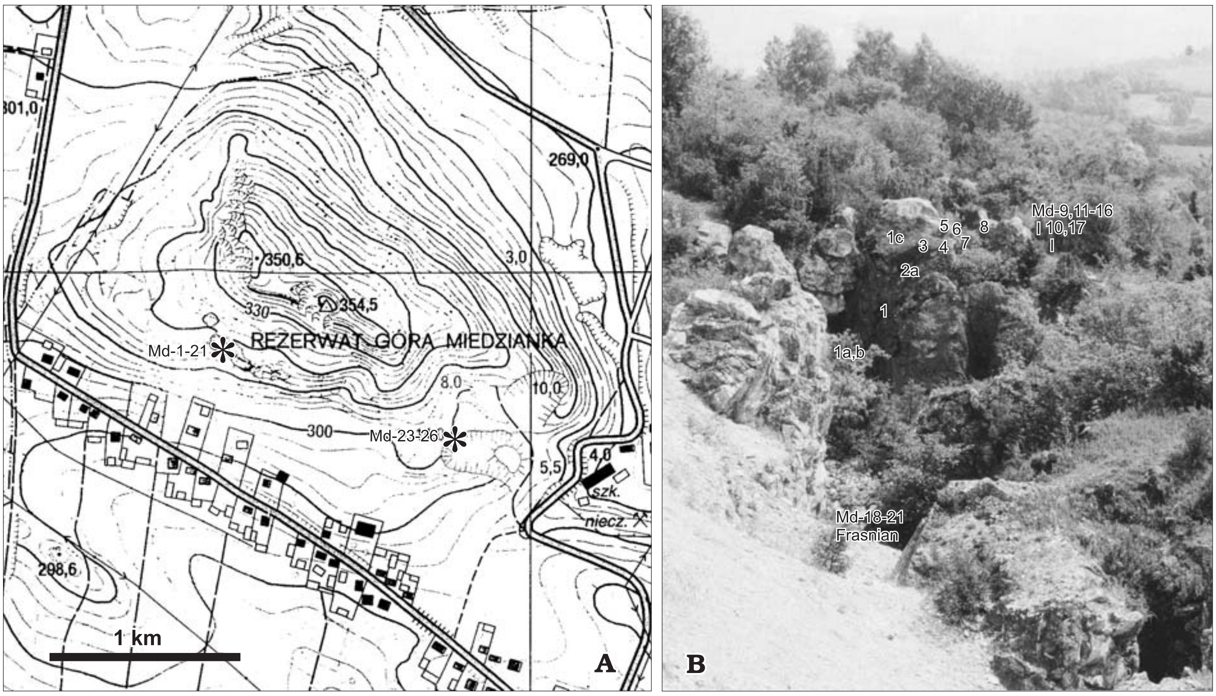


Fig. 4. Location of the Famennian exposures at Miedzianka in the Holy Cross Mountains (A) and places from where samples were taken (B); view from west.

zone have appeared suitable for study, located on opposite ends of it. In the ancient open mine on the SW of the hill remnants of two mining galleries are preserved. In tectonic blocks hanging above the entrance to the eastern gallery and on its eastern wall indistinct bedding is enhanced by weathering enabling sampling for stratigraphic purposes. Succesion is there reversed, with younger strata downhill.

Fossiliferous strata of the terminal Frasnian, with a brachiopod coquina with atrypid brachiopods, ahermatypic corals, and cephalopods are exposed in front of the entrance to the gallery on the northern wall of the mine (mentioned in Szulczewski 1989). Its age was determined by Czarnocki and Samsonowicz (1911) based on findings of *Manticoceras*. Siliceous lithistid sponges and silicified goniatite shells occur in the topmost part of the coquina, making the succession similar to that at Kowala (described below). The most unusual aspect of the conodont fauna is the complete lack of *Icriodus*, so abundant in the terminal Frasnian strata elsewhere, and abundance of *Manticolepis rhenana*. *M. winchelli* and "*Palmatolepis*" *linguiformis* are associated but *Lagovilepis bogartensis* and *Klapperilepis ultima* are missing. The environmental situation is thus somewhat similar to that at Kowala but fundamentally different from Płucki (see Dzik 2002). A spectrum of main conodont taxa for the succession was already given by Szulczewski (1989). My sampling revealed that there is no continuity between the Frasnian and Famennian here. The coquina is topped with a conglomerate (sample Md-27, Table 3), composed mostly of pebbles of a light grey limestone dissimilar to that immediately below in the section. The conglomerate matrix yielded an assemblage of the latest *K. triangularis* Zone species with a rather insignificant admixture of the latest Frasnian species. The latter is rather surprising, considering a rather high productivity of conodont samples from the coquina. Possibly, the pebbles were derived either from a not so high part of the Frasnian or they represent destroyed strata deposited at the beginning of the Famennian. There was thus a sedimentary discontinuity connected with an erosion event nearby marking a sea level drop in the earliest Famennian (Johnson *et al*. 1985).

A reddish organodetrital limestone initiates the well-bedded part of the succession. Beds of a cephalopod limestone occurred there once, from which Czarnocki and Samsonowicz (1911) extracted *Nehdenites verneuili*. A conodont assemblage with *Klapperilepis crepida* has been recovered by myself from loose blocks and samples from a tectonically brecciated zone in the exposure. A seemingly ordered succesion covers the *C. marginifera* and *L. styriacus* zones but conodonts show that it is repeated there. The youngest bed of the series near the dislocation in the middle of gallery is probably of early *L. styriacus* Zone age, whereas the southern block on the hill slope outside the mine extends to the *P. jugosus* Zone. The pattern of dislocations is so complex that the actual succession can be restored only tentatively and a probability remains that beds of different age are intercalated. As typical for the location, samples taken from apparently the same bed (indicated with consecutive lettering in Tables) may appear to be of different age.

The late Famennian is documented in the abandoned quarry at the SE foot of the hill. This is a marly shale with calcareous concretions tectonically inserted in the Frasnian massive limestone (Czarnocki and Samsonowicz 1911). Among concretions are nuclei of clymenias (*Cymaclymenia*). Czarnocki (1928, 1989) determined *Wocklumeria sphaeroides*, *Parawocklumeria paradoxa*, and several other species diagnostic of the latest Famennian. According to Czarnocki and Sujkowski (1931), Tournaisian black shales with phosphorite concretions and *Guerichia* once cropped out above the marly shale of the Famennian.

OSTRÓWKA

Exposures of the Famennian on the northern wall of the Ostrówka quarry are located only 3 km east of Miedzianka, but their facies development and stratigraphic completeness is dramatically different, as identified already by Czarnocki (1928). At present only a few beds of extremely condensed Famennian limestone can be found topping the Frasnian (Racki 1993) limestone with *Amphipora*, with an erosional discontinuity (Szulczewski *et al.* 1996). In extreme cases only two beds of the Famennian limestone are represented, the lower one representing the *P. trachytera* Zone, the upper one *D. trigonica* Zone (upper velifer and costatus zones; Szulczewski 1978). I sampled the most complete section among accessible ones in front of the Todowa Grząba hill, from where also slabs with clymenoid ammonoids were collected. The massive limestone underlying the organodetrital cephalopod limestone succession yielded a conodont assemblage (sample Ost-0) with *Conditolepis marginifera*, the dominant species being *Icriodus cornutus*. Conodonts of the *C. marginifera* Zone occur even below, possibly the source was a pocket within the limestone (Szulczewski *et al.* 1996) although no such structures were discernible in the sample. The first bed of black cephalopod limestone (sample Ost-1) contains *Palmatolepis trachytera* with reduced posterior process together with *Lagovignathus styriacus*; it is thus significantly younger than the conodont-yielding strata at Łagów-Dule described below. The bed immediately above (Ost-5) yielded *Palmatolepis rugosa* and *Tripodellus mancus*. A thin detrital limestone layer topping the succession yielded *Dasbergina trigonica* indicating the latest Famennian. Above, a marly shale with nodular limestone beds and concretions follow, with the *Scaliognathus anchoralis* fauna and probably reworked *Siphonodella* (Szulczewski *et al.* 1996; Dzik 1997).

Before intense quarrying a much more complete succession of the Famennian was exposed in a trench dug by Jan Czarnocki (1989, p. 23). Another section, only 1.8 m thick has been sampled for trilobites by Osmólska (1962). Wolska (1967) in her work on conodonts referred to Osmólska's section but it is unlikely that her samples truly were taken from it. Bed 2 of Osmólska (1962) is a black bituminous limestone evidently corresponding to beds 3 to 5 of Czarnocki (1989), the most fossiliferous clymeniid horizon accessible now, with *Stenoclymenia sandbergeri*. Among conodonts from that limestone (e.g. my sample Ost-12) there is *P. trachytera* (found in bed 7 by Wolska 1967) and *Lagovignathus styriacus* (bed 8). Wolska (1967) reported *C. marginifera* from strata 4 to 7, beds 1–3 being poor in conodonts. This makes data of Wolska of little use in correlating the succession of clymeniids described by Czarnocki (1989; see also Woroncowa-Marcinowska *in* Pajchlowa *et al.* 2003) with the conodont scheme, despite efforts of Szulczewski and Żakowa (1967). I dissolved small pieces of matrix from several of Czarnocki's specimens of clymeniids housed at the Museum of the State Geological Institute in Warsaw (earlier done also by Woroncowa-Marcinowska 2003 and Woroncowa-Marcinowska and Szrek 2004 and another specimen from the collection of the Instytut Paleobiologii PAN. This allows determination of the possible age of some of the beds. Sample taken from ammonoid specimen ZPAL AmVII/185 (Ost-185 on Table 17) contains *Tripodellus gonioclymeniae*, from IG 284.II.265 and IG 284.II.293 (Ost 265 and Ost-293) *Palmatolepis rugosa* has been extracted.

KOWALA

The studied material comes from the quarry of the cement plant Nowiny II located immediately south of the village Kowala, in proximity to the railroad section studied by Szulczewski (1971). This is the most complete and thickest section of the Famennian in the Holy Cross Mountains. Conodonts and ammonoids from both its Frasnian and Tournaisian parts have been already described by myself (Dzik 1997, 2002). Conodonts occur throughout the whole section but samples are usually of low productivity and specimens are covered with clay. Because of little use of this material to apparatus reconstruction I collected relatively few samples. The section has been studied stratigraphically also by Berkowski (2002).

The base of the Famennian is located within a unit of chert-bearing limestone with a wavy bedding, and is not discernible lithologically (Racki and Baliński 1998; Dzik 2002; Racki *et al*. 2002; Bond and Zatoń 2003). 5.5 m above, the limestone gradually becomes laminated and marly with bedding planes covered by large thalloid algae of possibly codiacean affinities (Racki *et al*. 2002, fig. 3b), *Concavicaris* crustaceans and ammonoid anaptychi. In sample Ko-155 from the base of this unit *Klapperilepis ultima* is already associated with *Tripodellus clarki* (or *Klapperilepis schuelkei*) and a few other species of *Klapperilepis*. 13 m above the base the first *Conditolepis prima* was encountered, and *K. rhomboidea* about 24 m from the base. Faults cut the section in this part and it remains difficult to estimate how much of it is missing or duplicated, but a sample taken about 2 m above the fault contains still approximately the same fauna with *K. rhomboidea*.

An unlabelled wooden box with fossiliferous marls similar to those from Kowala has been transferred to me by Zofia Kielan-Jaworowska, collected by her in 1946 for the late Jan Czarnocki. Among fossils there is a poorly preserved specimen possibly representing *Cheiloceras lagoviense* and the nautiloid *Gonatocyrtoceras* cf. *guerichi*. If truly collected at Kowala, it probably comes from near the fault, as indicated by conodonts (sample Ko?-168; Table 8).

A succession of about 93 m of marl with concretions and limestone intercalations continues from above the fault to the top of the Famennian and offers an unusually complete succession of conodonts and ammonoids. *Conditolepis quadrantinodosa* is present from at least 80 m below the top (sample Ko-161); *C. marginifera* about 7 m higher (Ko-163). In the black shale 63–65 m below the top of the section, pyritic nuclei of *Protornoceras* and associated ammonoids occur; the fauna was known earlier only as reworked in Quaternary clay at Sieklucki's brickpit in Kielce (Dybczyński 1913, Sobolew 1912a, 1914a, b; House 1970). The associated conodont assemblage includes *Conditolepis distorta* and *Palmatolepis ampla*.

The latter species is replaced (sample Ko-18) by *Palmatolepis trachytera* 40 m below the top and about 4 m below a very characteristic intercalation of a cardboard-like black shale with *Guerichia*, punctured but not breaking when hit by a hammer. This lithology marks the *Platyclymenia annulata* event (see Bond and Zatoń 2003). Limestone nodules immediately above the shale contain very well preserved juvenile conodont specimens (sample Ko-8a).

Another member of the *P. trachytera* lineage, *P. rugosa*, emerges 26 m below the top of the Famennian (sample Ko-181), associated there with *L. styriacus*. 4 m higher, *Pseudopolygnathus jugosus* (sample Ko-131, Ko-194) appears with increased contribution of limestone intercalations first. These higher Famennian strata, exposed now in the northern wall of the quarry, were identified by Czarnocki (1933) in trenches dug at this place. His section ranged from the greenish nodular marly limestone intercalating with shales containing an ammonoid assemblage with *Clymenia*. Calcitic skeletons of benthic organisms are represented there by rhabdomesid bryozoans and platyceratid gastropods.

A black shale intercalation splits a 1.5 m thick nodular greenish limestone above the more marly layers into halves. The limestone is topped with a thicker bed where *Dasbergina trigonica* first appears (sample Ko-123). This part of the section shows thus a rather low sedimentation rate as compared with that representing the *K. triangularis* to *P. trachytera* zones.

6.2 m of marl with limestone nodules follow then with alternation of olive green and red layers. This unit apparently corresponds to the most fossiliferous part of trenches yielding the diverse and well-preserved clymeniid assemblage with *Kalloclymenia* described by Czarnocki (1989). Unfortunately, in the trench sampled by myself (Dzik 1997) only nuclei of ammonoid conchs devoid of shells were found. All specimens collected from these beds belong to stratigraphically undiagnostic species of *Prionoceras* and *Sporadoceras*.

Above the last red nodular bed a 3.4 m thick succesion of olive shale and marls follows with rare nodular limestone intercalations and two beds of light greenish clay (possibly bentonite). *Wocklumeria sphaeroides* and *Parawocklumeria paradoxa* occur there. Two beds of nodular limestone, each about 0.3 m thick yielded the last Famennian-type conodonts, *Tripodellus gracilis*, and *Branmehla suprema* (sample Ko-75; Dzik 1997). Above is another black, burning shale 1.1 m thick (reported already by Czarnocki 1933, weathered in the trench studied by myself but now exposed in the quarry; Filipiak and Racki 2005) and 1 m thick bed of tuffite. The tuffite yielded the *Acutimitoceras* fauna of the terminal Famennian, which is taxonomically impoverished but rich in specimens. Similarly impoverished conodont *Protognathodus* assemblage was encountered in a laminated limestone intercalation 2 m above the tuffite and 2 m below the first occurrence of diagnostic Tournaisian conodonts (Dzik 1997). The Kowala section appears thus probably the most complete and fossiliferous among known succesions across the Devonian–Carboniferous boundary.

A borehole has been drilled in the vicinity of the quarry, described by Romanek and Rup (1990) and Żakowa and Radlicz (1990). Conodonts from the core were studied by Nehring-Lefeld (1990). The Frasnian–Fammenian boundary was incorrectly determined as coinciding with the top of massive limestone. The limestone strata above has yielded at depth 237.7 to 236.7 m specimens of *Belodella* (Nehring-Lefeld 1990, pl. 4: 12–13), the lineage terminating its occurrence with the end of the Frasnian of the Holy Cross Mountains. Apparently, similarly as in the outcrop (Racki and Baliński 1998; Dzik 2002), the boundary is located close to the top of the somewhat silicified limestone.

KADZIELNIA

The cephalopod limestone at Kadzielnia has been described palaeontologically for the first time by Gürich (1896), and Sobolew (1912*a*) determined its Famennian age. Wolska (1967) and Szulczewski (1971) sampled it for conodonts identifying the crepida to quadrantinodosa zones. Makowski (in Szulczewski 1971, p. 67) identified *Tornoceras sublentiforme* (his *T. acutum*) among cephalopods of the limestone. Nautiloids from this bed were described by myself (Dzik 1984). The *Cheiloceras* limestone rests at Kadzielnia immediately on the massive reefal Frasnian limestone and its basal bed contains a shallow-water conodont assemblage with dominant *Icriodus cornutus* and *Polygnathus praecursor*. The palmatolepidids emerge in great number in the main bed of the cephalopod limestone with randomly distributed large conchs of nautiloids and goniatites. The presence of advanced *Klapperilepis termini* and *Conditolepis prima* indicates the late *K. crepida* Zone.

A significant faunal change is expressed in the upper part of the overlying bed of pure limestone (sample Ka-3). Many species terminate their occurrence (including *Klapperilepis crepida*), whereas *K. rhomboidea*, *Conditolepis glabra*, *C. falcata*, and *C. klapperi* emerge. The change is so abrupt that a sedimentary discontinuity with significant gap in deposition seems likely. These species continue to the end of the sampled limestone succession. Above is a marly unit with nodular limestone intercalations yielding blind trilobites *Dianops* and poorly preserved cephalopods.

WIETRZNIA

The abandoned Wietrznia quarry in Kielce (now a nature sanctuary) is among the Holy Cross Mountains sections of the Frasnian most productive in conodonts (reviewed in Dzik 2002). The Famennian exposures there are less suitable for stratigraphic studies because of intense tectonics. Behind the northern wall of the quarry there is a dislocation zone with almost vertically dipping Famennian marls of various age in contact with units of the Frasnian, different in each exposure. Szulczewski (1989) interpreted the tectonics as synsedimentary. Although this seems possible as a result of breaking and differential settling of the underlying Frasnian reefal or mud mound body, the evidence for this remains weak. More likely, the Famennian pelagic strata in various outcrops represent tectonically shuffled different parts of the same lithologic column.

Among conodont samples available to myself, there is no material representing the earliest Famennian. The geologically oldest one is Wtr-34 taken from a tectonic breccia immediately below the large block left in the middle of the quarry. The conodont assemblage from there includes *Tripodellus schuelkei* with a wide angular platform. Probably the same breccia is exposed in the wall of the quarry nearby (block A? of Szulczewski 1989). It is topped with bedded limestone containing *T. clarki* (Wtr-27) associated with the first *Conditolepis*. The limestone succession with *Klapperilepis robusta* (Wtr-26) ends there with a sedimentary discontinuity penetrated with burrows. A succession of marls with nodular limestone intercalations starts from there. Early *K. termini* in the basalmost layer (Wtr-25) indicates some time gap at the discontinuity.

The first Famennian bed topping the Frasnian succession published in Dzik (2002) is probably of somewhat younger age, as suggested by advanced *T. variabilis*. The next portion of the Famennian has been sampled in the dislocated block in the middle of the quarry, where a series of laminated dark limestone and calcareous shale with pyritized radiolarians and phosphatized carapaces and appendages of the pelagic crustacean *Concavicaris* occurs. In a sample taken at the base of the block (Wtr-32), *K. crepida* has been identified; in a sample from limestone intercalation near the top of the exposed succession (Wtr-33), *Conditolepis prima* has been encountered. Nodules from the same unit brecciated in the wall east of the block have yielded poorly preserved goniatites.

JABŁONNA

This is perhaps the most intensely studied section of the Famennian in the Holy Cross Mountains. Unfortunately, it is also probably among the most tectonically disturbed. A trench has been dug there in 1949 by Czarnocki (1989, fig. 8) and ammonoids have been collected bed-by-bed. Some of the clymeniids have been described by Czarnocki (1989) and trilobites by Osmólska (1962). She described the section and correctly determined the age of bed 9 as corresponding to the *Cheiloceras* Stufe but her report of *Clymenia* (*Cymaclymenia* in Czarnocki 1989) in beds 14 and 18, the latter suggested to represent the *Wocklumeria* Stufe, remains a mystery. The material of unprepared goniatites and clymeniids from the trench has been transferred to myself in 1972 by Halszka Osmólska and conodonts have been extracted from the matrix. They indicate the *K. crepida* Zone extending from beds (my conodont samples J-) 3 to 16, material from beds 18–19 is not represented, the *P. trachytera* Zone is present in beds 20 to 24 (where also the first clymeniids are represented). The *L. styriacus* Zone is present in bed 26, and the *P. jugosus* Zone in bed 27. Higher strata are not represented among conodont samples, but bed 33 yielded *Kosmoclymenia* and *Epiwocklumeria*. As shown on the published sketch (Czarnocki 1989) much of the succession is represented by rubble and this may be the reason why bed 23, containing *C. marginifera*, does not fit in stratigraphically.

In 1962 another trench has been dug in approximately the same place and conodonts from there were described by Wolska (1967). Unfortunately, the strata exposed in the new trench have not been correlated with those from the old one. The first *Conditolepis prima* (*Palmatolepis glabra glabra* of Wolska 1967) has been encountered in bed 15 (attribution of specimen on her pl. 7:12 to bed 9 is probably a mistake), so the strata above probably correspond to bed 16 of Czarnocki. I sampled the remains of the trench in 1980 and the representation of the first occurrence of *C. prima* in continuous succession has been confirmed (sample J-46). *Synclydognathus ancestralis*, the species known elsewhere only from sample Wtr-32 at Wietrznia and presumably of very restricted occurrence, has been found in sample J-45a of my new series and in sample from bed 16, which seems to provide a rather firm ground for correlation. In fact this fits well also the distribution of *C. tenuipunctata* in both series.

Higher samples of Wolska were taken from the rubble and their spatial relationship in the section cannot be established. They correspond to the part of Czarnocki's trench above the dislocation. Bed 27 of Wolska (1967) corresponds to bed 20 of Czarnocki (1989). It appears thus that a significant part of the mid Famennian is not represented in the trenches.

A fundamentally different picture is presented by the core of borehole Jabłonna IG 1 (Żakowa *et al.* 1983). Although highly incomplete and punctuated by tectonic breccias in its lower part, it shows a relatively complete succession of the mid Famennian. The sampled section starts above a breccia, higher than in trenches, as *K. termini* is already represented there (depth 75.0 m), which thus corresponds probably to bed 3 of Czarnocki (1989). The first *C. prima* occurs at depth 74.0 m, immediately above another breccia. The first occurrence of *C. falcata* at depth 71.5 suggests a correspondence to bed 19 of Wolska, already within the breccia in Czarnocki's section. In fact, most of the core corresponds to this hiatus, with *K. rhomboidea* and *C. marginifera* occurring up to 64.5 m. Evidently there is a tectonic discontinuity above, corresponding to the upper unit in Czarnocki's trench.

The first appearance of *P. jugosus* at depth 63.5–63.7 suggests a correspondence to bed 27. *Dasbergina trigonica* has been found at depth 62.9 by Żakowa *et al.* (1983), which shows a succession closely similar to that at Dzikowiec. Apparently bed 33 of Czarnocki corresponds to this youngest Famennian limestone. A black shale with limestone nodules and tuffite at depth 61.7–61.8 probably represent the terminal Devonian Hangenberg event, in close analogy with the Kowala succession.

ŚCIEGNIA

This is the locality "Wzdół Plebański" of Kościelniakowska (1967). The sampled section is along the creek behind the allotment No. 16. This is a rather monotonous succession of nodular or grey-green wavy-bedded marly limestone with a spectacular intercalation of black clay of the *Platyclymenia annulata*

Event in the middle. Conodont samples are generally of rather low productivity. The oldest of them (Wzd-10) contains *Conditolepis distorta* and numerous *Alternognathus* specimens with a wide platform. In proximity to the black shale (sample Wzd-7) the first *Dasbergina* appears, and above it *Lagovignathus granulosus* has been found. 1.2 m above the black shale there is a tectonic discontinuity surface but probably not much of the section is missing as *L. granulosus* occurs still above it (sample Wzd-9). A significant rebuilding of the assemblage took place between this level and the topmost exposed bed (Wzd-13) with *Palmatolepis rugosa*. A significant dislocation separates this part of the section from that to the north, where there is a small exposure of an early Famennian nodular limestone within dark clays. The conodont assemblage contains *Conditolepis prima* and *C. gilberti*.

ŁAGÓW AND PŁUCKI

The oldest unit of the Famennian in the Płucki-Łagów section is the Lower Łagów Beds (dolne warstwy łagowskie), a rhythmic intercalation of grey nodular marly limestone and shales. The Beds were identified by Sobolew (1912b) and Czarnocki (1989) in Dule, where they are in tectonic contact with the overlying limestone strata of the Upper Łagów Beds along a fault. Such a rock crops out near the mouth of the ravine on both sides and the most complete exposure is in the backyard of the house number 73 on the Słupecka street. Lithologically identical strata crop out along the road to Nowa Słupia and are in continuity with the Płucki section. Conodont samples show their early Famennian age and the only lithic distinction at which the base of the Lower Łagów Beds could be defined is the top of the dark limestone and marl succession containing the Upper Kellwasserkalk horizon, terminating 4.0 m above it. The basal stratum (sample Pł-40) contains the first *Klapperilepis delicatula*.

The Słupecka 73 exposure is poorly fossiliferous, except for the cephalopod limestone beds, and conodonts extracted from the nodular limestone at the base contain a conodont assemblage with *Conditolepis falcata*. More than 4.0 m of the succession are exposed there below a cephalopod limestone bed with large *Maeneceras*, 20 cm thick. It is separated from the last bed of the nodular limestone with a sedimentary discontinuity and covered with a ferruginous stromatolite, marking another discontinuity surface. The limestone succesion above, with five beds separated by shale intercalations of thickness diminishing upwards, may conveniently be considered the basal part of the Upper Łagów Beds (górne warstwy łagowskie), together with the cephalopod limestone bed. The bed immediately underlying the cephalopod limestone contains *C. marginifera* and the same conodont assemblage occurs throughout the strata exposed above. *Palmatolepis ampla* appears for the first time in the bed immediately above the ferrugineous stromatolite.

This means that the *Cheiloceras* assemblage, which is rich in fossils, described by Sobolew (1914) and known to me only from loose blocks collected from the scree, must have been derived from lateral equivalents of the strata exposed at Słupecka 73, probably from fossiliferous limestone lenses.

A few specimens of the large nautiloid *Mecynoceras* transferred to me by Andrzej Piotrowski (Dzik 1985) were claimed to be collected on the left slope of the valley. I have not been able to confirm this location. The limestone matrix (sample Ł-Mec; Table 3) contains *Klapperilepis circularis* and *K. quadrantinodosolobata*, being thus older than any part of the Dule section. A lense of cephalopod limestone of this age was once exploited in a trench at Janczyce (Makowski 1991), about 20 km to east, in the same facies zone of the Holy Cross Mountains. An almost complete succession of the Famennian has been traced in the borehole Janczyce 1 by Matyja and Narkiewicz (1992, 1995).

Gürich (1896, 1901) was the first who identified fossils from the “Sacculus-Bank” on the right slope of the Niwa valley in Łagów, and determined their geological age. Sobolew (1911) published a list of fossils, mostly from no longer existing exposures of a fossiliferous limestone of the Upper Łagów Beds on the left slope of the valley. His more detailed stratigraphic and palaeontological work on the right side of the valley (Sobolew 1912*b*), in the slope exposure of ravine Dule, remains the main source of information on this classic locality. An interpretive sketch of the wall was published in Czarnocki (1989).

As a result of activity of fossil collectors at Dule, the ammonoid-bearing limestone lenses were already completely exploited when in 1974 I attempted to make a precise sampling in a few trenches dug across the exposure. The deepest lying bed reached by the trench is a massive synsedimentary brecciated limestone with pebbles of grey marly limestone identical with that occurring in the Lower Łagów Beds. In a sample of such pebble (Ł-39; probably contaminated with the matrix) *Conditolepis glabra* has been found. This supports its age older than the matrix (Ł-38), where only the more advanced member of the same lineage, *C. distorta*, occurs. The topmost part of the bed is rich in pyrite and contains phosphorite pebbles composed mostly of larval gastropod shells. Originally aragonitic molluscan shells are frequently replaced with pyrite, offernig surprisingly precise replicas of their original morphology (Dzik 1994). The tornoceratid goniatite *Pseudoclymenia* has been also found in this part of the bed. The overlying 2 m of a dark bedded limestone with marly shale intercalation contains several species of the cheiloceratids, with the dominant *Dimeroceras polonicum*. In this zone probably the most fossiliferous lens of the "Sacculus-Bank" of Gürich (1896) was located, accessible to collecting until 1971. No clymeniid has been found in this unit by myself and I guess that those reported by Sobolew (1914) and Czarnocki (1989) allegedly from this stratum were collected in the northern part of the exposure from a lens incorrectly correlated with it.

At the base of the black mudstone covering the fossiliferous limestone bed, numerous small limestone concretions (sample Ł-4) yielded *P. trachytera* and *L. granulosus*. Samples from beds of a black limestone above were barren of conodonts, but almost certainly they correspond to blocks of the black limestone with the heterocoral *Oligophylloides* (Ł-40) and clymeniids occurring in the scree. They all contain *P. trachytera*. Higher up in the section only undeterminable flattened clymeniids occur in the shale with intercalations of black limestone with the abundant bivalve *Guerichia* (well exposed behind the allotment Słupecka 59).

CORRELATION AND CHRONOLOGY

I believe that inserting units of chronostratigraphy or biochronology (recently reviewed by Lindsay 2003, but see Zalasiewicz *et al*. 2004) between those of geochronology and lithostratigraphy is of little purpose and results in unnecessary complication of terminology (Dzik 1995). While reasoning on age correlation based on paleontological evidence, it seems enough to separate clearly data and hypotheses on evolutionary events (unique but of low resolution) from faunistic or floristic expressions of environmental changes (potentially of high resolution but repeatable in principle).

The geochronology of the Famennian was originally based on ammonoid biostratigraphic subdivisions assumed to reflect evolution. There are reasons to believe that truly the ammonoids were the fastest evolving organisms of the Devonian and easiest to determine taxonomically (also owing to their low population variability). However, except for a few classical places in central Europe, Russia, Australia, and northern Africa, they are relatively rare fossils. It seems thus more practical and reliable to base subdivision of the Famennian on the evolution of conodonts even if they do not enable equally subtle subdivisions. This obviously requires a biological approach to their taxonomy (that is, study of their population variability) and all available morphological evidence has to be used (that is, data on the composition of their whole apparatuses). This attitude is followed here and, although ammonoids are also used to determine chronological succesion of events, the conodont-based zonation is the background standard to which all other ways of inference are supplementary.

Below a review of the evolutionary events that can be used for intercontinental correlation of the central European standard are reviewed in chronological order, starting from the beginning of the Famennian. To avoid misunderstanding, I refer to zones intented to be chronological units ("chrons") based on evolutionary events using full taxonomic names of the index taxa in italics. Early, mid, or late units within them do not have formally defined boundaries and are used in lower case. In names of biostratigraphic or ecostratigraphic zones only the species rank name is used in roman letters, without the genus name.

EVOLUTIONARY DATUMS

The classic Famennian conodont biostratigraphic scheme was proposed by Ziegler (1962, 1971). Since that time several improvements were introduced both by its author and other students (summarized by Ziegler and Sandberg 1984, 1990, and Schülke 1999). All of them followed the same basic way of inference, that is basing the correlation on the actual ranges of morphologies in the rock sections. Despite declared reference to the phyletic evolution of particular conodont lineages, the vertical concept of chronospecies or even a plain typology was applied. An expression of this methodological attitude is the "Famennian" concept of subspecies, as neither a geographic race nor a segment of evolutionary transition. Some of such understood subspecies are equivalent to regular biological species (e.g., "*Palmatolepis glabra acuta*") in the meaning applied by students of conodont apparatuses from other geological periods, others (e.g., "*Palmatolepis quadrantinodosa inflexa*") seem to be just morphotypes within population variability of a species. I insist on applying the populationl attitude to the fossil material and on defining the boundaries between chronospecies horizontally. The global correlation standard (less precise, but reliable) could then truly be based on the phyletic evolution of the most suitable conodont lineages.

Most of the traditional zonal subdivisions offered by Ziegler (1962) can easily serve this purpose after a minor redefinition, but those introduced by Ziegler and Sandberg (1984) are more difficult to apply. The main obstacle is that the evolution is reliably documented in very few tropical conodont lineages used in the Famennian biostratigraphy. Even in cases when this is potentially possible, a non-biological approach to taxonomy obliterates the observed evolutionary change. The three younger of the zonal units of Ziegler and Sandberg (1984) are deficient in this aspect. Thus, the zonal species "*Palmatolepis postera*" is probably only a marginal morphology in the population variability of *P. schindewolfi*. Although the origin of *P. schindewolfi* is traceable in the fossil record, its great population variability makes identification of transitional stages rather unreliable in small samples and several other conodont lineages in the same time span seem more practical as index fossils. The taxonomy and chronological boundaries of "*Palmatolepis expansa*" (claimed to be a member of the *Tripodellus gonioclymeniae* lineage) is uncertain and many of its occurrences reported in the literature are probably based on taxonomic misidentifications. The origin of the youngest species, "*Siphonodella*" *praesulcata* remains obscure and its identification is usually uncertain because of co-occurrence of homeomorphic species and lack of knowledge of the apparatus composition.

Therefore I propose to come back to the original zonal subdivision of the Famennian by Ziegler (1962) with only unavoidable corrections resulting from the progress in understanding of the taxonomy and evolution of the index species. All but the last zonal units (or rather datums) used here are based on the index species chosen by Ziegler (1962), nomenclatorially corrected. I am skeptical regarding reliability for intercontinental correlation of any earlier proposed time units of lower rank. Modified definitions of the evolutionary zones are given below with a brief review of other probable evolutionary changes within their time spans of possible correlative value.

***Klapperilepis triangularis* Zone**. — There is no evolutionary change, which could be used to define the base of the Famennian as currently understood (that is at the end of the Upper Kellwasserkalk environmental event corresponding to the base of triangularis zone in the Montagne Noire; Klapper *et al*. 1993; House *et al*. 2000) but just an ecologically controlled disappearance of a few warm-water pelagic species [in Schülke's (1999, p. 10) words, followed by a "mass occurrence of *Palmatolepis triangularis*"]. The subdivision of the latest Frasnian zone proposed by Girard *et al*. (2005) does not apply to the Holy Cross Mountains as in the Płucki section "*Palmatolepis*" *linguiformis* continues to the end of the Upper Kellwasser horizon together with all its conodont fauna, whereas in the Kowala section *Klapperilepis ultima* is missing in the latest Frasnian (Dzik 2002).

The change from *K. ultima* to *K. triangularis* took place somewhat later (Dzik 2002). This means that the earliest part of the Famennian, defined on the environmental change, has to be placed within the zonal unit based on the evolution, which starts in the latest Frasnian and continues to the earliest Famennian (I proposed *Ancyrodella curvata* as probably the most reliable marker of this kind for the base of the terminal part of the Frasnian; Dzik 2002).

Ziegler (1962) subdivided his triangularis Zone in three parts. The middle unit was defined on the first appearance of *Klapperilepis delicatula* and *Tripodellus clarki* (as understood in the present work). Both these lineages appeared in the Holy Cross Mountain by migration from elewhere (Dzik 2002) at approximately the same time as the evolutionary change from *Klapperilepis ultima* to *K. triangularis*. If applied to the local, central European biostratigraphy, this first unit corresponds thus to probably a very brief time between the end of the Frasnian and the base of the evolutionary *K. triangularis* Zone. The change to *K. protorhomboidea*, as proposed by Schülke (1999), moves the boundary between the units a little but the origin of the new index species is equally cryptic and difficult to trace. The upper unit of Ziegler's triangularis Zone is defined on the appearance of *Conditolepis tenuipunctata*. This is probably a true evolutionary event, in effect of narrowing the platform of P_1 element and widening the platform of P_2 elements of the ancestral *Conditolepis lobicornis*, but the exact course of evolution remains to be demonstrated. Anyway, this may be a useful datum for the global correlation, better than the origin of *K. robusta* proposed by Schülke (1999), the ancestry of which remains unknown.

The change from *Klapperilepis* to *Palmatolepis* (Dzik 2005) may appear useful for correlation in the middle of the Zone. Near the end of the zone, the triramous P_2 elements originated in the lineage of *Tripodellus* but transitional populations are polymorphic and co-occur with more conservative lineages of the same genus which makes their application to dating rather unreliable. The transition from *Klapperilepis protorhomboidea* to *K. rhomboidea* is of even less importance because of rarity of these species and their great population variability.

***Klapperilepis crepida* Zone**. — The zonal index species originated from *K. robusta*, as shown by Schülke (1999). Both chronospecies are variable and transitional populations contain modal morphologies of both of them. The significant overlap in their ranges as interpreted by that author is thus probably a result of application of the vertical species concept. Schülke (1999) proposed to define the base of the zone on the origin of "*Palmatolepis abnormis sandbergi*". This is a good evolutionary datum, as long as M elements are used to identify the (sub)species. Unfortunately, the most common P_1 elements are individually hardly distinguishable from those of the ancestral *K. triangularis*. The transition took place much earlier than the first appearance of *K. robusta*, thus well within the *K. triangularis* Zone in its traditional meaning.

In the Holy Cross Mountains, sections *K. robusta* changes into *K. termini* with a gradual increase in the height of denticle rows. This transformation is of correlative value and Ziegler (1962) used it to define the boundary between the lower and middle parts of the Zone. It remains unclear whether the different time of appearance of *K. crepida* and *K. termini* is related to their evolution, results of migrations or an artifact of taxonomy. Another fast evolving lineage of the zone is that of *Conditolepis tenuipunctata* → *C. glabra*, the basis of Ziegler's upper part of the Zone. This is a phyletic change that has to be carefully recognized. Apparently, Schülke (1999) applied there the vertical species concept, which resulted in a chronological overlap of successive species.

Ziegler (1962) introduced the rhomboidea Zone located between crepida and quadrantinodosa zones based on the appearance of *Klapperilepis rhomboidea*. This species is clearly a successor of *K. protorhomboidea*. The evolutionary change was slow and difficult to trace because of a wide population variability and morphologic simplicity of P_1 elements. The appearance of *K. rhomboidea* in the Holy Cross Mountains is an ecological event of questionable correlative value. Probably its oldest occurrence is at Kadzielnia (sample Ka-3) where it co-occurs with the late *K. termini*. Im Łagów, Kowala and Miedzianka the species co-occurs with *C. quadrantinodosa* and disappears before its change into *C. marginifera*.

***Conditolepis quadrantinodosa* Zone**. — The highly variable index species *C. quadrantinodosa* originated from *C. klapperi*, but the change has not been traced in any section. Some time after this event, *C. inflexoidea* originated allopatrically in respect to *C. quadrantinodosa* and then returned to the area of occurrence of the *C. quadrantinodosa* → *C. marginifera* lineage. This probably enforced both sympatric populations to narrow their variability (character displacement). *C. inflexoidea* variability was reduced mostly to the morphotype with oval platform and narrow crest along its anterior lobe. In fact, a remarkable rebuilding of conodont assemblages is connected with the entrance of *C. klapperi* to the Kadzielnia succession. Perhaps it would be reasonable to define the base of the Zone at this event, but the origin of *C. klapperi* remains cryptic.

***Conditolepis marginifera* Zone**. — Ziegler (1962) used the disappearance of *C. inflexoidea* as the basis for distinguishing his two parts of the *C. quadrantinodosa* Zone. This is clearly an ecological phenomenon and not a reliable basis for time correlation. The change from *C. quadrantinodosa* to *C. marginifera* is not so much connected with introduction of any evolutionary novelty but rather with decrease in population variability. Anyway, these species occur usually in large number of specimens and their taxonomical identification seems rather easy. Ziegler and Sandberg (1984) proposed the origin of their subspecies "*Palmatolepis marginifera utahensis*" as the marker for the base the upper unit but the biological meaning of this taxon remains to be settled.

Perhaps the origin of *Palmatolepis ampla* from *P. perlobata* is also of potential correlative value within this zone but these lineages apparently split allopatrically.

***Palmatolepis trachytera* Zone**. — The zone, with its lower boundary defined at the origin of the nominal species was introduced by Ziegler and Sandberg (1984). The transition from *P. ampla* is still inadequately documented but very likely. The oldest population of *P. trachytera* share the presence of sharp posterior lobes with its ancestor. In the original meaning, this was the boundary between the lower and middle part of Ziegler's (1962) velifera Zone, based on the appearance of *Scaphignathus velifer* (transferred to marginifera Zone as its uppermost unit by Ziegler and Sandberg 1984). This lineage of shallow-water conodonts is under a strong environmental control in its distribution and was rightly abandoned as the basis for global time correlation. Unfortunately, this refers also to the appearance of *Dasbergina granulosa*, the basis for recognition of the uppert part of the velifera (or the whole trachytera) Zone.

The origin of *Lagovignathus granulosus* from *L. lagoviensis* is of potential correlative value in the younger part of the zone.

***Lagovignathus styriacus* Zone**. — The change from *Lagovignathus granulosus* to the nominal species defines the base of the zone, as introduced by Ziegler (1962). Ziegler and Sandberg (1984) renamed it as the postera Zone defined on the origin of "*Palmatolepis perlobata postera*" which seems to be a morphotype of *P. schindewolfi*. The origin of *L. styriacus* seems to be a much more reliable basis for the age correlation.

Of potential correlative value is also the associated *Palmatolepis rugosa*. As shown by the morphology of the P_2 element, this is a member of the *P. trachytera* lineage but in sections studied by myself there is always a gap in their distribution, thus the transition cannot be demonstrated.

Ziegler and Sandberg (1984) proposed the origin of *T. mancus* as the lower limit of their upper postera Zone but this is a rare species of unclear relationship to both the ancestral *T. gracilis* and its possible successor *T. gonioclymeniae*. Although of potential correlative value this event remains to be tested.

***Pseudopolygnathus jugosus* Zone**. — The upper part of Ziegler's styriaca Zone was defined on the appearance of *P. jugosus*. The origin of icrion with three rows of denticles in this *Pseudopolygnathus* (or perhaps rather *Dasbergina*) lineage seems to be rather well documented. The unit corresponds roughly to the traditional costatus Zone together with Ziegler and Sandberg's (1984) lower expansa Zone. The taxonomic status of "*Palmatolepis expansa*" proposed to define the lower boundary of the zone, remains to be clarified. As mentioned already above, no such species has been encountered in the Holy Cross Mountains or the Sudetes. I see also no possibility to trace in the available material the evolutionary origin of "*Siphonodella*" *praesulcata*, defining its upper limit.

Ziegler's costatus Zone was defined on the appearance of *Pseudopolygnathus ziegleri*, as understood in this work. Unlike *P. jugosus*, the origin of this species remains cryptic and its occurrence, similar to other Famennian and Tournaisian species of the genus, is rather chaotic, evidently as a result of a high ecological sensitivity. This refers as well to *P. aculeatus*, chosen by Ziegler and Sandberg (1984) to define their middle expansa Zone. Even the change from *P. ziegleri* to *P. ultimus*, of potential correlative value (defining the upper expansa Zone), may be misleading. At Kowala the ancestral species reappeared after some time of occurrence of *P. ultimus*.

Tripodellus gonioclymeniae, used by Ziegler (1962) to define the middle and upper parts of the costatus Zone remains of cryptic origin, although its origin from *T. mancus* is likely. The lineage originated probably allopatrically from *P. gracilis* but the allegedly transitional role of "*Palmatolepis expansa*" (Ziegler and Sandberg 1984) is far from proven.

***Dasbergina trigonica* Zone**. — The origin of the nominal species of this newly proposed zone from *Dasbergina marburgensis* is shown by a transition series in the upper part of the clymeniid limestone at Dzikowiec in the Sudetes. The zone roughly corresponds to Ziegler and Sandberg's (1984) praesulcata Zone. The topmost part of the unit includes the *Protognathodus kockeli* fauna. The latter immigrated to the equatorial zone together with an impoverished cold-water ammonoid fauna near the end of the Famennian (if defined at the end of the Hangenberg black shale environmental event). The exact time and place of origin of *P. kockeli* remains to be determined and the three units within the praesulcata Zone, defined on the disappearance of *T. gonioclymeniae* and entrance of *P. kockeli*, are of clear ecostratigraphic nature.

CONODONT ECOSTRATIGRAPHY

Like any other application of evolutionary changes to age correlation, the conodont zonation of the Famennian allows only a crude approximation to chronological relationships among fossiliferous strata. It is thus tempting to refine the stratigraphic resolution by using short-term environmental changes of possibly

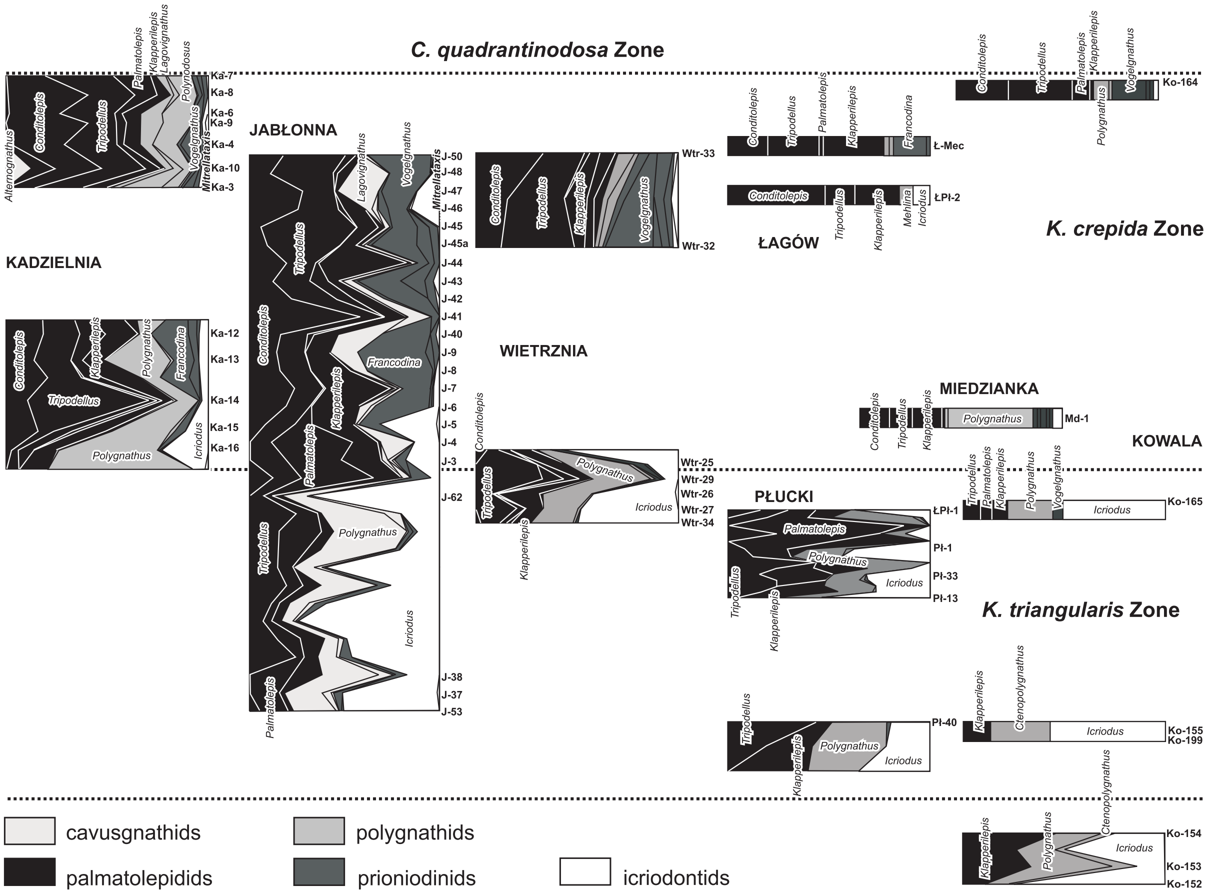


Fig. 5. Logs of percent contribution of conodont elements representative of the main lineages for samples from the early Famennian of the Holy Cross Mountains. Relative position of samples standardized in reference to proposed chronologic subdivisions.

wide extent. The easiest and probably most reliable technique of such a correlation is the palynological methodology of comparing changes in percentage contribution of ecologically sensitive taxa, the procedure frequently used in connecion with conodont biofacies analysis.

Such "palynological" logs based on the Famennian conodonts (Figs 5, 6) appear promising for the within-region correlation but much more research is needed to approach truly useful results. It has appeared that much more dense sampling would be necessary than done by myself for the apparatus study. Only one succession is sampled well enough in this respect, that is the upper part of the Kowala section (Fig. 6). A rather clear pattern of alternation of presumably shallow- (and cold?-) water faunas dominated by *Pseudopolygnathus* and more open-sea palmatolepidid-rich assemblages is visible in the log. Three cycles cover there the *P. trigonicus* Zone and another three the *P. jugosus* Zone. In the coeval part of the Dzikowiec section these cycles are not so clearly recognizable, mostly because of a relatively deeper-water environment. Unlike Kowala, immediately after the transgressive event near the beginning of the *P. jugosus* Zone a relatively stable environment was established there.

Except for the trench at Kowala, the sampling is too sparse to show convincingly such a pattern, but some large-scale cycles are shown by the distribution of the open-sea palmatolepidids and shallow-water icriodontids. The distribution of *Conditolepis falcata*, the dominant species in the Holy Cross Mountains late Famennian, seems meaningful. There are three peaks in its distribution separated by the dominance of *Icriodus* (at Miedzianka), polygnathids (Łagów) or both taxa (at Kowala). Two such peaks correspond to the *C. marginifera* Zone, the *P. trachytera* Zone corresponds to a probable shallowing, and the third peak covers at least the lower part of the *L. styriacus* Zone. More dense sampling would probably reveal a smaller scale cyclicity within each of those events, as suggested by the record at Łagów, where the late *C. marginifera* Zone deepening seems to be split into two events and a similar cyclicity as in Kowala may have occurred in

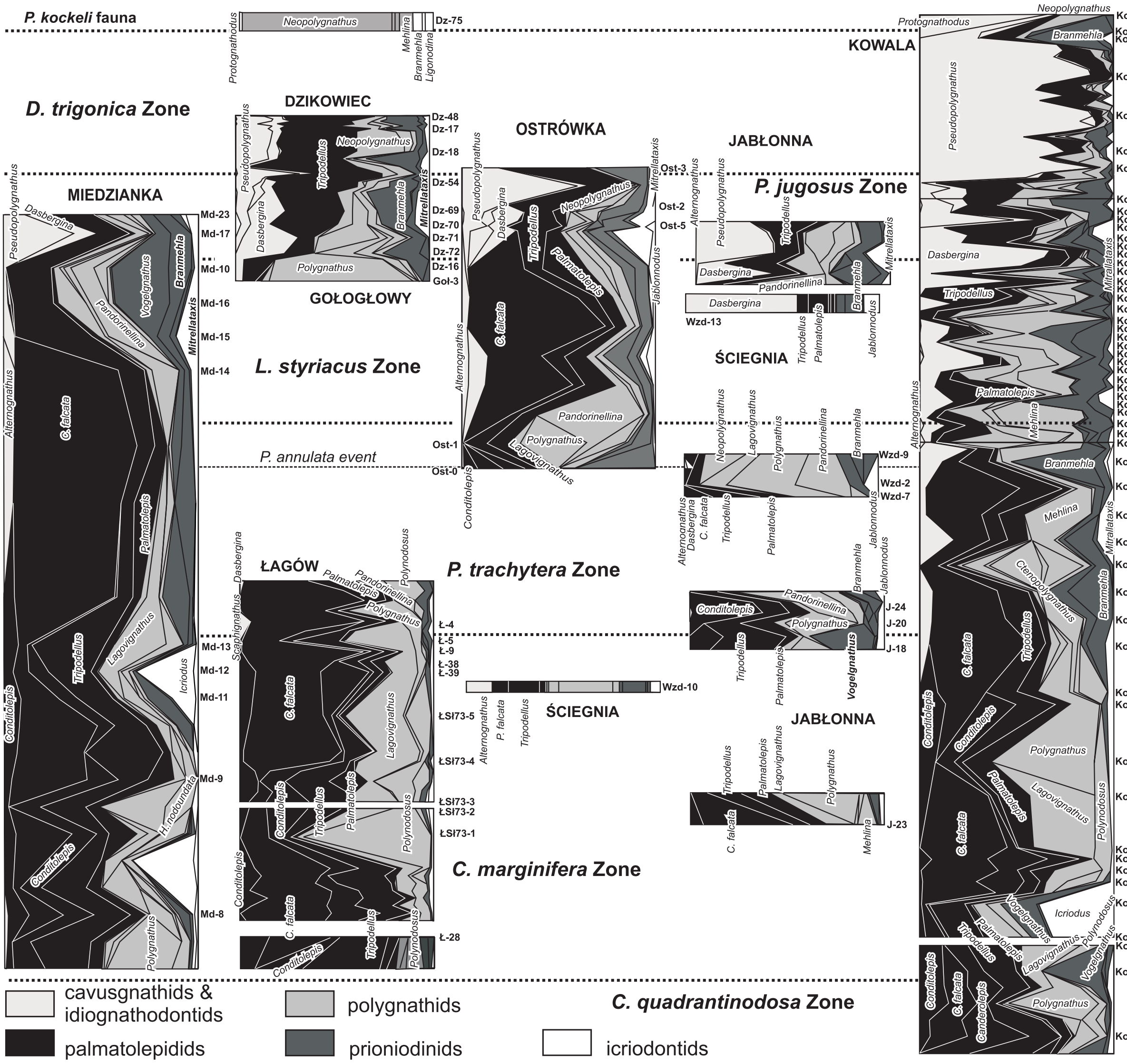


Fig. 6. Logs of percent contribution of conodont elements representative of the main lineages for samples from the early Famennian of the Sudetes and Holy Cross Mountains. Relative position of samples standardized in reference to proposed chronologic subdivisions.

the *P. trachytera* Zone. The complex tectonics makes sampling difficult at this site, and it is even less reliable in this respect at Miedzianka.

The *K. crepida* Zone is characterized by a rather stable environment, except for its transgressive base. In *K. triangularis* Zone and the earliest Famennian strata deposited before this Zone, several peaks in abundance of *Icriodus* are recognizable but incomplete sections do not allow use of their potential correlative value. This may be of potential value in establishing a high resolution chronology of the Late Devonian, as a similar rythmicity seems to be expressed also in the Chinese sections (Wang and Ziegler 2002).

Unfortunately, the relatively complete record is available only for rather deep-water environments of the Famennian of Poland. Shallow-water succesions are known from exposures only in the Cracow region (Baliński 1995) although they have been reached by numerous drillholes in Silesia (Narkiewicz 1978; Belka 1998), Pomerania (Matyja 1993), and the Lublin region (Matyja and Żbikowska 1985). The cores yielded conodont faunas with many species unknown in the area sampled by myself. These include bizarre *Ctenopolygnathus rarus* (Baliński, 1995), *Omolonognathus transformis* Gagiev, 1979 (Baliński 1995), *Mashkovia silesiensis* Belka, 1998, and *Icriodus chojnicensis* Matyja, 1972. Potential occurrence of similar assemblages in the Holy Cross Mountains is suggested by the isolated sample from Karczówka containing ornate new species of *Mitrellataxis*. The same species have been identified in the single productive sample from coeval strata at the Żbik ravine near Dębnik collected by myself.

METHODS

Ammonoid conchs and other macrofossils on which this study is based, have been extracted from the rock and illustrated using standard, widely used techniques and equipment, which do not need to be described in detail. A somewhat more sophisticated method has been applied to chemical extraction of microfossils. These were mostly phosphatic conodont elements or fish teeth and scales, but also secondarily phosphatized or pyritized ammonoid conchs. Because the treatment of samples may influence results of extraction, the procedure is presented below.

CONODONT ELEMENT EXTRACTION

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. The large fraction was screened after being dried 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. Residues rich in clay, developing mud cracks after being dried, were washed again. Dry residues with high content of non-phosphatic debris were separated in the electromagnetic mineralogical separator, after coming again through a 1 mm sieve to remove aggregates blocking the funnel of the separator. The angle and amperage of separation were chosen separately for each series of similar samples. It was avoided to proceed with separation too fast or to remove much more than half of the low-magnetic fraction of the residue in one pass. Commonly the separation was repeated a few times. Only in case of silica-rich samples from the Sudetes were heavy liquids used in separation.

The specimens are kept loose in plastic slides (*Franke Zellen*) instead of being glued to the paper, as is the American practice. The reason for this is that gluing of a very large number of specimens is time consuming and makes moving and segregation of specimens (necessary to arrange them in apparatus sets, as explained below) difficult. It may also be destructive to fragile specimens. All together 235,031 specimens have been taxonomically identified and counted. Some samples were dissolved for additional material at late stages of preparation of the work and some minor inconsistencies in data presented on Tables 1–19 may result from this.

Measurements (published in Dzik 2002 and 2005) 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 appear 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 posterior lobe of all specimens, both dextral and sinistral, was oriented towards the right while drawn.

RECONSTRUCTION OF CONODONT APPARATUSES

The most efficient way to restore conodont apparatuses at the present stage of knowledge is by inventing working hypotheses on their composition to falsify and verify them while collecting new samples (Dzik 1991). All the elements in each sample have to be separated into morphological classes to match them into sets of particular species. It is helpful to consider the shape, robustness of denticulation and coloration of elements at this stage of reasoning. In this study, the elements within a large Franke cell were arranged in piles with a hair mounted on a holder. Sets representing the icriodontids, prioniodinids, polygnathids, and palmatolepidids were then transferred to separate cells and the separation was continued until series of all the element types for each species were arranged. Their various combinations represent hypotheses to be tested.

In principle, the whole series of element types of a species has to be represented in a large sample. Each of the identified morphological classes can thus be attributed to a multielement species. First, the already known apparatuses were identified and removed. Provisional grouping of residual elements was attempted to fit the better known apparatuses. This was then tested by repeating the same procedure with successive samples. Usually such concepts are soon falsified (obviously, this requires that samples are significantly different in species composition, being taken from various horizons and kinds of the rock). The remaining, not rejected hypotheses on the apparatus composition are further tested by looking for a possibly close relative (preferably belonging to the same evolving lineage) with morphologically similar elements in particular apparatus locations. The whole phylogenetic tree has to be logically consistent in its every aspect, including continuity in a homologous series of elements between species.

The main obstacle in reconstructing the Late Devonian conodont apparatuses is the deficiency of non-platform elements in samples (their unbalancing). As a result only the apparatuses of numerically dominant species are reliably known at present and many reconstructions of Famennian apparatuses remain incomplete.

A special aspect of apparatus reconstructions is that phylogenetically related sympatric species share some of the element types. More precisely, their population variability may appear wider than the difference between species. In such cases the specimens not attributable to particular species have to be counted together for the whole species group (as given in the Tables 1–19) or separated arbitrarily (as included in logs of percent contribution).

TAXONOMY

Not only the apparatus study but also taxonomic decisions have been taken separately for each sample. The population approach to the species-level taxonomy was used. Already while assembling elements into apparatuses, the specimens within a sample were separated into morphologic classes on the basis of the unimodal distribution of morphologic characters, more or less objectively.

No nomenclatorial taxonomic considerations were undertaken until a reasonable stability of the hypothesis on the apparatus composition was reached by repeated tests. Species have been defined on the basis of the most diagnostic characters within the apparatus, irrespective of whether the characteristic element is easy to recover (bears a platform) or not. Only after the apparatus structure of a species is established, can single specimens be safely identified taxonomically with precision expressing their diagnostic value. This means that it is waste of time to attempt species identification separately for each element. The morphology alone is usually not enough to determine its species identity. It may even happen that this is done despite the morphology, if a specimen appears to be an end member of a continuous spectrum of population variability. Instead, its co-occurrence in the same sample with taxonomically identifiable specimens is relied on (for detailed discussion of methodology see Dzik 1991).

INFERENCE ON EVOLUTION

The method of chronophyletics (Dzik 1995, 2005) has been used to study the course of evolution. Data on species derived from particular samples were arranged according to their position in time and to the morphologic differences. This is enough to enhance possible chronomorphoclines represented by successions of populations, more or less continuous in their morphological gradation. The fossil record of some Famennian conodonts appears virtually complete, enabling application of stratophenetics to document their evolution biometrically (Dzik 2005). This kind of research has not been widely applied only because of technical limitations: there are too many species to be identified and described to make application of the time-consuming biometrics practical.

Hypotheses on the course of evolution produced with application of chronophyletics are falsifiable by retrodiction (Dzik 1995, 2005) and this is basically the same kind of reasoning as that used in testing the apparatus reconstructions.

CONODONT APPARATUSES

The most striking aspect of a conodont oral apparatus is its subdivision into morphologic (and functional) units, represented anteriorly by the sharp, incisor-like elements of the M series (usually only a single pair), the comb-like elements of the S series in the middle (usually 9 elements), and the robust, usually molarized P series at the posterior end (usually two pairs). The notation system for the elements within series follows here the proposal of Purnell *et al.* (2000). Their position and orientation in the animal body is relatively well recognized, although only a fraction of taxa is known from articulated natural assemblages of elements and some minor differences in views remain. Descriptives for orientation of all elements are based on their serial homology with the platform series elements, not on the actual orientation in the apparatus (Fig. 7). The apparatus is a highly diversified structure, offering a lot of information on mechanisms of its morphogenesis, possible function, and evolution.

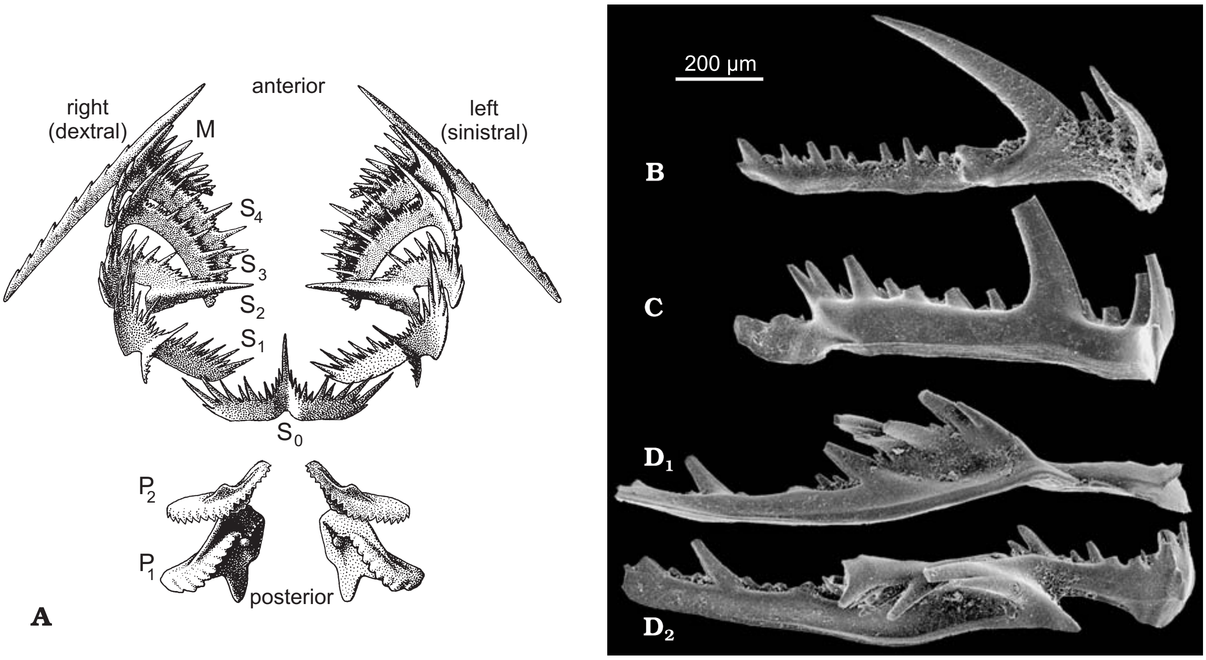


Fig. 7. **A**. Apparatus of the best known palmatolepidid conodont, the latest Frasnian *Lagovignathus bogartensis* (Stauffer, 1938). Reconstruction based on the cluster described by Lange (1968; with orientation of S_0 reversed and S_1 arbitrarily chosen, slightly modified after Dzik 1991), seen from its ventral side. Descriptives for elements' orientation used in the text given. **B**–**D**. Regeneration and pathological malformation of ramiform polygnathid conodont elements $S_{3–4}$ from the *C. quadrantinodosa* Zone at Miedzianka (sample Md-2) with regerating processes and two specimens displaced and unified during life (D); specimens ZPAL cXVI/2126, 2128, and 2127.

PATTERNS OF MOLARIZATION

A morphologic gradient is usually expressed in conodont apparatuses, the most robust and the sharpest elements being those located at the opposite ends of the apparatus. In numerous conodont lineages of various age the occlusal surface of the posteriorly located elements of the apparatus increased their working surface, apparently in connection with their grinding function (e.g., Sweet 1988). This is an aspect of molarization, analogous to that in mammalian evolution. In rare cases the evolutionary expansion of a robust appearance reached as far as the anteriormost elements of the apparatus (for instance in the Silurian *Johnognathus*). The patterns of molarization varied, but three ways to reach the needed effect were usually chosen by natural selection: development of a platform, icrion or peniculus.

Platform. — This is the most common kind of molarization. The platform is a thickening of the element wall immediately above the margin of the basal cone. This may be connected with a narrowing of the basal

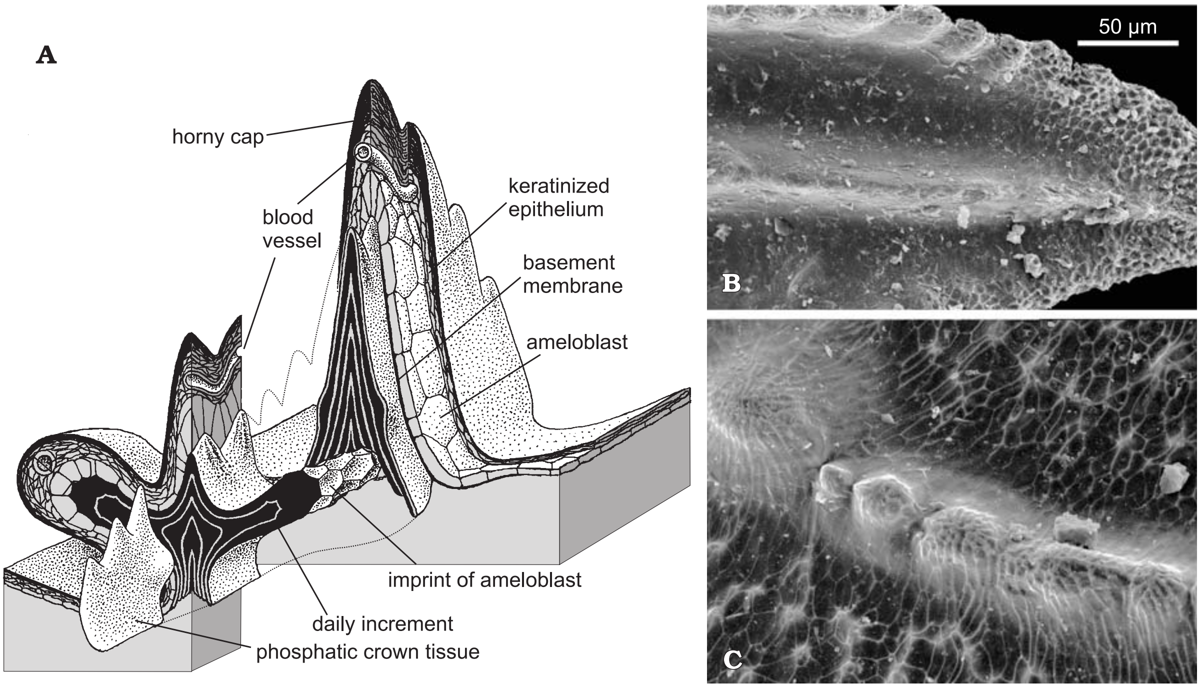


Fig. 8. **A**. Diagrammatic presentation of the model of conodont element growth and morphogenesis with assumption that the phosphatic tissue was an internal skeleton under a keratinous working surface (modified after Dzik 2000). **B**. Imprints of ameloblasts restricted to the most intensely growing part of the P_1 element, presumably the basement membrane did not develop there, being restricted to the central part of the platform; *Polygnathus semicostatus* Branson *et* Mehl, 1934 from the *P. trachytera* Zone at Łagów (sample Ł-27; specimen ZPAL CVI/2570; see also Fig. 62P). **C**. Imprints of ameloblasts covering whole platform of the P_1 elements element, with apparent proliferation centers at tips of denticles; *Klapperilepis ultima* (Ziegler, 1958) from the pre-*K. triangularis* Zone strata at Płucki (sample Pł-36; specimen ZPAL CVI/1509; see also Fig. 79E).

cavity and finally its inversion (as is the case with the polygnathid and palmatolepidid apparatuses). The margin of the platform may as well remain narrow and its growth then follows an expansion of the deep basal cavity (as is the case with the Ordovician balognathids). This difference does not affect the shape of the occlusal surface (as well exemplified by the Carboniferous *Cavusgnathus* and *Mestognathus*). Nevertheless, the platform of an element with a narrow basal cavity is much more massive and its development required much more expense of calcium phosphate. This is probably why the cold-water conodonts generally developed platform elements with a thin wall whereas in tropical environments, where access to calcium is unlimited, the conodonts developed massive elements.

Icrion. — This is a way to molarize alternative to the platform, although it may develop as the terminal stage in the evolution of a platform. The molarized area is formed by tips of denticles of the blade followed by parallel rows of accessory denticles of the same height (Dzik 1991). Icrion is usually of a fusiform shape and its denticles tend to be arranged in transverse ridges. Almost always this kind of molarization characterize elements with a deep basal cavity and thin walls, typical of relatively cold-water environments (the most common being the icriodontids and idiognathodontids). Rarely it developed also in elements with inverted basal cavity.

Peniculus. — This is a modification of the icrion with very numerous, needle-like denticles forming a kind of brush (Lindström and Ziegler 1965). This structure developed in its typical form in three groups of polygnathid conodonts: the Givetian to Frasnian *Skeletognathus* lineage, the Frasnian ancyrodellids, and Famennian relatives of *Mehlina*. It remains to be determined whether it originated only once in a clade composed by those conodonts or it is just an effect of a regulatory mechanism controlling the element growth. Usuallly the peniculus was a juvenile feature and changed into a regular platform after the basal cavity inverted. Despite the suggestion by Lindström and Ziegler (1965), this does not seem to be a case of pathology.

GROWTH OF ELEMENTS

The conodont elements grew by adding layer by layer of calcium phosphate on its occlusal (working) surface. This is a close analogy (perhaps even homology) to the enamel of vertebrate teeth and scales. It seems thus reasonable to expect that mechanisms controlling the histogeny of elements were similar to those regulating development of vertebrate teeth. The main difference is that conodont elements did not erupt. There is a variety of opinions how they acted mechanically while being secreted (reviewed in Dzik 2000).

Morphogenesis. — Any conodont element, irrespective of its final size and shape, started its development as a minute phosphatic cone (Fig. 8A). One may guess that formation of the cusp of the cone was controlled by similar factors as the development of enamel-built cusps of Recent vertebrate teeth, that is in effect of formation of an "enamel knot" in the secretive epithelium above (Dzik 2000). With the subsequent growth of early conodonts (*Mitrellataxis* and *Jablonnodus* may represent this archaic pattern in the Famennian), the element increased the thickness of its wall and height of the cusp, changing its shape only a little. In more derived conodonts, elements expanded basally into processes or a platform until enough space for a morphogenetic field emerged to allow formation of additional coniform units (denticles or tubercles). The number of denticles is thus more or less strictly correlated with the element size (Dzik and Trammer 1980). This aspect of the element growth radically influences their morphology and to avoid misleading differences and similarities, the specimens are illustrated here in the same magnification, whenever possible.

More or less prominent longitudinal ridges ornamenting elements probably developed under morphogenetic control of a similar kind as the denticles. Apart from them, the element surface may be smooth or ornamented with a reticulate pattern. By analogy with Recent fish scales, it may be speculated that the smooth surface was secreted under a relatively well-developed basement membrane of the secretory epithelium, whereas in fast-growing regions, where the membrane was missing, particular secretory cells (ameloblasts) directly contacted with the phosphatic tissue, leaving imprints on its surface (Dzik 2000). Reticulate ornamentation characterizes usually tips of denticles and margins of the platform (Fig. 8B), but in some conodonts (for instance the palmatolepidids) it covers the whole element surface. Although initiation of tubercles or denticles was connected with proliferiation of ameloblasts (Dzik 2000), their size did not change during subsequent growth (von Bitter and Norby 1994). In rare cases (*Playfordia*, *Guizhoudella*), the element surface is covered with minute tubercles.

***Sinuosa* larva**. — In early members of platform conodont lineages, juvenile P_1 elements with conical basal cavity developed an incipient platform above the basal cone, sometimes at some distance from it. This separation of structures was gradually obliterated as an effect of the expansion and thickening of the platform. At the end of growth the conical basal cavity is represented only by an indistinct pit. In some lineages, however, the inverted cavity of the masive platform replaced the cone rather abruptly and even in mature elements a prominent basal cone is recognizable as a discrete unit. Such a drastic change in the ontogeny apparently represents a profound functional and physiological transformation. Changes of this kind have to be referred to as a metamorphosis; the early stage marked by so distinct a discontinuity is a larva (Fig. 9).

In *Neopolygnathus* this larval stage lasted 12–14 days, as indicated by the growth increments (assuming these are daily) and then the inverted basal cavity developed below the dorsally located incipient platform. The platform and its basal cavity expanded in all directions, finally enclosing the conical unit (Fig. 9). In the lineage of *Tripodellus* a gradual evolution in the extent of the larval stage can be traced. In early members of the lineage, there is no recognizable conical element stage in taxonomically identifiable juvenile specimens. It developed in populations from the *C. marginifera* Zone, being recognizable only on one side of the P_1 element. Such specimens are traditionally referred to as *Palmatolepis sinuosa*, so I propose the name "sinuosa larva" for this developmental stage. These conodonts, classified here in *T. schleizius*, metamorphosed after 5 to 15 days. In later populations from the *P. trachytera* Zone the change occurred after 25–35 days (*Tripodellus gracilis*). In even more advanced *Tripodellus gonioclymeniae*, which apparently originated as a result of a shortening of the postlarval growth and earlier maturation (neoteny), the conical cavity existed until the end of the element growth. An impressive case of parallelism in this respect is the development in approximately the same time of a strongly asymmetric larval basal cone in the completely unrelated polygnathid *Lagovignathus*? *dissimilis*. The sinuosa larva also in this case expanded almost to the end of the element growth.

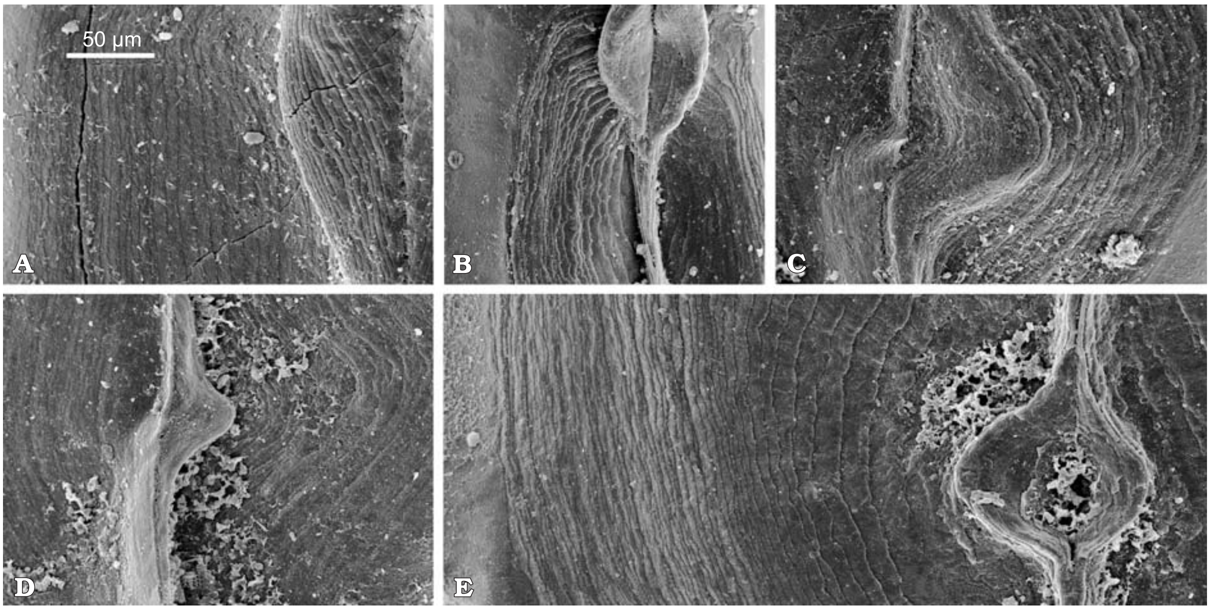


Fig. 9. "Sinuosa" larva of the Famennian conodonts and evolution of timing of its metamorphosis. Bases of P_1 elements with presumably daily increments are shown. **A**. *Alternognathus beulensis* Ziegler *et* Sandberg, 1984 from the *P. trachytera* Zone at Ściegnia (Wzdół Plebański, sample Wzd-10; ZPAL CVI/2371, see also Fig. 110B). **B**. *Neopolygnathus communis* (Branson *et* Mehl, 1934) from the *P. trachytera* Zone at Kowala (sample Ko-15; specimen ZPAL cXVI/2510, see also Fig. 70G). **C**. *Tripodellus schleizius* (Helms, 1963) from the *P. trachytera* Zone at Kowala (sample Ko-8; specimen ZPAL cXVI/2932) with relatively late metamorphosis. **D**. *T. minutus* (Branson *et* Mehl, 1934) from slightly older strata of the same zone and locality (sample Ko-9a; specimen ZPAL cXVI/2942) with earlier occurring metamorphosis. **E**. *Ancyrognathus* sp. n. from the *K. crepida* Zone at Jabłonna (sample J-65; specimen ZPAL cXVI/2577; see also Fig. 76D).

It can only be speculated why the sinuosa larva developed in these lineages. In the case of the polygnathids, juvenile specimens may possibly have depended on yolk or were bred in a kind of pouch. Alternatively, perhaps they fed on a kind of food different from that used by adults, not needing the grinding action of the platform series elements. The latter explanation does not refer to *Tripodellus*, as no change of the occlusal surface corresponds there to modifications of the base.

Termination of growth. — Although conodont elements in most samples show great differences in size and no doubt they functioned while growing, probably the growth of most of them terminated under genetic control. This is not so apparent in the case of elements growing almost isometrically, but even then a concentration of growth lines may indicate its termination.

The growth increments (Fig. 9), frequently well visible within the basal cavity (or on the surface of the inverted basal cavity), show a surprisingly regular and rhythmic distribution. In elements of medium size they count 60–70. If these are daily increments, conodonts reached their maturity approximately after two to three months. As noted above, the change from a coniform to inverted basal cavity in *Neopolygnathus* occurred after two weeks.

The increased density of increments is not the only expression of ceased growth. Much more impressive and convincing is the change in the curvature of processes. The tip of prominently denticulated elements is frequently recurved, developing a barb-like form, with the terminal denticle pointing in the same direction as the process. Such an element could grow further only in the height of its denticles, with the length of processes remaining constant. This phenomenon is common in so many unrelated taxa, that one may suggest that the ontogeny of all conodonts was controlled in a similar way.

Regeneration. — A restoration of broken cusps and denticles to their original shape is a common phenomenon in conodont elements, although variably distributed among samples and species. This is proof that these skeletal structures were involved in a mechanical action and permanently covered with secretory soft tissue. Less common is the regeneration of whole processes. It appears that at the beginning the mechanism of regeneration of processes was similar to that of single denticles. The newly formed bud was morphologically simple and somewhat irregular in appearance (Fig. 8). However, a regular process similar to its juvenile counterpart emerged subsequently. Apparently the whole set of morphogenetic machinery reestablished, with complex and regularly distributed *Anlagen* of denticles. As the basal structure of the process was obviously destroyed prior to regeneration, the only source of morphogenetic factors was the secretive tissue above. The mechanism of the morphogentic control directed by a vascular network above the element was proposed by myself and it seems unavoidable to accept the presence of a truly mechanically resistant, perhaps keratinous cup arming the internal mineral skeleton of conodont elements (Dzik 2000).

DESCRIPTION AND CLASSIFICATION OF CONODONTS

Because of the large number of taxa described in this paper formal synonymy lists are not given and only the most important synonyms are commented on. The stratigraphic and geographic distribution data refer only to Poland and to type specimens and species. For most of the earlier named Famennian species such data can be extracted from publications in respect to platform P_1 elements but it might be misleading to transfer them mechanically to apparatus taxa. They have to be confirmed by apparatus studies, until now performed to a very limited extent (e.g., Klapper and Philip 1971; van den Boogaard and Kuhry 1979; Metzger 1994; Schülke 1999).

Emended diagnoses, referring to apparatus composition wherever possible, are given for genera and species (and some families). The characters listed in a diagnosis are intended to differentiate taxa at the same rank and only those included in the same taxon of higher rank. The diagnoses are hierarchical in the sense that characters shared by all members of the higher rank taxon (plesiomorphies) are ignored in characterizing lower rank taxa. These characters may serve to diagnose the higher rank taxon only if they are, or their combination is, unique to the taxon. To distinguish species homoemorphic in some aspects, so common among conodonts, it it thus necessary to consider the whole hierarchical set of diagnoses, up to the taxonomic rank unifying such forms similar to each other in result of convergent evolution.

Phylum **CHORDATA** Bateson, 1886
Class **CONODONTA** Eichenberg, 1930
Order **Prioniodontida** Dzik, 1976
Family **Icriodontidae** Müller *et* Müller, 1957

Diagnosis. — P_2 elements of the apparatus usually with icrion on the external process, elements of the S series more or less reduced, simplified morphologically and bearing processes with unmineralized bases of denticles.

Remarks. — The icriodontids have their roots in the Ordovician and the original aspect of their apparatus is a triramous P_1 element with icrion on its probably ventral (*sic*!) process and a set of ramiform complex elements similar to other prioniodontids but with a tendency to reduce denticulation in some of them or separate particular denticles on the processes that became less and less mineralized (e.g., Dzik 1994). At the beginning of the Devonian this change was already advanced, the anterior process in P_1 element being represented only by an expansion of the base, but the dorsal process still preserved denticulation (Serpagli 1982). The Devonian lineage of *Latericriodus* with this kind of apparatus continued until the mid Givetian represented there by its type species (Bultynck 2003). A further reduction of the dorsal process in the late Emsian resulted in the emergence of the lineage of *Icriodus*, with only one process represented in the P_1 element (Klapper and Ziegler 1967). This branch continued to the mid Famennian, in some parts of its occurrence represented by several separate lineages. Meanwhile additional processes with icrion developed in offshoots of *Latericriodus* or the icrion was replaced with a single row denticles in others. As a result of the disapearance of the icrion in the late Frasnian, the lineage of *Pelekysgnathus* originated. Probably from this lineage emerged conodonts lacking the P series elements at all and, in replacement, changing their coniform elements of the rest of the apparatus into robust structures, eventually developing a kind of icrion (*Fungulodus*). Rare specimens from the Famennian of the Holy Cross Mountains seem to document the evolution from *Latericriodus* to the late Famennian *Antognathus*, but also the early evolution of *Pelekysgnathus* and apparatuses composed exclusively of “simple cones” (Fig. 121).

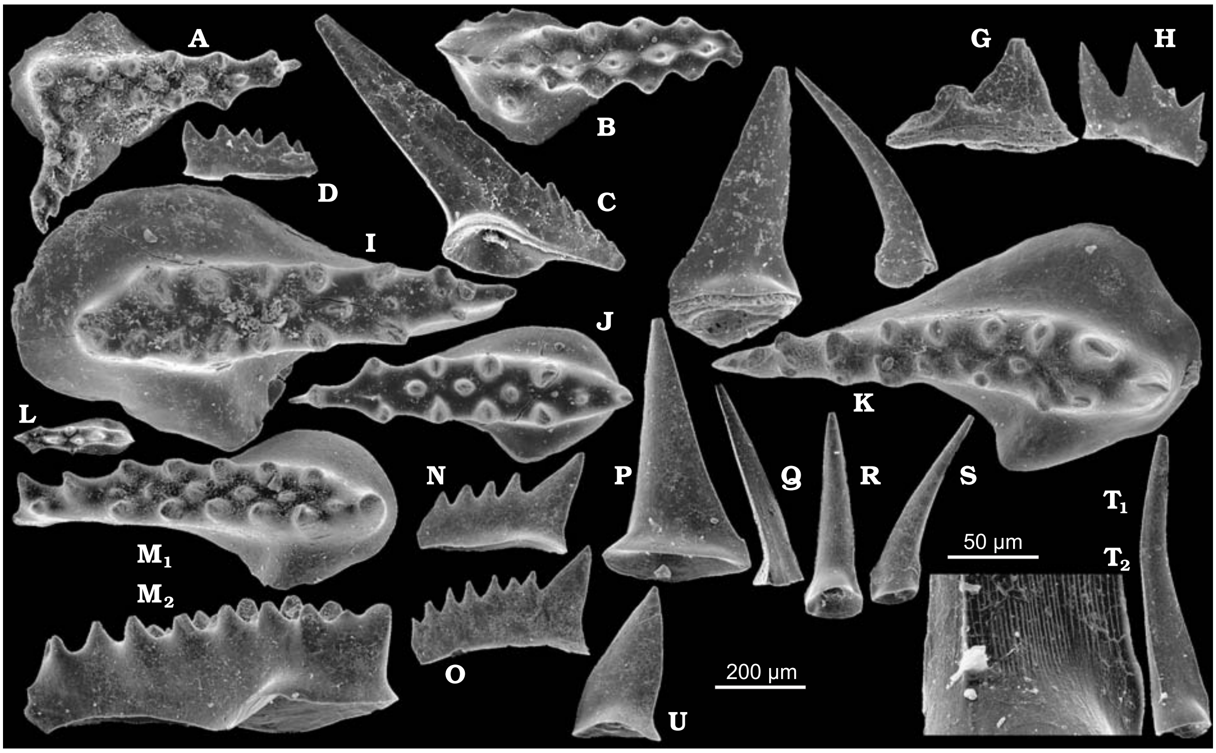


Fig. 10. Primitive Famennian icriodontids from the Holy Cross Mountains in occlusal (A, B), K, I–L_1, and posterior views. **A**. *Latericriodus* sp.; left P_1 element from the *Klapperilepis triangularis* Zone at Jabłonna (sample J-53a); specimen ZPAL cXVI /1705. **B**, **C**. *Latericriodus* (or *Antognathus*) *rarus* sp. n.; left P_1 (holotype) and P_2 elements from the *L. styriacus* Zone at Ostrówka (sample Ost-5); specimens ZPAL cXVI/1797–1798. **D**–**U**. *Icriodus alternatus* Branson *et* Mehl, 1934 from the earliest Famennian at Płucki (D–K, sample Pł-36) and the *K. triangularis* Zone at Jabłonna (L–U, sample J-53a); P_1 (C, I–K, M–O), P_2 (E, P), and S (F–H, P–U) elements ZPAL cXVI/1528, 1526, 1530, 1531, 1532, 1604, 1527, 1529, 1606, 1605, 1613, 1614, 1607, 1609, 1611, 1612, 1610, and 1608. Note pathologically multicusped S elements (G, H) and difference in height of the cusp between juvenile P_1 elements of different age (cf. D *versus* N).

Genus *Latericriodus* Müller, 1962

Type species: *Icriodus latericrescens* Branson *et* Mehl, 1938.

Diagnosis. — Fusiform icrion on the ventral process, well denticulated dorsal process with a tendency to develop icrion on it and to reduce completely the rudimentary, undenticulated anterior process.

Remarks. — The earlier described late Famennian icriodontid species with additional denticulated processes, attributed to *Antognathus* (Sandberg and Ziegler 1979) differ from those of the early Devonian *Latericriodus* mostly in their irregular shape and denticulation and in bending of the posterior process in the opposite direction (ventral, not dorsal). This may not be enough to substantiate a generic level distinction, as the specimens described below are morphologically and stratigraphically transitional. Unquestionable *Latericriodus* is unknown above the Givetian varcus Zone but its occurrence is generally disjunct (Bultynck 2003) and there are reports on its occurrence in the earliest Frasnian (Sandberg *et al.* 1994, Aboussalam 2003).

Latericriodus sp.
(Figs 10A and 121)

Material. — One specimen.

Remarks. — The early Famennian P_1 element from Jabłonna seems transition between those of the latest Givetian *Latericriodus latericrescens* (Branson *et* Mehl, 1938) (Klapper *in* Ziegler 1975) and the late Famennian *Antognathus mowitzaensis* (Sandberg and Ziegler, 1979) (Sandberg and Dreesen 1984), and this nicely corresponds to its geological age. *Latericriodus* (or *Antognathus*) *rarus* sp. n. from Ostrówka and Kowala may be another connecting link in this long-lasting but mostly cryptic lineage.

Occurrence. — The *K. triangularis* Zone at Jabłonna.

Latericriodus (or *Antognathus*) *rarus* sp. n.
(Figs 10B, C and 121)

Holotype: P_1 element ZPAL cXVI /1797 (Fig. 10B).

Type horizon and locality: Sample Ost-5, late Famennian *L. styriacus* Zone at Ostrówka, Holy Cross Mountains.

Derivation of name: Referring to rarity of this species in the Holy Cross Mountains.

Material. — Four specimens.

Diagnosis. — Icrion of P_1 element with additional denticle lateral to the cusp.

Remarks. — The specimens from Ostrówka and Kowala may represent the first stage in development of an additional process characterizing species of *Antognathus* (see Sandberg and Dreesen 1984). Taking the P_1 element alone, it seems likely that the process developed *de novo* and is not homologous with the differently oriented process in *Latericriodus* sp. However, the association of a surprisingly primitive, denticulated P_2 element of seemingly Early Devonian morphology suggests that this is rather a kind of late Devonian "living fossil".

Occurrence. — The late *L. styriacus* Zone at Kowala and Ostrówka.

Genus ***Icriodus*** Branson *et* Mehl, 1938

Type species: *I. expansus* Branson *et* Mehl, 1934 from the Givetian Mineola Limestone near Big Springs, Missouri (Klapper *in* Ziegler 1975).

Icriodus alternatus Branson *et* Mehl, 1934
(Figs 10D–U and 121)

Type horizon and locality: Probably Saverton Shale near Monroe City, Missouri, early Famennian (Klapper *in* Ziegler 1975).

Material. — 10,161 specimens.

Diagnosis. — In icrion of P_1 elements denticles of the middle row weaker than those of lateral rows and alternating with them; cusp transverse to the base.

Remarks. — In the earliest Famennian sample Pł-36 (Fig. 10D–K) P_1 elements of *Icriodus* are highly variable. Most of them show a fusiform icrion with small tubercles of the middle row. In narrow specimens they tend to disappear. The basal cavity is generally large and wide, although in rare specimens it may be narrower, similar to geologically younger populations of the lineage. Juveniles show small and straight cusp, initially associated with a single ventral denticle that usually merges the central row but frequently it is laterally displaced. With growth, the cusp became prominent and somewhat inclined, which results in development of a ridge along its occlusal surface; the resulting appearance restores to some degree the separation of the cusp from the icrion typical of juveniles. In profile view, the icrion is virtually straight, only slightly convex in some specimens. Contribution of such specimens to the somewhat younger sample J-53a (Fig. 10D–K) seems slightly higher. Associated non-platform elements range in shape from triangular to needle-like, with no apparent morphological classes (possible exceptions are the widest and most robust specimens, probably representing P_2 elements; Fig. 121). All show sharp edges and relatively flat appearance but in sample Wtr-27 several robust specimens with subquadrate or subtriangular section of the base occur. They differ from elements of much younger *Mitrellataxis circularis* in their widely expanding basal cone.

Occurrence. — From the base of the Famennian to the early *K. crepida* Zone in all studied localities. The species occurs also in the Dębnik area (Baliński 1995).

Icriodus cornutus Sannemann, 1955
(Figs 11 and 121)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Ziegler 1975).

Material. — 2,104 specimens.

Diagnosis. — Cusp of P_1 element inclined dorsally, narrow icrion of P_1 elements with irregularly distributed denticles of the middle row, which are sometimes slightly higher than those of lateral rows; in mature specimens they merge to produce irregular transverse ridges.

Occurrence. — At Jabłonna, the lineage of *Icriodus* reappears with this species after a gap in occurrence, when *Pelekygnathus* was the dominant icriodontid; in Kadzielnia there seems to be a continuity between *I. alternatus* and *I. cornutus* within the *K. crepida* Zone. Transitional samples show a great population variabil-

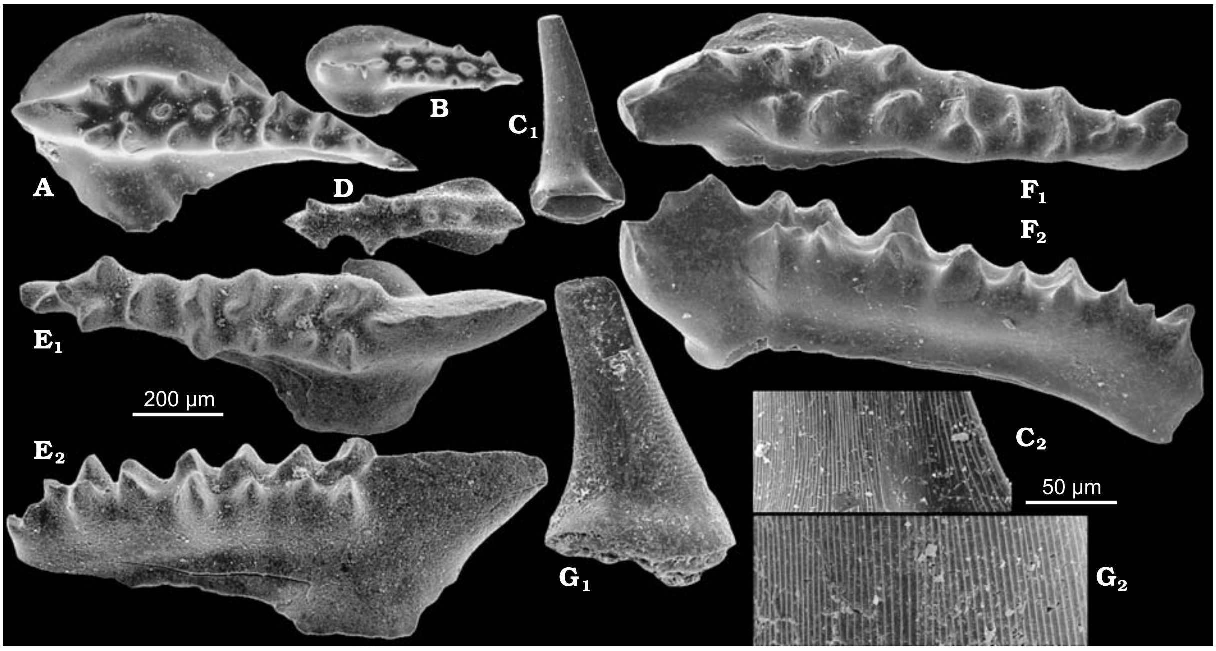


Fig. 11. Mid Famennian icriodontid *Icriodus cornutus* Sannemann, 1955 from Kadzielnia in the Holy Cross Mountains. **A–C**. Ancestral population from the late *K. triangularis* (sample Ka-16) with almost vertical cusp, transitional from *I. alternatus*; P_1 (A, B) and P_2 (C) elements ZPAL cXVI /1646, 1648, and1647. **D–G**. Advanced populations with prominent and strongly inclined cusp from the *K. crepida* Zone (D, E, sample Ka-2; F, G, Ka-14); P_1 (D–F) and P_2 (G) elements ZPAL cXVI /1650, 1649, 1644, and 1643, respectively. Note striation of coniform elements somewhat resembling that in *Mitrellataxis*.

ity, with specimens of morphologies similar to holotypes of *I. alternatus*, *I. cornutus*, and *I. costatus* occurring together. In samples J-65 and Ka-14 robust P_1 specimens similar to the holotype of *Icriodus costatus* (Thomas, 1949) from the late Famennian Maple Hill Shale at Burlington, Iowa (Klapper *in* Ziegler 1975) are associated with equally robust non-platform elements ornamented with longitudinal striae. Robust P_1 elements of this species somewhat resemble those of the Carboniferous *Eotaphrus* and perhaps this may be their more appropriate generic affiliation.

Rare specimens from the *P. trachytera* Zone are probably reworked. *Icriodus* apparently did not survive *C. marginifera* in the Holy Cross Mountains area, but *I. chojnicensis* Matyja, 1972 from Pomerania and the Lublin area (Matyja 1972, 1993; Matyja and Żbikowska 1974) may be a continuation of the lineage in marginal parts of the Variscan basin.

Genus ***Pelekysgnathus*** Thomas, 1949

Type species: *P. inclinatus* Thomas, 1949 from the late Famennian Maple Mill Shale in Washigton County, Iowa.

Diagnosis. — Icriodontids with P_1 elements bearing only the ventral process (as in *Icriodus*) with a single row of denticles.

Pelekysgnathus planus Sannemann, 1955
(Figs 12A–Q and 121)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955a).

Material. — 1,113 specimens.

Diagnosis. — The blade of P_1 elements straight in profile view or gently convex, with the cusp not separated from other denticles or slightly higher but almost straight.

Remarks. — The early form of *Pelekysgnathus planus* from the earliest Famennian shows a linear profile of the blade with a weak denticulation and the cusp not separated from other denticles, similarly as in the Frasnian (Dzik 2002). In samples of somewhat younger age, for instance J-53a (Fig. 12A), along with such specimens a new morphology emerged, with a dominant cusp and sharp, separate denticles. The blade remains short, however, which only partially results from generally small size of elements. In later (typical)

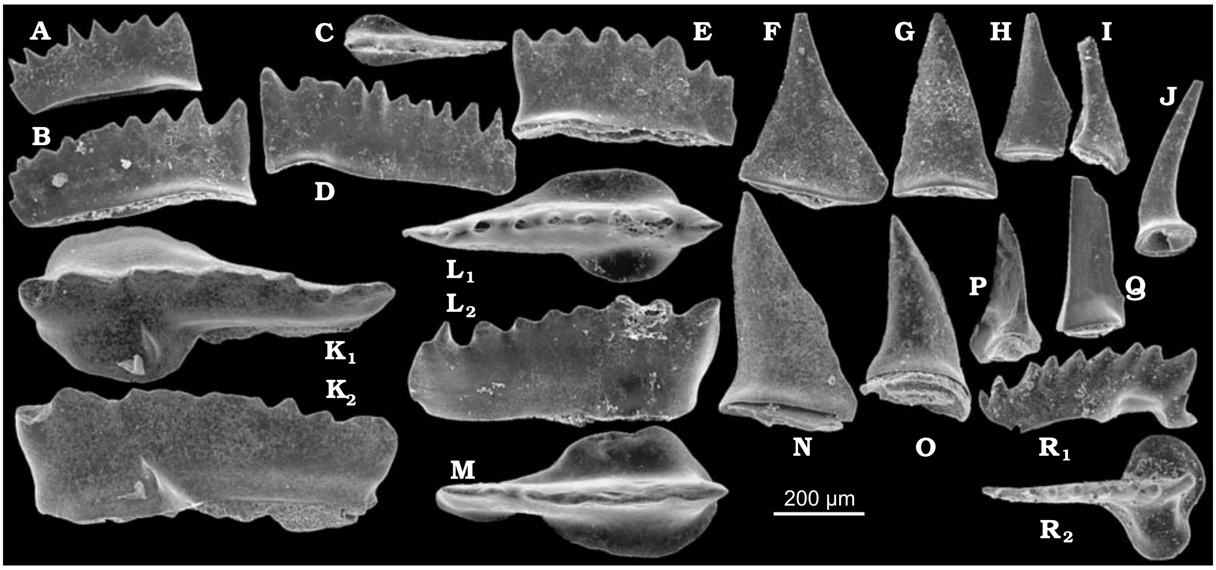


Fig. 12. Icriodontids without icrion from the Famennian of the Holy Cross Mountains and Sudetes. **A**–**Q**. *Pelekysgnathus planus* Sannemann, 1955 from the early Famennian at Jabłonna (A, H, sample J-53a; B–G, I, J, sample J-5,) and Karczówka (K–Q); P_1 (A–E, K–M) and P_2 (F, N) and S (G–J, O–Q) elements ZPAL cXVI /1615, 1618, 1620, 1619, 1621, 1622, 1623, 1617, 1624, 1616, 1628, 1630, 1629, and 1631–1634, respectively. **R**. *Dollymae*? *guizhouensis* Wang *et* Wang, 1978 from the late Famennian at Dzikowiec (sample Dz-48); P_1 element ZPAL cXVI /1645.

forms with a gently inclined cusp, the profile of the blade is convex, similar as in the holotype (Sannemann 1955a). Mature robust elements show a weak denticulation. Associated non-platform elements (e.g., J-03) represent two separate classes of triangular elements (probably P_2) wider than in *Icriodus alternatus* and more robust needle-like elements.

Occurrence. — Continues from the latest Frasnian to the *C. marginifera* Zone (Ł-13); specimens from the *P. jugosus* Zone at Ostrówka are probably reworked.

Genus ?*Dollymae* Hass, 1959

Type species: *D. sagittula* Hass, 1959 from the late Tournaisian Chappel Limestone of Texas.

Diagnosis. — Dorsal process in P_1 elements with a ingle row of denticles and the basal cavity expanded on both sides up to developing denticulated processes.

Dollymae? *guizhouensis* Wang *et* Wang, 1978

(Figs 12R and 121)

Type horizon and locality: Late Famennian of Daihua Formation at Daihua, Guizhou, China; associated with *Wocklumeria* and *Bispathodus* (Wang and Wang 1978).

Material. — Six specimens.

Diagnosis. — Undenticulated, tranversely widened basal cone in P_1 elements, additional denticulation ventrally of the cusp.

Remarks. — The incipient denticulation below the cusp makes this very rare latest Famennian species unlike other species of *Pelekysgnathus*. As noticed already by Over (1992), the lateral expansion of the base suggests that this may be the beginning of the lineage represented in the Tournaisian by *Dollymae bouckaerti* Groessens, 1977 and *Eotaphrus bultyncki* (Groessens, 1977), subsequently diversified into elaborate Carboniferous forms.

Occurrence. — The *D. trigonica* Zone at Kowala and Dzikowiec.

Family **Jablonnodontidae** fam. n.

Diagnosis. — Apparatus composed of only coniform elements mimicking those of the Ordovician protopanderodontids.

Remarks. — Interpretation of taxomic affinities of the Famennian “simple cones” is a difficult task. The geologically youngest conodont being unquestionably a continuation of the early Paleozoic coniform conodonts is *Belodella*, the panderodontid which did not survive to the Famennian. The last occurrences of that peri-reefal species are latest Frasnian in age (e. g., Dzik 2002). The seemingly coniform conodont elements of the coeval icriodontids are mostly isolated denticles of elements with otherwise unmineralized processes. At least three lineages of the icriodontids persisted into the Famennian. Their coniform denticles are of virtually the same morphology as those of geologically older species, being associated with icrion-bearing P_1 elements. Yet, “simple cones” occur in abundance also in horizons and whole sections of the Famennian where icriodontid P_1 elements are missing. Some of them are very similar to the Ordovician protopanderodontids or distacodontids. The Famennian *Mitrellataxis* of Chauff and Price (1980; growth increments within the basal cavity show that this is a conodont, not a fish scale, as suggested for the related *Fungulodus* by Wang and Turner 1985) is a homeomorph of the early Ordovician *Clavohamulus*. Elements indistinguishable from those of the Ordovician *Drepanoistodus* have been described as parts of the apparatus of Famennian *Pelekysgnathus* (Sandberg and Dreesen 1984). In the Holy Cross Mountains such elements occur abundantly in some samples (Table 1). No recurrent association with the P_1 elements of *Pelekysgnathus* or *Icriodus* has been noticed, and wherever those are represented in a reasonable number, they are associated with flat and wide triangular elements like those from older strata (e.g., Dzik 2002).

It is tempting to assume that these are cases of further reduction in mineralization of the icriodontid oral apparatus. Perhaps in some cases this actually took place. Nevertheless, some other associations of coniform elements show a recurrent morphological differentiation closely resembling that in the early Palaeozoic protopanderodontid conodonts. Although not all element types represent truly discrete classes and morphological transitions are more common than in undoubted protopanderodontids, the similarity is striking and extends even to development of geniculation in some elements, mimicking the Ordovician distacodontids (Sandberg and Dreesen 1984). A possibility of such an affinity cannot be excluded, as much of the Famennian conodont fauna is of cryptic origin. It emerged as an effect of extensive migration events and the present knowledge of the Silurian and Devonian simple cones is still very limited outside restricted regions of Europe.

The alternative, that this is a case of secondary introduction of regularity to earlier rather indifferent morphologic variability of the icriodontid denticles is supported by the relatively late emergence of these conodonts and the tremendous time gap separating them from the last indisputable protopanderodontids (end of the Ordovician). If these were secondarily simplified icriodontids, then all the platform series locations were either lost, or reduced to the cusp.

There are thus two possible solutions to the problem of the Famennian “simple-cones”: (1) these are denticles of elements from an icriodontid lineage with completely reduced P elements or (2) these are survivors of the Ordovician protopanderodontids, that is a Lazarus lineage not recognized previously from the whole Silurian and most of the Devonian. Until this issue is settled, the material of simple cones not belonging to *Icriodus* and *Pelekysgnathus* is here described provisionally in terms of coniform apparatus terminology.

Genus ***Mitrellataxis*** Chauff *et* Price, 1980

Type species: *M. chevronella* Chauff *et* Price, 1980 from the Maple Mill Shale at Kalona Clay Pit, Iowa; *Scaphignathus velifer* Zone.

Diagnosis. — Robust coniform elements with shallow or inverted basal cavities of circular outline.

Remarks. — The Famennian “simple cones” are of three kinds: some are ornamented with prominent longitudinal ribs (typical *Mitrellataxis*), others show a virtually smooth surface (*Jablonnodus*), yet others developed irregular tuberculation with ameloblasts imprints, thus developing a kind of icrion (*Fungulodus–Conchodontus*; Over 1992). A fine striation occurs also in robust icriodontid denticles (Over 1992) although there seems to be a morphologic gap between them and *Mitrellataxis*. A similar gap separates smooth icriodontid denticles and elements of *M. circularis*, resembling rather denticles of robust prioniodinids. *Mitrellataxis conoidalis* may be the connecting link between robust coniform elements of *Icriodus* and more derived species of its genus; this is the sole reason why it is classified among the Prioniodontida.

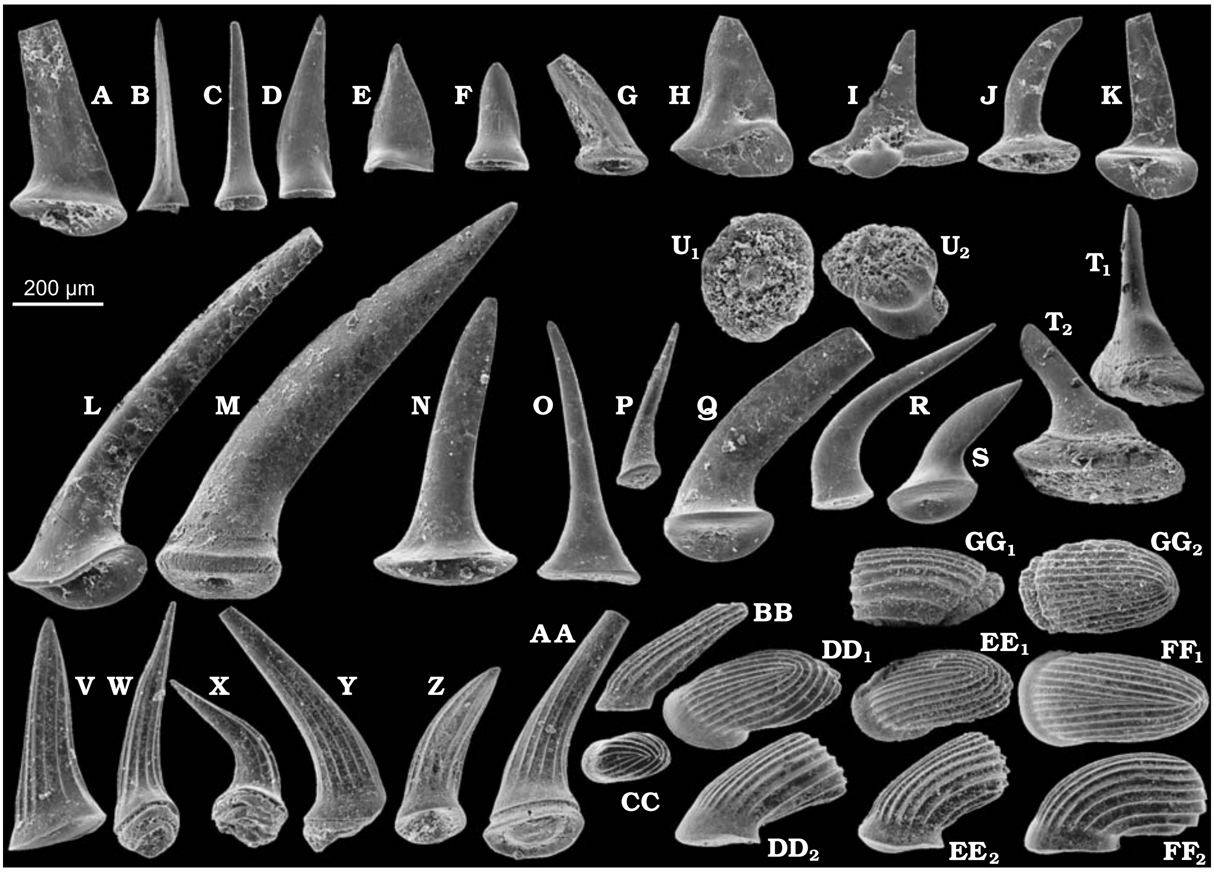


Fig. 13. Possible Famennian icriodontids with completely reduced platform series in the apparatus. **A**–**K**. *Mitrellataxis*? *asymmetrica* sp. n. from the *L. styriacus* Zone at Ostrówka (sample Ost-12); specimens ZPAL cXVI /1575, 1567, 1576, 1573 (holotype, D), 1574, 1572, 1571, 1569, 1568, 1570, 1566, respectively. **L**–**T**. *Mitrellataxis circularis* (Wang *et* Wang, 1978) from the same sample and from Kowala (T, sample Ko-8), specimens ZPAL cXVI /1578–1580, 1584, 1585, 1583, 1581, 1582, and 1577. **U**. *Mitrellataxis coronella* Chauff and Price, 1980 from the *P. jugosus* Zone at Kowala (sample Ko-63); specimen ZPAL cXVI /2334; **V**, **X**. *Mitrellataxis conoidalis* sp. n. from the *K. crepida* Zone at Jabłonna (bed 5); specimens ZPAL cXVI /1627 (holotype, V), 1625 and 1626. **Y**–**GG**. *Mitrellataxis ornata* sp. n. from the late *K. triangularis* Zone at Karczówka, (Y–FF) and early Famennian at the Żbik ravine in Dębnik near Cracow; specimens ZPAL cXVI/1636, 1635, 1637, 1642, 1641, 1638, 1639, 1640, and 2963, respectively (holotype, FF).

Mitrellataxis conoidalis sp. n.
(Figs 13V–X and 121)

Holotype: Specimen ZPAL cXVI/1627 (Fig. 13V).

Type horizon and locality: Bed 5, early Famennian *K. crepida* Zone at Jabłonna, Holy Cross Mountains.

Derivation of the name: Referring to conoidal shape of elements.

Material. — 34 specimens.

Diagnosis. — All elements with a sharp conical cusp ornamented by longitudinal ribs; relatively deep basal cavity.

Remarks. — From *M. chevronella* and *M. ornata*, the new species differs in having only conical elements, from *M.*? *asymmetrica* and species of *Jablonnodus* in presence of longitudinal ribs.

Occurrence. — The late *K. triangularis* (J-37) to the *K. crepida* zones at Kadzielnia, Jabłonna, and Wietrznia.

Mitrellataxis ornata sp. n.
(Figs 13Y–GG and 121)

Holotype: Specimen ZPAL cXVI/1640 (Fig. 13FF).

Type horizon and locality: Sample of cephalopod limestone taken by Dymitr Sobolew, early Famennian late *K. triangularis* Zone at Karczówka, Holy Cross Mountains.

Derivation of the name: Referring to ornate ribbing of the cusp.

Material. — 35 specimens.

Diagnosis. — Most specimens with blunt apex and ovoid appearance of the cusp, rare conical elements; all bear sharp longitudinal ribs merging in a chevron pattern on the external surface of the cusp or passing continuously across the tip.

Remarks. — From the morphologically closest *M. chevronella* differs in a more regular and less robust appearance of cusps and usually flat or concave basal cavity. In the type sample of *M. ornata* sharply conical elements also occur. Whether they belong to the same apparatus or represent sympatric occurrence of *M. conoidalis* requires testing with more material.

Occurrence. — The type locality and early Famennian of Żbik ravine in Dębnik near Cracow.

Mitrellataxis? *asymmetrica* sp. n.
(Fig. 13A–K)

Holotype: Specimen ZPAL cXVI/1673 (Fig. 13D).

Type horizon and locality: Sample Ost-12, late Famennian *L. styriacus* Zone at Ostrówka, Holy Cross Mountains.

Derivation of the name: Referring to the asymmetry of most elements.

Material. — 52 specimens.

Diagnosis. — Sharp conical cusp with lenticular section, smooth surface and sharp edges.

Remarks. — From typical species of *Mitrellataxis*, the new species differs in a smooth surface of the cusp, from *M. circularis* in sharp-edged cusp and generally narrow base. The idea that the Famennian "simple cones" are isolated denticles of secondarily simplified icriodontids fits especially this species. The elements show linearly extending bases, quite long in some specimens, and they may be easily visualised as being distributed along a non-minerized process.

Elements of *M.*? *asymmetrica* resemble most the coniform elements of *Icriodus* (e.g., that on Fig. 10U) differing only in that no incipient denticles or angulations develop near the bese, as is usual in at least some elements of *Icriodus*. This is thus either a case of homeomorphy or the species is the end-member of an icriodontid lineage with reduced P_1 elements. Wang (1989) illustrated a similar element from the *Polygnathus perbonus* Zone of the Emsian under the name *Drepanodina subcircularis* Wang, 1981. This may mean that the lineage was long-lasting.

Occurrence. — Sparsely occurring in many samples ranging from the *P. trachytera* Zone at Kowala and Jabłonna to the *L. styriacus* Zone at Ściegnia and Ostrówka.

Mitrellataxis circularis (Wang *et* Wang, 1978)
(Figs 13L–T and 121)

Type horizon and locality: Late Famennian of Daihua Formation at Daihua, Guizhou, China; associated with *Wocklumeria* and *Pseudopolygnathus*.

Material. — 3,295 specimens.

Diagnosis. — Cusp with oval cross section, elements variable in shape but not forming discrete morphologic classes, shallow basal cavity usually filled with tissue.

Remarks. — Despite general similarity of smooth elements, relationship of this species to *Jablonnodus* is not likely because they do not group in any recurrent morphologic classes. They rather resemble in colour and shape cusps and denticles of associated robust prioniodinids. It cannot be excluded that this is actually a prioniodinid with uncalcified bases of processes. That these were truly denticles of uncalcified processes of icriodontids or prioniodinids is supported by the linear elongation of the basal body, with a longitudinal furrow (Fig. 13T).

The only illustrated specimen of *Drepanodus circularis* Wang *et* Wang, 1978 has a short cusp, which makes it similar to *M. conoidalis* sp. n., so the taxonomic identification proposed here requires confirmation by the Chinese topotype material.

Occurrence. — Ranges from the late *K. triangularis* Zone to the top of the Famennian in almost all localities.

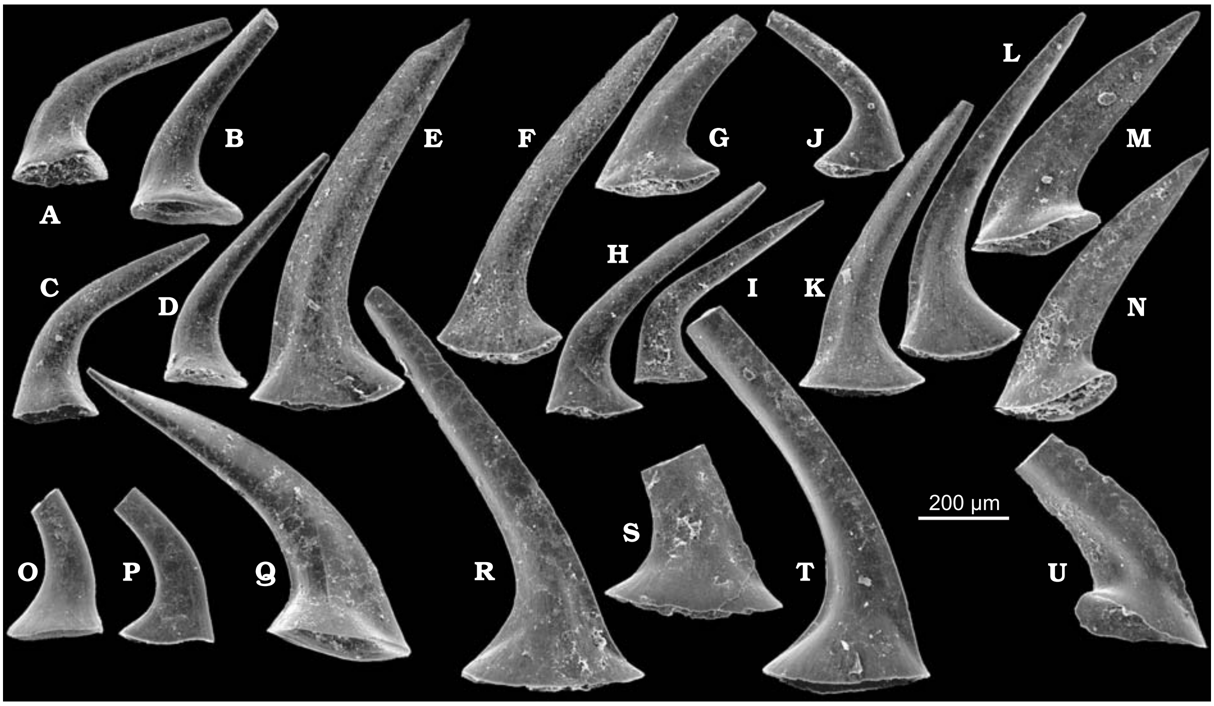


Fig. 14. Simple-cone *Jablonnodus oistodiformis* sp. n. from the early *P. trachytera* Zone at Jabłonna (bed 24; A–N) and the *L. styriacus* Zone at Ostrówka (O–U, sample Ost-12) in the Holy Cross Mountains; all in posterior view. A, B, O, P. Right and left P_1? elements; specimens ZPAL cXVI/1545, 1546, 1560, and 1564, respectively. C, D, Q. Right and left P_2 (?) elements 1546, 1548, and 1559. E, F, R, S. S_0? elements 1549, 1550, 1562 and 1561. G–L, T. Right and left $S_{1–4}$? elements 1551–1557 and 1563. M, N, U. Right and left M? elements 1557, 1558, and 1565.

Mitrellataxis coronella Chauff *et* Price, 1980
(Figs 13U and 121)

Type horizon and locality: Unnamed basal shale member of the Sulphur Springs Formation, probably lower costatus Zone (Chauff and Price 1980).

Material. — Single specimen from sample Ko-116 at Kowala, *P. jugosus* Zone.

Diagnosis. — Waistlike constriction near the base, small low cusp in the middle of flat occlusal surface, relatively deep basal cavity.

Remarks. — The only specimen found has the occlusal surface partially covered with clay but the conical tip in the centre and ribs around the margin are clearly recognizable.

Genus ***Jablonnodus*** gen. n.

Type species: *J. oistodiformis* sp. n. from the Famennian of the Holy Cross Mountains, Poland.

Diagnosis. — Tendency to develop geniculate “oistodontiform” and symmetrical “erectiform” elements in the apparatus, homeomorphic with the Ordovician Distacodontidae; weak morphologic disparity between probable P and S series.

Remarks. — Mound (1968) and Wang and Wang (1978) illustrated several such elements under the generic name *Drepanodina*. Unfortunately, the holotype of *Drepanodina lachrymosa* Mound, 1968 from the late Famennian Upper Wabamun Group of Alberta, the type species of the genus, is probably a denticle of *Pelekysgnathus*, as suggested by the appearance of its base.

Jablonnodus oistodiformis sp. n.
(Figs 14 and 121)

Holotype: M element ZPAL cVI/1557 (Fig. 14M).

Type horizon and locality: Bed 24, mid Famennian *P. trachytera* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: Referring to some similarity of one element in the apparatus to that of the Ordovician genus *Oistodus*.

Material. — 934 specimens.

Diagnosis. — Possible M elements almost geniculate, cusp of most elements with sharp edges and bases with oval contour.

Remarks. — Elements of the species are characteristic in their *Drepanoistodus*-like appearance and are easy to separate from other associated simple-cones. It is not ecologically associated with species of *Mitrellataxis* with smooth elements and samples rich in the latter do not contain *J. oistodiformis.* Identification of discrete element types of the apparatus was possible owing to their abundance in samples Ost-12 and J-24 (Table 17).

Elements tentatively identified as belonging to the platform series have a strongly bent cusp. They form two classes differing in outline of the base (Fig. 121), those with rounded triangular outline are provisionally proposed to be P_1 elements, base outline of possible P_2 elements is circular. Elements with a rather erect cusp show the symmetry transition series from the strictly symmetrical probable S_0 elements through those with the base flattened from one side ($S_{1–2}$) to those having flattening on both sides ($S_{3–4}$). A separate class is represented by probable M elements with the whole cusp strongly inclined to the base and very asymmetric.

From other species of the genus, *J. oistodiformis* differs in the shape of possible M elements and relatively distinct classes of the element types (at least P, S, and M). Sandberg and Dreesen (1984, pl. 3: 10, 11, 23, 24) illustrated even more advanced, fully geniculate elements associated with equally derived other elements from the late Famennian (expansa Zone) of Colorado and England. In each of those localities they co-occur with different icriodontids. The lineage seems thus to have been evolving rather fast.

Occurrence. — Probably the late *C. marginifera* Zone at Jabłonna, Miedzianka and Łagów, certainly the *P. trachytera* Zone at Jabłonna, Kowala, Łagów and Ostrówka, possibly continued to the early *L. styriacus* Zone at Jabłonna and Ostrówka.

Jablonnodus erectus sp. n.
(Figs 15 and 121)

Holotype: P_1 element ZPAL cVI/1587 (Fig. 15B).

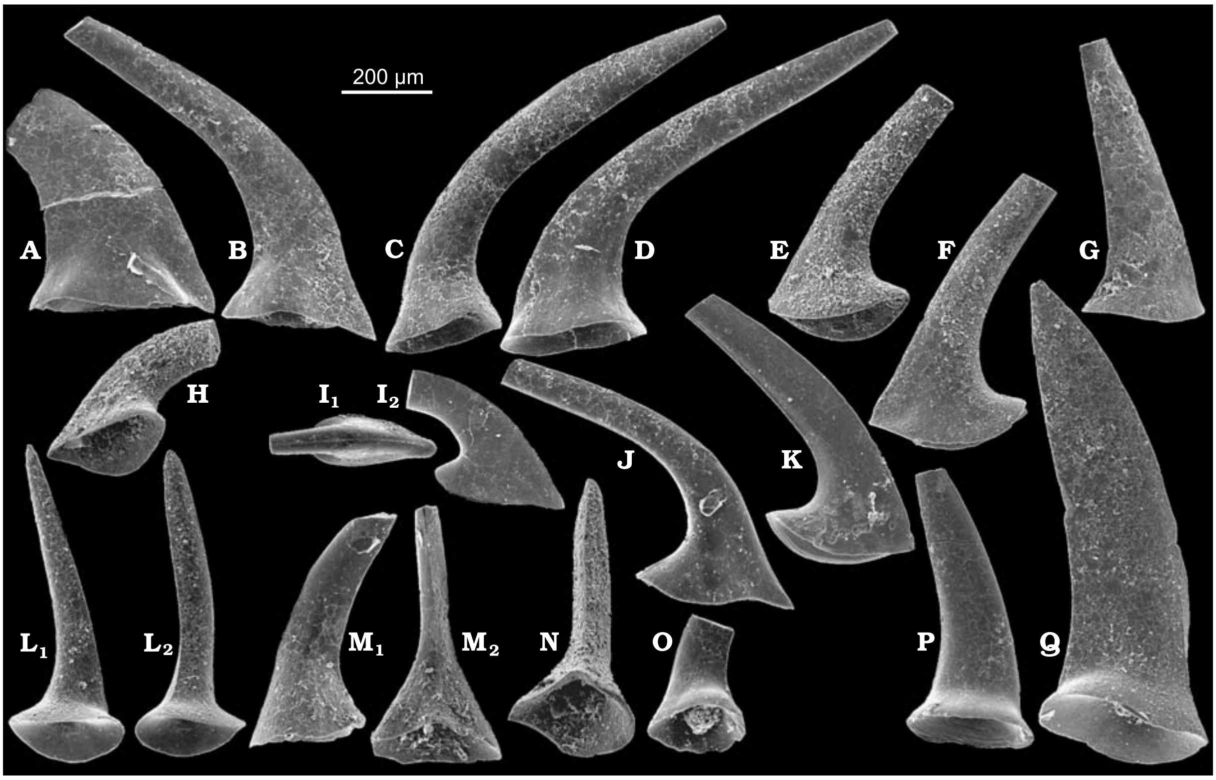


Fig. 15. Simple-cone *Jablonnodus erectus* sp. n. from the late *Lagovignathus styriacus* Zone at Ostrówka (A–L, N–Q, sample Ost-265) and the early *P. jugosus* Zone at Jabłonna (M, bed 27) in the Holy Cross Mountains; in posterior, ventral (I_1) and medial (L_2 and M_2) views. A, B. Left P_1? elements; specimens ZPAL cXVI /1586-1587, respectively. C, D. Right P_2 (?) elements 1588, 1589. E, F, H–L. Right and left $S_{2–4}$? elements 1591, 1593, 1596, 1600, 1590, 1592, and 1597. G, M. S_0? elements 1602 and 1601. N–O. Right S_1? elements 1598, 1599. P, Q. Left M? elements 1595 and 1594.

Type horizon and locality: Sample Ost-284.II.265, late Famennian *L. styriacus* Zone at Ostrówka, Holy Cross Mountains.

Derivation of name: Referring to erect cusp in the symmetrical element of the apparatus.

Material. — 937 specimens.

Diagnosis. — Possible M elements with erect cusp, bases of most elements with irregularly eye drop contour.

Remarks. — Sample Ost-265 offers enough material to allow identification of discrete element types and their homology with those of the stratigraphically older *J. oistodiformis*. Probable P_1 elements bear wide sharp ridges and have a characteristic outline of the base, acutely narrowing at ends and swollen in the middle but with one side strongly depressed. Such a depression is present in the outline of the otherwise rounded base of rather gracile probable P_2 elements (Fig. 121). Elements of the symmetry transition series are similar to those of *J. oistodiformis* except for being somewhat more robust; probable M elements are less inclined.

From the other species of the genus, *J. erectus* differs in the shape of possible M elements and the wide cusp of probable P_2 elements. Their basal cavity is relatively shallow and wide. P elements show also a characteristic external extension of the base.

Occurrence. — Possibly the top of the *K. crepida* Zone at Jabłonna, the *C. marginifera* and *P. trachytera* Zone at Łagów, the *L. styriacus* Zone at Ostrówka, Miedzianka, and Ściegnia; the *P. jugosus* Zone at Kowala and Ostrówka.

Order **Ozarkodinida** Dzik, 1976

Family **Prioniodinidae** Bassler, 1925

Genus ***Ligonodina*** Bassler, 1925

Type species: *L. pectinata* Bassler, 1925 from the mid Frasnian of New York (Huddle 1968).

Diagnosis. — The anteriormost element of the apparatus (M) with a wide and flat cusp.

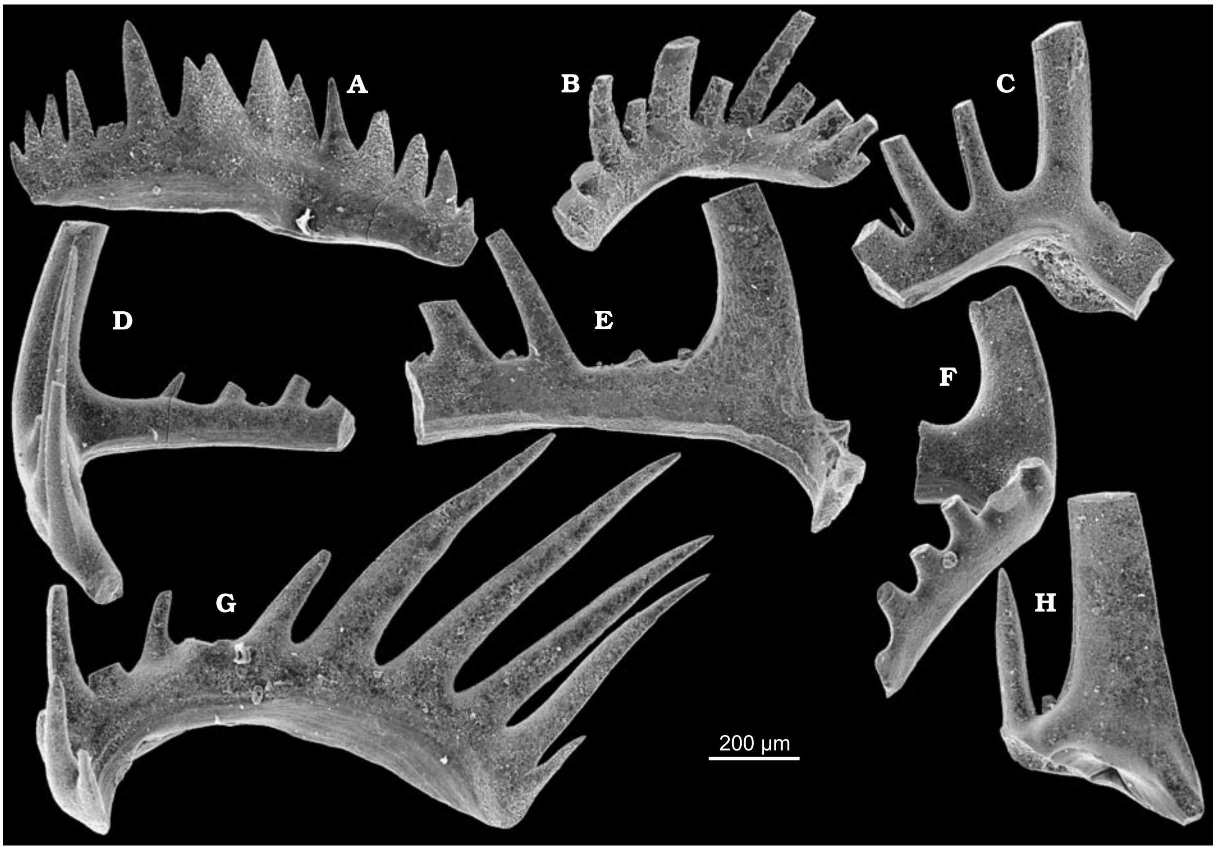


Fig. 16. Specifically undetermined early Famennian prioniodinid *Ligonodina* sp. from the *K. triangularis* Zone at Jabłonna (sample J-58) in the Holy Cross Mountains. P_1 (A), P_2 (B), S_0 (D), S_1 (C), S_2 (G?), $S_{3–4}$ (E, F), and M (H) elements; specimens ZPAL cXVI/11728, 1729, 1731, 1730, 1733, 1734, 1732, and 1735, respectively.

CORRIGENDUM

In the printed version of this volume instead of the proper photographic plate for Figure 17,
the plate of Figure 18 was erroneously inserted (and repeated in its place).
The correct Figure 17 is given here on the reverse side of this page.

Fig. 17. Early Famennian successors of the main prioniodinid lineage of *Ligonodina* from the Holy Cross Mountains. **A**, **B**. *Ligonodina pectinata* Bassler, 1925 from the earliest Famennian at Płucki (sample Pł-40); S_4 (A) and M (B) elements ZPAL cXVI/1712, 1713. **C**–**T**. *Ligonodina albidens* sp. n. from the late *K. triangularis* and *K. crepida* zones at Jabłonna (bed 7, C; J-6, D–G; J-45a, H–N) and Wietrznia (M–T, sample Wtr-21); P_1 (H and P), P_2 (C and I), S_0 (J and R), S_1 (K?), $S_{2–4}$ (D, F, L, O, N, Q, and S), and M (E, G, M, and T) elements; specimens ZPAL cXVI/1722, 1725, 1726, 1724, 1727, 1736–1739, 1742, 1743 (holotype, M), 1740, 1741, 1750, 1753, 1751, 1752, and 1754, respectively.

Ligonodina pectinata Bassler, 1925
(Figs 16?, 17A, B, and 122)

Type horizon and locality: Rhinestreet Shale Member of the West Falls Formation at Weyer, New York (Huddle 1968).

Material. — 419 specimens, some of doubtful specific affinity.

Diagnosis. — Prominently denticulated dorsal process and large triangular cusp of the M element, relatively shallow basal cavities of all elements.

Remarks. — Identification of this species in the earliest Famennian is based on rather weak evidence: one juvenile M element from sample Pł-40 (Fig. 17B), which may be an extreme variety of *Ctenopolygnathus* and a robust but teratologically deformed specimen from sample Pł-1. This refers also to the generalized prioniodinids from the *K. triangularis* Zone at Jabłonna (Fig. 16). In younger Famennian strata from other localities much more derived prioniodinids are represented. Unfortunately, other elements in the apparatus are usually of little diagnostic value and even if several names are available for the Famennian prioniodinids, among them *Ligonodina delicata* Branson *et* Mehl, 1934, with the type occurrence in the Saverton Shale at Sees Creek, Missouri (Mound 1968 introduced a new name for it because of homonymy at that time, but there is no longer need for it). From the same reason several occurrences of the species are identified only tentatively.

In the Frasnian populations of the species there is some uncertainty regarding distinction between S_1 and P_1 elements, both showing a wide population variability. Position in the apparatus of the elements with short and strongly twisted ventral process and relatively high cusp (Dzik 2002, figs 7A and 8A, B) remains controversial. In the latest Frasnian samples undoubted P_1 elements have been identified (Dzik 2002, fig. 8C), with robust denticles, a high cusp, and arched dorsal process. In the Famennian their homologues show a less prominent denticulation but more blade-like appearance. This may be a case of directional evolution.

In the basalmost Famennian sample at Miedzianka (Md-27) wide M elements closely similar to those of *L. albidens* sp. n. co-occur with robust $S_{3–4}$ elements resembling somewhat those of *Idioprioniodus uncadinoides* sp. n. This may be a population transitional between *L. pectinata* and *L. albidens* but the material (conglomerate!) may contain reworked Frasnian specimens as well.

CORRIGENDUM

The correct Figure 17

Fig. 17. Early Famennian successors of the main prioniodinid lineage of *Ligonodina* from the Holy Cross Mountains. **A**, **B**. *Ligonodina pectinata* Bassler, 1925 from the earliest Famennian at Płucki (sample Pł-40); S$_4$ (A) and M (B) elements ZPAL cXVI/1712, 1713. **C**–**T**. *Ligonodina albidens* sp. n. from the late *K. triangularis* and *K. crepida* zones at Jabłonna (bed 7, C; J-6, D–G; J-45a, H–N) and Wietrznia (M–T, sample Wtr-21); P$_1$ (H and P), P$_2$ (C and I), S$_0$ (J and R), S$_1$ (K?), S$_{2–4}$ (D, F, L, O, N, Q, and S), and M (E, G, M, and T) elements; specimens ZPAL cXVI/1722, 1725, 1726, 1724, 1727, 1736–1739, 1742, 1743 (holotype, M), 1740, 1741, 1750, 1753, 1751, 1752, and 1754, respectively.

Occurrence. — Only the earliest Famennian at Płucki, possibly also the late *K. triangularis* Zone at Jabłonna and Miedzianka.

Ligonodina albidens sp. n.
(Figs 17C–T and 122)

Holotype: Specimen ZPAL cXVI/1743 (Fig. 17M).

Type horizon and locality: Sample J-45a, early Famennian *K. crepida* Zone at Jabłonna, Holy Cross Mountains.

Derivation of the name: The name refers to albid coloration of denticles in this species.

Material. — 417 specimens.

Diagnosis. — Short triangular process of M element, external processes of the symmetry transition elements few in number.

Remarks. — The wide cusp of M elements indicates relationship of the species to the *Ligonodina* main lineage but remaining elements of the apparatus are highly derived morphologically. This species is rather easily recognizable owing to sparsely distributed prominent denticles of adult elements and short external processes of S elements, only single denticles representing them in the S_0 element. In this respect and general appearance of non-M elements, the species resembles the geologically younger *Lagovidina obliqua* sp. n. but relationship between these species remains unclear and may be a result of homeomorphy. The species occurs both in the deeper-water area of Jabłonna and shallower environment of Wietrznia located above the Frasnian mudmound.

Occurrence. — The late *K. triangularis* and *K. crepida* zones at Jabłonna, Wietrznia, Kadzielnia and Miedzianka.

Ligonodina multidens sp. n.
(Figs 18 and 122)

Holotype: Specimen ZPAL cXVI/1659 (Fig. 18I).

Type horizon and locality: Sample Md-1, early Famennian late *K. triangularis* Zone at Miedzianka, Holy Cross Mountains.

Derivation of the name: Referring to relatively numerous denticles on M element.

Material. — 25 specimens.

Diagnosis. — Straight and relatively long, almost transversely oriented process of M element with denticles of relatively uniform height.

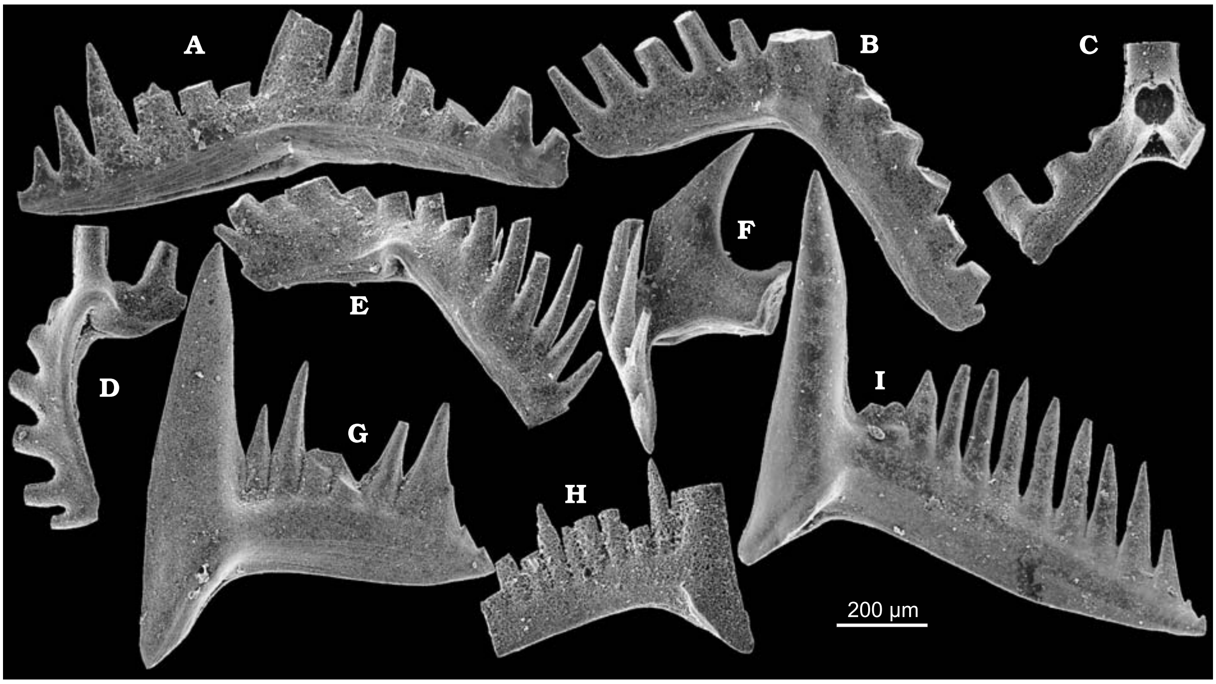


Fig. 18. Generalized early Famennian prioniodinid *Ligonodina multidens* sp. n. from Kadzielnia (A, F, and H, sample Ka-2; B–E, and G, sample Ka-3) and Miedzianka (I, sample Md-1) in the Holy Cross Mountains. P_1 (A), P_2 (B), S_0 (C), S_1 (D), S_2 (E), $S_{3–4}$ (F), and M (G–I) elements; specimens ZPAL cXVI/1651–1656, 1658, 1657, and 1759 (holotype, I), respectively.

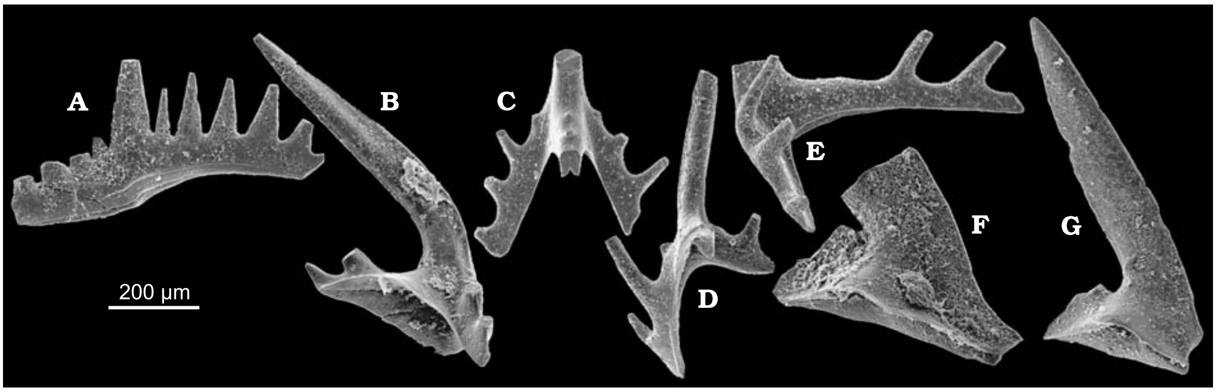


Fig. 19. Simplified early Famennian prioniodinid *Ligonodina latibasalis* sp. n. from Jabłonna (A–F, sample J-45a) and Wietrznia (G, sample Wtr-32) in the Holy Cross Mountains. P_1 (A), P_2 (B), S_0 (C), S_{1-2} (D), S_{3-4} (E), and M (F, G) elements; specimens ZPAL cXVI/1744–1749 (holotype, F), and 1755, respectively.

Remarks. — The apparatus of the species is rather generalized in appearance and may be a successor of a Frasnian lineage. Available material is rather limited and in some cases it is difficult to decide to which of associated prioniodinid species particular elements belong. However, the morphology of M elements seems distinctive enough to substantiate separation at the species level; its wide and transversely oriented process supports the generic affiliation.

Occurrence. — The late *K. triangularis* to *K. crepida* zones at Miedzianka and Kadzielnia.

Ligonodina latibasalis sp. n.
(Figs 19 and 122)

Holotype: Specimen ZPAL cXVI/1749 (Fig. 19F).

Type horizon and locality: Sample J-45a, early Famennian *K. crepida* Zone at Jabłonna, Holy Cross Mountains.

Derivation of the name: The name refers to widened bases of most elements.

Material. — 153 specimens.

Diagnosis. — Reduced dorsal process of M element with a few low denticles, widely gaping basal cavities of P_2 element and shortened processes of S elements with few large denticles.

Remarks. — The morphologically simplified appearance of elements makes generic affiliation of this probably paedomorphic prioniodinid rather uncertain.

Occurrence. — The *K. crepida* Zone at Jabłonna, Wietrznia and probably Łagów.

Ligonodina sudetica sp. n.
(Figs 20 and 122)

Holotype: Specimen ZPAL cXVI/1887 (Fig. 20I).

Type horizon and locality: Sample Dz-8, late Famennian *P. jugosus* Zone at Dzikowiec, the Sudetes.

Derivation of the name: Referring to the Sudetes Mountains, where the material was found.

Material. — 257 specimens.

Diagnosis. — High arched elements with flat sharp denticles, M elements with triangularly narrowed base, undenticulated, pointed external process and variable length and orientation of internal process.

Remarks. — Because of the unusually wide range of variability it is not certain if truly only one prioniodinid species is represented in the late Famennian of Dzikowiec. However, there seems to be a complete gradation between extreme morphologies of the most characteristic M elements (Fig. 20I–L). Also the generic affiliation of the species is uncertain and it may as well belong to *Idioprioniodus*. In fact, some of its M elements resemble those of *Ligonodina pectinata*, others *Idioprioniodus ruptus* sp. n. The most characteristic aspect of most elements of *L. sudetica* is elongation of their cusps and sharp denticles and relatively short processes.

Occurrence. — The *P. jugosus* and *D. trigonica* zones at Dzikowiec and possibly Kowala.

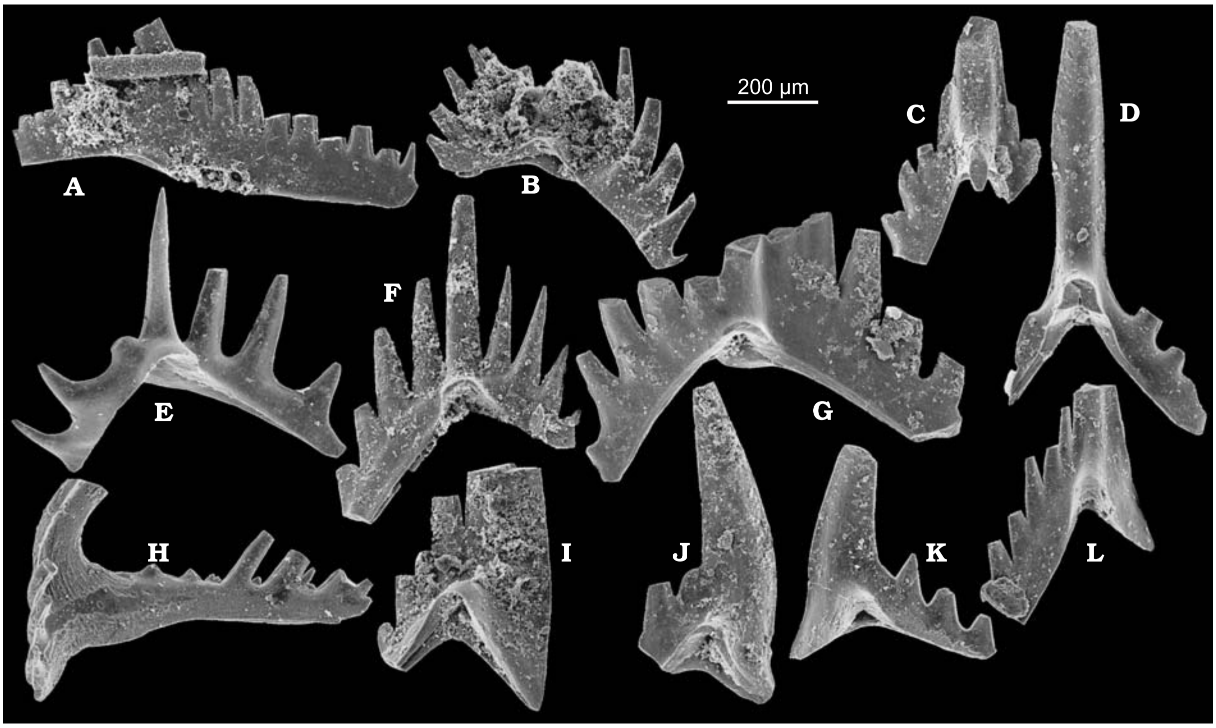


Fig. 20. Problematic late Famennian prioniodinid *Ligonodina sudetica* sp. n. from Dzikowiec, the Sudetes (A, D, H, and L, sample Dz-9; B, C, F, and I, sample Dz-8; E, G, J, and K, sample Dz-10). P_1 (A), P_2 (B), S_0 (C, D), S_1 (E), S_2 (F, G), S_{3-4} (H), and M (I–L) elements; specimens ZPAL cXVI/1877, 1886, 1885, 1878, 1880, 1884, 1881, 1879, 1887 (holotype, I), 1883, and 1876, respectively.

Genus ***Pluckidina*** Dzik, 2002

Type species: *Pluckidina lagoviensis* Dzik, 2002 from the late Frasnian of the Holy Cross Mountains, Poland.

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

Pluckidina lipperti (Bischoff, 1956)
(Figs 21 and 123)

Type population: Upper Kellwasserkalk of Schmidt's quarry near Braunau.

Material. — 183 specimens.

Remarks. — The earliest Famennian *Pluckidina* is of a rather generalized morphology (Fig. 21A–F). It may be distinct taxonomically from the latest Frasnian type population of the species but with so few specimens available it is difficult to identify possible differences. The material seems to fit within the range of its variability. The population from the *K. crepida* Zone at Jabłonna (Fig. 21G–N) shows a somewhat more robust denticulation. Whether this reflects an evolutionary change or only ecophenotypic adaptation remains to be elucidated.

Coeval, but usually allopatric, species of *Ligonodina* differ from those of *Pluckidina* mostly in the shape of the high arched S_1 elements (also M elements) and generally more delicate denticulation of S elements. The angular appearence of S_1 elements is an indication of the proximity to early gondolellids.

Occurrence. — From the beginning of Famennian to the early *K. triangularis* Zone at Płucki and the late *K. triangularis* to *K. crepida* zones at Jabłonna.

Pluckidina purnelli sp. n.
(Figs 22 and 123)

Holotype: Specimen ZPAL cXVI/1681 (Fig. 22G).

Type horizon and locality: Bed 24, mid Famennian *P. trachytera* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: In recognition of Mark Purnell's research on prioniodinid apparatuses.

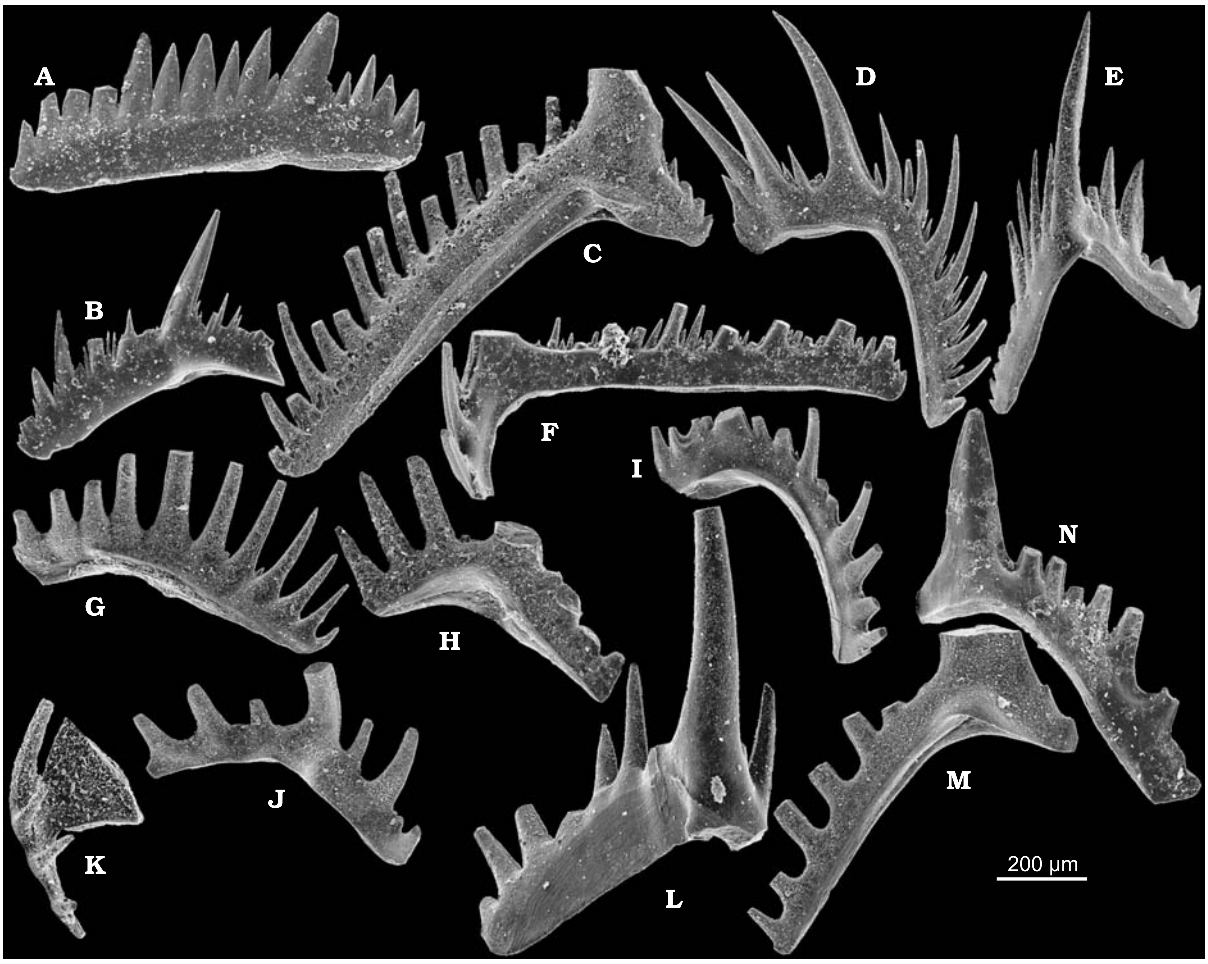


Fig. 21. Early Famennian successors of the prioniodinid lineage of *Pluckidina lipperti* (Bischoff, 1956) from the beginning of the *K. triangularis* Zone at Płucki (samples Pł-36, A, B, and F) somewhat younger strata at the same locality (sample Pł-1, D, E) and transition from the *K. triangularis* to *K. crepida* Zone at Jabłonna (G, I, and M, sample J-53; J, sample J-60; N, bed 6; H, K, L, bed 7) in the Holy Cross Mountains. P_1 (A, G), P_2 (B, H and J), S_0 (F), S_1 (E and L), S_2 (D and I), S_{3-4} (K), and M (M, N) elements; specimens ZPAL cXVI/1706, 1707, 1711, 1709, 1708, 1710, 1714, 1715, 1717–1719, 1716, 1720 and 1721, respectively.

Material. — 83 specimens.

Diagnosis. — Straight, almost transversely oriented inner process of M element with prominent denticles, relatively long external process of S_{3-4} elements extending almost along the same line as the cusp.

Remarks. — This is a rather generalized prioniodinid but the shape of the M element makes it different from all other Famennian prioniodinids occurring in the region. Also the delicate and mostly alternating denticulation of elements is rather unusual for the prioniodinids enabling rather easy separation of its elements from those of associated members of the family. The species has a rather short range of occurrence in the Holy Cross Mountains but probably was represented in the whole area, as it has been found at Jabłonna and Ostrówka, which are relatively distant from each other.

Occurrence. — The *P. trachytera* Zone at Jabłonna and the *L. styriacus* to *P. jugosus* zones at Ostrówka.

Genus ***Lagovidina*** gen. n.

Type species: *Lagovidina obliqua* sp. n.

Diagnosis. — Inverted basal cavity in all elements, M element with a short dorsal process and strongly bent cusp, probable P_2 with the dorsal process angularly bent close to the base and a tendency to develop an additional process near the bending.

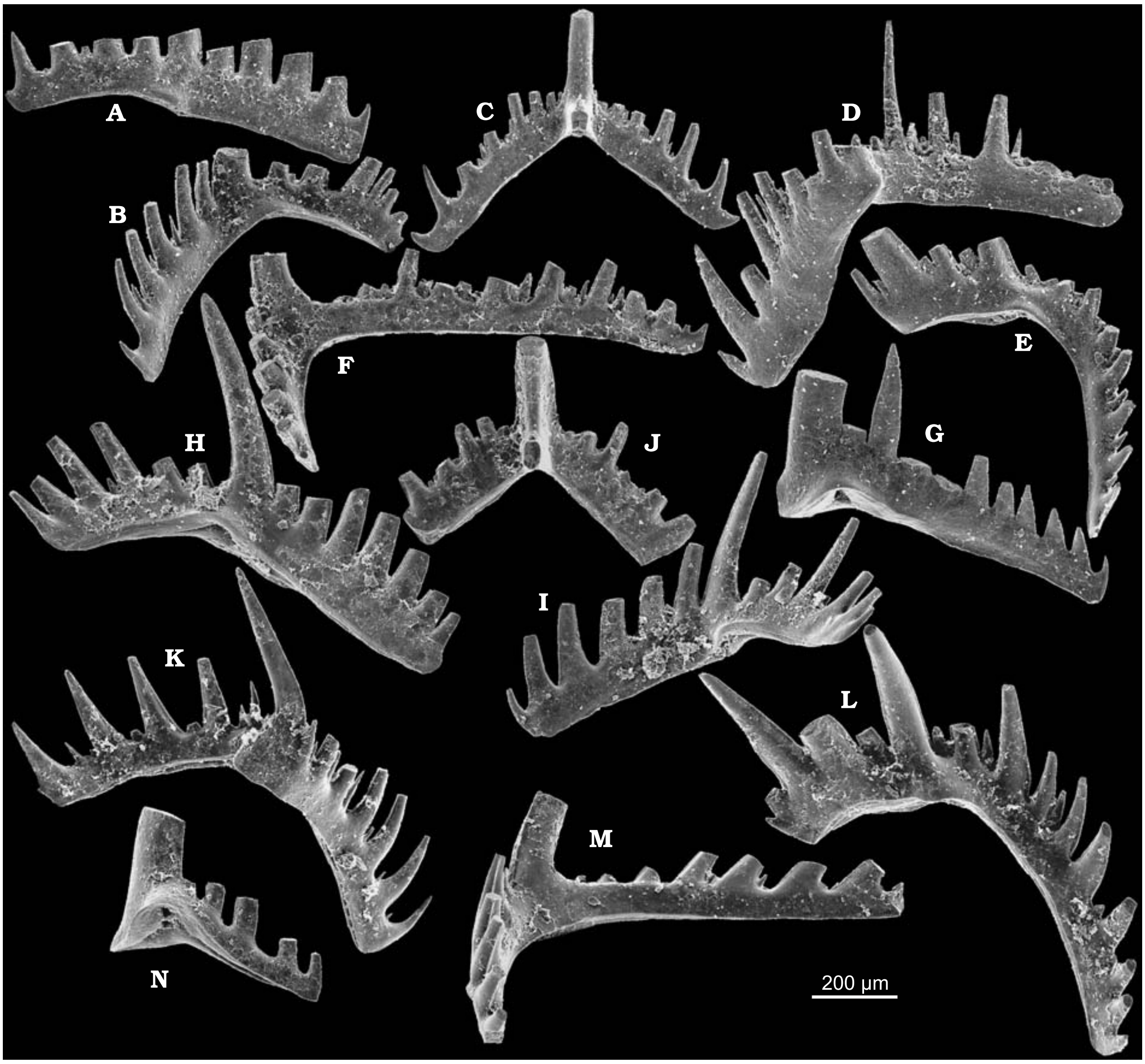


Fig. 22. Late Famennian prioniodinid *Pluckidina purnelli* sp. n. from the *P. trachytera* Zone at Jabłonna (A–G, bed 24) and the *L. styriacus* Zone at Ostrówka (H–N, sample Ost-12) in the Holy Cross Mountains. P_1 (A and H), P_2 (B and I), S_0 (C and J), S_1 (D and K), S_2 (E and L), S_{3-4} (F and M), and M (G and N) elements; specimens ZPAL cXVI/1675–1888 (holotype, G), respectively.

Lagovidina obliqua sp. n.

(Figs 23 and 122)

Holotype: Specimen ZPAL cXVI/1674 (Fig. 23R).

Type horizon and locality: Sample Ł-28, early Famennian *C. quadrantinodosa* Zone at Łagów, Holy Cross Mountains.

Derivation of name: Referring to the skewed base of M elements.

Material. — 625 specimens.

Diagnosis. — M element with triangular outline and straight base, P series with short processes and a high cusp, P_1 element with the inner process bifurcating, P_2 element strongly bent and twisted, sometimes developing additional anterior process.

Remarks. — The lineage emerged at Kadzielnia together with *Klapperilepis crepida* and *Tripodellus lobus* and continued after the disappearance of these species. This oldest population shows a laterally bent dorsal process of the P_2 element without additional branch and a slight angulation at the base of M elements. In a probably slightly younger sample from Miedzianka (Md-1), still containing *K. crepida*, the dorsal process of the P_2 element is already bifurcated but the cusp is relatively small in most specimens. Probably this is

Fig. 23. Derived prioniodinid *Lagovidina obliqua* sp. n. from the late *K. triangularis* Zone at Jabłonna (F, sample J-53a), the *K. crepida* Zone at Kadzielnia (A and G, sample Ka-7; B, C, and H, sample Ka-6; D, E, I, and J, sample Ka-3) and Miedzianka (sample Md-1, K–N), and the *C. quadrantinodosa* Zone at Łagów (O–S, sample Ł-28). P_1 (A, D, F, K, and P), P_2 (B, E, L, and O), $S_{1–2}$ (N), $S_{3–4}$ (C, M, and Q; note that the latter is a cluster of two elements), and M (G–J, R) elements; specimens ZPAL cXVI/1907, 1663, 1664, 1660, 1661, 1723, 1906, 1665, 1662, 1905, 1666, 1667, 1669, 1668, 1671, 1670, 1673, 1674 (holotype, R), and 1672, respectively.

a case of a gradual evolution but the material is not abundant enough to demonstrate this reliably and to substantiate erection of more chronospecies. Moreover, the co-occurrence of *L. multidens* sp. n., with some of its elements somewhat similar to those of early members of *Lagovidina*, makes their separation not completely sure. Phylogenetic relationship of *L. multidens* and *Ligonodona albidens* to the new species is unclear. A puzzling aspect of the apparatus structure of the latter species is that it also contains probable P_2 element

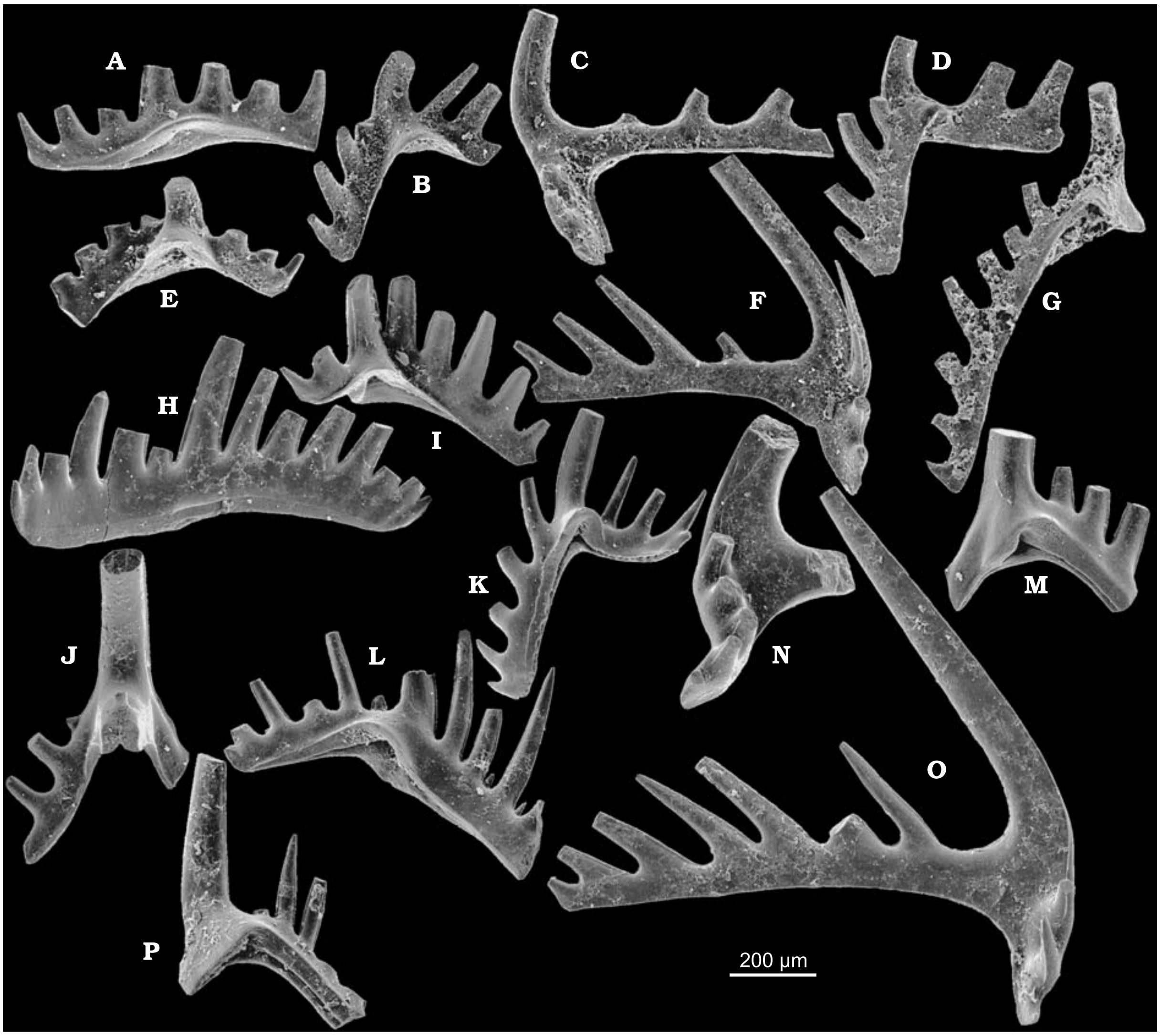


Fig. 24. Possible ancestor of Carboniferous prioniodinids, *Idioprioniodus ruptus* sp. n. from the *P. trachytera* Zone at Jabłonna (A–G, bed 24) and the *L. styriacus* Zone at Miedzianka (M ,N, sample Md-14), and Ostrówka (H–L, O, P, sample Ost-12). P_1 (A and H), P_2 (B and I), S_0 (C and J), S_1 (D and K), S_2 (E and L), $S_{3–4}$ (F, N, and O), and M (G, M, and P) elements; specimens ZPAL cXVI/1695 (holotype, G), 1698–1702, 1697, 1696, 1703, and 1704, respectively.

with a high cusp and inner process which tends to bifurcate. Whether this is a result of parallel evolution or shared inherited character, remains to be clarified.

Occurrence. — Early form in the *K. crepida* Zone at Kadzielnia, typical form in the *C. quadrantinodosa* and the early *C. marginifera* zones at Łagów and Miedzianka.

Genus ***Idioprioniodus*** Gunnell, 1933

Type species: *Idioprioniodus typus* Gunnell, 1933 from the Stephanian (Missourian) Kansas City Group.

Diagnosis. — M element with strongly aborally bent anterior process.

Idioprioniodus ruptus sp. n.
(Figs 24 and 123)

Holotype: Specimen ZPAL cXVI/1695 (Fig. 24G).

Type horizon and locality: Bed 24, mid Famennian *P. trachytera* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: Referring to the “ruptured” appearance of the external process in a ramiform element.

Material. — 905 specimens, some of questionable affinities.

Diagnosis. — At least some large $S_{3–4}$ elements show angular twisting of the external process, otherwise generalized morphology of the apparatus.

Remarks. — Most of the collected *Idioprioniodus* specimens are juvenile. Only sample Md-14 from Miedzianka yielded fragmentary but mature elements that show the unique morphology of $S_{3–4}$ elements. The origin of the species is cryptic; somewhat similar forms are known among Frasnian *Pluckidina* species (see Dzik 2002).

Occurrence. — The *C. marginifera* to *D. trigonica* zones at Kowala, Miedzianka and Ostrówka.

Idioprioniodus uncadinoides sp. n.
(Figs 25A–H and 123)

Holotype: Specimen ZPAL cXVI/1890 (Fig. 25F).

Type horizon and locality: Bed 27, late Famennian early *P. jugosus* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: Referring to the similarity of some elements to *Uncadina* gen. n.

Material. — 23 specimens.

Diagnosis. — Robust $S_{3–4}$ elements with short, prominently denticulated external process and wide inner process bearing disproportionally small, inclined denticles.

Remarks. — The apparatus reconstruction of this species is poorly supported despite the characteristic appearance of its diagnostic $S_{3–4}$ elements. Such elements in sample Wtr-25, from the *K. triangularis* Zone at Wietrznia, are associated with the set of other elements of *Idioprioniodus*. It has to be noted, however, that this sample significantly differs in age from those with the most typical specimens and the robust appearance of the inner process may be in this case a "gerontic" feature. A somewhat similar appearance is exhibited by the medial process of the S_0 element of *Trichognathus tumida* of Branson and Mehl (1934, pl. 16: 28). Some support to so wide a gap in stratigraphic occurrence is offered by a finding of a juvenile specimen with a similar aspect from coeval strata at Jabłonna (sample J-45a, Fig. 25G), in co-occurrence with *Uncadina unca*. This specimen resembles also *Guizhoudella*.

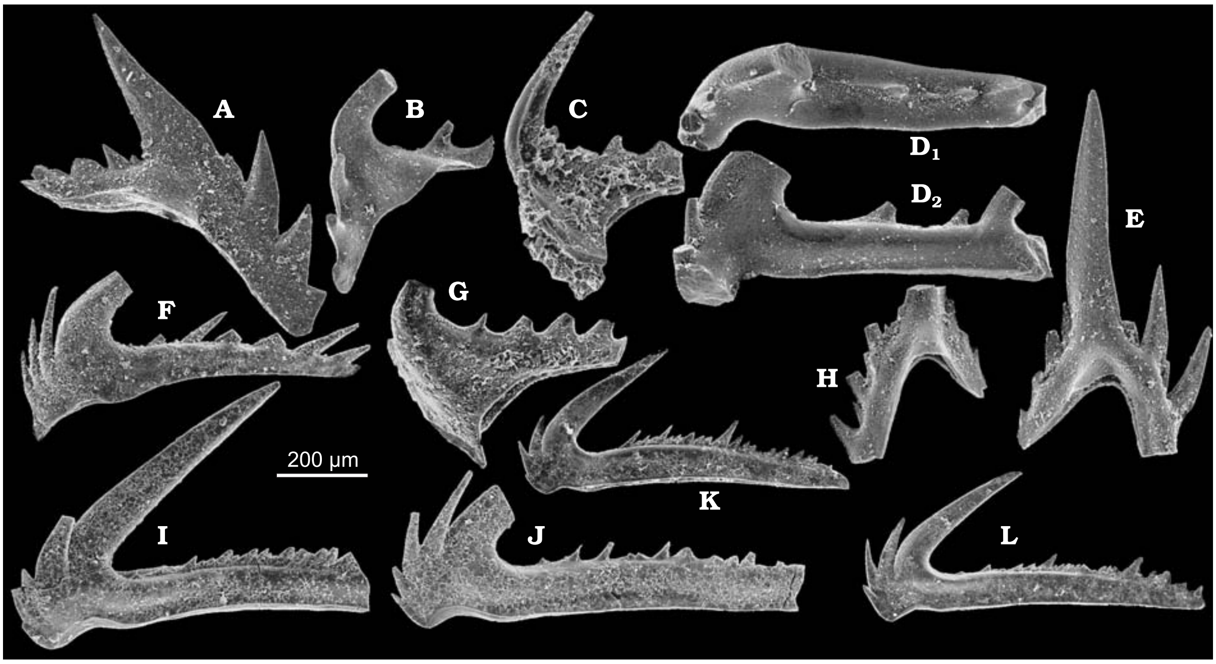


Fig. 25. Aberrant prioniodinid *Uncadina* and its poorly known possible less derived relative. **A**–**H**. *Idioprioniodus uncadinoides* sp. n. from the *K. triangularis* Zone at Wietrznia (uncertain taxonomic identity; A, D, E, and H, sample Wtr-25) and Jabłonna (G, sample J-45a), and the *P. jugosus* Zone of the same locality (B, C, F, bed 27). P_1 (A?), P_2 (B), S_0 (C), $S_{3–4}$ (D, F, and G), and M (E and H) elements; specimens ZPAL cXVI/1893, 1888, 1889, 1894, 1895, 1890 (holotype, F), 1891, and 1896, respectively. **I**–**L**. *Uncadina unca* (Bischoff, 1956) from the *K. triangularis* Zone at Jabłonna (sample J-45a). S elements, specimens ZPAL cXVI/1897, 1998, 1900, 1899, respectively.

Occurrence. — The *K. triangularis* to *K. crepida* zones transition at Wietrznia and the *P. jugosus* Zone at Jabłonna and Kowala.

Genus ***Uncadina*** gen. n.

Type species: *Hindeodella unca* Bischoff, 1956 from the Early Famennian at the Bicken quarry in the Rhenish Slate Mountains.

Diagnosis. — Only one type of asymmetric element with short, prominently denticulated external process, strong cusp and robust inner process with disproportionally delicate denticulation.

Remarks. — Despite a great number of collected elements only one type of them has been identified. It seems unlikely that any other element kind was associated with them. All are more or less asymmetric and resemble prioniodinid S_{3-4} elements, especially those of *Idioprioniodus uncadinoides* sp. n. This is the only basis for classification of the genus among prioniodinids.

Uncadina unca (Bischoff, 1956)

(Figs 25I–L and 123)

Type horizon and locality: *Klapperilepis crepida* Zone at the Bicken quarry in the Rhenish Slate Mountains.

Material. — 724 specimens.

Diagnosis. — As for the genus.

Occurrence. — The *K. crepida* Zone at Jabłonna and Wietrznia.

Genus ***Guizhoudella*** Wang *et* Wang, 1978

Type species: *Guizhoudella triangularis* Wang *et* Wang, 1978 from the Late Famennian of Daihua Formation at Daihua, Guizhou, China.

Diagnosis. — Ramiform elements of the apparatus with surface granular in places; denticles fused into wide, denticulated blades.

Remarks. — Most elements of the apparatus of *Guizhoudella dinodontoides* sp. n. are homeomorphic with those of *Dinodus leptus* Cooper, 1939. In the Tournaisian samples of the latter species delicate ramiform S and M elements co-occur with closely similar P_2 elements (*Elictognathus*) that have been suggested to belong to the *Siphonodella* apparatus (Sweet 1988). The only species of "*Siphonodella*" which could be matched with these sets of non-P_1 elements in the material studied by myself (Dzik 1997) is "*S.*" *lobata*. The Famennian species is so similar to that from the Tournaisian that its independent origin is difficult to accept. The problem thus emerges how the "*Elictognathus*" and "*Siphonodella*" elements originated, if they truly belonged to the same apparatus. It has to be noted that in *Dinodus* no tuberculation of *Guizhoudella* (or *Playfordia*, see Dzik 2002) type occurs. Instead, the elements show distinct imprints of ameloblasts.

"*Elsonella*" *rhenana* Lindström *et* Ziegler, 1965 from the latest Givetian hermanni-cristatus Zone (Lindström and Ziegler 1965) differs from *G. dinodontoides* sp. n. only in a low-angle arrangement of processes in the probable S_1 element. This suggests that the stratigraphic distribution of the Famennian *Guizhoudella* species reflects their evolution, in which the apparatus became gradually disorganized, with increased variability and irregular appearance of elements. It would then depart from the *Dinodus*-like morphology. The long-lasting *Guizhoudella* species lineage appears to be cryptic for most of its range.

Guizhoudella triangularis Wang *et* Wang, 1978

(Figs 26 and 124)

Type horizon and locality: Sample ACE 366 with *Tripodellus gonioclymeniae*, Daihua Formation at Daihua, Guizhou, China (Wang and Wang, 1978).

Material. — 28 specimens.

Diagnosis. — Elements with thin walls of the very deep basal cone, strongly curved cusps; sharp, numerous denticles.

Remarks. — The holotype of the type species represents an S_1 element. S_{3-4} elements from the same sample were named *Belodella bilinearis* by Wang and Wang (1978). This is so bizarre a conodont that identification of its elements does not cause any difficulties, even if they are very rare in samples. Some specimens

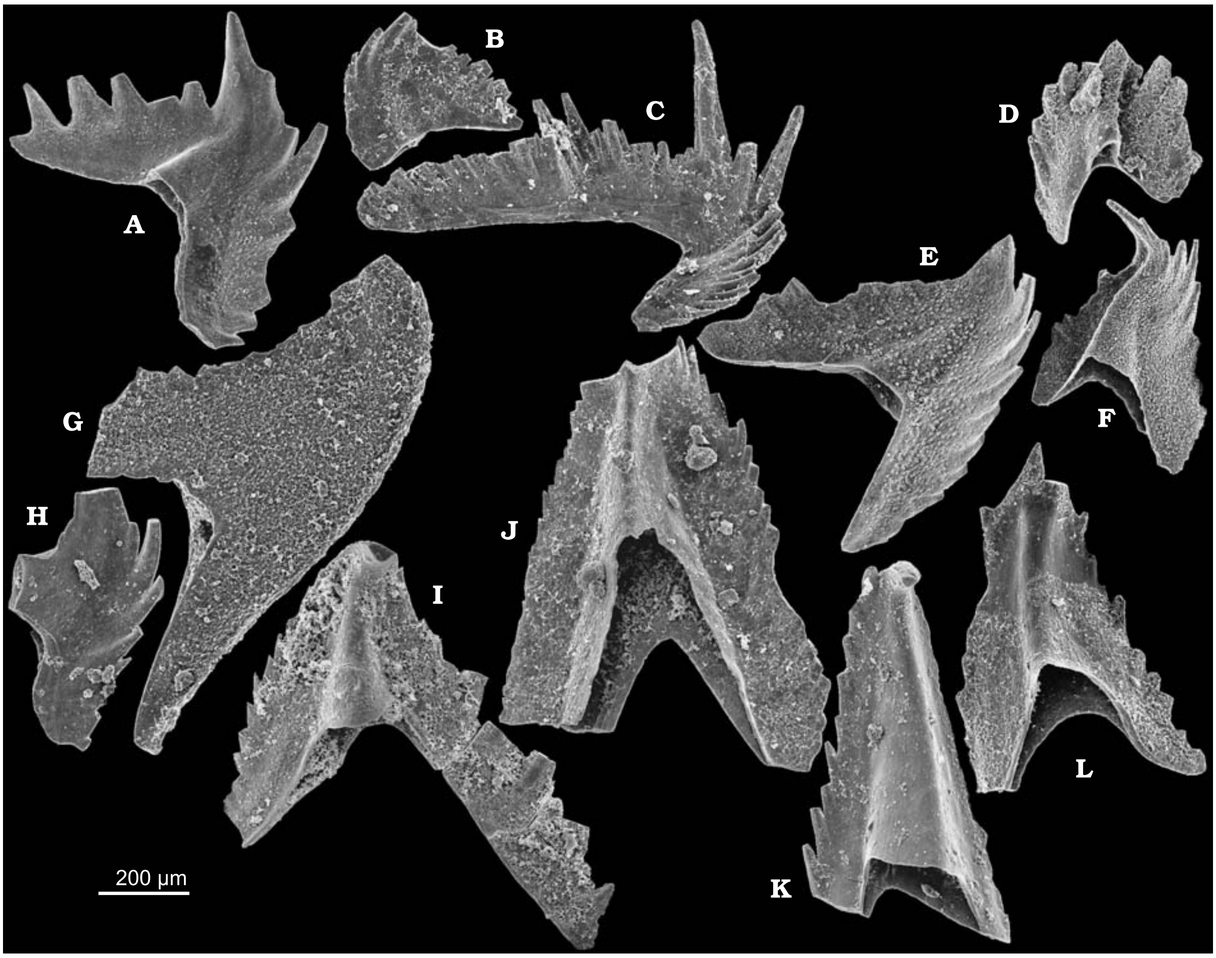


Fig. 26. Bizarre probable prioniodinid *Guizhoudella triangularis* Wang *et* Wang, 1978 from the *P. jugosus* Zone at Ostrówka (sample Ost 185, A, B, D–F and Ost-265, G), the *K. crepida* Zone at Jabłonna (C, sample J-46; L, bed 27; J, sample J-66), the late *K. triangularis* Zone at Wietrznia (I, sample Wtr-27) in the Holy Cross Mountains, and the *P. jugosus* Zone at Dzikowiec (H, sample Dz-8) in the Sudetes. P_1 (A?), P_2 (B?), S_0 (C), $S_{1–2}$ (D and F), $S_{3–4}$ (E, G, and H), and M (I–L) elements; specimens ZPAL cXVI/1806, 1808, 1775, 1807, 1809–1811, 1862, 1909, 1901, 1861, and 1892, respectively.

resemble P elements of typical prioniodinids (Fig. 26A) but variability is so wide that recognition of discrete element types may not be possible.

Occurrence. — The *L. styriacus* to *D. trigonica* zones at Jabłonna, Kowala, Ostrówka, and Dzikowiec.

Guizhoudella dinodontoides sp. n.

(Figs 27 and 124)

Holotype: Specimen ZPAL cXVI/1933 (Fig. 27E).

Type horizon and locality: Sample J-45a, early Famennian *K. crepida* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: Referring to the similarity of elements to *Dinodus*.

Material. — 12 specimens.

Diagnosis. — Relatively small basal cone and wide, flat denticles; processes of ramiform elements with a low platform forming a ribbon-like structure along their basal parts.

Remarks. — Similar to the type species, the new species is also long ranging and extremely variable, but species distinction is rather certain. Only juveniles lacking characteristic denticulation and ribbon-like platform (e.g., Fig. 27Q, R) may be misidentified. Much less certain is identification and homology of particular element types. Two elements from sample Md-14 may represent the platform series (Fig. 27A, B) if they truly belong to the species (they lack the tuberculation occurring in undoubted specimens). Alternatively, the platform series is represented by elements with relatively straight processes but otherwise similar to other el-

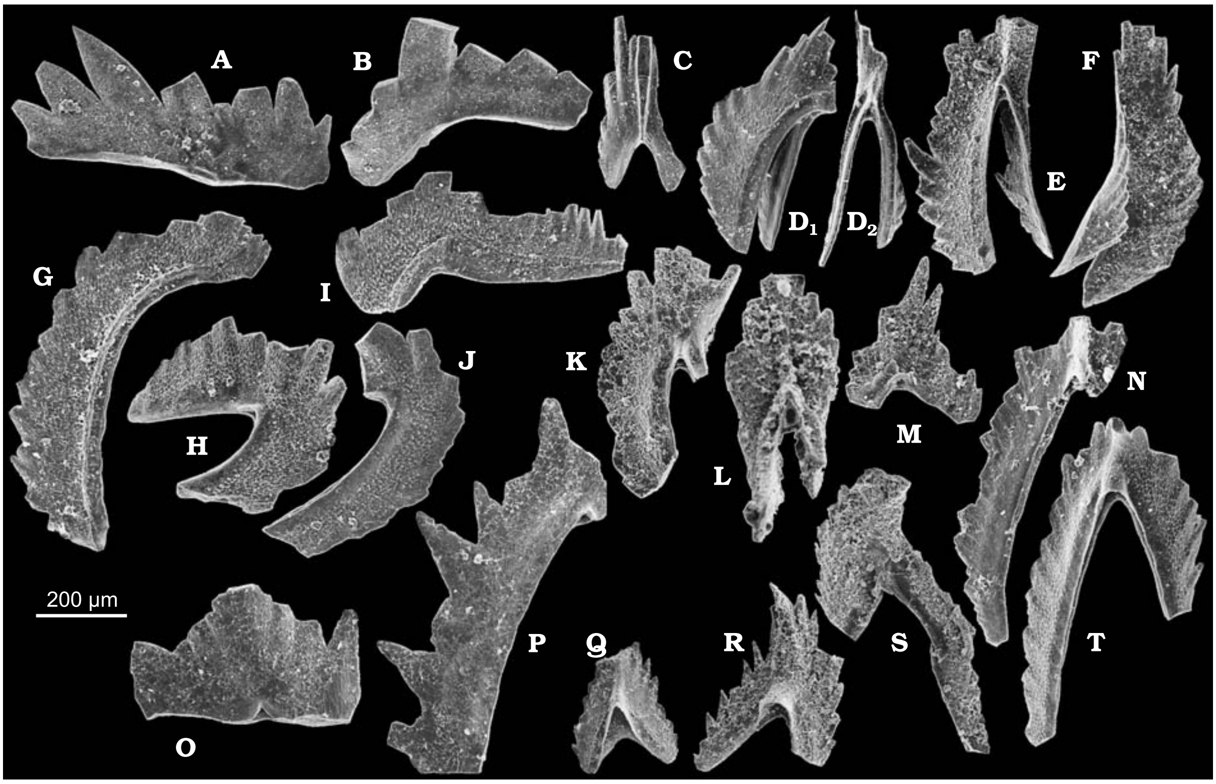


Fig. 27. Bizarre probable prioniodinid *Guizhoudella dinodontoides* sp. n. from the *L. styriacus* Zone at Miedzianka (sample Md-14, A, B, H, J, T), Jabłonna (C–F, K, M, O–S, sample J-45a; L, bed 12), and Kowala (G, I, sample Ko-18; N, sample Ko-154) in the Holy Cross Mountains. P_1 (A?), P_2 (B?), S_0 (C and L), S_1 (D, E, F, and K), S_2 (H? and I?), $S_{3–4}$ (G, and I)), and M (M, N, O–T) elements; specimens ZPAL cXVI/1801, 1802, 1813–1815, 1333, 1799, 1809–1811, 1862, 1909, 1901, 1861, and 1892, respectively.

ement types (Fig. 27G and I). The elements S_0 and S_1 may or may not have the medial process, but it seems to be always rather short in length, unlike the probably homeomorphic Carboniferous *Dinodus*.

Occurrence. — Rare from the beginning of the Famennian at Kowala through the *K. crepida* Zone at Jabłonna, Kadzielnia and Kowala to the *L. styriacus* Zone at Miedzianka.

Family **Gondolellidae** Lindström, 1970

Diagnosis. — The P_1 elements with more or less reduced dorsal process, otherwise the apparatus with a generalized polygnathid-like structure; the prioniodinid affinities disclosed only by the "enantiognathus" appearance of S_1 elements.

Remarks. — The oldest undoubted gondolellid *Gondolella* are known from the late Carboniferous (von Bitter and Merrill 1998). Its apparatus differs from that of *Branmehla* only in the morphology of element lacking dorsal process but bearing a platform along the ventral process. Juvenile elements of *Branmehla* closely resemble the paedomorphic Permian and Triassic gondolellid *Neospathodus*.

Genus ***Branmehla*** Hass, 1959

Type species: *Spathodus inornatus* Branson *et* Mehl, 1934 from the Fammennian Saverton Shale, Missouri.

Diagnosis. — Non-platform P_1 elements with a short dorsal process, dominant cusp together with neighboring denticles gives the element an angular outline; transversely expanding short basal cavity.

Branmehla bohlenana (Helms, 1959)

(Figs 28, 29, and 124)

Type horizon and locality: Bed 8 in the limestone quarry at Bohlen near Saalfeld, lower *Clymenia* beds.

Material. — 1,664 specimens.

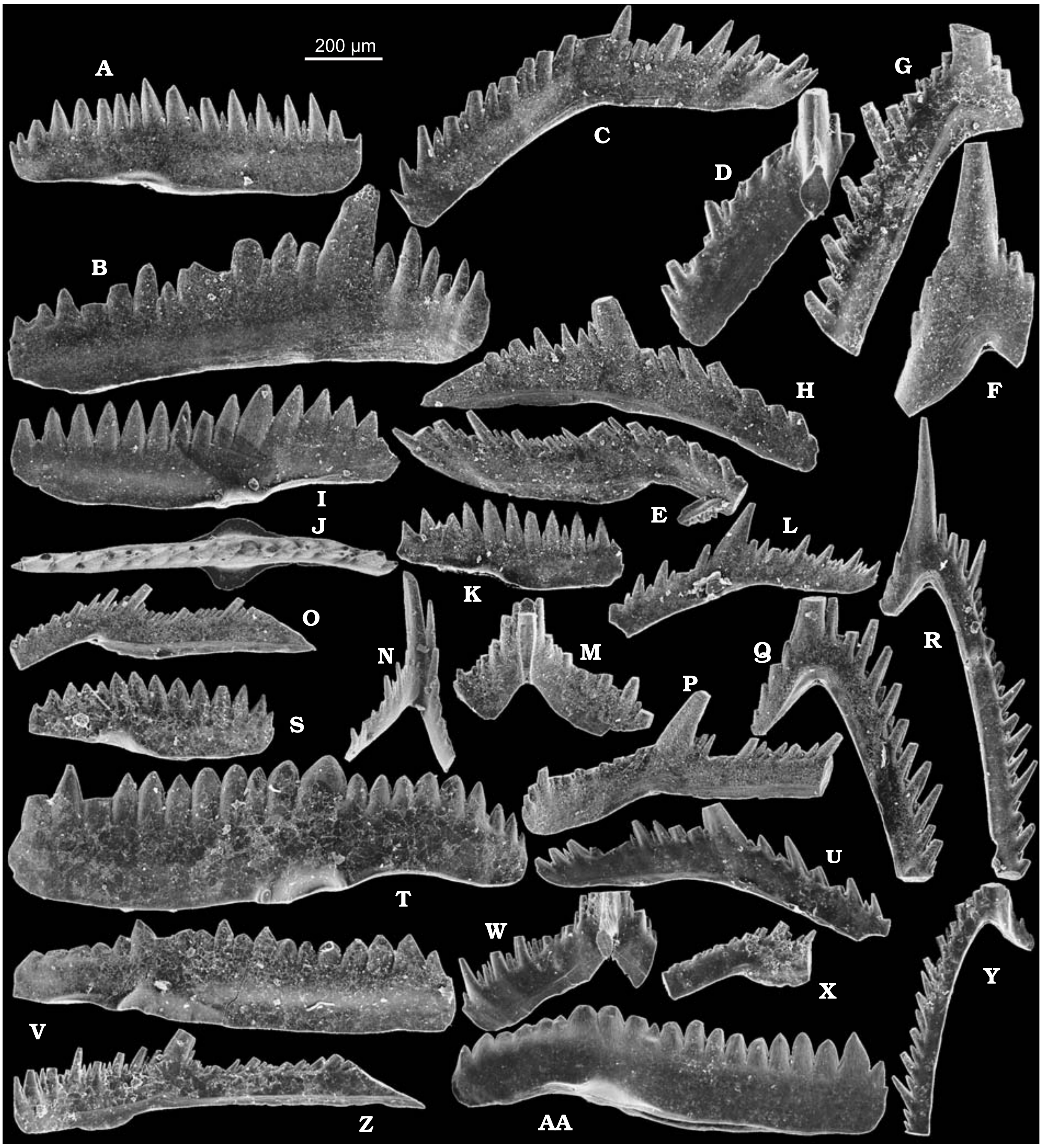


Fig. 28. Early gondolellid *Branmehla bohlenana* (Helms, 1959) from the *C. quadrantinodosa* Zone at Łagów (A–F, sample ŁSł73-2) and the *K. crepida* zones at Wietrznia (G, sample Wtr-21) and the *L. styriacus* Zone at Miedzianka (H–R, sample Md-14) and Ostrówka (S, T, sample Ost-5; W–AA, sample Ost-15,) in the Holy Cross Mountains. P_1 (A, B, I–K, T–V, and AA), P_2 (E, H, L, and U), S_0 (D, M, and W), S_1 (N), S_2 (E, O, and X), S_{3-4} (P and Z), and M (F–G, Q, R, and Y) elements; specimens ZPAL cXVI/1970, 1969, 1971–1974, 1968, 1978, 1975, 1977, 1976, 1979–1985, 1988, 1986, 1990, 1987, 1991, 1992, 1994, 1993, and 1989, respectively.

Diagnosis. — Elongated and rather robust P_1 element with relatively low cusp.

Remarks. — The geologically oldest populations of *Branmehla* from Łagów (sample ŁSł73-2; Fig. 28) closely resemble the earliest Famennian *Pluckidina lipperti* (Fig. 21A–E) and that species is likely to be its ancestor. The main difference is in the morphology of the M element, which is higly arched in *B. bohlenana* (note that the geologically later *Pluckidina lipperti* from the *K. crepida* Zone exhibits the same tendency; Fig. 21N).

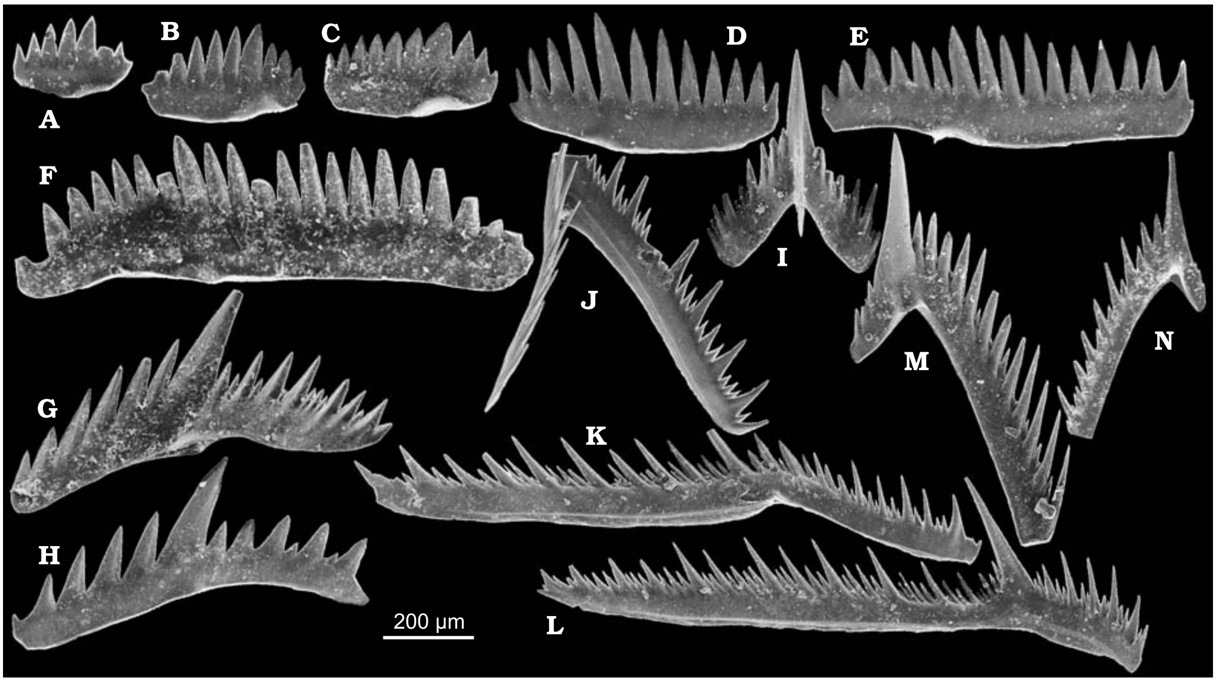


Fig. 29. Juvenile specimens of early gondolellid *Branmehla bohlenana* (Helms, 1959) from the *P. trachytera* Zone at Kowala (sample Ko-8a) in the Holy Cross Mountains. P_1 (A–F), P_2 (G, H), S_0 (I), S_1 (J), S_2 (K), S_{3-4} (L), and M (M and N) elements; specimens ZPAL cXVI/2339, 2338, 530, 2337, 2336, 529, 526, 2340–2344, 2335, and 521, respectively.

The transition from *B. bohlenana* to *B. inornata* is gradual and it is virtually impossible to delimit these species even if for most of their range they occur allopatrically. In the rather representive sample Ost-12 from the *L. styriacus* Zone some elements can be found that are indistinguishable from those of the type species of the genus. They grade into the modal morphology of *B. bohlenana* and are thus considered extreme morphologies within the same species. In fact, the morphology of *B. inornata* is typical mostly for juvenile specimens. In the course of ontogeny denticles are added without increasing the element height and as a result the dominantion of the cusp seems to disappear. Ontogenetic extension of the dorsal process is connected with its lateral bending, which gives it the characteristic appearance.

The species is rather variable, especially in respect to the denticulation of P_1 elements. Denticles are wide and short, densely distributed in some specimens (Fig. 28S), or elongate and sparsely distributed in others (Fig. 29D).

Panderodella subrecta of Holmes (1928, p. 31, pl. 10:15) from the Chattanooga Sshale may be conspecific and thus a senior synonym of the species.

Occurrence. — Possibly ancestral population in the *K. crepida* Zone at Wietrznia, the typical form from the *C. quadrantinodosa* Zone to the end of the Famennian at Łagów, Miedzianka, Kowala, Ostrówka, and Dzikowiec.

Branmehla inornata (Branson *et* Mehl, 1934)
(Figs 30 and 124)

Type horizon and locality: Probably the Saverton Shale near Monroe City, Missouri (Klapper *in* Ziegler 1975).

Material. — 6,049 specimens.

Diagnosis. — P_1 elements with high, sharp denticles, which decrease linearly in size with distance from the cusp, to give the element a polygonal profile.

Remarks. — Mature P_1 elements of this species resemble juveniles of *B. bohlenana* and its origin is clearly paedomorphic. They rarely occur sympatrically but then juveniles are difficult to tell apart.

Occurrence. — From the *P. trachytera* Zone to the end of Famennian at Kowala, Ostrówka, and Dzikowiec.

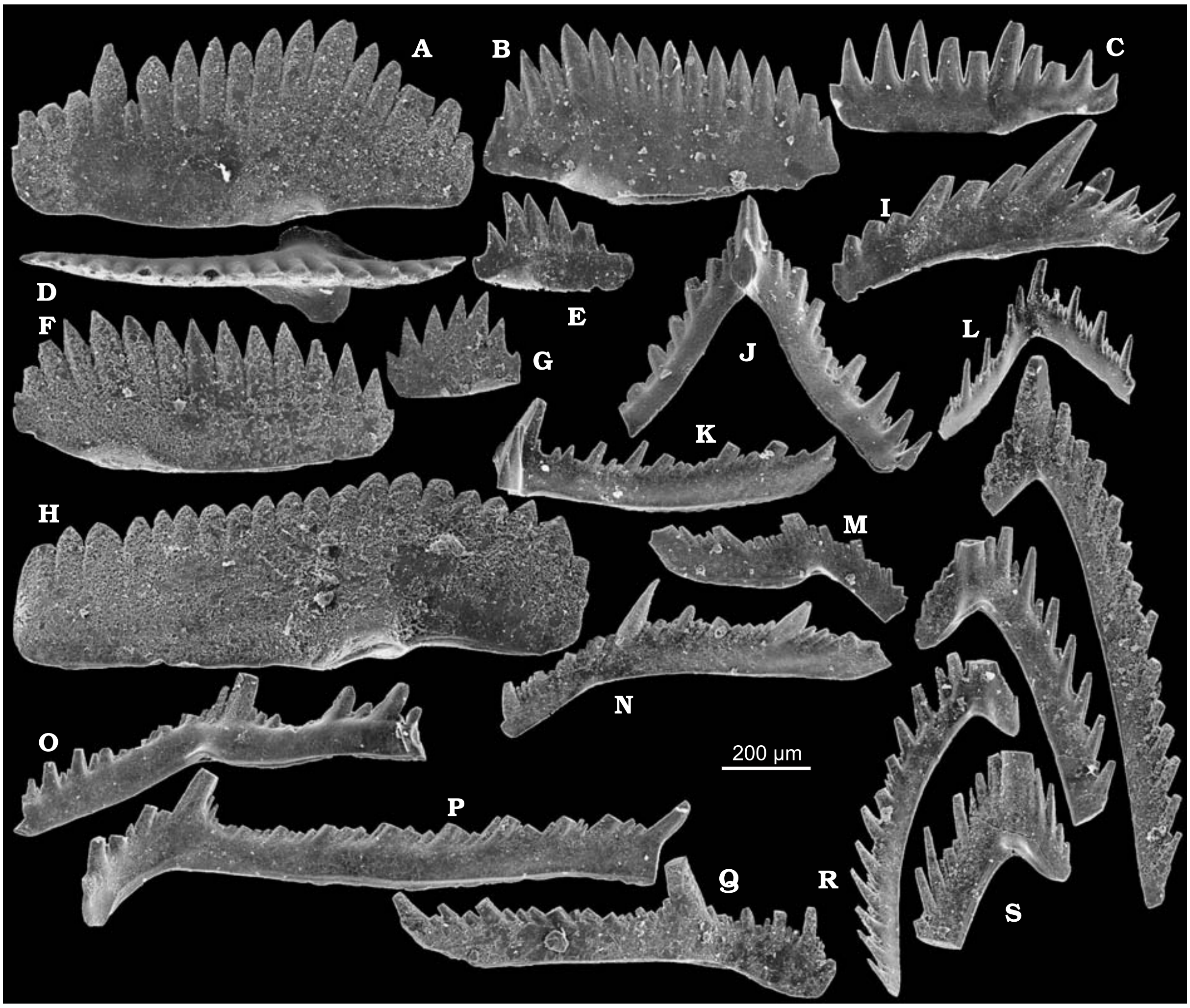


Fig. 30. Paedomorphic early gondolellid *Branmehla inornata* (Branson *et* Mehl, 1934) from the *P. jugosus* Zone at Jabłonna (A, F, G, and S, bed 27) and Ostrówka (B–E, I–R, and T, U, sample Ost-185; H, sample Ost-5) in the Holy Cross Mountains. P$_1$ (A–H), P$_2$ (I), S$_0$ (J, K), S$_1$ (L), S$_2$ (M–O), S$_{3-4}$ (P, Q), and M (R–U) elements; specimens ZPAL cXVI/1995, 2000, 2001, 1999, 2002, 1996, 1997, 2003, 2004–2008, 2011, 2009, 2010, 2014, 1998, 2012, and 2013, respectively.

Branmehla suprema (Ziegler, 1962)
(Figs 31B–I and 124)

Type horizon and locality: Sample 2c from the Hönnetal road section in the Rhenish Slate Mountains, topmost costatus Zone.

Material. — 1,539 specimens.

Diagnosis. — Dorsal process of P$_1$ element laterally bent, widely gaping basal cone.

Remarks. — P$_2$ and S elements are relatively robust, as compared with other species of the genus. *Spathodus fissilis* Branson *et* Mehl, 1934 from the Saverton Shale near Monroe City, Missouri may be conspecific.

P$_1$ element of this species somewhat resembles that of *B. inornata* in profile view and many morphologically transitional specimens occur.

Occurrence. — Probable ancestral population near the end of the *C. marginifera* at Kowala; undoubted from the *L. styriacus* Yone to the end of Famennian at Jabłonna, Kowala and Dzikowiec.

Branmehla disparilis (Branson *et* Mehl, 1934)
(Figs 31A and 124)

Type horizon and locality: Probably the Saverton Shale near Monroe City, Missouri (Ziegler 1975).

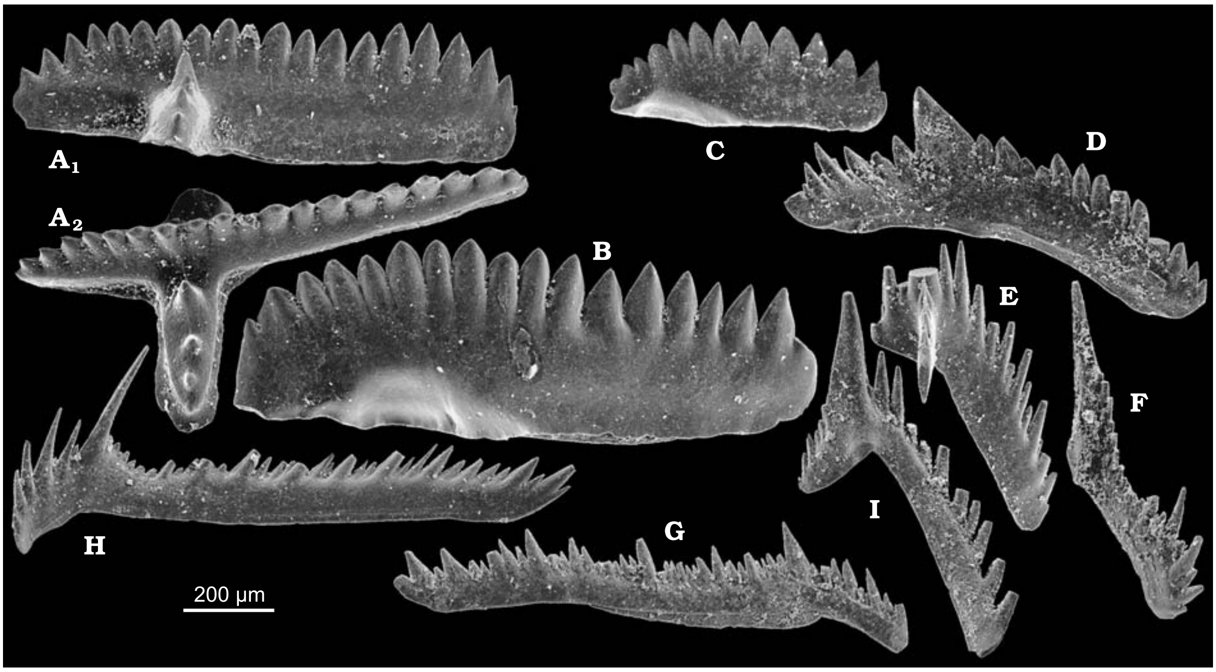


Fig. 31. Advanced late Famennian species of *Branmehla* from the *D. trigonica* Zone at Ostrówka (sample Ost-3) in the Holy Cross Mountains. A. *Branmehla disparilis* (Branson *et* Mehl, 1934). P_1 element; specimen ZPAL cXVI/2016. B–I. *Branmehla suprema* (Ziegler, 1962). P_1 (B, C), P_2 (D), S_0 (E), S_1 (F), S_2 (G), $S_{3–4}$ (H), and M (I) elements; specimens ZPAL cXVI/2017–2024, respectively.

Material. — Four specimens.

Diagnosis. — Base of P_1 elements laterally expanded to form denticulated transverse processes.

Remarks. — Even more prominent lateral process may develop in P_1 elements, as shown by Perri and Spaletta (1991). Probably the species originated from *B. suprema*, the lateral process being derivative of the asymmetric expansion of the base.

Occurrence. — The latest Famennian at Dzikowiec and Ostrówka.

Family **Spathognathodontidae** Hass, 1959

Diagnosis. — Biramous S_0 element, other elements of S series with relatively short processes.

Remarks. — Despite the great time gap between the Carboniferous occurrences of conodonts with biramous symmetrical elements in the apparatus (*Hindeodus* and *Synclydognathus*) and similar Silurian *Ozarkodina*, it was proposed by myself that they represent the same clade (Dzik 1991). The occurrence of *Synclydognathus* in the early Famennian significantly reduces this gap and confirms the hypothesis of their close relationship. One of the new Famennian species appears closely similar in its apparatus organization to coeval *Apatognathus*, earlier classified among prioniodinids.

Genus ***Synclydognathus*** Rexroad *et* Varker, 1992

Type species: *Prioniodus geminus* Hinde, 1900 from the Viséan of Scotland.

Diagnosis. — M and $S_{1–2}$ elements morphologically similar, with high-arched arrangement of processes that are subequal in length.

Remarks. — Apparatus reconstructions of the Carboniferous species were presented by Sweet (1988; as *Hindeodus scitulus*), Rexroad and Varker (1992), and Dzik (1997, under misspelled name *Syncladognathus*). In the high-arched appearance of S elements the genus is closely similar to *Apatognathus*, to which it seems closely related. The main difference is in the morphologically non-simplified elements of the platform series.

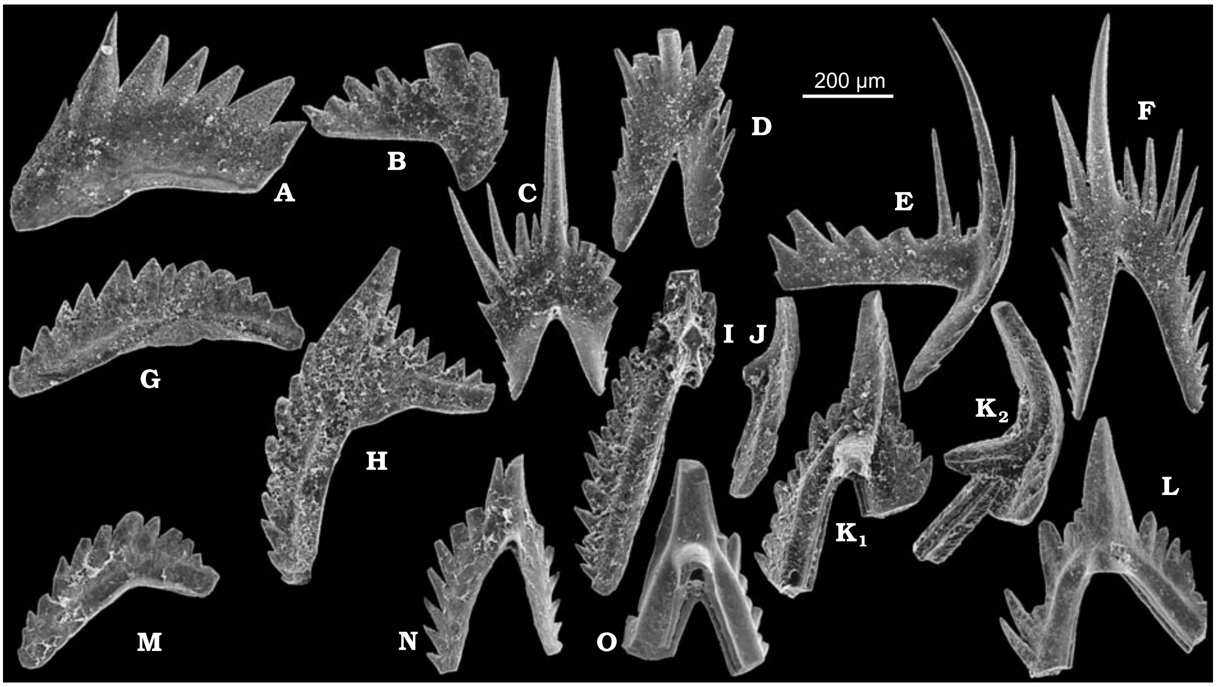


Fig. 32. Famennian ozarkodinids *Synclydognathus* from the Holy Cross Mountains. **A**–**F**. *Synclydognathus ancestralis* sp. n. from the *K. crepida* Zone at Wietrznia (sample Wtr-32). P_1 (A), P_2 (B), S_0 (C), S_{1-2} (D), S_{3-4} (E), and M (F) elements; specimens ZPAL cXVI/1819–1824 (holotype, F), respectively. **G**–**K**. *Synclydognathus triramosus* sp. n. from the *P. trachytera* Zone at Jabłonna (bed 24). P_1 (G), P_2 (H), S_0 (I, J), and M (K) elements; specimens ZPAL cXVI/1838, 1842, 1839, 1840 (holotype, K), respectively. **I**–**M**. *Synclydognathus* sp. from the *L. styriacus* Zone at Ostrówka (sample Ost-12). P_2 (J), and M (I, K–M) elements; specimens ZPAL cXVI/2384–2386.

Synclydognathus ancestralis sp. n.
(Figs 32A–F and 121)

Holotype: Specimen ZPAL cXVI/1824 (Fig. 32F).

Type horizon and locality: Sample Wtr-32, early Famennian *K. crepida* Zone at Wietrznia, Holy Cross Mountains.

Derivation of name: Referring to ancestral position to other species of the genus.

Material. — 109 specimens.

Diagnosis. — Flat elements with elongated sharp denticles.

Remarks. — The new species differs from the type species (Rexroad and Varker 1992) in the delicate, relatively underived appearance of elements. *Falcodus*, as interpreted by myself (Dzik 1997) may be another descendant lineage related to this species.

Occurrence. — The *K. crepida* Zone at Wietrznia and Jabłonna.

Synclydognathus triramosus sp. n.
(Figs 32G–K and 121)

Holotype: Specimen ZPAL cXVI/1841 (Fig. 32K).

Type horizon and locality: Bed 24, mid Famennian *P. trachytera* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: Referring to triramous appearance of non-P elements.

Material. — 14 specimens.

Diagnosis. — All elements of the apparatus with a narrow platform extending along processes and robust regular denticulation; S_0 element with a short denticulated medial process.

Remarks. — From the morphologically closest Carboniferous type species (Rexroad and Varker 1992), differs in arched profile of P_1 and incipiently triramous S_0 and M elements.

Occurrence. — Only the type horizon and locality.

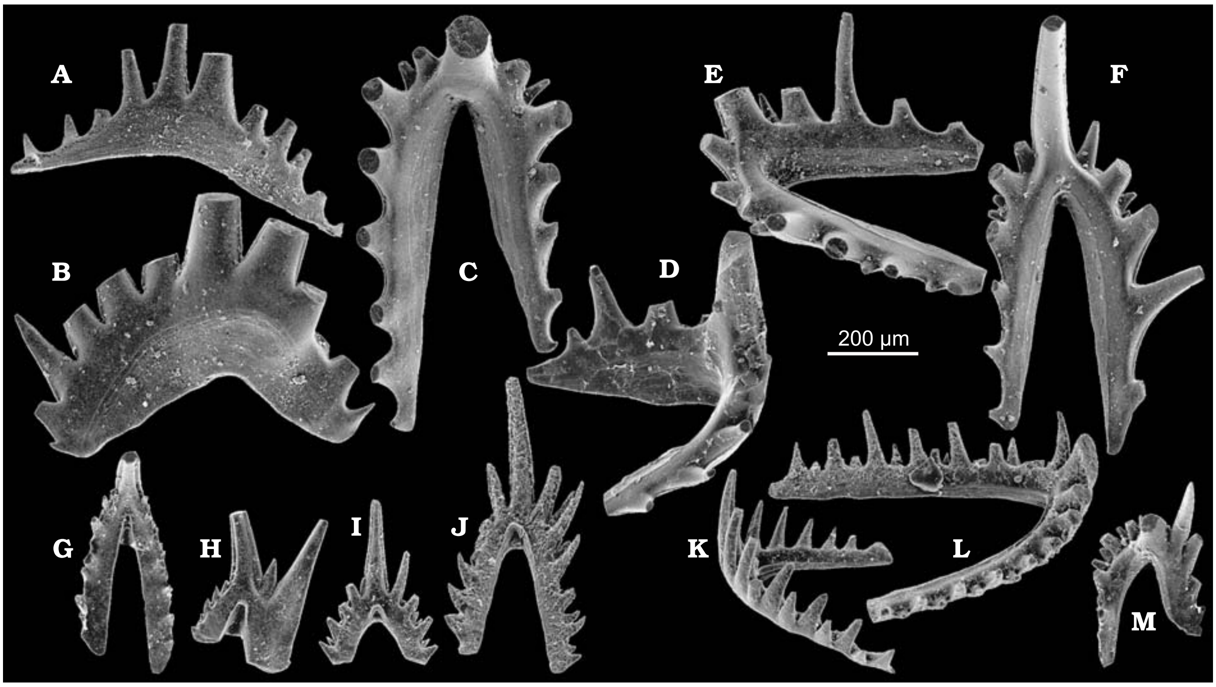


Fig. 33. Famennian ozarkodinids *Apatognathus* from the Holy Cross Mountains. **A–F**, **I–M**. *Apatognathus provarians* Nicoll, 1980 from the late *K. crepida* Zone at Łagów (A–F, sample ŁSł73-2; M, sample Ł-27) and the *K. triangularis* Zone at Jabłonna (I–L, sample J-45a). P (A, B), S_0 (I), S_{1-2} (C, J), S_{3-4} (D, E and K, L), and M (F) elements; specimens ZPAL cXVI/1825–1827, 1830, 1829, 1828, 1834–1837, and 1831, respectively. **G**, **H**. *Apatognathus varians* Branson *et* Mehl, 1934 from the *P. jugosus* Zone at Ostrówka (sample Ost-185). S_{1-2} (G) and M (H) elements; specimens ZPAL cXVI/1833 and 1832.

Synclydognathus sp.
(Fig. 32I–M)

Material. — Five specimens.

Remarks. — Rare specimens from sample Ost-12 may represent a new species of *Synclydognathus* representing another link between the early Famennian and Carboniferosus members of the lineage.

Occurrence. — The *L. styriacus* Zone at Ostrówka.

Genus ***Apatognathus*** Branson *et* Mehl, 1934

Type species: *Apatognathus varians* Branson *et* Mehl, 1934 from the Famennian of central Missouri.

Diagnosis. — Narrow robust processes and sparsely distributed denticles of all elements; closely similar morphology of elements within M, S, and P series.

Remarks. — Nicoll (1980) presented a succession of *Apatognathus* species in the Caning Basin that is probably an evolutionary series. The change is expressed mostly in the morphology of the M element. In *A. provarians* from the *K. crepida* Zone alternating denticles of the same aspect as those in S elements occurred. In *A. klapperi* from the *C. marginifera* Zone they formed a prominent fan without alternation of size. One denticle dominated in *A. varians* from the *P. trachytera* to *D. trigonica* zones. Nicoll (1980) pointed out also a gradual change in the pattern of denticle alternation. This succession is confirmed by the material from the Holy Cross Mountains although the available material of possible *A. klapperi* is too limited to determine this species with confidence.

Apatognathus provarians Nicoll, 1980
(Figs 33A–F, I–M, and 121)

Type horizon and locality: Lower Napier Formation in the Canning Basin of Australia, late *K. crepida* Zone.

Material. — 203 specimens.

Diagnosis. — Processes of S and M elements arched, larger denticles of M element of relatively uniform size.

Remarks. — Apparatus reconstruction was presented by Nicoll (1980) and is fully confirmed by the new European material (Fig. 121).

Occurrence. — The *K. crepida* Zone at Jabłonna, Wietrznia, Kadzielnia and Kowala.

Apatognathus varians Branson *et* Mehl, 1934
(Fig. 33G, H)

Type horizon and locality: Famennian at Dixie, Missouri (Ziegler 1977, p. 313).

Material. — 106 specimens.

Diagnosis. — Processes of S and M elements narrowly disposed, M element with one large denticle of almost the cusp size.

Remarks. — Apparatus reconstruction was presented by Nicoll (1980) and the few available specimens from the Holy Cross Mountains seem to represent its part (Fig. 121). The diagnostic features are shown by one of the type specimens of Branson and Mehl (1934, pl. 17:3).

Occurrence. — The *K. marginifera* zone at Jabłonna; rare in all the studied localities from the *P. trachytera* to *D. trigonica* zones.

Family **Francodinidae** fam. n.

Diagnosis. — A tendency to bifurcate processes of S elements starting from S_1 and expanding towards S_4, all elements more or less arched in profile view, M-elements tending to develop A-shaped appearance, triramous symmetrical element of the apparatus.

Remarks. — This is a well-defined clade but difficult to diagnose morphologically. The branch probably started with a *Mehlina*-like (or *Pandorinellina*-like, depending of which morphology of M elements is primitive) ancestral form having arched profile of denticulation in P_1 elements, strongly aborally bent external process in S elements and a rather prominent external process in M elements. From this hypothetical form (similar to *Vogelgnathus proclinatus* sp. n.) as a result of diminution of the adult size (paedomorphosis) the lineage of *Vogelgnathus* emerged characterized by a surprisingly primitive appearance of the apparatus for the late Devonian. *Urbanekodina undata* gen. et sp. n. seems to be the end member of this evolutionary trend (Fig. 125), with its elements showing a bizarre mixture of palmatolepidid and spathognathodontid aspects.

The lineage of *Francodina* at its beginning preserved large size of elements inherited from a *P.*? *vogelgnathoides*-like ancestor (Fig. 126). The prioniodinid-like apparatuses of *Francodina* species probably originated as a result of released developmental control of the element morphology. The most surprising aspect of this is the transformation of M elements, otherwise the most morphologically stable element in the post-Ordovician conodont apparatuses. In advanced *F. franconica* both its processes achieved a similar length, the external process becoming ribbon-like in *Sweetodina lagoviensis* sp. n. The most unusual aspect of the apparatus of *Planadina plana* is the undenticulated internal process of M elements – the situation opposite to that typical for virtually all ozarkodinine conodonts (but similar to the Ordovician prioniodontids, e.g., *Prioniodus elegans*). Despite its seemingly *Ligonodina*-like appearance it is apparently a francodinid, and its prominent external process originated by modification of a ribbon-like structure similar to that of *S. lagoviensis*.

Genus ***Vogelgnathus*** Norby *et* Rexroad, 1985

Type species: *Spathognathodus campbelli* Rexroad, 1957 from the Namurian (Chesterian) of Illinois (see Norby and Rexroad, 1985; van dem Boogard 1992).

Diagnosis. — Minute and morphologically generalized elements of a spathognathodontid appearance but with triramous S_0 elements.

Vogelgnathus variabilis sp. n.
(Figs 34 and 125)

Holotype: Specimen ZPAL cXVI/1859 (Fig. 34R).

Type horizon and locality: Sample J-53a, early Famennian *K. triangularis* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: Referring to extreme variability in shape of P_1 elements.

Material. — 748 specimens.

Diagnosis. — M elements with relatively short and transversely arranged inner process; cusp of P_1 element only slightly longer than other denticles.

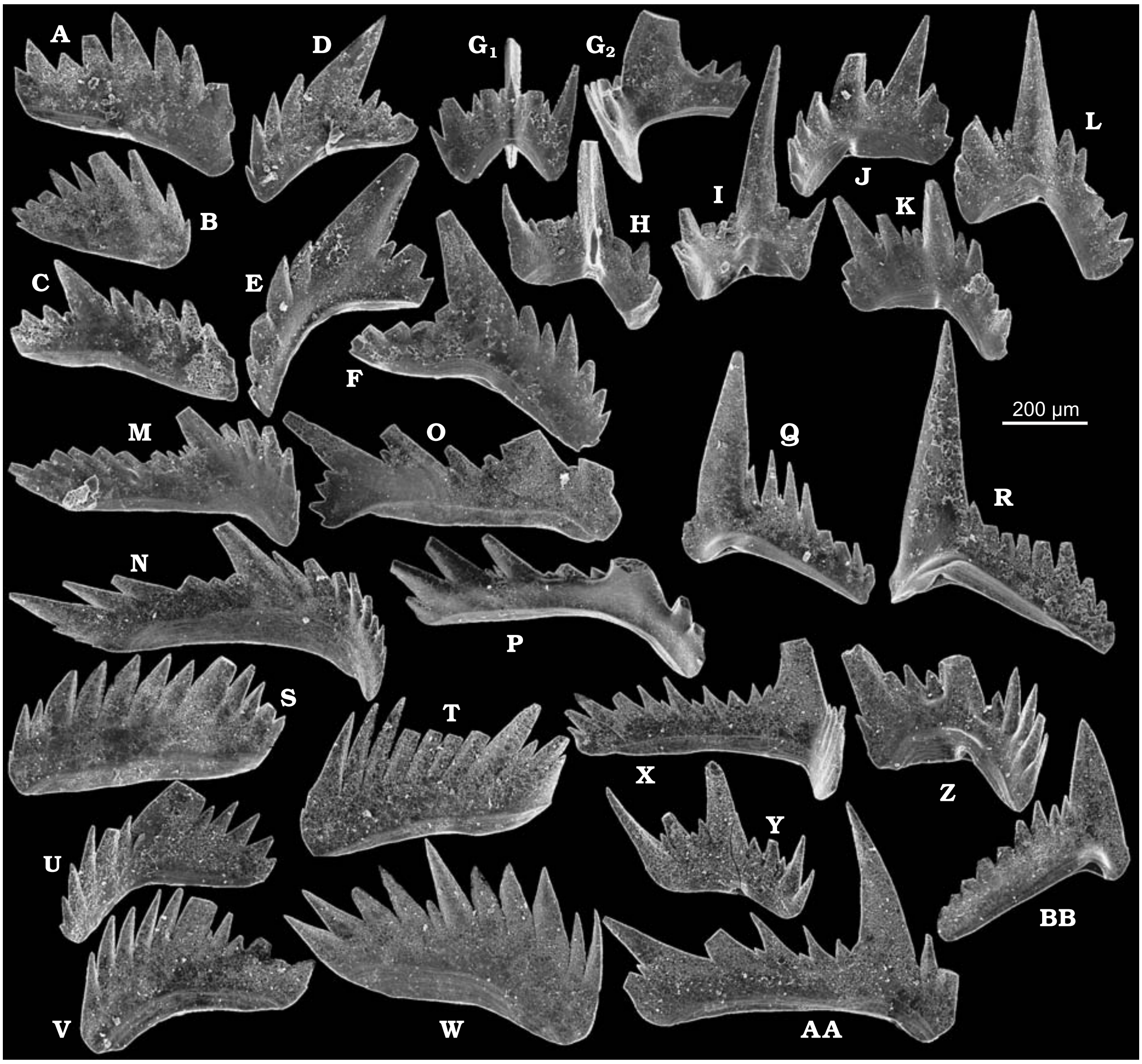


Fig. 34. Earliest francodinid *Vogelgnathus variabilis* sp. n. from the early Famennian *K. triangularis* Zone at Jabłonna (A–R, sample J-53a; S–BB, sample J-58) in the Holy Cross Mountains. P_1 (A–C and S, T), P_2 (D–F and U–W), S_0 (G and X), S_1 (H, I, and Z), S_2 (J–L and Y), $S_{3–4}$ (M–P and AA), and M (Q, R, and BB) elements; specimens ZPAL cXVI/1844, 1843, 1845, 1847, 1848, 1846, 1849, 1850, 1852, 1851, 1853–1856, 1858, 1857, 1860, 1859 (holotype, R), 1946, 1947, 1950, 1949, 1948, 1951, 1953, 1952, 1954, and 1952, respectively.

Remarks. — This is the geologically oldest species of the genus. Its unusual variability and small size suggests a paedomorphic origin and release of selection pressure on the apparatus morphology. Possibly the associated *Mehlina kielcensis* sp. n. is close to its ancestor, as suggested by similar M and P_1 elements but other elements of the apparatus are non-paedomorphic. Alternative to this ancestry is the relationship to *Pandorinellina*? *vogelgnathoides* but this would require a cryptic occurrence of the latter lineage during the *K. triangularis* Zone. As generally the francodinids show punctuated distribution, this is not unlikely.

In late populations of the species (e.g., J-58, Fig. 34S–BB) most M elements show a rounded tip of the external process, which is typical for its successor, *V. proclinatus*.

Occurrence. — The *K. triangularis* Zone at Płucki and Jabłonna.

Vogelgnathus proclinatus sp. n.
(Figs 35 and 125)

Holotype: Specimen ZPAL cXVI/1932 (Fig. 35N).

Type horizon and locality: Sample Wtr-21, early Famennian *K. crepida* Zone at Wietrznia, Holy Cross Mountains.

Fig. 35. Paedomorphic francodinid *Vogelgnathus proclinatus* sp. n. from the early Famennian *K. crepida* Zone at Jabłonna (A–G, sample J-45a; O–Z, sample J-44) and Wietrznia (H–N, sample Wtr-21) in the Holy Cross Mountains. P_1 (A, H, Q–S, and X), P_2 (B, I, and Y), S_0 (C, J, and P), S_1 (D, K, and U), S_2 (E, L, and T), $S_{3–4}$ (F, M, O, and W), and M (G, N, V, and Z) elements; specimens ZPAL cXVI/1919–1932 (holotype, N), 1933, 1942, 1938, 1937, 1939, 1943, 1942, 1934, 1944, 1935, 1940, and 1945, respectively.

Derivation of name: Referring to the proclined cusp of P_1 element.

Material. — 2,727 specimens.

Diagnosis. — Relatively long and high-arched inner process of M element, high and proclined cusp of P_1 element.

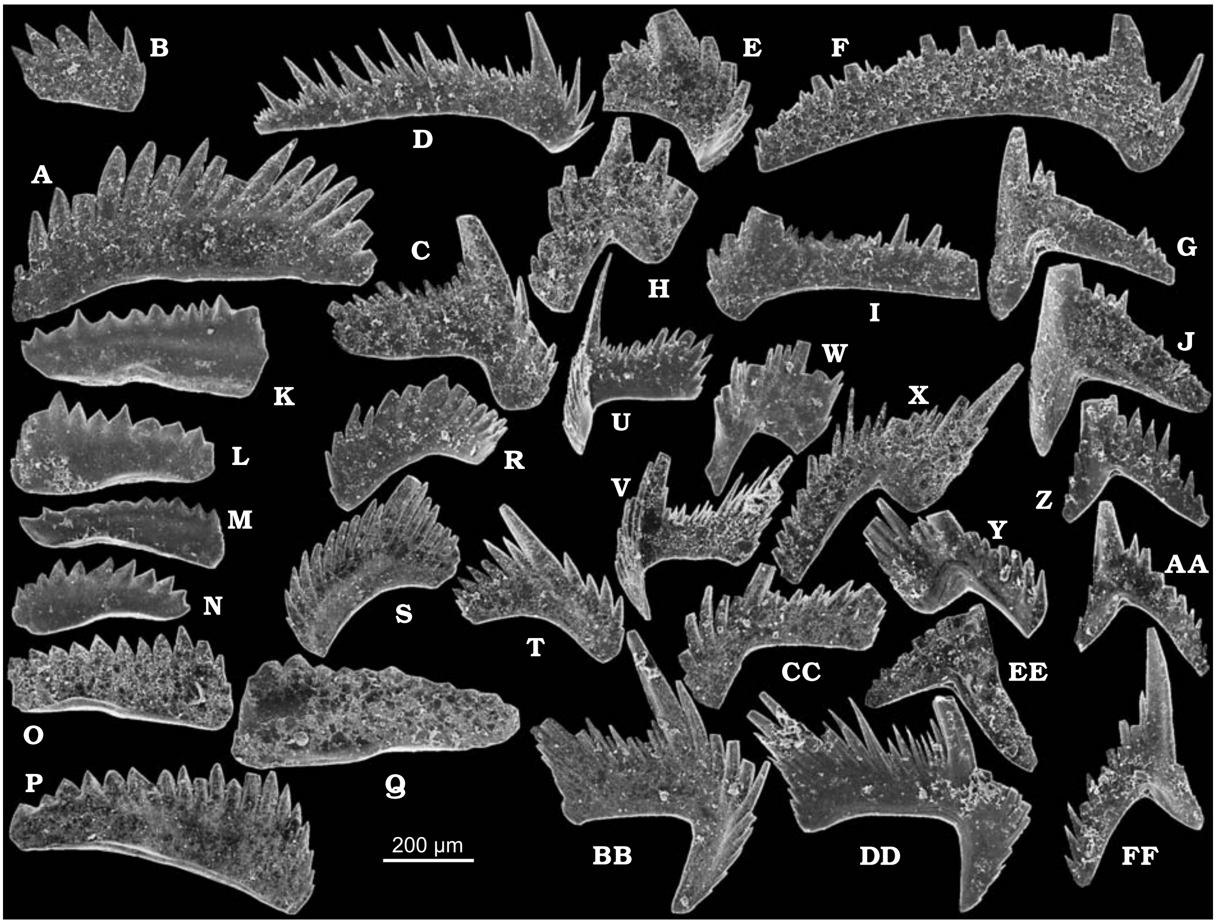


Fig. 36. Derived species of the francodinid *Vogelgnathus* from the early Famennian of the Holy Cross Mountains. **A**–**J**. *V. arcuatus* sp. n. from the *K. crepida* Zone at Wietrznia (A, H–J, sample Wtr-21; B–G, sample Wtr-32). P_1 (A, B), P_2 (C), S_0 (D, E), S_2 (H), S_{3-4} (F and I), and M (G and J) elements; specimens ZPAL cXVI/1966, 1956, 1957, 1959 (holotype, D), 1958, 1960, 1964, 1963, and 1965, respectively. **K**–**FF**. *V. unicus* (Klapper *et al.*, 2004) in co-occurrence with *K. rhomboidea* from Kowala (K, M, sample Ko-164; L, N, UY, Z, and DD, sample Ko-163) and Łagów (O–Q, SS–T, VX, AA–CC, EE, FF, sample Ł-28). P_1 (K–Q), P_2 (R–T), S_0 (U, V), S_1 (W), S_2 (X, Y), S_{3-4} (BB–DD), and M (AA and DD–FF) elements; specimens ZPAL cXVI/2040, 2033, 2041, 2034, 2045, 2044, 2043 (holotype, Q), 2035, 2046, 2047, 2036, 2048, 1373, 2049, 2037, 2039, 2052, 2050, 2051, 2038, 2054, and 2053, respectively.

Remarks. — Specimens of this species from sample J-44 attained a much larger size than typical for *Vogelgnathus* (Fig. 35O, V, X). They are robust and bear long and sharp tips of outer processes in S_{3-4} and M elements but preserve the unique paedomorphic aspects of the genus generally connected with small element size.

Occurrence. — The *K. crepida* to *C. marginifera* zones at Jabłonna, Kadzielnia, Kowala, and Wietrznia.

Vogelgnathus arcuatus sp. n.
(Figs 36A–J and 125)

Holotype: Specimen ZPAL cXVI/1959 (Fig. 36D).

Type horizon and locality: Sample Wtr-32, early Famennian *K. crepida* Zone at Wietrznia, Holy Cross Mountains.

Derivation of name: Referring to the arched S_{3-4} element.

Material. — 47 specimens.

Diagnosis. — S_0 and S_{3-4} elements bearing very long ribbon-like processes with arched profile.

Remarks. — P_1 elements (Fig. 36A) tentatively attributed to this species resemble some large specimens of *V. proclinatus* in bearing numerous denticles and an undifferentiated cusp.

Occurrence. — The *K. crepida* Zone at Wietrznia and Miedzianka.

Vogelgnathus unicus (Klapper, Uyeno, Armstrong *et* Telford, 2004)
(Figs 36K–FF and 125)

Type horizon and locality: Sample COB-19 from depth 101.5–101.7 m, upper member of the Long Rapids Formation of Ontario, rhomboidea Zone.

Material. — 1,801 specimens.

Diagnosis. — Short denticles of P_1 elements, merging together into a blade with undulated margin in adult specimens; M elements with short processes of subequal length.

Remarks. — The type series of P_1 elements of *Mehlina*? *unica* Klapper *et al*., 2004 is characteristic enough in the pattern of denticulation to make identification of this species rather safe, even if the rest of its apparatus was not identified by Klapper *et al*. (2004). The similarity of P_1 elements to geologically older *Mehlina robustidentata* sp. n. may be accidental but a possibility cannot be excluded that *V. unicus* and *V. variabilis* independently paedomorphically developed from closely related species classified here in *Mehlina*. If truly this was the case, as suggested by the sympatric occurrence of these species of *Vogelgnathus*, the range of the genus should be enlarged to preserve its monophyly.

Occurrence. — The *K. crepida* Zone at Jabłonna; the *C. quadrantinodosa* to *P. trachytera* zones at Łagów, Miedzianka, and Kowala.

Vogelgnathus branmehloides sp. n.
(Figs 37A–R and 125)

Holotype: Specimen ZPAL cXVI/2066 (Fig. 37K).

Type horizon and locality: Bed 27, late Famennian *P. jugosus* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: From similarity of P_1 elements to those of *Branmehla inornata*.

Material. — 2,560 specimens.

Diagnosis. — High arched profile of P_1 elements, with dominant cusp.

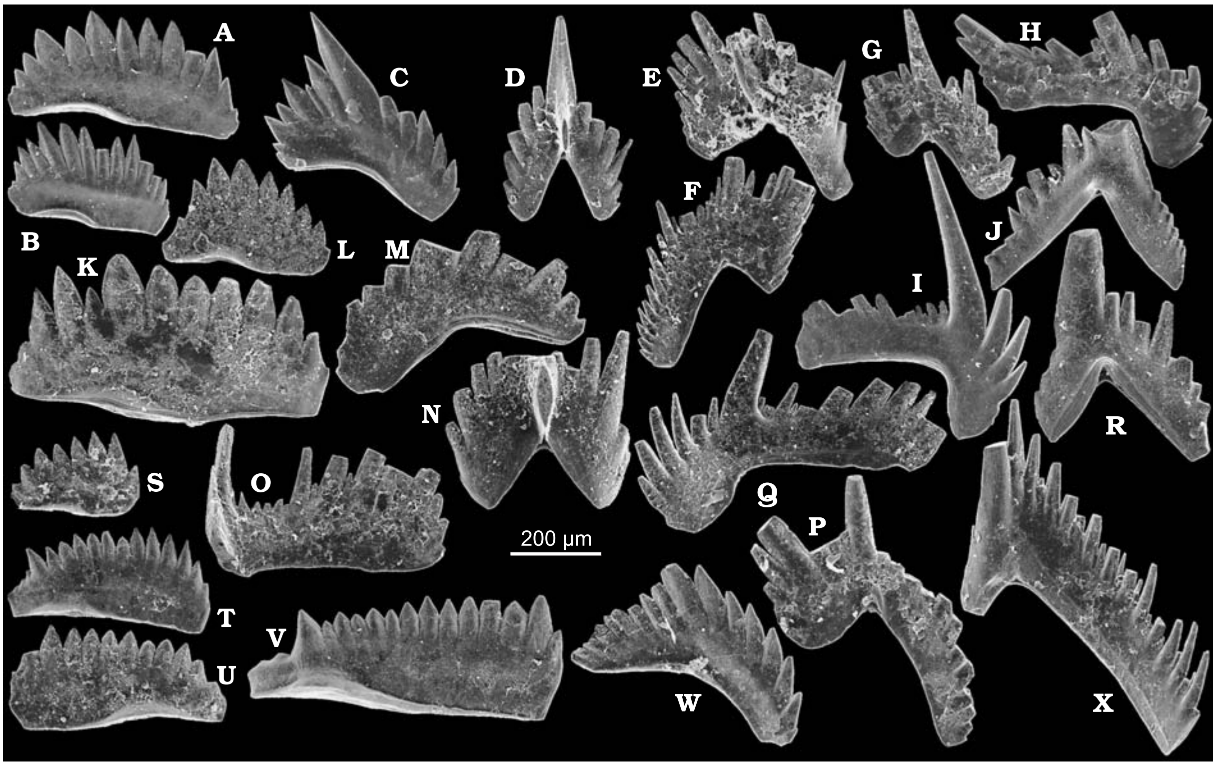


Fig. 37. Late species of the francodinid *Vogelgnathus* from the mid Famennian of the Holy Cross Mountains. **A**–**R**. *V. branmehloides* sp. n. from the *L. styriacus* Zone at Ostrówka (A–J, sample Ost-12) and the *P. jugosus* Zone at Jabłonna (K–R, bed 27). P_1 (A, B and K, L), P_2 (C and M), S_0 (D and N, O), S_1 (E), S_2 (F, G, and P), S_{3-4} (H–I and Q), and M (J and R) elements; specimens ZPAL cXVI/2059, 2056, 2060–2063, 2057, 2058, 2064–2066 (holotype, K), 2067–2073, respectively. **S**–**X**. *V. werneri* (Ziegler, 1962) from the *L. styriacus* Zone at Ostrówka (sample Ost-12). P_1 (S–V), P_2 (W?), and M (X?) elements; specimens ZPAL cXVI/2077, 2075, 2076, 2074, 2078, 2079, respectively.

Remarks. — The apparatus reconstruction of this species has been proposed by myself (Dzik 1991, fig. 12B) under the name *Pinacognathus*(?) sp. Its provisional taxonomic affiliation referred to the similarity of its P_1 elements to Carboniferous elements at that time classified in *Pinacognathus*, which later appeared to represent P_2 elements probably of *Siphonodella* (Dzik 1997). The M and S elements are closely similar to stratigraphically older *V. unicus*, being different only in bearing less numerous, usually not alternating denticles. But P_1 elements of these species are unlike each other, rather precluding any direct ancestor-descendant relationship.

Occurrence. — The *P. trachytera* to *P. jugosus* zones at Jabłonna, Kowala, Miedzianka, and Ostrówka.

Vogelgnathus werneri (Ziegler, 1962)
(Figs 37S–X and 125)

Type horizon and locality: Sample 1132 from the Hönnetal section in the Rhenish Slate Mountains, upper velifer Zone.

Material. — 959 specimens.

Diagnosis. — Conical cusp of P_1 element dominating over nearby denticles but lower than denticles near the end of ventral process; dorsal process with rudimentary denticles.

Remarks. — Minute elements indistinguishable from *Spathognathodus breviatus* Wang *et* Wang, 1978 co-occur with other ones typical of this species and probably also their type specimens are juveniles of this species. Already Van dem Boogard (1992) noticed a similarity of *Spathognathodus werneri* Ziegler, 1962 to *Vogelgnathus campbelli*. Apparatus composition of the species is poorly known and non-P_1 elements are here only provisionally attributed to it.

Occurrence. — From the *C. marginifera* Zone at Miedzianka to the *L. styriacus* Zone at Kowala, Ostrówka and Jabłonna. Ecologically associated with *V. branmehloides*. The species occurs also in the Dębnik area (Baliński 1995).

Genus ***Urbanekodina*** gen. n.

Type species: *Urbanekodina undata* sp. n. from the mid Famennian of the Holy Cross Mountains.

Derivation of name: After Adam Urbanek, to recognize his contribution to understanding the palaeobiology and evolution of colonial clonal organisms.

Diagnosis. — Minute elements with truncated processes.

Urbanekodina undata sp. n.
(Figs 38 and 125)

Holotype: Specimen ZPAL cXVI/2026 (Fig. 38B).

Type horizon and locality: Sample Md-8/9, mid Famennian *P. trachytera* Zone at Miedzianka, Holy Cross Mountains.

Derivation of name: Referring to undulating course of denticles in S elements.

Material. — 206 specimens.

Diagnosis. — As for the genus.

Remarks. — S elements of the apparatus of this species are superficially similar to juvenile homologous elements of the apparatus of the palmatolepidid *Conditolepis*, with which they co-occur. They differ in in-

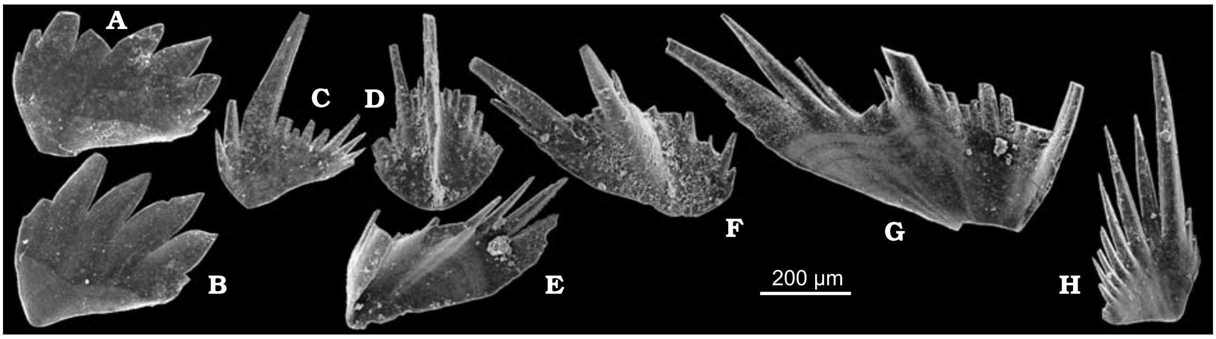


Fig. 38. Extremely paedomorphic francodinid *Urbanekodina undata* sp. n. from the *P. trachytera* Zone at Miedzianka (sample Md-8/9) in the Holy Cross Mountains. P_1 (A, B), P_2 (C), S_0 (D), S_1 (E), S_2 (F), S_{3-4} (G), and M (H) elements; specimens ZPAL cXVI/2025, 2026 (holotype, B), and 2027–2032, respectively.

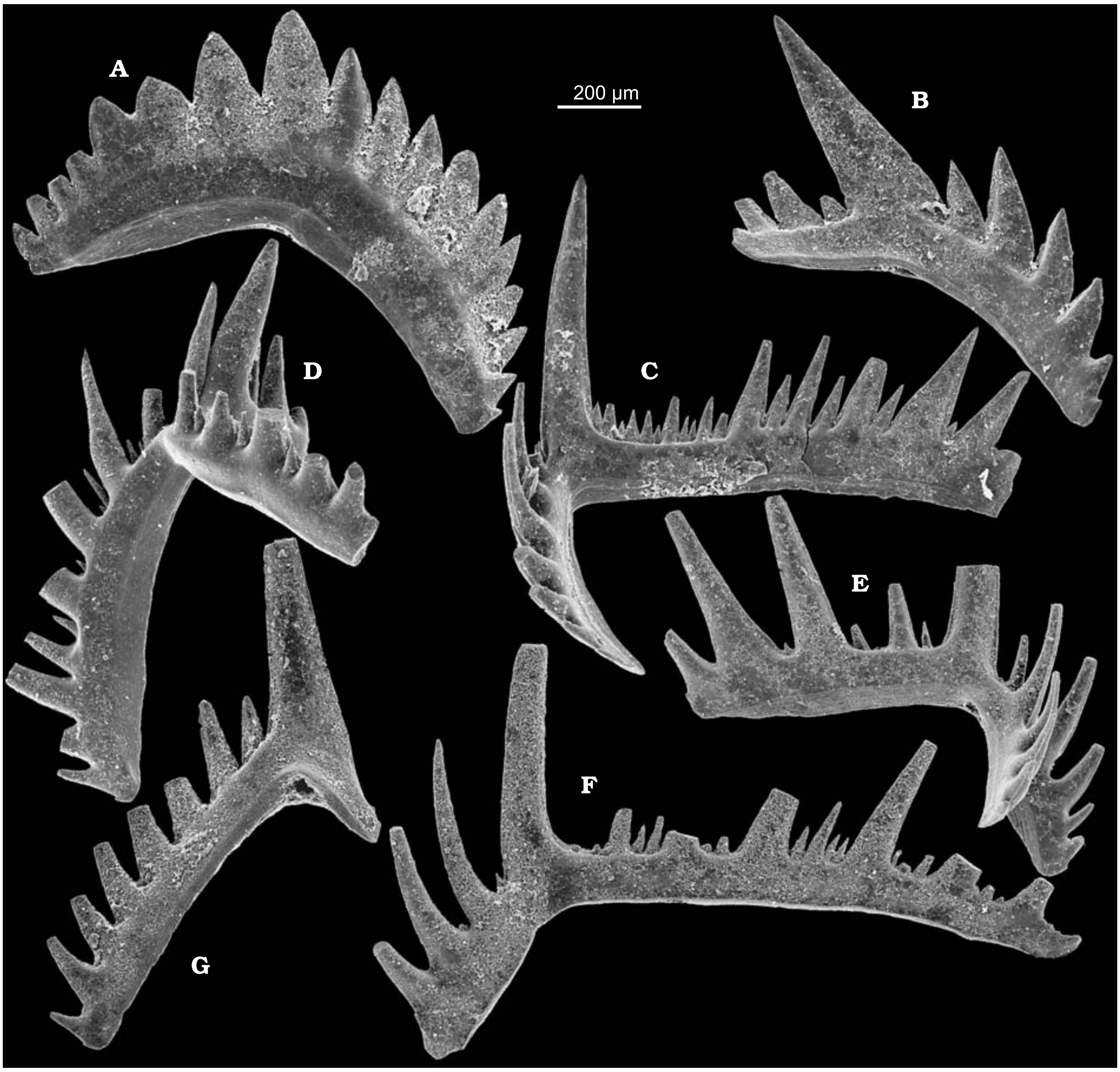


Fig. 39. Large-size francodinid *Francodina santacrucensis* sp. n. from the *K. crepida* Zone at Jabłonna (bed 8) in the Holy Cross Mountains. P_1 (A), P_2 (B), S_0 (C), S_1 (D), S_2 (E), S_{3-4} (F), and M (G) elements; specimens ZPAL cXVI/1756–1761 (holotype, E).

verse angular appearance, the external process being "truncated" in such a way that the first denticles are the largest in the row. The almost complete reduction of the medial process in S_0 elements is probably a paedomorphic feature. The origin of this bizarre conodont from *Vogelgnathus* seems likely but not proven. The alternative palmatolepidid relationship would require even deeper transformations.

Occurrence. — Possibly in the late *K. triangularis* Zone at Kowala, rare in all localities except for Miedzianka, ranging from the *C. quadrantinodosa* to *L. styriacus* Zone.

Genus ***Francodina*** gen. n.

Type species: *Ligonodina franconica* Sannemann, 1955 from the *Cheiloceras* Stufe of Frankenwald.

Derivation of name: After Frankenwald, from where most of the elements of the apparatus were first described by Sannemenn (1955*a*).

Diagnosis. — S_1 and S_2 elements in the apparatus triramous.

Remarks. — Morphology of P series and M elements of the oldest species of this genus is similar to that of *Vogelgnathus variabilis* sp. n., which appears somewhat earlier in the Holy Cross Mountains Famennian. Although the transition remains to be demonstrated, it seems likely. Poorly preserved specimens resembling

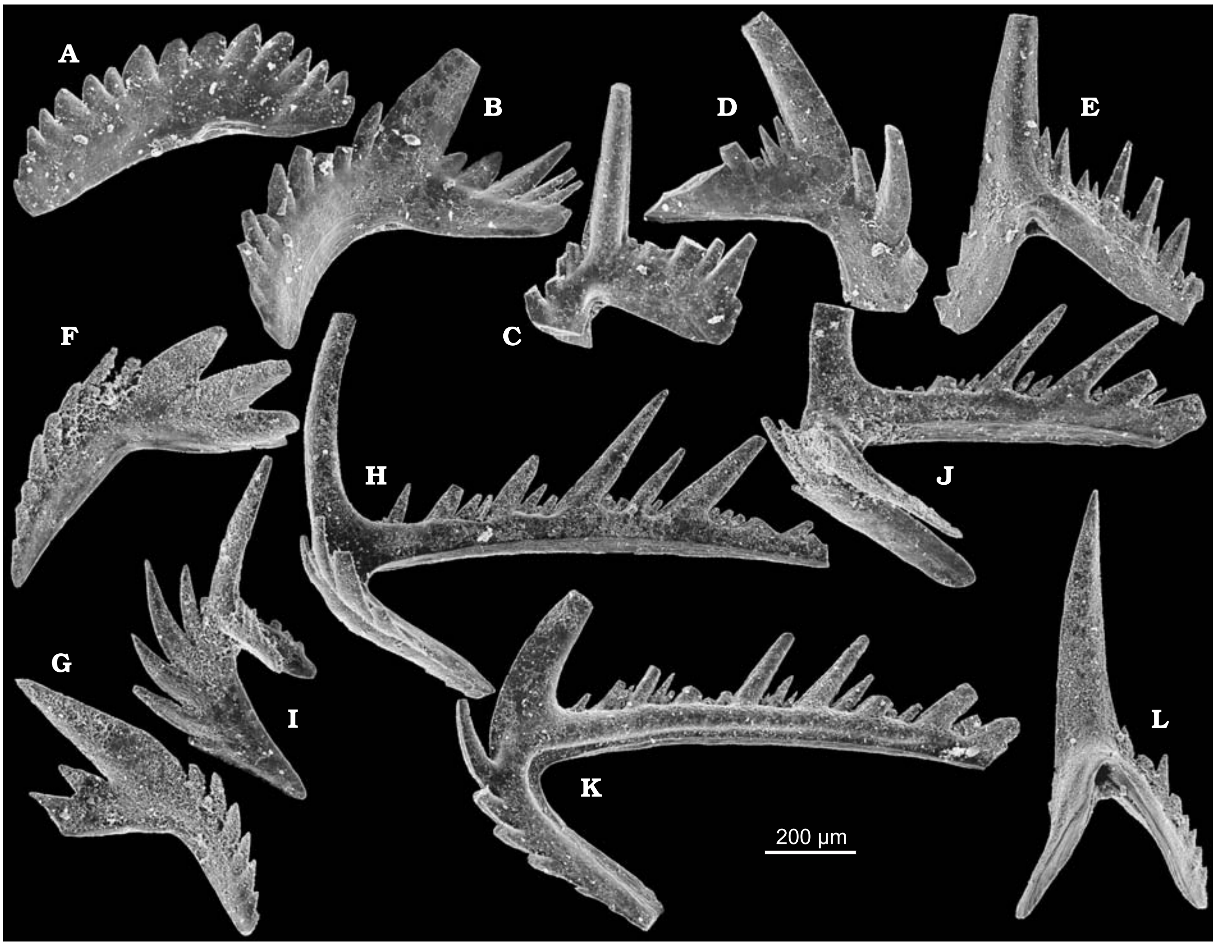


Fig. 40. Species of *Francodina* from the *K. crepida* Zone at Jabłonna in the Holy Cross Mountains. **A–E**. Population transitional between *F. santacrucensis* sp. n. and *F. franconica* (Sannemann, 1955) (sample J-46). P_1 (A), P_2 (B), S_1 (C), S_{3-4} (D), and M (E) elements; specimens ZPAL cXVI/1770–1774. **F–L**. *F. franconica* (Sannemann, 1955) (bed 8). P_1 (F), P_2 (G), S_0 (H), S_1 (I), S_2 (J), S_{3-4} (K), and M (L) elements; specimens ZPAL cXVI/1763–1769.

F. santacrucensis sp. n. occur at Wietrznia in sample Wtr-19 representing the late *K. triangularis* Zone. Triramous elements are missing among them and it is possible, although far from proven, that they represent the ancestral population of the lineage.

Francodina santacrucensis sp. n.
(Figs 39, 40A–E, and 126)

Holotype: Specimen ZPAL cXVI/1760 (Fig. 39E).

Type horizon and locality: Bed 8, early Famennian *K. crepida* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: From Latin name of the Holy Cross Mountains.

Material. — 1,121 specimens.

Diagnosis. — S elements with processes emerging under a wide angle.

Remarks. — Unlike the probably related species of *Vogelgnathus*, elements of *F. santacrucensis* are of large size, even as compared with the largest known conodonts of the Famennian. There seems to be an increase in mature size in the evolution of the lineage, probably a reversal from the tendency to paedomorphism, which was probably behind the origin of the branch of francodinids. *Pandorinellina*? *vogelgnathoides* sp. n. (Fig. 125) is somewhat similar to this oldest *Francodina* in showing a tendency to bifurcation of the external process of S_1 elements and arched contour of P_1 elements. Its S elements, however, are still of a rather generalized polygnathid appearance and the species is known from significantly younger strata.

Occurrence. — The *K. crepida* Zone at Jabłonna, Wietrznia, and Kadzielnia.

Francodina franconica (Sannemann, 1955)
(Figs 40F–L and 126)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955a).

Material. — 1,593 specimens.

Diagnosis. — M element with equal length of high-arched processes, external process of S elements strongly recurved.

Remarks. — Sannemann's (1955a) *Apatognathus inversus*, *Ligonodina franconica*, *Roundya franca*, *Tripodellus flexuosus* and Helms' (1959) *Roundya prava* and *Tripodellus tenuis* all were based on elements of the species, which are very characteristic and easy to identify even in association with other francodinids and prioniodinids. Elements of the P series are similar to each other in profile view but differ in curvature: P_1 elements are twisted whereas P_2 are laterally bent. S_1 element mimics elements of the palmatolepidid *Tripodellus*. The species co-occurs sympatrically for most of its range with *F. santacrucensis*, which is apparently more primitive and closer morphologically to the common ancestor. A possibly relic population transitional between them occurs at Jabłonna (J-46, Fig. 40A–E) and may represent another species of the genus.

Occurrence. — Possibly the latest *K. triangularis* Zone at Wietrznia; the *K. crepida* Zone at Jabłonna, Wietrznia and Kadzielnia.

Genus ***Sweetodina*** gen. n.

Type species: *Ligonodina monodentata* Bischoff *et* Ziegler, 1956 from the late Famennian of the limestone quarry NE Weitershausen.

Derivation of name: In recognition of the great contribution to the paleontology of conodonts by Walter C. Sweet (The Ohio State University, Columbus).

Diagnosis. — S elements with a tendency to planar disposition of processes, the external one pointed.

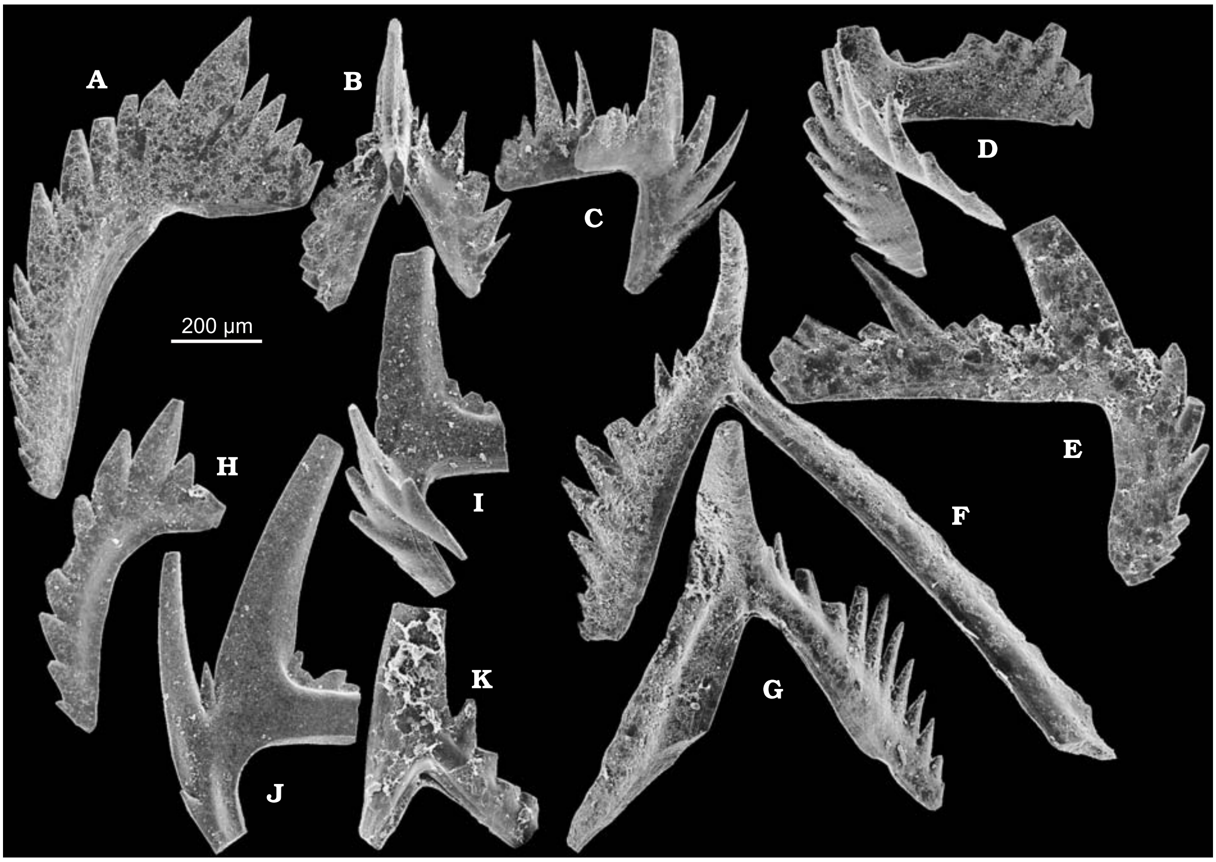


Fig. 41. Advanced francodinid *Sweetodina* from the late *K. crepida* Zone at Łagów in the Holy Cross Mountains. **A**–**G**. *S. lagoviensis* sp. n. (sample Ł-28). P_{1-2} (A), S_0 (B), S_1 (C), S_2 (D), S_{3-4} (E), and M (F, G) elements; specimens ZPAL cXVI/1787–1792 (holotype, F). **H**–**K**. Early population of *S. monodentata* (Bischoff and Ziegler, 1956) (sample ŁSł73-2). P_{1-2} (H), S_2 (I), S_{3-4} (J), and M (K) elements; specimens ZPAL cXVI/1793–1796.

Remarks. — Distinctions between element types of *Sweetodina* are obliterated by the unusualy high variability. There seems to be no morphologic difference between elements of the P series.

Sweetodina lagoviensis sp. n.
(Figs 41A–G and 126)

Holotype: Specimen ZPAL cXVI/1791 (Fig. 41F).

Type horizon and locality: Sample Ł-28, mid Famennian *C. quadrantinodosa* Zone at Łagów, Holy Cross Mountains.

Derivation of name: From latinized name of the type locality.

Material. — 436 specimens.

Diagnosis. — M element with elongated processes, the outer process ribbon-like, inner strongly denticulated.

Remarks. — This is probably a local, allopatrically developed species as it is preceded in the Łagów section by the less derived (in respect to M, but not S_3 element morphology) *S. monodentata* and succeeded by the same species in the region. The bizarre appearance of the M element makes it different from all other Devonian conodonts and only the similarity to *F. franconica* allows recognition of its affinity.

Occurrence. — The *C. quadrantinodosa* to *C. marginifera* (possibly *P. trachytera*) zones at Łagów and Miedzianka.

Sweetodina monodentata (Bischoff *et* Ziegler, 1956)
(Figs 41H–K, 42, and 126)

Type horizon and locality: Late Famennian limestone at quarry NE Weitershausen.

Material. — 480 specimens.

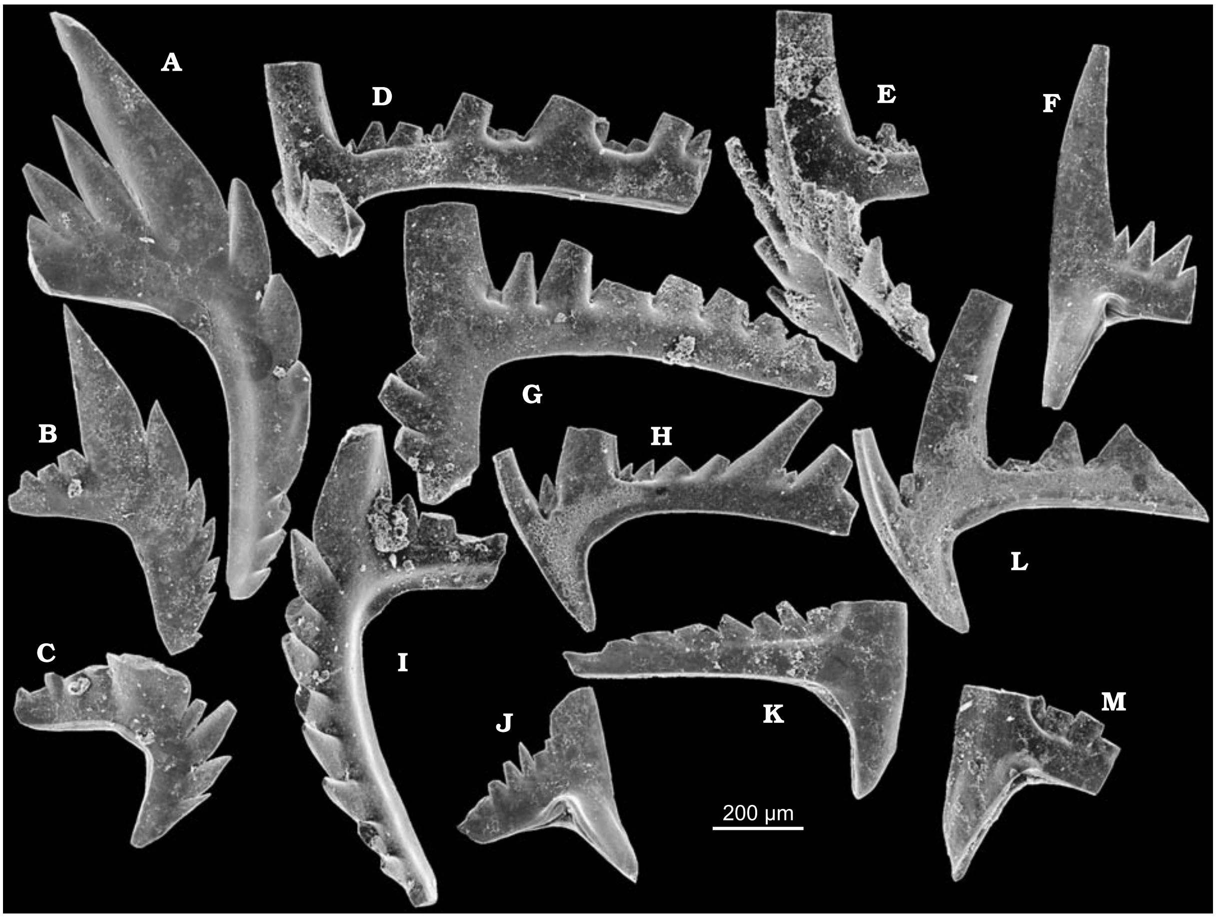


Fig. 42. Late populations of the francodinid *Sweetodina monodentata* (Bischoff *et* Ziegler, 1956) from the late *L. styriacus* Zone at Ściegnia (Wzdół Plebański; sample Wzd-13, A–C, F, J, K) in the Holy Cross Mountains and late *P. jugosus* and *D. trigonica* zones at Dzikowiec (sample Dz-8, D, E, Dz-7, G, I, J, and Dz-10, H) in the Sudetes. P_{1-2} (A–C, I), S_0 (D), S_{1-2} (E), S_3 (H and L), S_4 (K), and M (J and M) elements; specimens ZPAL cXVI/1863–1965, 1873, 1874, 1867, 1870, 1875, 1869, 1868, 1866, 1871, 1872, respectively.

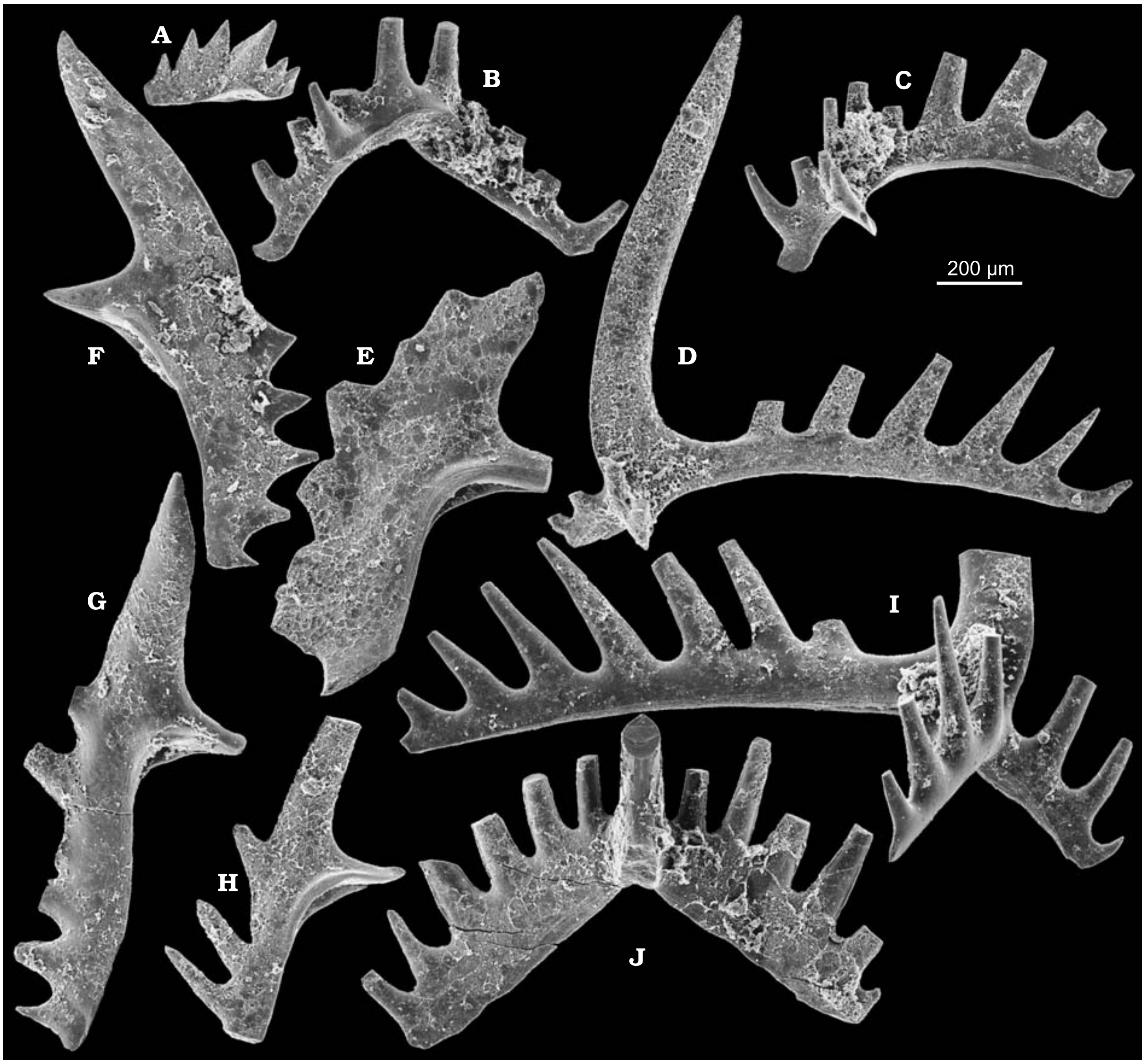


Fig. 43. The advanced francodinid *Planadina plana* (Helms, 1959) from the early *P. jugosus* Zone at Jabłonna (A, D, and F, bed 27), the *C. quadrantinodosa* Zone at Łagów (B, C, sample ŁSł73-5), and the *L. styriacus* Zone at Ostrówka (E, H, and J, sample Ost-5; G and I, sample Ost-12) in the Holy Cross Mountains. P_1 (A?), S_0 (J?), S_1 (B?), S_2 (C, I), S_{3-4} (D), and M (E–H) elements; specimens ZPAL cXVI/1776, 1779, 1780, 1777, 1783, 1778, 1785, 1782, 1784, and 1781, respectively.

Diagnosis. — M element with subequal length of short processes, outer process undenticulated and sharplz pointed, inner one with a few denticles; outer process of S_{3-4} elements with enlarged proximal denticle.

Remarks. — Along with the type species, also the types of *Ozarkodina homoarcuata* and *Neoprioniodus postinversus* of Helms (1959) belong to the same apparatus. The early population of the species from Łagów (Fig. 41H–K) differs from that of the late Famennian only in more highly arched processes of the M element, in this respect resembling probably ancestral *Francodina* and its successor, *S. lagoviensis*. Enlarged denticle in S_3 element indicates some degree of advancement so *S. lagoviensis* probably did not originate in place from this population but only shared with it common ancestry. That this element type represents only a single location in *S. monodentata* is suggested by the occurrence of similar elements lacking denticulation on the outer process and with denticles of the inner process almost uniform in size. They are thus transitional morphologically between S and M element types. Inner process in M elements is short and oriented almost perpendicular to the cusp in late populations.

Occurrence. — Probably the *C. quadrantinodosa* Zone at Kowala and Łagów, widespread from the *P. trachytera* Zone to the end of Famennian.

Genus *Planadina* gen. n.

Type species: *Roundya plana* Helms, 1959 from the *Platyclymenia annulata* Zone, Bohlen near Saalfeld.

Derivation of name: Taken from the name of the type species.

Diagnosis. — Triramous in all S elements, M element with strongly bent, ribbon-like external process and transversely oriented undenticulated inner process.

Remarks. — This genus is unusual in that the denticulated and elongated process in its M elements is not the inner one, as in virtually all other ozarkodinid and prioniodontid conodonts, but the outer one. Such a bizarre morphology can be explained if the ancestor of *Planadina* was like *Francodina franconica* or *Sweetodina lagoviensis* in this respect, that is with both processes elongated and bearing low and wide denticles. Especially the denticulation of the ribbon-like process in the latter species is appealing as a possibly ancestral state because it forms a kind of undulating ridge. A mysterious aspect of this apparatus is that no undoubted P series elements have been identified (except for one questionable specimen of small size; Fig. 43A). A possibility emerges that $P_{1–2}$ elements attained the same shape as the M elements. In fact some of them resemble platform series elements of *Sweetodina* (Fig. 43F).

Planadina plana (Helms, 1959)
(Figs 43 and 126)

Type horizon and locality: Bed 7 (“Wagner Bank”) of *Platyclymenia annulata* Zone, Bohlen near Saalfeld (Helms 1959).

Material. — 396 specimens.

Diagnosis. — As for the genus.

Remarks. — A single element of a rather robust appearance associated with those of *P. plana* (Fig. 43A) may or may not represent P series.

Occurrence. — Possibly the *K. crepida* Zone at Kadzielnia; widespread from the *C. marginifera* to *P. jugosus* zones at Łagów, Miedzianka, Ostrówka, Kowala, and Dzikowiec.

Family **Polygnathidae** Bassler, 1925

Diagnosis. — Triramous S_0 elements and narrow basal cavity of P_1 elements with a tendency to inversion, frequently connected with development of a platform; apparatus generalized.

Remarks. — The Polygnathidae originated at the beginning of the Devonian from *Ozarkodina*, a member of the Spathognathodontidae, by developing a medial process in S_0 elements and elongation of processes in other S elements. *Pandorinellina* probably represents this first lineage continued without significant changes to the Famennian.

Genus *Pandorinellina* Müller *et* Müller, 1957

Type species: *Pandorina insita* Stauffer, 1940 from the latest Givetian Lithograph City Formation of Minnesota (G. Klapper, personal communication 2005).

Diagnosis. — P_1 elements developing more or less expanded basal cavity with virtually flat surface, lacking platform; relatively high-arched M elements, other elements of a generalized polygnathid appearance.

Remarks. — *Hindeodontoides* of Rexroad and Merrill (1996), with the Viséan type species *H. spiculus*, is an alternative nomenclatorial option for species affiliated here in *Pandorinellina*. *Dasbergina* is rooted in the *Pandorinellina* lineage and the transition from *P. vulgaris* to *D. stabilis* seems to be continuous.

Pandorinellina? *vogelgnathoides* sp. n.
(Figs 44 and 125)

Holotype: Specimen ZPAL cXVI/1912 (Fig. 44A).

Type horizon and locality: Sample Ka-5, early Famennian *K. crepida* Zone at Kadzielnia, Holy Cross Mountains.

Derivation of name: Referring to similarity to *Vogelgnathus*.

Material. — 350 specimens.

Diagnosis. — Gently arched profile of P_1 elements at denticle tips, robust S elements with straight, rather short processes; high arched long processes of M element.

Remarks. — An almost complete set of elements of the species is offered by sample J-68 from Jabłonna. At first glance they are similar to non-platform elements of *Polygnathus* but no single specimen of this genus

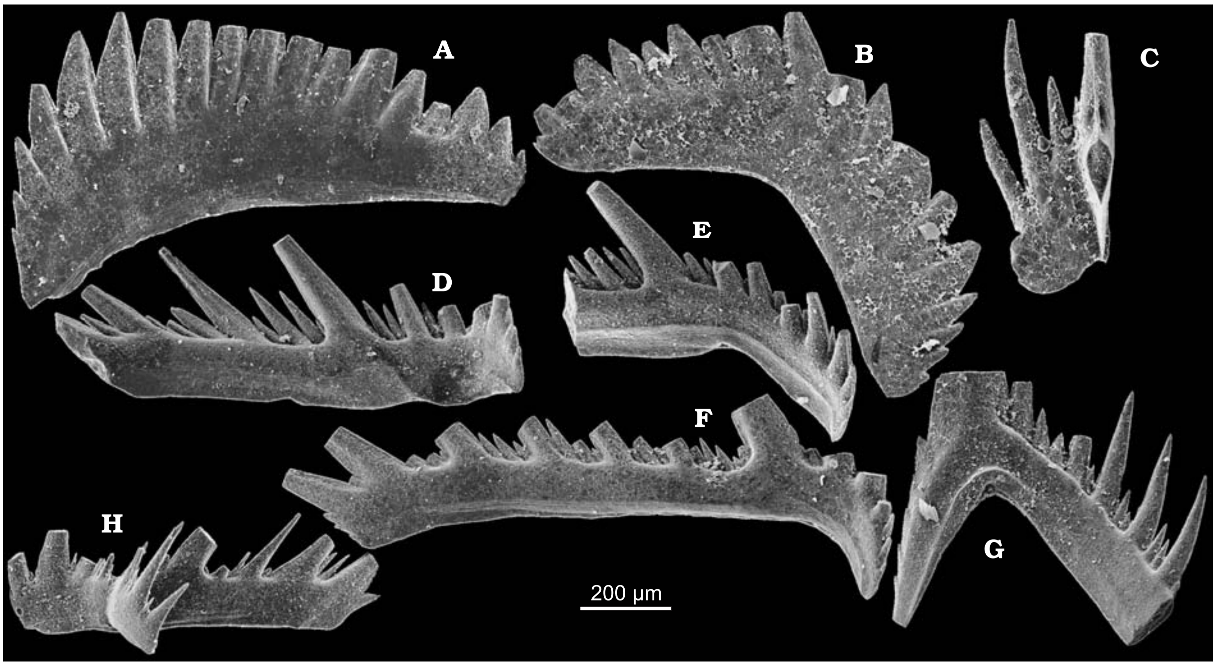


Fig. 44. Enigmathic non-platform polygnathid with possible francodinid affinities *Pandorinellina*? *vogelgnathoides* sp. n. from the *K. crepida* Zone at Kadzielnia (A–G, sample Ka-5; H, sample Ka-3) in the Holy Cross Mountains. P_1 (A), P_2 (B), S_0 (C), S_1 (D and H), S_2 (E), S_{3-4} (F), and M (G) elements; specimens ZPAL cXVI/1912–1918 (holotype, A), and 1903, respectively.

is represented in the sample. Much more numerous but high-diversity samples from Kadzielnia allow distinguishing probable P_1 and P_2 elements. The apparatus somewhat resembles that of the francodinids and generally short processes give it a paedomorphic appearance. The species cannot be ancestral to the first francodinid, *Vogelgnathus*, because of the large size of elements, their straight processes, and too young geological age. Among S_1 elements with short straight processes at Kadzielnia there are specimens with an additional process developing at the element bend. This is another francodinid feature and it cannot be excluded that *P.*? *vogelgnathoides* is a case of evolutionary reversal within the francodinids.

Occurrence. — The *K. crepida* Zone at Jabłonna and Kadzielnia.

Pandorinellina vulgaris sp. n.
(Figs 45A–L and 127)

Holotype: Specimen ZPAL cXVI/2181 (Fig. 45B).

Type horizon and locality: Bed 24, mid Famennian *P. trachytera* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: *Vulgaris*, usual, referring to its indifferent appearance and abundance.

Material. — 3,244 specimens.

Diagnosis. — Sharp denticles of P_1 elements of roughly similar height, basal cone with a willow leaf-like contour extending to about two thirds ot the dorsal process, rest of the base narrow.

Remarks. — The species differs from the Frasnian *P. insita* in the more regular distribution of height of denticles, which close to the dorsal tip are arranged in a gently convex profile. This character makes the species transitional to the *Protognathodus* and *Dasbergina* lineages. The associated *Alternognathus* at non-platform ontogenetic stages shows already a wide spacing in distribution of denticles in the dorsal part of the P_1 element.

The rather large sample Ost-12 shows mature P_1 elements with a robust appearance, the blade being somewhat thickened below denticles, but never developing a true platform. The basal cavity is very narrow. Juvenile specimens with their sharp denticles and flat appearance somewhat resemble *Mehlina*, as well as juveniles of the associated *Mehlina*. The main difference at this stage of ontogeny is in a denser and more irregular denticulation in *Mehlina transita*, which also relatively early developed an incipient platform and inverted basal cavity. Some P_1 specimens of *Branmehla* may also resemble this species but they show wider and shorter basal cavity and are more or less bent.

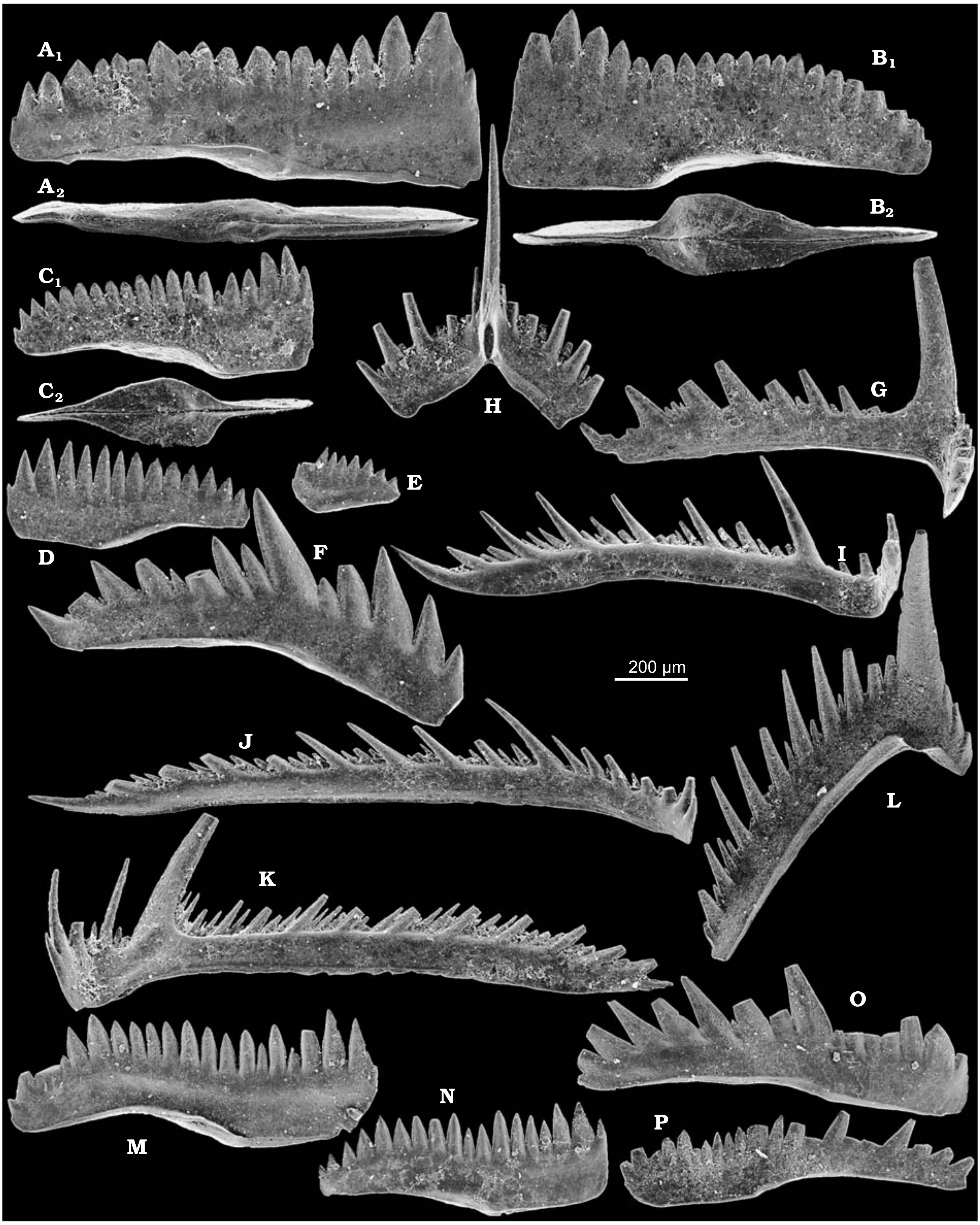


Fig. 45. Underived non-platform polygnathids *Pandorinellina* from the late Famennian of the Holy Cross Mountains. **A**–**L**. *P. vulgaris* sp. n. from the *P. trachytera* Zone at Jabłonna (bed 24). P_1 (A–E), P_2 (F), S_0 (G, H), S_1 (I), S_2 (J), S_{3-4} (K), and M (L) elements; specimens ZPAL cXVI/2180–2191 (holotype, B), respectively. **M**–**P**. *Pandorinellina fragilis* sp. n. from the *P. jugosus* Zone at Ostrówka (sample Ost-185) in the Holy Cross Mountains. P_1 (M, N) and P_2 (O, P) elements; specimens ZPAL cXVI/2192–2195 (holotype, P), respectively.

Occurrence. — The *C. marginifera* Zone at Łagów, the *P. trachytera* to *P. jugosus* zones at Jabłonna, Kowala, Miedzianka, Ostrówka, and Dzikowiec.

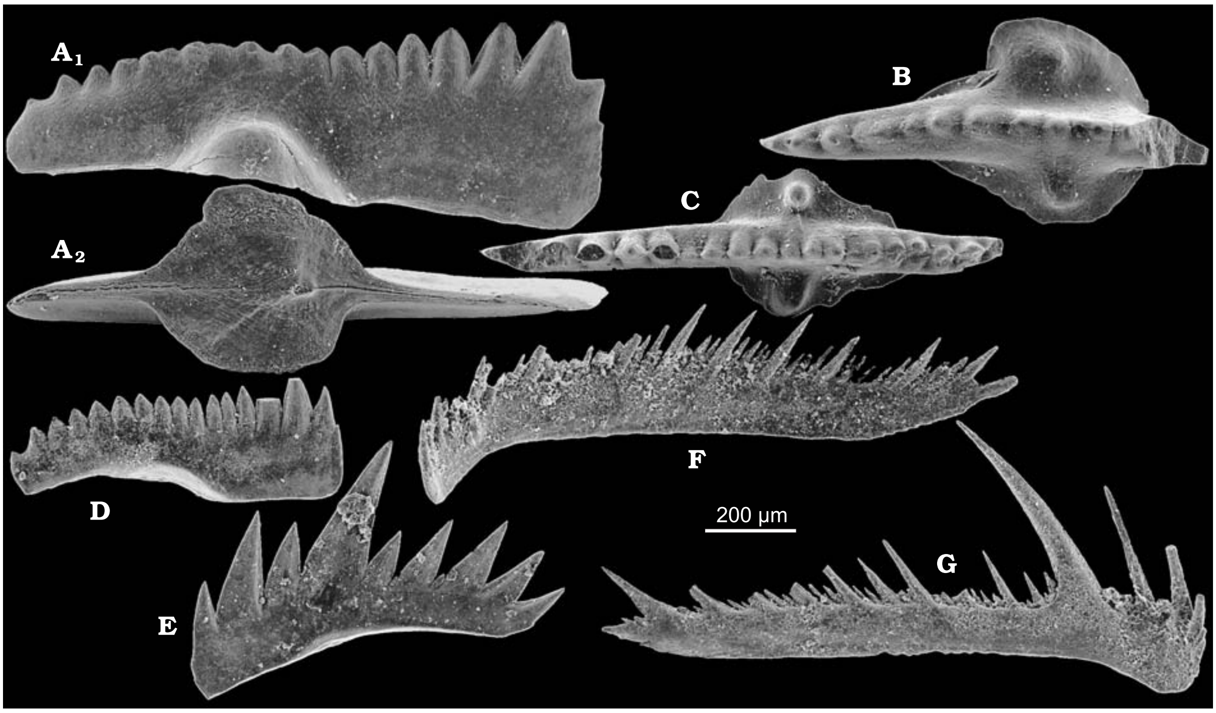


Fig. 46. Non-platform polygnathid *Pandorinellina bituberculata* sp. n. from the *P. jugosus* Zone at Jabłonna (sample J-51) in the Holy Cross Mountains. P_1 (A–D), P_2 (E), S_2 (F), and $S_{3–4}$ (G) elements; specimens ZPAL cXVI/2199–2205 (holotype, A), respectively.

Pandorinellina fragilis sp. n.
(Figs 45M–P and 127)

Holotype: Specimen ZPAL cXVI/2195 (Fig. 45P).

Type horizon and locality: Sample Ost-185, late Famennian *P. jugosus* Zone at Ostrówka, Holy Cross Mountains.

Derivation of name: Referring to fragility of specimens.

Material. — 219 specimens.

Diagnosis. — Extremely flat P_2 elements with irregular denticulation.

Remarks. — The species is closely similar to *P. vulgaris* and almost certainly is its successor. It is highly variable and single specimens may not be specifically determinable. These species seem to occur allopatrically.

Occurrence. — The late *P. jugosus* to early *D. trigonica* zones at Ostrówka.

Pandorinellina bituberculata sp. n.
(Figs 46 and 127)

Holotype: Specimen ZPAL cXVI/2199 (Fig. 46A).

Type horizon and locality: Sample J-51, late Famennian *P. jugosus* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: Referring to two tubercles developing on the base.

Material. — 49 specimens.

Diagnosis. — Robust blade of P_1 elements, mature elements tend to develop large tubercle on each side of the widened basal cone, which is subcircular in outline and restricted to the mid-length of the blade.

Remarks. — The species is another successor of *P. vulgaris* representing the opposite to the tendency in *P. fragilis* towards a robust appearance of all elements. Juveniles of the ancestor and successor are indinstinguishable and can be attributed to its species only on the basis of co-occurrence with adult specimens and geological age. Because of this, the species affiliation of the late Famennian populations of *Pandorinellina* known exclusively from immature specimens remains tentative. This is especially troublesome with the Kowala section, where acid treatment of limestone samples produces mostly juvenile specimens of *Pandorinellina*, whereas washing of the intercalating clay (e.g., Ko-131) supplies robust mature specimens. From unknown reason the population dynamics of the species depended on whether limy mud or fine clay was depos-

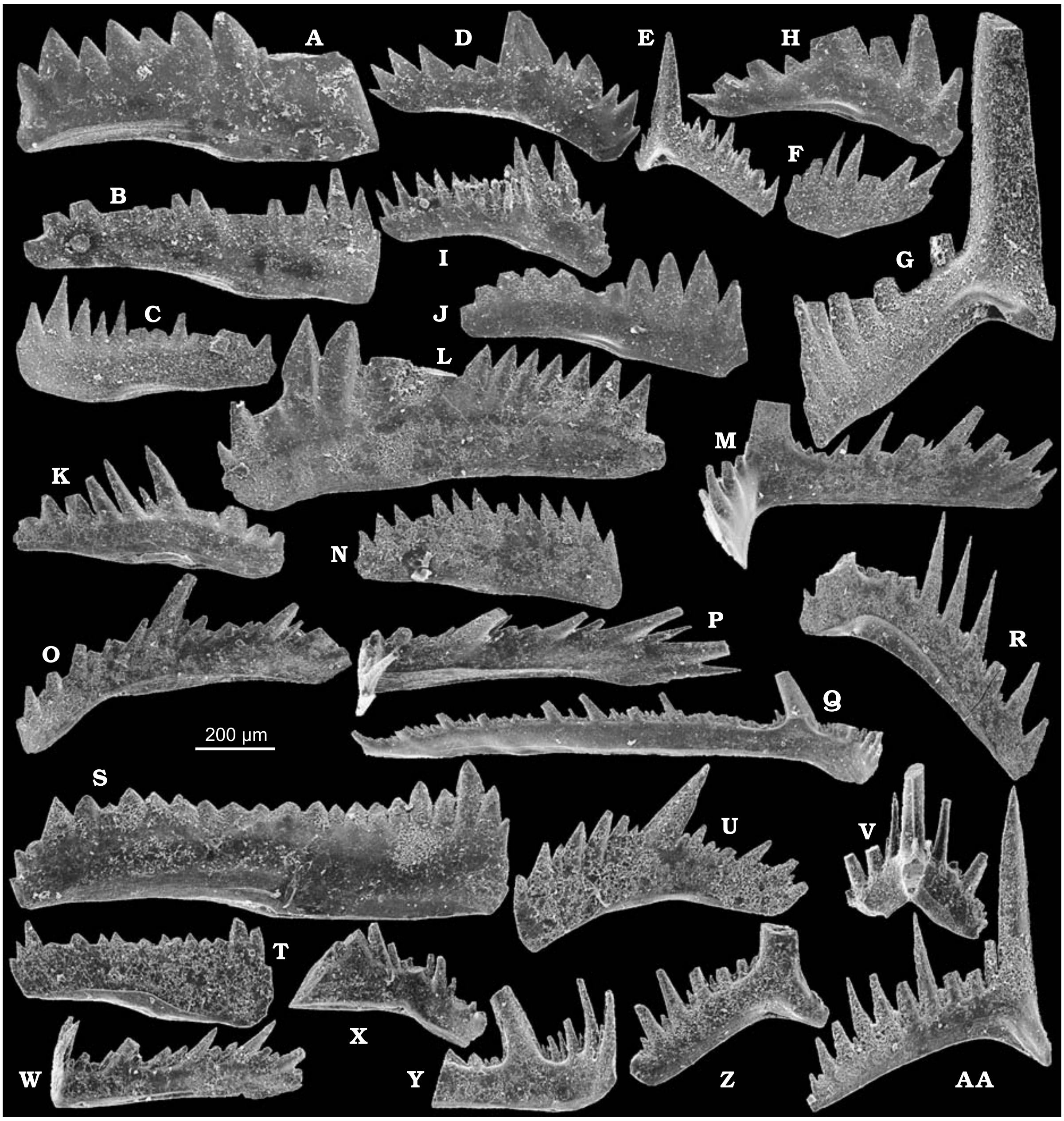


Fig. 47. Non-platform polygnathids *Mehlina*. **A**–**R**. *M. kielcensis* sp. n. from the *K. triangularis* Zone at Płucki (A–G, sample Pł-1) and Jabłonna (H, I, and J, sample J-53a), and the *K. crepida* Zone at Jabłonna (K–R, bed 3) in the Holy Cross Mountains. P_1 A–C, F, J–L, and N), P_2 (D, H, I, and K), S_0 (M), S_1 (P), S_2 (O), S_{3-4} (Q), and M (E, G, and R) elements; specimens ZPAL cXVI/2080–2082 (holotype, A), 2084, 2085, 2083, 2086, 2088, 2089, 2087, 2095, 2090, 2093, 2091, 2095, 2094, 2096, and 2097, respectively. **S**–**AA**. *Mehlina robustidentata* sp. n. from the *K. crepida* Zone at Jabłonna (S and BB, bed 8; U–AA, sample J-45a) in the Holy Cross Mountains. P_1 (S, T), P_2 (U), S_0 (V), S_1 (W), S_2 (X), S_{3-4} (Y), and M (Z and AA) elements; specimens ZPAL cXVI/2098 (holotype, S), 2100–2106, and 2099, respectively.

ited. Although the taxonomy of the *P. vulgaris*-group is inconveniently difficult to apply, the distinctions between species seems rather well substantiated.

Occurrence. — The *L. styriacus* to *P. jugosus* zones at Jabłonna, Ostrówka, Kowala, and Dzikowiec.

Genus *Mehlina* Youngquist, 1945

Type species: *Mehlina irregularis* Youngquist, 1945 from the late Frasnian Independence Shale (Amana Beds) of Iowa.

Diagnosis. — Polygnathids with very flat P_1 elements having extremely narrow basal cavity, inverted in later ontogeny, lacking platform; M elements with relatively short and transversely arranged inner process.

Remarks. — The morphologic distinction between *Pandorinellina* and *Mehlina* is far from being apparent and it is further obliterated by their population variability. Nevertheless, these are branches of platform-lacking polygnathids separate already in the Frasnian and throughout their stratigraphic occurrence giving rise to several lineages of conodonts with platform- or icrion-bearing P_1 elements. Even if practical application of their taxonomy may cause difficulties, it is reasonable to distinguish them at the generic level because of phylogentic consequences.

Mehlina kielcensis sp. n.
(Figs 47A–R and 127)

Holotype: Specimen ZPAL cXVI/2080 (Fig. 47A).

Type horizon and locality: Sample Pł-1, early Famennian *P. triangularis* Zone at Płucki, Holy Cross Mountains.

Derivation of name: From latinized name of Kielce, the capital of the Holy Cross Mountains region.

Material. — 527 specimens.

Diagnosis. — Mature P_1 with relatively few (10–15) denticles, all elements of generalized morphology.

Remarks. — This is the oldest member of the Famennian lineage of *Mehlina*. From its probable ancestor *M. irregularis*, it differs in having more robust and less numerous denticles in P_1 elements; the latter character makes it different from the successor, *M. robustidentata* sp. n. Despite a wide population variability, samples containing these species are relatively easily distinguishable on the basis of P_1 elements. A possibly related lineage is represented by *Vogelgnathus variabilis* (the oldest member of the Francodinidae; Fig. 125), different in a paedomorphic appearance and small size of elements.

Occurrence. — From the beginning of Famennian to the early *K. crepida* at Płucki, Jabłonna and Kadzielnia.

Mehlina robustidentata sp. n.
(Figs 47S–AA and 127)

Holotype: Specimen ZPAL cXVI/2098 (Fig. 47S).

Type horizon and locality: Bed 8, early Famennian *K. crepida* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: Referring to robust appearance of denticulation of the P_1 element.

Material. — 426 specimens.

Diagnosis. — P_1 element with numerous (15–20) robust denticles and long blade.

Remarks. — The species shows some similarities to *Alternognathus pseudostrigosus* from slightly younger strata (the oldest member of the Cavusgnathidae; Fig. 137) and may be its ancestor. The change would involve development of a somewhat irregular platform in the P_1 element.

Occurrence. — The late *K. crepida* to *C. marginifera* zones at Jabłonna and Łagów.

Mehlina strigosa (Branson *et* Mehl, 1934)
(Figs 48, 49D, E?, and 127)

Type horizon and locality: Famennian at Dixie, Missouri (Ziegler 1977, p. 313).

Material. — 2,050 specimens.

Diagnosis. — P_1 element with numerous (15–30) sharp-pointed denticles.

Remarks. — This is a highly variable species. From its predecessor, *M. robustidentata*, it differs not only in the pattern of denticulation but also in a tendency to develop somewhat widened flat basal cone in the P_1 element. In this respect it is somewhat similar to *Dasbergina stabilis*, from which it differs in the much higher sharp denticles on the dorsal process and, of course, the rest of the apparatus. Moreover, the widened basal cone of *Dasbergina* extends to the dorsal tip of the element. In P_1 elements of *Pandorinellina vulgaris* the basal cone is restricted to mid-length and is wide. Some extreme elements may be difficult to attribute to particular species of these genera. In fact only P_1 and M elements are diagnostic at the generic level.

S_1 elements with additional process (Fig. 48O) co-occurring with other elements of the species are tentatively attributed to it, but similar elements are also associated with *Dasbergina micropunctata* (Fig. 138). This issue remains to be clarified.

Occurrence. — Widespread in the late *C. marginifera* to *P. jugosus* zones of the Holy Cross Mountains.

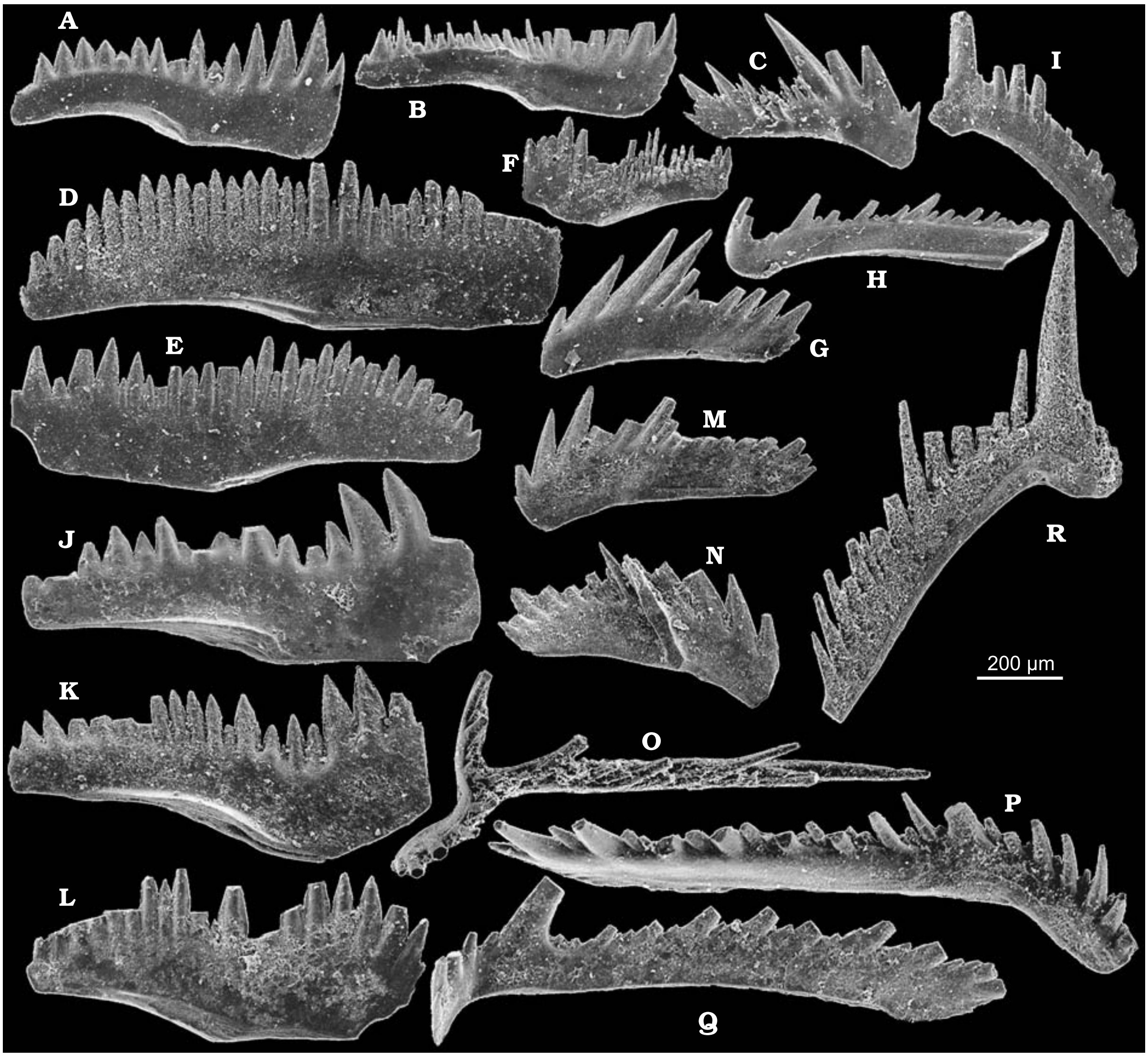


Fig. 48. Non-platform polygnathids *Mehlina strigosa* (Branson *et* Mehl, 1934) from the *P. trachytera* Zone at Kowala (A–C, sample Ko-15) and the *P. jugosus* Zone at Ostrówka (D–I, sample Ost-185) and Jabłonna (J–R, bed 27) in the Holy Cross Mountains. P_1 (A, B, DF, and J–L), P_2 (C, G, M, N), S_0 (M), S_1 (M and triramous O), S_2 (P), S_{3-4} (Q), and M (I and R) elements; specimens ZPAL cXVI/2107–2124, respectively.

Mehlina lunaria sp. n.
(Figs 49A, B and 127)

Holotype: Specimen ZPAL cXVI/2125 (Fig. 49A).

Type horizon and locality: Sample Ka-2, early Famennian *K. crepida* Zone at Kadzielnia, Holy Cross Mountains.

Derivation of name: Referring to semilunar outline of the element.

Material. — Two specimens.

Diagnosis. — Whole P_1 element transformed into elaborate peniculus built of bifurcating lateral processes radiating from the center of element.

Remarks. — This is a commonly occurring species with bizarre elements. Sannemann (1955a, pl. 1:10) reported it from the *K. crepida* Zone of the Frankenwald, Wolska (1967) from coeval strata at Jabłonna in the Holy Cross Mountains. At first glance it does not resemble a conodont at all. When seen from the base (Fig. 49A_3, B_2) it shows bifurcation of lateral processes that resulted in developing so unusual pattern of the peniculus. Also the basally pointed outline in lateral view is consistent with the characterictic appearance of P_1 elements of *Mehlina*. A peniculus developed widely in other members of the *Mehlina–Polynodosus* branch (Figs 47I, 48C, F, 49C–E, and 50A, G), as well as in the possibly related Frasnian *Ancyrodella*

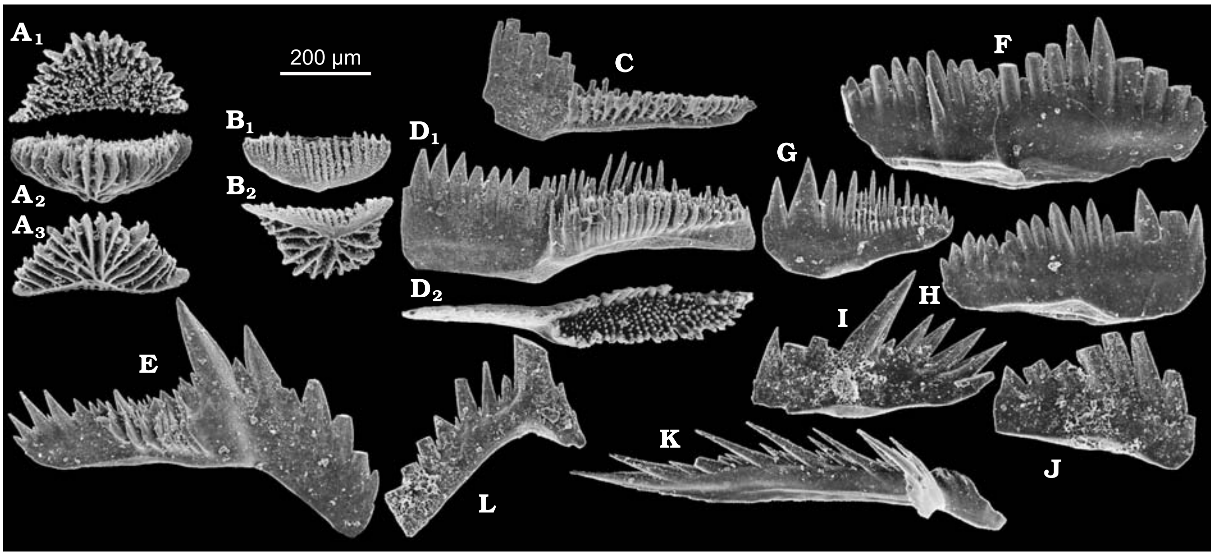


Fig. 49. Species of *Mehlina* bearing peniculus at adult stages and pathological polygnathid elements. **A**, **B**. *Mehlina lunaria* sp. n. from the *K. crepida* Zone at Kadzielnia (sample Ka-2). P_1 elements; specimens ZPAL cXVI/2125, 2126 (holotype, A). **C**–**E**. Extreme icrion-bearing elements of *Polynodosus transitus* sp. n. from the *P. trachytera* Zone at Jabłonna (C, bed 24) and *Mehlina strigosa* from the *C. quadrantinodosa* Zone at Miedzianka (D, E, sample Md-2). P_1 (D), P_2 (C and E); specimens ZPAL cXVI/2130, and 2178, 2179. **F**–**L**. *Mehlina sudetica* sp. n. from the *P. jugosus* Zone at Dzikowiec (F, L, sample Dz-10; G–K, sample Dz 54). P_1 (F–H), P_2 (I, J), S_1 (K), and M (L) elements; specimens ZPAL cXVI/2981, 2984, 2983 (holotype, H), 2985, 2986, and 2982, respectively.

(Lindström and Ziegler 1965) and the difference between them and *M. lunaria* is actually not great. An almost complete gradation can be assembled. The relatively stable morphology of P_1 elements of *M. lunaria* sp. n. (shown by both mine and earlier published specimens) and the morphologic gap between its morphology and variability expressed by other known peniculi indicates that this is a separate species.

Occurrence. — The *K. crepida* Zone at Kadzielnia.

Mehlina sudetica sp. n.
(Figs 49F–L and 127)

Holotype: Specimen ZPAL cXVI/2983 (Fig. 49H).

Type horizon and locality: Sample Dz-54, late Famennian *P. jugosus* Zone at Dzikowiec, Sudetes.

Derivation of name: From the Sudetes, where the type population occurs.

Material. — 285 specimens.

Diagnosis. — P_1 element with relatively short blade armed with numerous sharp but relatively robust denticles with a tendency to develop peniculus at late ontogenetic stages.

Remarks. — This is clearly a close relative and successor of *M. strigosa*. Co-occurrence of triramous S_1 elements may also be an expression of proximity to that species. The main difference is in P series elements, with P_1 element being more compact and robust than in *M. strigosa*, whereas in P_2 elements the tendency to develop peniculus seems to be not represented (not all specimens of *M. strigosa* show it).

Occurrence. — The *P. jugosus* and *D. trigonica* zones at Dzikowiec.

Genus ***Polynodosus*** Vorontzova, 1993

Type species: *Polygnathus nodocostata* Branson *et* Mehl, 1934 from the Famennian at Dixie or Noel (not specified) of Missouri (Branson and Mehl 1934, Helms 1961).

Diagnosis. — Platform of P_1 elements with tubercles tending to be arranged in ridges parallel to the blade, other elements robust, similar to those of *Mehlina*.

Remarks. — That *Polynodosus* is a derivative of *Mehlina* is suggested not only by the similarity of their apparatuses, in fact quite generalized, but also by the common development of a peniculus in at least some species (*P. nodoundatus* and *P. diversus*). There are at least four separate lineages within the genus. The least derived is represented by *P. transitus* and *P. lauriformis*, with relatively small and simple platform. In the lin-

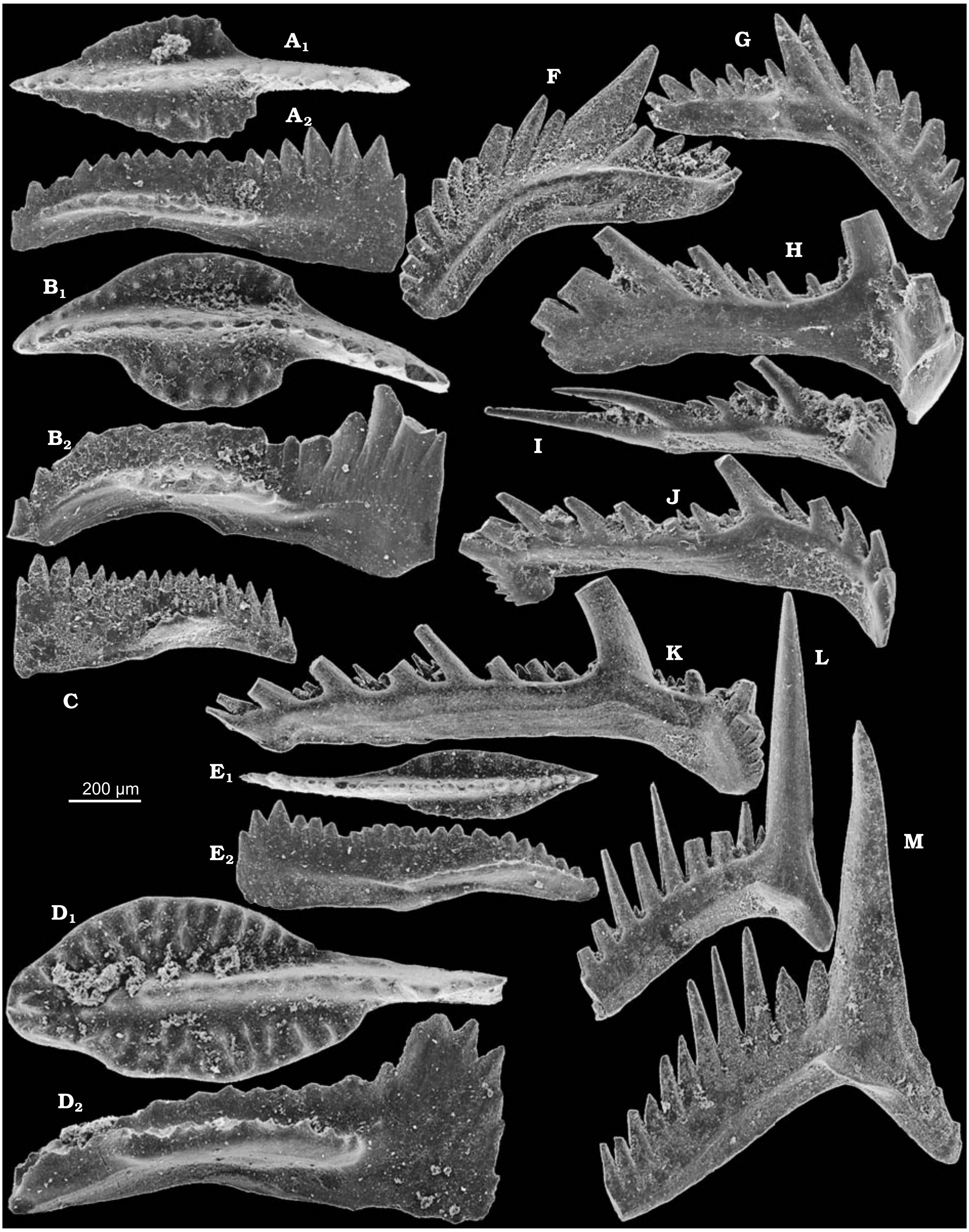


Fig. 50. Platform-bearing derivative of *Mehlina*, a population of robust *Polynodosus transitus* sp. n., including possible *P. lauriformis* (Dreesen *et* Dusar, 1974) (D, E), from the *C. quadrantinodosa* Zone at Łagów (sample Ł-26) in the Holy Cross Mountains. P_1 (A–E), P_2 (F, G), S_0 (H), S_1 (I), S_2 (J), $S_{3–4}$ (K), and M (L and M) elements; specimens ZPAL cXVI/2145 (holotype, A), 2144, 2146, 2156, 2155, 2147–2152, 2154, and 2153, respectively.

eage of *P. confluens* → *P. triphyllatus* the platform is extensive, and develops a constriction at mid-length. Even earlier in ontogeny the platform in the *P. diversus* → *P. nodoundatus* lineage originated. *P. perplexus* may or may not be a continuation of the latter, but the transition has not been traced. Probably it gave rise to

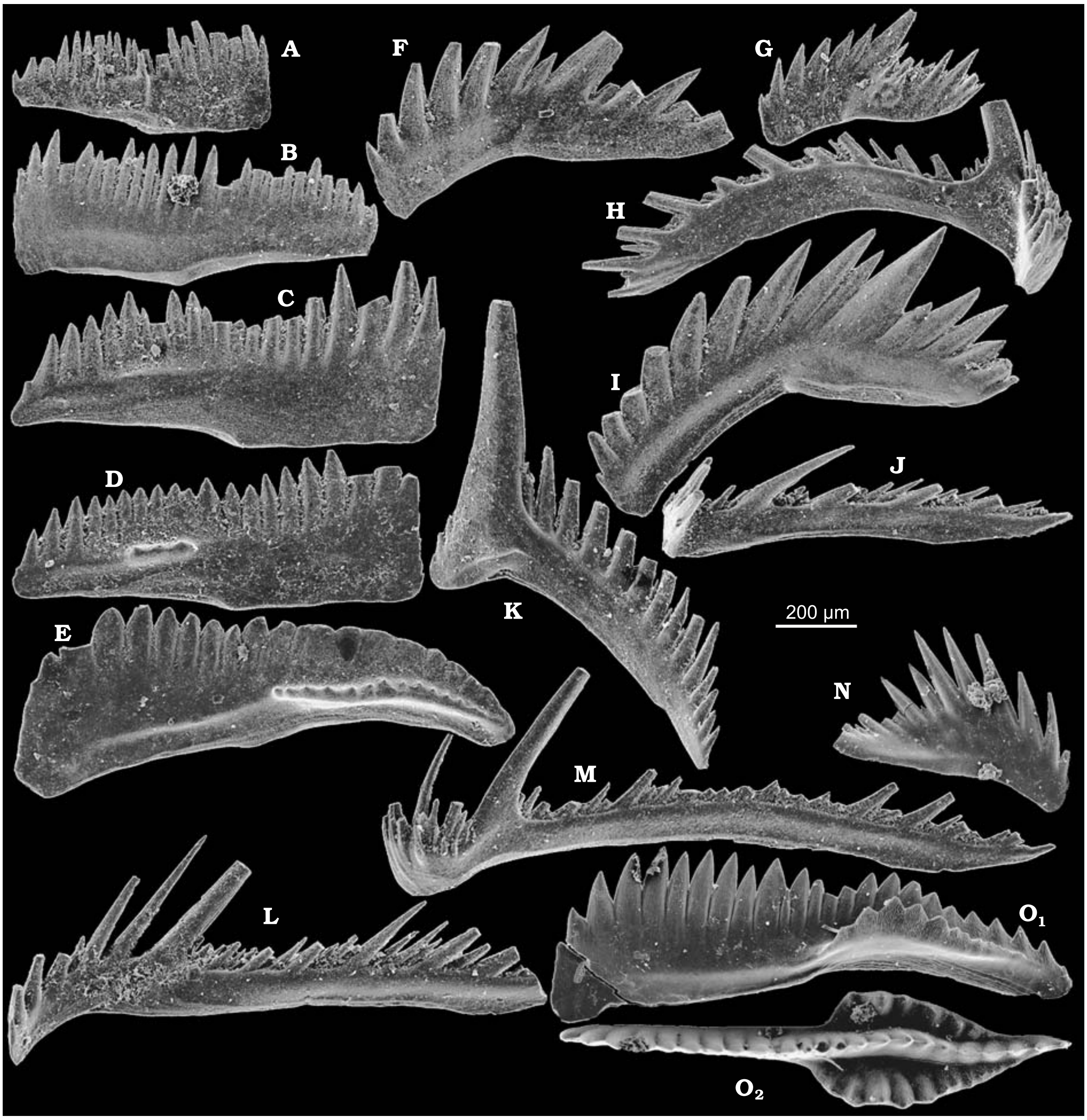


Fig. 51. Platform-bearing derivative of *Mehlina*, *Polynodosus* from the Famennian of the Holy Cross Mountains. **A**–**M**. Late population of gracile *Polynodosus transitus* sp. n. from the *P. trachytera* Zone at Jabłonna (bed 24). P_1 (A–E), P_2 (F, G, and I), S_0 (H), S_1 (J), S_2 (L), S_{3-4} (M), and M (K) elements; specimens ZPAL cXVI/2131–2135, 2137–2139, 2136, 2140, 2143, and 2141, 2142, respectively. **N**, **O**. *P. lauriformis* (Dreesen *et* Dusar, 1974) from the *L. styriacus* Zone at Ściegnia (sample Wzd-13). P_1 (O) and P_2 (N) elements; specimens ZPAL cXVI/2260 and 2259.

Hemilistrona, in which an elaborate platform developed in the P_1 elements. Late members of *Polynodosus* are almost homeomorphic to *Polygnathus* and they were earlier believed to originate from that lineage of ancient platform-bearing polygnathids.

Polynodosus transitus sp. n.
(Figs 50, 51A–M, and 127)

Holotype: Specimen ZPAL cXVI/2145 (Fig. 50A).

Type horizon and locality: Sample Ł-26, mid Famennian *C. quadrantinodosa* Zone at Łagów, Holy Cross Mountains.

Derivation of name: Referring to transitional position between *Mehlina* and *Polynodosus*.

Material. — 5,272 specimens.

Diagnosis. — Platform of the P_1 element of variable width, usually weakly developed and restricted to the middle part of the element, its dorsal tip sharply pointed.

Remarks. — This is a species of a generalized morphology and particular element types of closely similar morphology occur in several other polygnathids. It is the whole apparatus composition (*Mehlina*-like), not the P_1 element alone, that allows to distinguish it from, say, *Ctenopolygnathus angustidens*.

Juvenile specimens of the species are closely similar to those of *Mehlina* and an incipient platform developes relatively late in their ontogeny in a form of ridges at the middle height of the blade. The tendency to develop peniculus, so characteristic for *Mehlina* is apparent at early ontogenetic stages (Fig. 51A and C). The morphology of P_1 elements is very variable which makes delimitation of the species, both within samples and in respect to its stratigraphic range, difficult. From *M. lauriformis* (Dreesen *et* Dusar, 1974) probably representing a more advanced stage in the development of the lineage, it differs in having a heart-shaped outline of the platform. However, even in relatively early populations of *P. transitus*, specimens with elongated platform of laurus-leaf outline occur (Fig. 50D, E). They may or may not represent a separate species. In fact, the population from the Lower Łagów Beds is represented by a sample dominated by robust platform elements. Probably this is a result of low juvenile mortality, in opposition to the younger population from Jabłonna, where the platform is missing in most specimens of generally small size.

Polygnathus aff. *fallax* Helms *et* Wolska, 1967 from the *C. marginifera* Zone of Guangxi (Wang 1989, p. 110, pl. 39: 5) represents the same species.

Occurrence. — Widespread in the Holy Cross Mountains in the *C. quadrantinodosa* to *P. trachytera* zones.

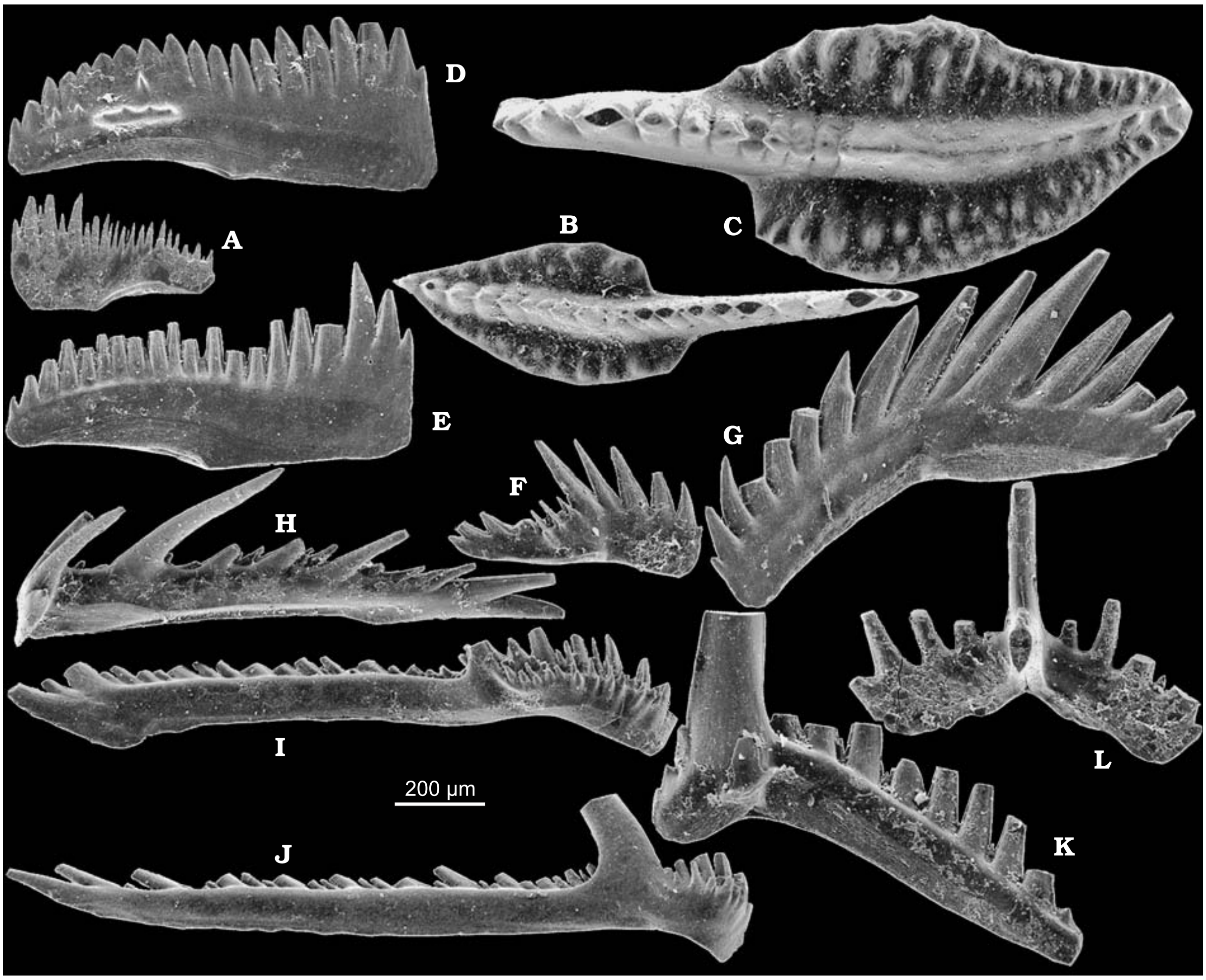


Fig. 52. Platform-bearing derivative of *Mehlina*, *Polynodosus lauriformis* (Dreesen *et* Dusar, 1974) from the *L. styriacus* Zone at Ostrówka (A–E and J, K, sample Ost 12; F–I and L, sample Ost 11) in the Holy Cross Mountains. P_1 (A–E), P_2 (F, G), S_0 (L), S_1 (H), S_2 (I), S_{3-4} (J), and M (K) elements; specimens ZPAL cXVI/2162, 2161, 2160, 2163, 2164, 2167, 2166, 2168–2170, 2165, and 2171, respectively.

Polynodosus lauriformis (Dreesen *et* Dusar, 1974)
(Figs 51N, O, 52, and 127)

Type horizon and locality: Sample 3 from the Hamoir Néblon supérieur section near Liege, Belgium (Dreesen and Dusar 1974).

Material. — 367 specimens.

Diagnosis. — Laurus leaf-shaped platform ornamented with nodes, restricted to its margin in juvenile specimens and covering the whole platform surface in adults.

Remarks. — From the coeval *Lagovignathus fallax* differs in the coarse ornamentation of the platform and the composition of the apparatus, from its probable ancestor *P. transitus* in a more regular outline of the platform. In samples Ł-24 and Ł-26 specimens morphologically indistinguishable from *P. lauriformis* (Fig. 50D–F) co-occur with those of *P. transitus* and transitional specimens are rare. Whether these are sympatric species or just a case of population variability, remains to be clarified. There is a possibility that *P. lauriformis* is a more off-shore counterpart of *P. transitus*.

Occurrence. — From the *C. marginifera* to *L. styriacus* zones at Kowala, Wzdół, Miedzianka, and Ostrówka.

Polynodosus confluens (Ulrich *et* Bassler, 1926)
(Fig. 53)

Type horizon and locality: "Hardin sandstone" near Mount Pleasant, Tennessee (Huddle 1968).

Material. — 1,011 specimens.

Diagnosis. — Platform of P_1 elements leaf-like in outline and slightly constricted at mid-length, bears more or less distinctly developed ridges parallel to the blade in its ventral part and is uniformly tuberculated in the dorsal part; P_2 elements robust but with peniculus at early stages.

Remarks. — The apparent separation of the dorsal part of the platform from the ventral part by an incipient constriction, visible in the topotype material (Huddle 1968, pl. 141-4), leaves little doubt that this is a relative of *P. triphyllatus*. Peniculus and platform with rows of tubercles parallel to the blade in juveniles (Fig. 53B and F) disclose affinities with *Polynodosus transitus*. The similarity of adult P_1 specimens to those of *Polylophodonta* is thus only convergent.

In the Holy Cross Mountains and Thuringian samples from the early *Cheiloceras* Stufe, together with specimens closely similar to the lectotype another morphotypes occur, classified by Helms (1961) in his *Polygnathus flaccida*. Such forms have not been illustrated by Huddle (1968) among the topotype American specimens. This may be due to the small number of exclusively mature specimens rpresented in his sample. In fact, the incompletely preserved holotype of *Polygnathus pennatuloideus* of Holmes (1928), co-occurring with *P. confluens* in the Chattanooga Shale near Huntsville, Alabama may represent a robustly ornamented morphotype of the same population.

There is a possibility of somewhat bimodal (dimorphic) distribution of morphologies of this element but it is obscured by a very wide range of population variability. Possibly the specimens with finely tuberculated dorsal part of the platform are counterpairs of those with wide strongly ribbed platform but there is a common reversal in asymmetry within the pair.

Occurrence. — The *K. crepida* Zone at Kadzielnia and Kowala.

Polynodosus triphyllatus (Ziegler, 1962)
(Figs 54A–I and 128)

Type horizon and locality: Pebble in the late Permian conglomerate of Rossenray in the Rhenish Slate Mountains.

Material. — 1,106 specimens.

Diagnosis. — Platform of P_1 element strongly constricted in the midlength.

Remarks. — According to Helms (1961) and Vorontzova (1993) a few chronospecies of polygnathids with ornate platform preceded this species in its lineage. In my material there seems to be a continuity between *P. confluens* and *P. triphyllatus* and gradual increase in depth of platform constriction, the character highly variable within each sample.

Juvenile elements described as *Polygnathus* cf. *P. diversus* by Metzger (1994), who identified P_2 elements and illustrated their ontogeny, probably belong to a population transitional between *P. confluens* and *P. triphyllatus*, as suggested by co-occurrence with mature P_1 elements.

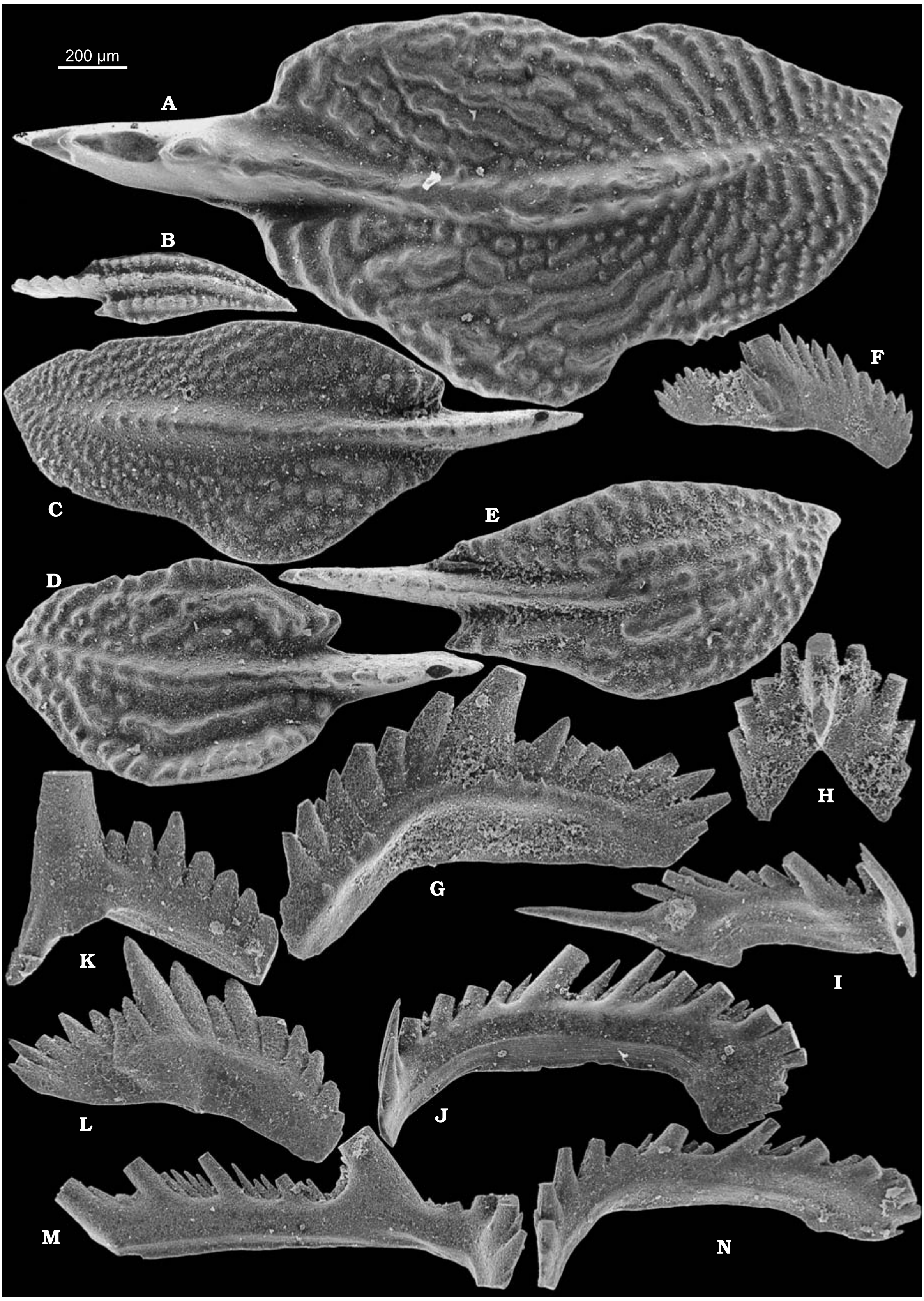


Fig. 53. Elaborate platform-bearing *Polynodosus confluens* (Ulrich *et* Bassler, 1926) from the *K. crepida* Zone at Kadzielnia (A and J, sample Ka-7; B and D, sample Ka-6; C, E–I, K, L, and N, sample Ka-4; M, sample Ka-10) in the Holy Cross Mountains. P_1 (A–E), P_2 (F, G, and L), S_0 (H), S_1 (I), S_2 (J and N), S_{3-4} (M), and M (K) elements; specimens ZPAL cXVI/2634, 2630, 2621, 2631, 2624, 2622, 2623, 2625, 2626, 2633, 2628, 2629, 2632, and 2627, respectively.

Nomenclatorial problems connected with this species have been discussed by Glenister and Klapper (1966, p. 834).

Occurrence. — The *C. quadrantinodosa* to *C. marginifera* zones at Kowala, Łagów and Miedzianka.

Polynodosus nodoundatus (Helms, 1961)
(Figs 54M–O and 128)

Type horizon and locality: Grey, thick-bedded limestone of the *Prolobites* Zone at Großen Buschteich near Rödersdorf, Thuringia (Helms 1961).

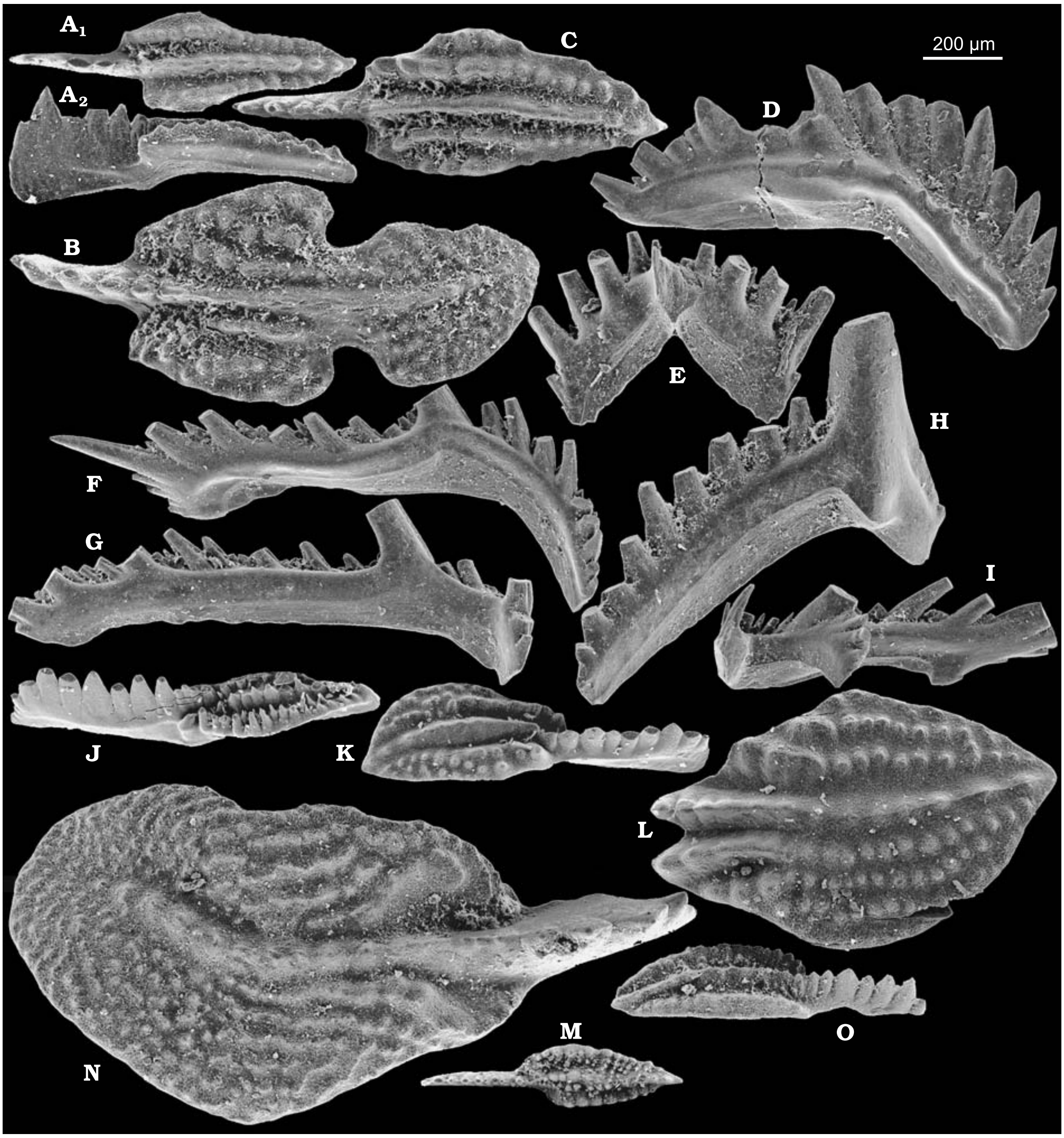


Fig. 54. Advanced species of *Polynodosus*. **A**–**I**. *P. triphyllatus* (Ziegler, 1960) from the *C. quadrantinodosa* Zone at Łagów (A, B, sample Ł-26; C–I, sample Ł-27) in the Holy Cross Mountains. P_1 (A–C), P_2 (D), S_0 (E), S_1 (aberrant with additional process, I), S_2 (F), S_{3-4} (G), and M (H) elements; specimens ZPAL cXVI/2157, 2158, 2496–2500, 2502, and 2501, respectively. **J**–**L**. *Polynodosus diversus* (Helms, 1959) from the *L. styriacus* Zone at Miedzianka (sample Md-14). P_1 elements; specimens ZPAL cXVI/2635–2637, respectively. **M**–**O**. *Polynodosus nodoundatus* (Helms, 1961) from the *C. quadrantinodosa* Zone at Łagów (sample ŁSł73-3). P_1 elements; specimens ZPAL cXVI/2638, 2640, and 2639, respectively.

Material. — 276 specimens.

Diagnosis. — Blunt apex of widened platform in mature P_1 element tending to develop a depression in the middle, ornamented with irregularly distributed tubercles.

Remarks. — In no sample available to me is the species the only platform-bearing polygnathid and is almost always subordinate in number. Only in sample Md-12 a significant number of P_1 elements have been encountered. They co-occur with robust P_2 elements of morphology indistinguishable from those attributed to *P. triphyllatus*. This speaks in favor of the proposed generic affiliation of *P. nodoundatus*. Presumably this is another derivartive of *P. confluens*.

Occurrence. — The *C. marginifera* Zone at Łagów, Kowala, Miedzianka, and Ostrówka.

Polynodosus diversus (Helms, 1959)
(Figs 54J–L and 128)

Type horizon and locality: With *S. velifer* 4.5 m below the top of bed 5 at Bohlen near Saalfeld, Thuringia (Helms 1959).

Material. — 58 specimens.

Diagnosis. — Juvenile P_1 elements with a robust peniculus, mature elements with rows of parallel nodes along the oval platform with greatest width in its dorsal part.

Remarks. — Only subadult specimens of the species have been known previously (Helms 1959; Austin *et al*. 1985), but in sample Md-14 from Miedzianka there is a gradation from morphs with a rather narrow platform to fragmentary large specimens with multiple rows of denticles. The species may be related to *P. nodoundatus*.

Occurrence. — The *C. marginifera* and *L. styriacus* Zone at Miedzianka.

Genus ***Ctenopolygnathus*** Müller *et* Müller, 1957

Type species: *Polygnathus angustidiscus* Youngquist, 1945 from the Frasnian Independence Shale of Iowa.

Diagnosis. — Polygnathids with robustly appearing platform that does not reach the dorsal ("posterior") tip in most of the P_1 elements even at late ontogenetic stages.

Remarks. — The morphology of *Ctenopolygnathus* is so simple and underived that there is a great chance of its convergent origin. If this is true, the only guide to taxonomic identity of species included in the genus is their stratophenetically traced relationship to the type species.

Bardashev *et al*. (2002) introduced several generic rank names for early polygnathids, defined on the morphology of the platform in P_1 elements, without reference to the apparatus composition. They are apparently understood as polyphyletic grades in the evolution of the branch. Among them is the redefined *Ctenopolygnathus* in a meaning rather fundamentally different from that applied by myself (Dzik 2002).

Ctenopolygnathus brevilamina (Branson *et* Mehl, 1934)
(Figs 55, 56, and 129)

Type horizon and locality: Early Famennian at Dixie and Noel, Missouri (Branson and Mehl 1934, p. 246).

Material. — 933 specimens.

Diagnosis. — P_1 elements with subparallel margins of the platform almost approaching the tip of the blade in mature specimens.

Remarks. — This species was earlier illustrated by myself (Dzik 2002) as *Ctenopolygnathus* sp. A from the Kellwasserakalk and *C*. sp. B from the basal Famennian at Płucki. Non-platform elements of the apparatus are of a rather primitive morphology, with short processes. Their growth was terminal, as indicated by hooked tips of processes, but termination may have taken place at very different sizes. Generally, species of *Ctenopolygnathus* are extremely variable and their identification requires samples with many specimens. The Frasnian *P. angustidiscus* had a generally shorter and even more variable platform of P_1 elements. However, even in *C. brevilamina* there are specimens which did not develop platform even late in their ontogeny (Fig. 56A), others have a wide platform resembling that of *Immognathus* (Fig. 56K). Quite frequently the dorsal tip of the element, which lacks a platform, developed a prominent denticulation of the blade.

The unstable morphology of elements of the apparatus suggests that *Ctenopolygnathus* originated by paedomorphosis, possibly from rather advanced polygnathids. In its Famennian evolution the original derived status seems to be partially re-established.

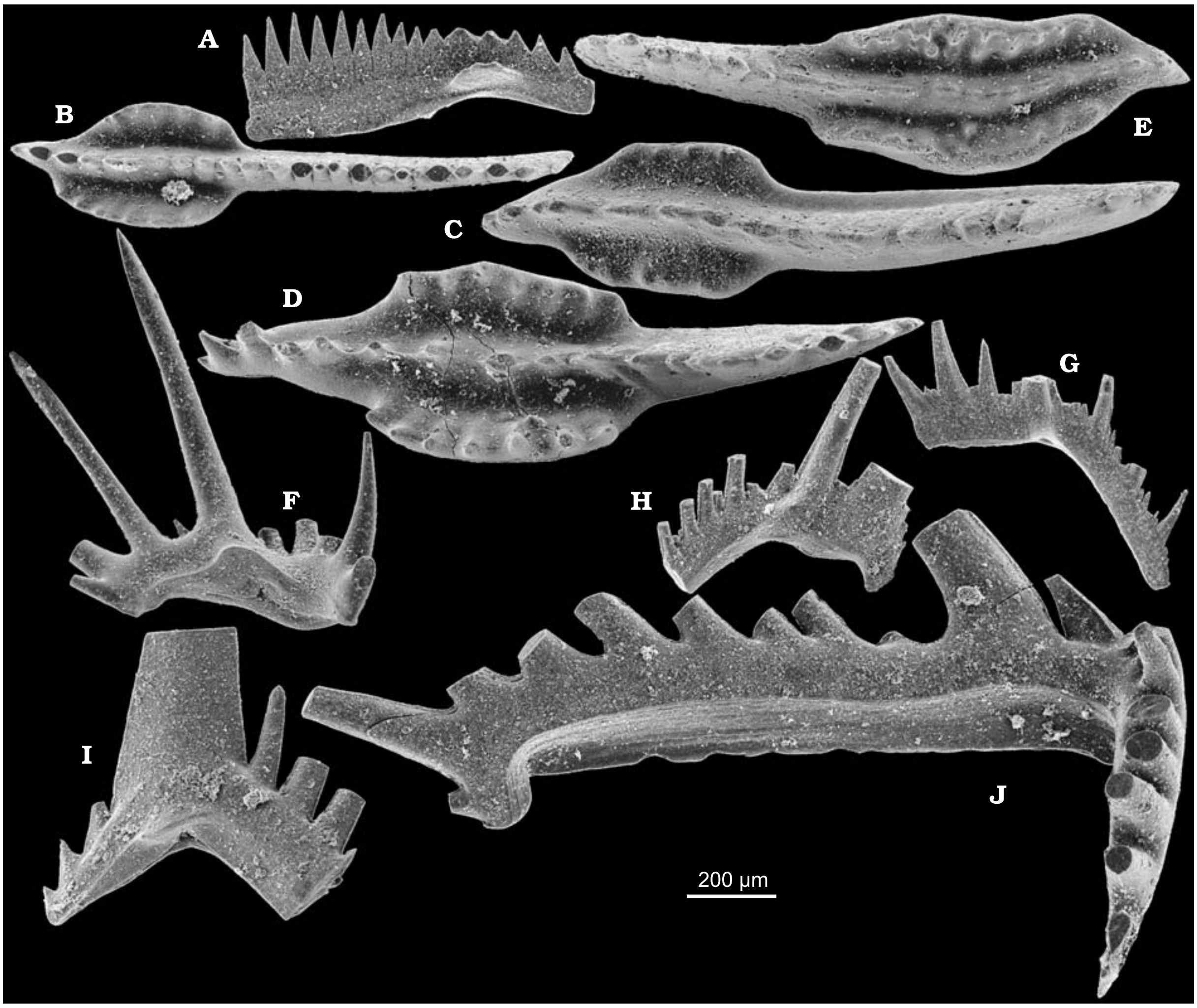


Fig. 55. *Ctenopolygnathus brevilamina* (Branson *et* Mehl, 1934), a polygnathid with probably secondarily reduced platform and paedomorphic appearance of elements, from the *K. triangularis* Zone at Płucki (sample Pł-1) in the Holy Cross Mountains. P_1 (A–E), S_1 (F), S_2 (G, H), S_{3-4} (J), and M (I) elements; specimens ZPAL cXVI/2393–2401 (holotype, E), and 2392, respectively.

Occurrence. — From the top of the Frasnian at Płucki to the *K. crepida* Zone at Jabłonna, Wietrznia and Kadzielnia; possibly also in younger strata at Ostrówka. The species was probably widespread in the early Famennian; it occurs also in the Dębnik area (Baliński 1995).

Genus ***Immognathus*** gen. n.

Type species: *Polygnathus streeli* Dreesen, Dusar *et* Groessens, 1976 from the costatus Zone of Belgium.

Derivation of name: In recognition of contribution of Immo Schülke to knowledge of apparatuses and evolution of the Famennian conodonts.

Diagnosis. — S_1 element with additional ventral process, P_1 elements tend to develop a relatively wide, flat or inverted basal cavity delimited by an escarpment extending to the element tip.

Remarks. — As shown by the apparatus structure, the similarity to the *Alternognathus* lineage in the form of the basal cavity of P_1 elements is a case of homeomorphy. *Immognathus* is probably a direct successor of the *Ctenopolygnathus* lineage and in the oldest samples (e.g., J-42) transitional morphologies of P_1 elements between these genera occur, that is the platform does not reach the element tip in juveniles and the basal cavity may be rather small and narrow in the same elements. Such elements are associated (e.g., sample J-44) with S_1 elements showing an additional ventral process. Notably, in the somewhat older bed 7 closely similar platform elements are associated with S_1 elements of *Ctenopolygnathus* morphology. This suggests that an evolutionary transition is recorded in the Jabłonna section. Mature specimens of *Immognathus* devel-

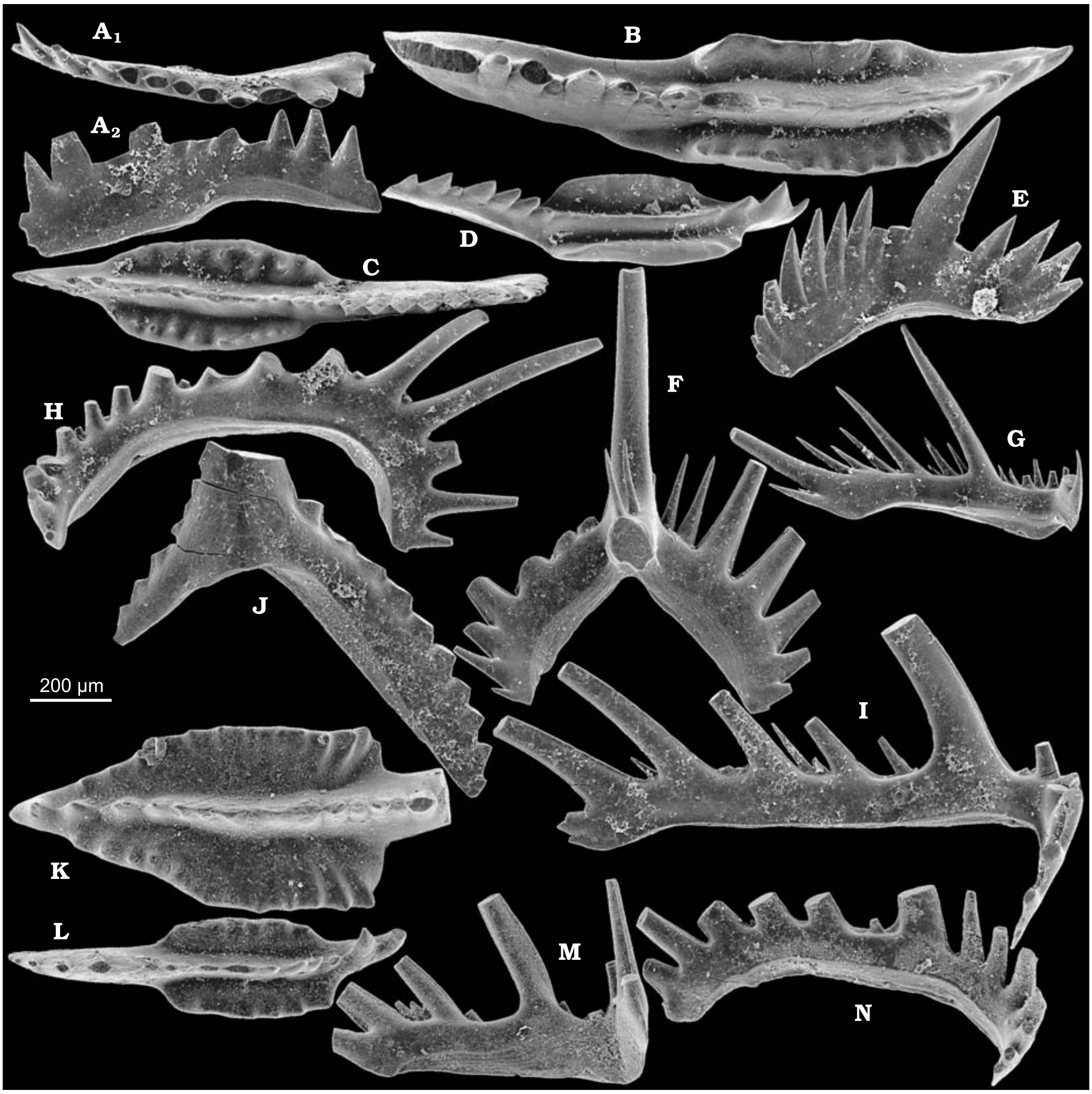


Fig. 56. Simplified polygnathid *Ctenopolygnathus brevilamina* (Branson *et* Mehl, 1934) from the *K. triangularis* Zone at Kowala (A, B, F–J, sample Ko-154; C–E, sample Ko-143) and Jabłonna (K–M, sample J-53a) and the *K. crepida* Zone at Kadzielnia (N, sample Ka-3) in the Holy Cross Mountains. P_1 (A–D, K, L), P_2 (E), S_0 (F), S_1 (G and M), S_2 (H and N), S_{3-4} (I), and M (J) elements; specimens ZPAL cXVI/2406, 2405, 2402–2404, 2407–2411, 2414, 2412, 2413, and 2415, respectively.

oped asymmetry in platform shape similar to that in *Polygnathus webbi*. *Polygnathus rarus* of Baliński (1995) from the Dębnik area may be another member of this branch.

Immognathus streeli (Dreesen, Dusar *et* Groessens, 1976)
(Figs 57 and 129)

Type horizon and locality: Sample YG 9 taken at theYves-Gomezée road section, Belgium with *Icriodus costatus*, lower costatus Zone (Dreesen *et al*. 1976).

Material. — 738 specimens.

Diagnosis. — Platform of P_1 elements ornamented with marginal tubercles extending admedially as short transverse ridges; in juveniles platform does not reach the dorsal tip of the blade.

Remarks. — Bifurcation of the ventral process in S_1 elements may be somewhat irregular and additional bifurcation may occur (e.g., in sample J-44).

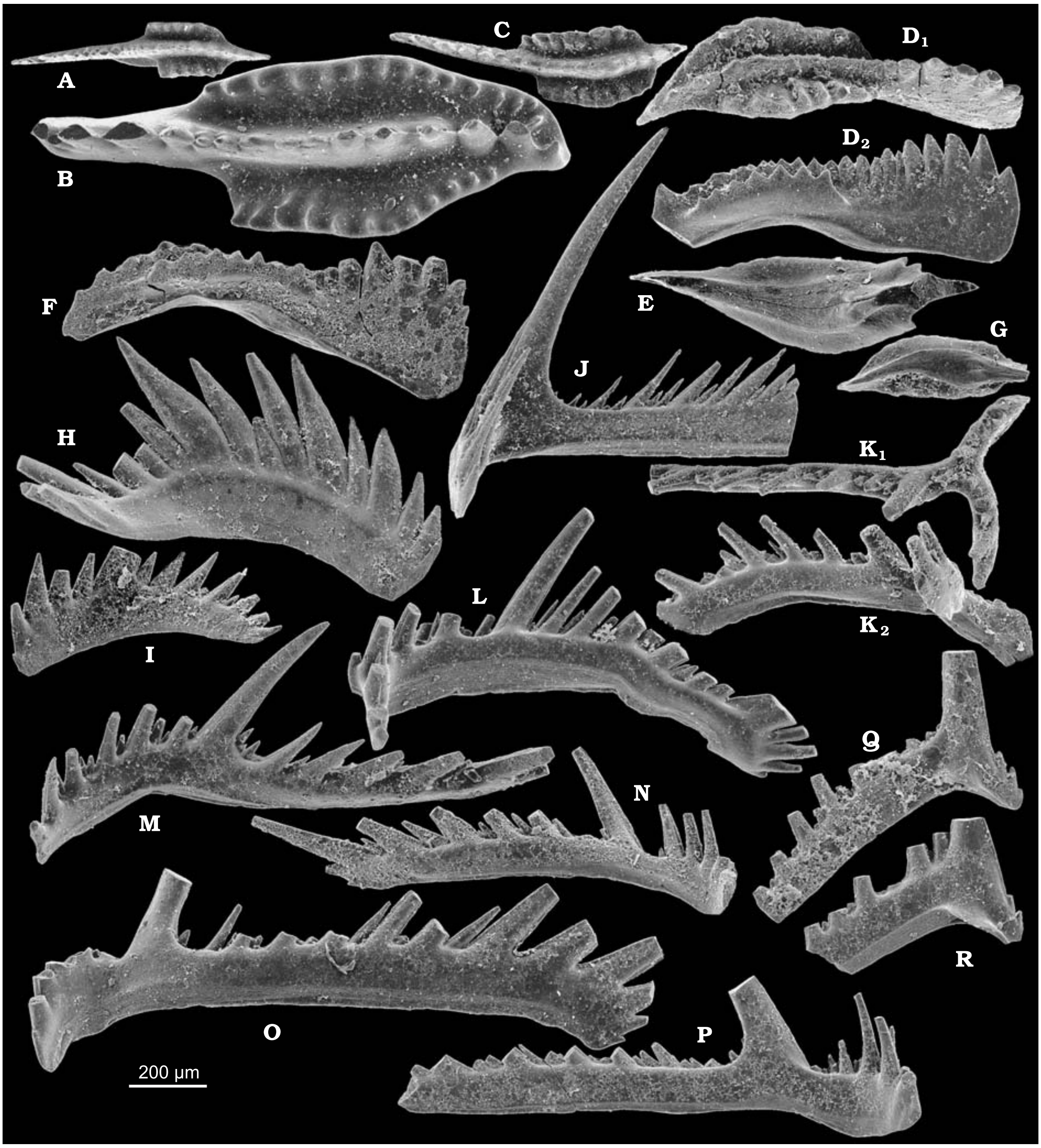


Fig. 57. Polygnathid with *Siphonodella*-like basal cavity, *Immognathus streeli* (Dreesen, Dusar *et* Groessens, 1976) from the *K. crepida* Zone at Wietrznia (A–E, H, J, L, M, Q and O, sample Wtr-21) and Jabłonna (G, I, K, N, P, and R, sample J-45a) in the Holy Cross Mountains. P_1 (A–G), P_2 (H, I), S_0 (J), S_1 (K, L), S_2 (M, N), $S_{3–4}$ (O, P), and M (Q, R) elements; specimens ZPAL cXVI/2417, 2418, 2427, 2425, 2416, 2428, 2426, 2420, 2429, 2419, 2430, 2421, 2422, 2431, 2423, 2432, 2424, and 2433, respectively.

Occurrence. — The *K. crepida* to *P. trachytera* zones at Jabłonna, Kowala and Miedzianka.

Immognathus rhabdotus (Schäfer, 1976)
(Figs 58B, D–L, and 129)

Type horizon and locality: Bed 21 in trench dug at Dasberg near Hövel, Rhenish Slate Mountains (Schäfer 1976).

Material. — 47 specimens.

Diagnosis. — P_1 elements with transversely ribbed platform tending to become flat dorsally in mature specimens and with parallel sides over most of its length.

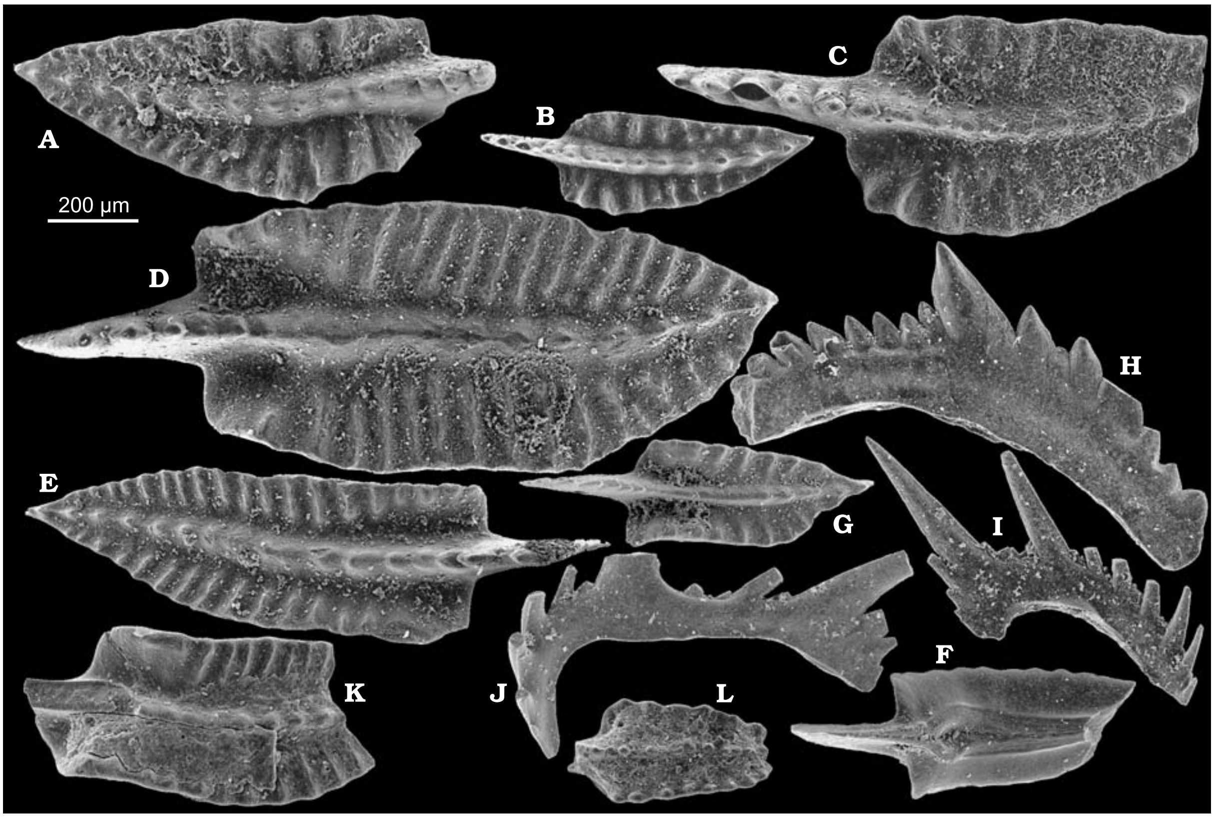


Fig. 58. Late Famennian *Siphonodella*-like polygnathids. **A**, **C**. *Polygnathus pennatulus* Ulrich *et* Bassler, 1926 from the *L. styriacus* Zone at Ostrówka (sample Ost-12) in the Holy Cross Mountains, possibly end members of population variability of *Hemilistrona perplexa*. P_1 elements; specimens ZPAL cXVI/2653–2654. **B**, **D**–**L**. *Immognathus rhabdotus* (Schäfer, 1976) from the *D. trigonica* Zone at Ostrówka (B, D, sample Ost-293; E–J, sample Ost-3) and Kowala (K, sample Ko-98) in the Holy Cross Mountains. P_1 (A–G, K, L), P_2 (H), S_2 (I), and $S_{3–4}$ (J) elements; specimens ZPAL cXVI/2673, 2720–2722, 2726, 2723–2725, 2391, and 2388, respectively.

Remarks. — In sample Ost-3 P_1 elements of this species dominate among polygnathids, being associated with robust ramiform elements of the *Ctenopolygnathus* type (Fig. 58I, J) that supports the generic placement of the species. Subadult P_1 elements of this species are virtually homeomorphic with those of *Pinacognathus*? *praesulcatus*. The difference is best visible in juveniles, having ventrally wider platform than in *P. praesulcatus* and in larger elements, with basal cavity of less angular section. If the partial apparatus reconstruction of the Tournaisian *Pinacognathus*? *sulcatus* proposed by myself is correct (Dzik 1997), all these species may belong to the same lineage. The generic name *Immognathus* may then appear appropriate to them and is to be transferred to the family Elictognathidae to ensure its monophyly.

From stratigraphically older *Polygnathus*? *pennatulus* the species differs in a less triangular outline of the platform and in lanceolate basal cone.

The P_1 elements of similar morphology from the boundary strata between the Famennian and Tournaisian, were identified by Bouckaert and Groessens (1976), Over (1992), and Sanz-López *et al.* (1999) as *Polygnathus inornatus* (with a Tournaisian type population, classified in *Pinacognathus* by Dzik 1997) and as *Pseudopolygnathus graulichi* by Austin *et al*. (1985). The lineage continued to the Carboniferous possibly represented there by *Pinacognathus inornatus* (E.R. Branson, 1934) (e.g., Dzik 1997). *P. graulichi*, with a very large basal cone, is rather a member of the *Dasbergina* lineage. Relationships and nomenclature of these latest Famennian and early Tournaisian forms requires clarification.

Occurrence. — The *L. styriacus* to *D. trigonica* zones at Ostrówka.

Genus ***Polygnathus*** Hinde, 1879

Type species: *Polygnathus dubius* Hinde, 1879 from the North Evans Limestone at Eighteenmile Creek in New York (Klapper and Philip 1971).

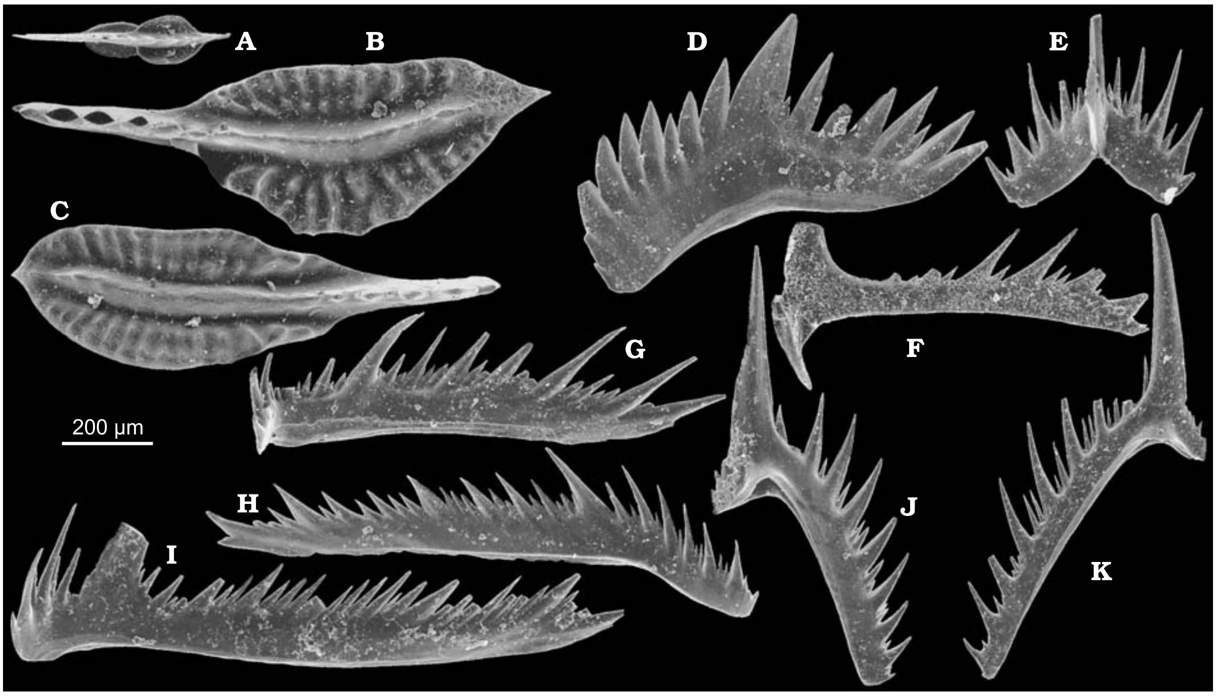


Fig. 59. Direct successor of the Frasnian lineage of asymmetric platform-bearing polygnathids, *Polygnathus praecursor* Matyja, 1993 from the earliest pre-*K. triangularis* Zone of the Famennian at Płucki (sample Pł-36) in the Holy Cross Mountains. P_1 (A–C, juvenile and probable adults; note that sinistral and dextral specimens are not mirror-images), P_2 (D), S_0 (E, F), S_1 (G), S_2 (H), S_{3-4} (I), and M (J, K) elements; specimens ZPAL cXVI/1535, 1533, 1534, 1536–1541, 1543, and 1542, respectively.

Polygnathus praecursor Matyja, 1993
(Figs 59, 60, 61, and 130)

Type horizon and locality: Depth 4636–4637 m in the borehole Unisław-2, Western Pomerania, Lower or Middle triangularis Zone (Matyja 1993).

Material. — 5,369 specimens.

Diagnosis. — Strong asymmetry in pairs of P_1 elements, mature elements with carina distinct to its tip.

Remarks. — The apparatus of an earliest Famennian population of the species from the Montagne Noire was restored by Schülke (1999) under the name *Polygnathus brevilaminus*. The type population of the latter species is different from *P. praecursor* in showing a more irregular development of the platform in P_1 elements and more robust appearance of the whole apparatus, and was classified in *Ctenopolygnathus* by Dzik (2002).

The earliest Famennian population of true *Polygnathus* from the Holy Cross Mountains was identified by myself (Dzik 2002) as belonging to the *Polygnathus semicostatus* lineage. At that time only juvenile platform specimens were known. More numerous material from that locality and other sites in the Holy Cross Mountains shows a significant difference between the earliest and mid Famennian members of the lineage and their classification in separate species, as proposed by Matyja (1993), is here supported.

The species seems to be a continuation of the Frasnian *P. webbi* lineage and discrimination of their boundaries with morphology alone may not be possible.

Occurrence. — From the beginning of Famennian to the early *K. crepida* Zone at Płucki, Kowala, Jabłonna, and Kadzielnia.

Polygnathus semicostatus Branson *et* Mehl, 1934
(Figs 8B, 62, and 130)

Type horizon and locality: Famennian at Dixie, Missouri (Ziegler 1977, p. 313).

Material. — 1,896 specimens.

Diagnosis. — Tongue-like dorsal end of the platform in P_1 element much narrower than the main part, ornamented with continuous transverse ribs.

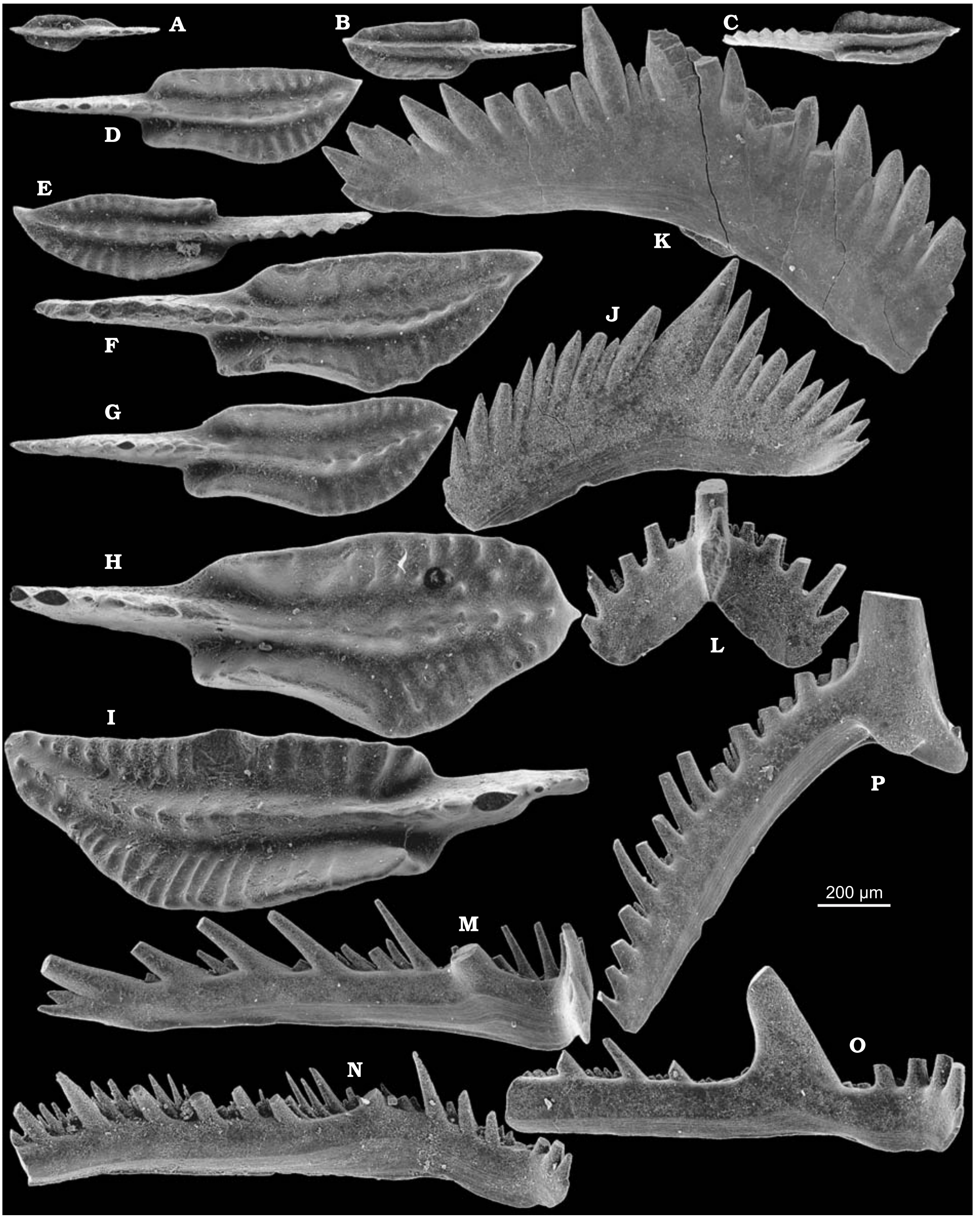


Fig. 60. Typical platform-bearing polygnathid *Polygnathus praecursor* Matyja, 1993 from the *K. triangularis* Zone at Jabłonna (A–H, sample J-53a; I, K–P, sample J-58; J, sample J-59) in the Holy Cross Mountains. P_1 (A–I, ontogenetic series of element pairs), P_2 (J, K), S_0 (L), S_1 (M), S_2 (N), S_{3-4} (O), and M (P) elements; specimens ZPAL cXVI/2434, 2436, 2435, 2437–2449, respectively.

Remarks. — The P_1 elements of the species differ from superficially similar elements of the Eifelian *P. linguiformis* in the mode of arching of the platform and in having a shorter blade (Dreesen and Orchard 1974). The geologically oldest specimens showing platform ornamentation typical for this species occur in

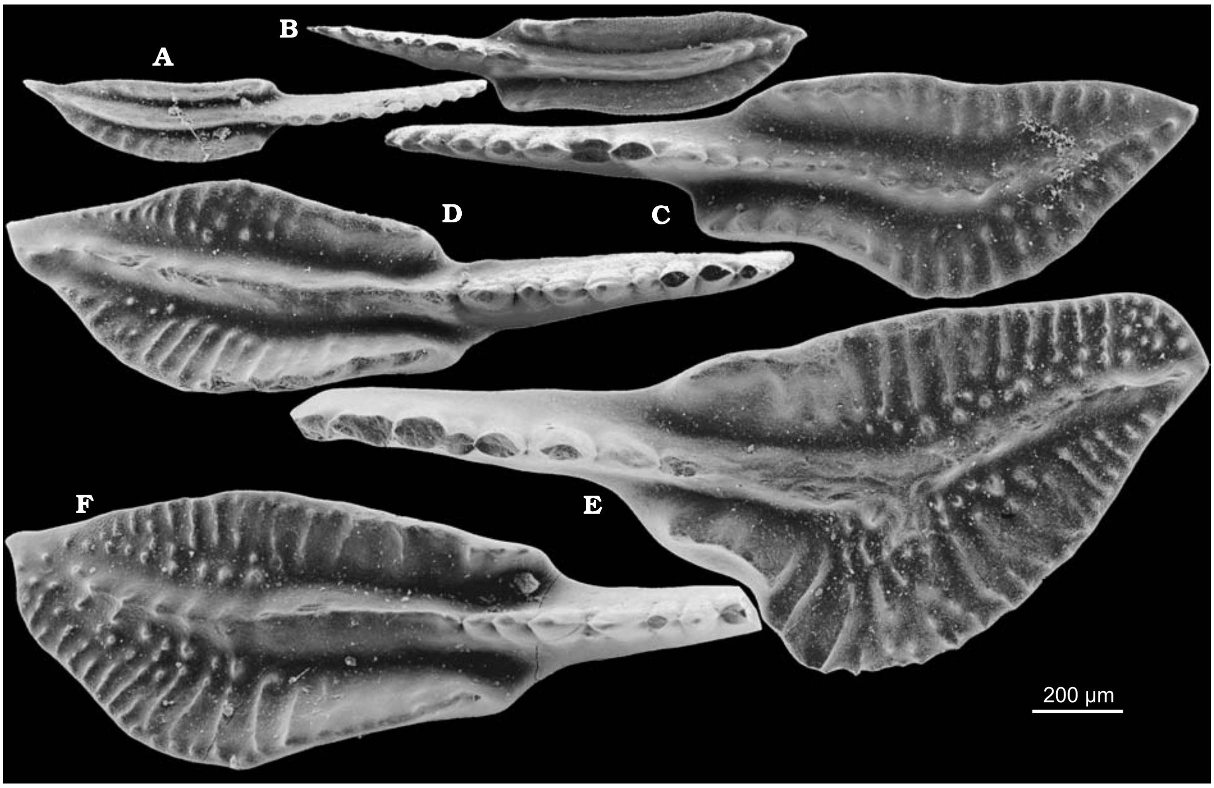


Fig. 61. Late population of *Polygnathus praecursor* Matyja, 1993 from the late *K. triangularis* Zone at Kadzielnia (sample Ka-16) in the Holy Cross Mountains. P_1 elements; specimens ZPAL cXVI/2487, 2486, 2488, 2490, 2489, and 2491, respectively.

samples Ka-3 and Ka-10 at Kadzielnia. They are associated with the dominant morph, in which tubercles near the dorsal end of the platform tend to be arranged into densely distributed transverse ribs, classified by Matyja (1974) in her *P. szulczewskii*. The type specimen of that species seems to be a dextral element of the early *P. semicostatus*, as suggested by its co-occurrence in the same sample (Minkowice 1 borehole depth 2385.4–2391.4; cf. Matyja 1974 and Matyja and Żbikowska 1974, pl. 6:8) with a sinistral element of *P. semicostatus*. Such initially profound apparatus asymmetry tends to disappear in the evolution of *P. semicostatus*. This is connected with a wider appearance of the ventral part of the platform, which no longer develops vertical margins. The same refers to *P. planirostratus* Dreesen *et* Dusar, 1974. *Polygnathus limbatus* Matyja, 1993 from the lower marginifera zone of the Chojnice borehole in western Pomerania seems to be a juvenile of *P. semicostatus*.

There is an interesting aspect of changes in the pattern of variability in the evolution of *P. semicostatus*. In the preceding *P. praecursor* the asymmetry in the P_1 element pair is stable, that is the sinistral element is narrower and with no apparent elevation of the anterior margin of the platform. In early populations of *P. semicostatus* rare dextral elements with “sinistral” morphology (and opposite) appear. In late populations such an inversion in asymmetry is very common. In effect both dextral and sinistral elements became dimorphic, with some intermediate forms, too. This loss of strict control of asymmetry is coeval with the general increase in population variability. Apparently the developmental mechanisms were losing their rigidity.

P. semicostatus is probably the most variable of all the Famennian polygnathids (Dreesen and Orchard 1974). This refers also to the organization of its basal cavity. In samples Ko-15, ŁSł73-2 and Ł-27 specimens with a depression in the base (the character used to define *Neopolygnathus*) occur (Fig. 70H–J), otherwise they do not differ from the associated typical elements of the species. Moreover, specimens with a virtually smooth narrow part of the platform occur, similar to *Polygnathus* sp. A of Matyja and Żbikowska (1974) from the crepida Zone of the borehole Minkowice 1 in the Lublin area or *Polygnathus padovanii* of Perri and Spalletta (1990) from coeval strata of the Carnic Alps. Combination of these two characters in specimens from Łagów (sample Ł-27) results in a morphology virtually indistinguishable from *Neopolygnathus communis*. Such specimens have been classified as *Polygnathus depressus* by Metzger (1989).

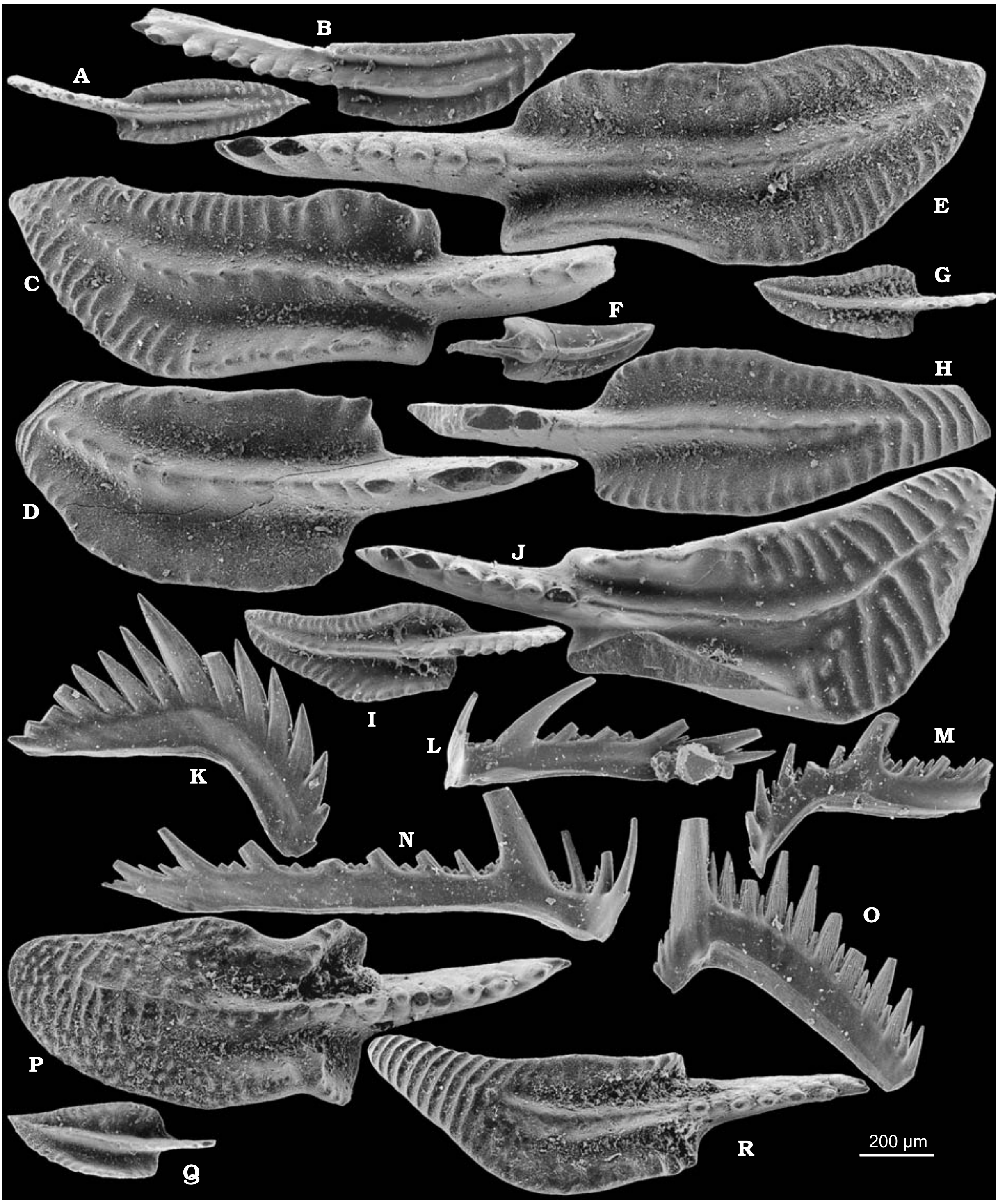


Fig. 62. *Polygnathus semicostatus* Branson *et* Mehl, 1934 from the *P. trachytera* Zone at Kowala (A, B, F, G, I–O, sample Ko-15), *K. crepida* Zone at Kadzielnia (C–E, H, sample Ka-3), and the *C. quadrantinodosa* Zone at Łagów (T, X, sample Ł-32; Q, sample Ł-27) in the Holy Cross Mountains. P_1 (A–J, P–R), P_2 (K), S_1 (L), S_2 (M), S_{3-4} (N), and M (O) elements; specimens ZPAL cXVI/2517, 2516, 2493, 2495, 2492, 2514, 2515, 2494, 2495, 2519–2509, 2520–2524, 2526, 2570, and 2525, respectively.

As indicated by the distribution of imprints of ameloblasts, the dorsal part of the platform was more intensely secreted than the ventral one.

Occurrence. — The late *K. crepida* to *L. styriacus* zones at Jabłonna, Kadzielnia, Wietrznia, Kowala, Miedzianka, and Ostrówka. The species occurs also in the Dębnik area (Baliński 1995).

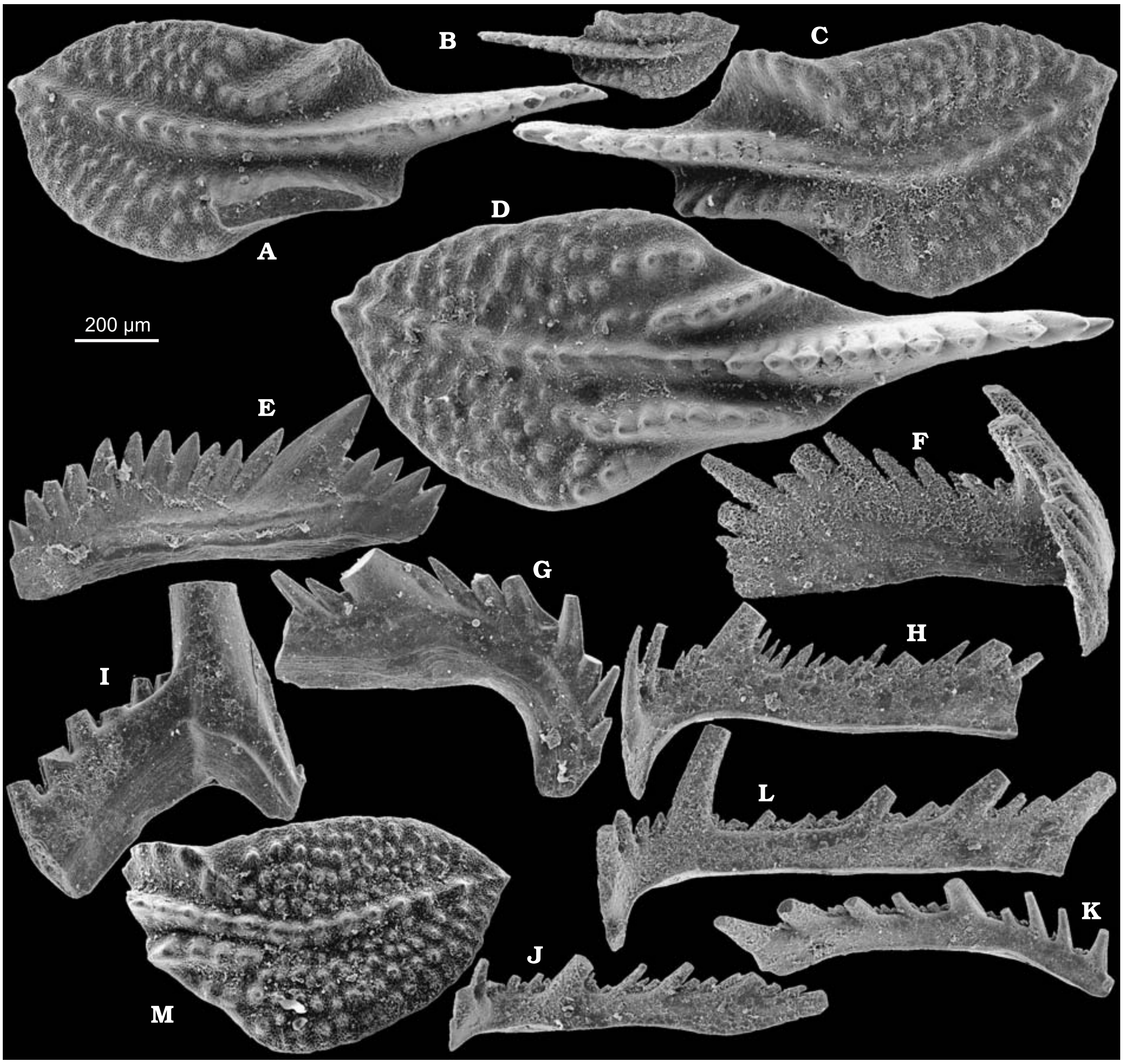


Fig. 63. Problematic *Polygnathus*? *experplexus* (Sandberg *et* Ziegler, 1979) from the *L.styriacus* Zone at Ostrówka (A, D–F, sample Ost-12; B, C, I–K, sample Ost-293) in the Holy Cross Mountains and Dzikowiec (L, sample Dz-71) in the Sudetes. P_1 (A–D, L), P_2 (E), S_0 (F), S_1 (J?), S_2 (G, K?), S_{3-4} (H, L), and M (M?) elements; specimens ZPAL cXVI/2656, 2680, 2681, 2672, 2664–2668, 2683–2685, and 2971, respectively.

Polygnathus? *experplexus* Sandberg *et* Ziegler, 1979
(Figs 63 and 130)

Type horizon and locality: Upper styriacus Zone, Box Member of Percha Shale east of Santa Rita, New Mexico (Sandberg and Ziegler 1979).

Material. — 554 specimens.

Diagnosis. — P_1 elements with two tuberculated rostral ridges and lobate platform ornamented with tubercles.

Remarks. — The origin of the species remains unsettled. P_1 elements show some similarity to *Hemilistrona perplexa*, but the apparatus is rather different and its morphology may suggest an origin from *Polygnathus praecursor*. In early populations of probable *P.*? *experplexus* the mature P_1 elements are convex centrally (near the cusp), wheareas in typical populations the corresponding part of the platform is gently concave.

Occurrence. — The *L. styriacus* and *P. jugosus* zones at Jabłonna, Ostrówka, Kowala, and Dzikowiec.

Polygnathus extralobatus Schäfer, 1976

(Figs 64A–K and 130)

Type horizon and locality: Bed 65 in the trench at Dasberg near Hövel, Rhenish Slate Mountains (Schäfer 1976).

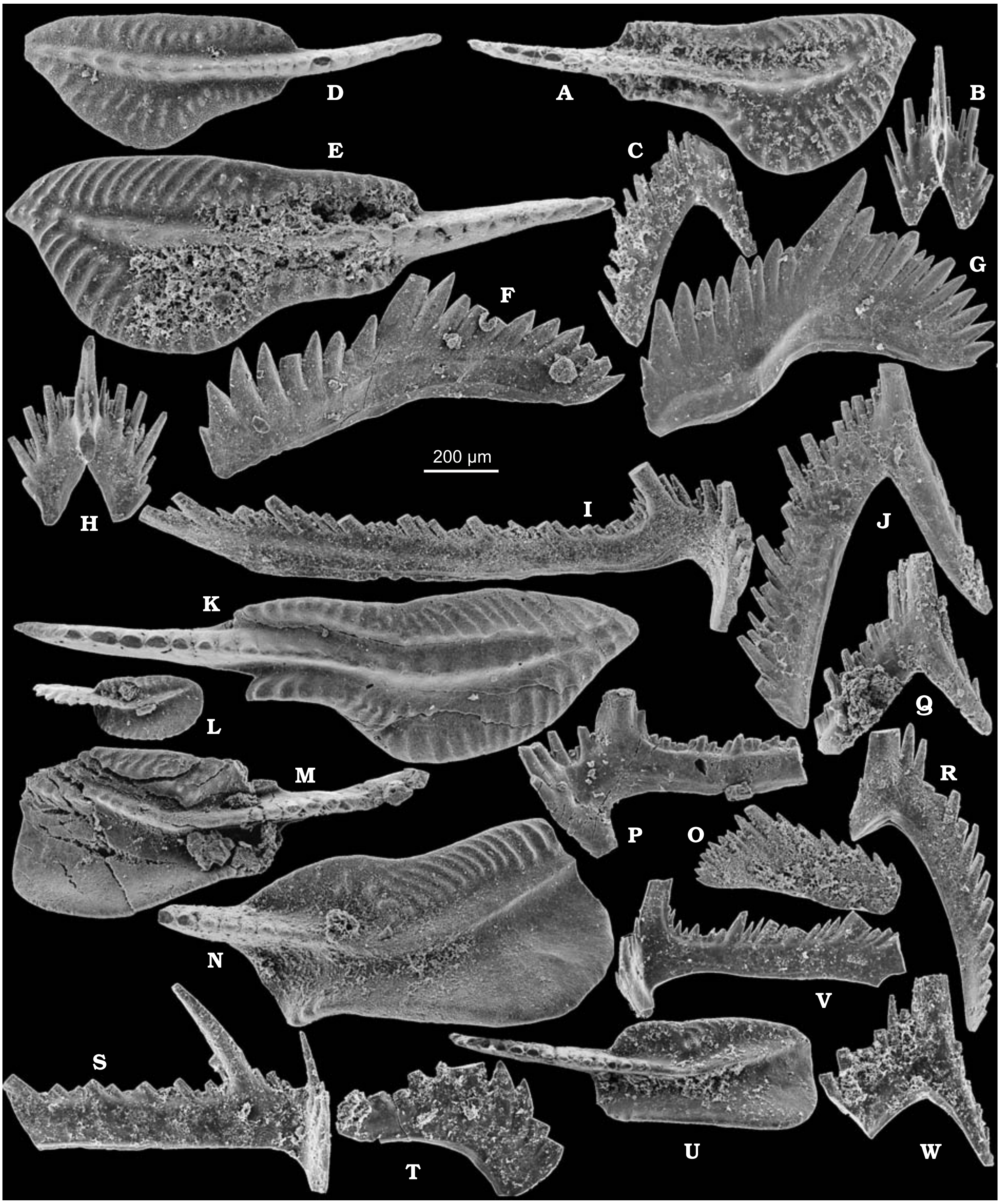


Fig. 64. Late Famennian polygnathids from the *P. jugosus* Zone at Ostrówka (D, N, O–R, sample Ost-265) and Jabłonna (E–J, bed 27) in the Holy Cross Mountains, Gołogłowy (K–M, Q, sample Goł-3) and Dzikowiec (A–C, sample Dz-53) in the Sudetes. **A**–**K**. *Polygnathus extralobatus* Schäfer, 1976. P_1 (A, D, E, K), P_2 (F, G), S_0 (B, H), S_{3-4} (I), and M (C, G) elements; specimens ZPAL cXVI/2968–2970, 2686–2690, and 2715, respectively. **L**–**W**. *Polygnathus znepolensis* Spassov, 1965. P_1 (L–N, U), P_2 (O, T), S_{3-4} (P, S), and M (Q, R, V) elements; specimens ZPAL cXVI/2697, 2698, 2691, 2717, 2699-2700, 2718, 2719, 2975, 2973, 2972, 2974, and 2976, respectively.

Material. — 1,014 specimens.

Diagnosis. — Widened dorsal part of the platform in P_1 element covered with obliquely running transverse ribs, discontinuous near the carina.

Remarks. — The species is so close to its stratigraphic predecessor, *P. obliquicostatus* Ziegler, 1962 that the ancestor-descendant relationship between them seems almost certain (Schäfer 1976). That species has not been encountered in the material available to me so the lineage probably entered the Holy Cross Mountains after the widening of the platform lobe was completed. *P. semicostatus* seems to be a likely ancestor of *P. obliquicostatus*.

Occurrence. — The *P. jugosus* and *D. trigonica* zones at Kowala, Jabłonna, and Gołogłowy.

Polygnathus znepolensis Spassov, 1965
(Figs 64L–W and 130)

Type horizon and locality: Summit of Krast hill at Berainci, Bulgaria (Klapper *in* Ziegler 1975).

Material. — 445 specimens.

Diagnosis. — Anterior part of the platform in P_1 element ornamented with oblique ribs, posterior lobe wide and gently convex, smooth.

Remarks. — This is a species widely occurring in shallow-water Late Famennian environments (Schäfer 1976). In the holotype of *P. znepolensis* re-illustrated by Klapper (*in* Ziegler 1975, pl. 5: 7) the posterior lobe of the platform bears robust radiating ridges, which have not been encoutered in any of the mature specimens in the Polish material. Possibly the holotype belongs thus to *P. extralobatus*, its close relative and probable ancestor. Both species co-occur at Gołogłowy and Ostrówka. In the oldest samples containing the species only minute juvenile specimens occur. This may reflect either a high juvenile mortality in extreme environments atypical for the species or its paedomorphic origin.

Occurrence. — The late *L. styriacus* and *P. jugosus* zones at Jabłonna, Ostrówka, Kowala, Gołogłowy, and Dzikowiec. The species occurs also in the Dębnik area (Baliński 1995).

Polygnathus procerus Sannemann, 1955
(Figs 65A–C and 131)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955a).

Material. — 832 specimens.

Diagnosis. — P_1 elements with almost symmetrical, willow-leaf-shaped platform, relatively flat in mature elements, ornamented with tubercles.

Remarks. — The P_1 elements of the species differ from juveniles of *P. volhynicus* in a less concave occlusal surface and less asymmetric outline of the platform, from *P. kadzielniae* in its lanceolate outline. Apparatus of the species was restored by Schülke (1995).

Occurrence. — The *K. triangularis* and *K. crepida* zones at Płucki, Jabłonna, Kadzielnia, Wietrznia, and Miedzianka.

Polygnathus volhynicus Drygant, 1986
(Figs 65D–O and 131)

Type horizon and locality: Depth 725–780 m in the borehole Volodymyr Volynsky, Ukraine, *K. crepida* Zone (Drygant 1986).

Material. — 1,893 specimens.

Diagnosis. — P_1 elements with asymmetric platform, in juveniles lanceolate and narrow; its raised margins ornamented by transverse ribs; no apparent asymmetry in pairs; carina separate to its tip even in mature elements.

Remarks. — Juveniles show a deeper separation of the blade from marginal parts of the platform (Drygant 1986) than in *P. procerus*, its probable ancestor. From *P. praecursor*, associated in some samples, the species differs in the lack of asymmetry of elements and their narrow appearance at juvenile (but not earliest) stages. Specimens of *P. squalidus* Drygant, 1986, co-occurring with those of *P. volhynicus* in the borehole Volodymyr Volynski are closely similar to mature specimens from Karczówka, and these names may be synonyms.

Occurrence. — The late *K. triangularis* Zone at Karczówka. The species occurs also in the Dębnik area (Baliński 1995).

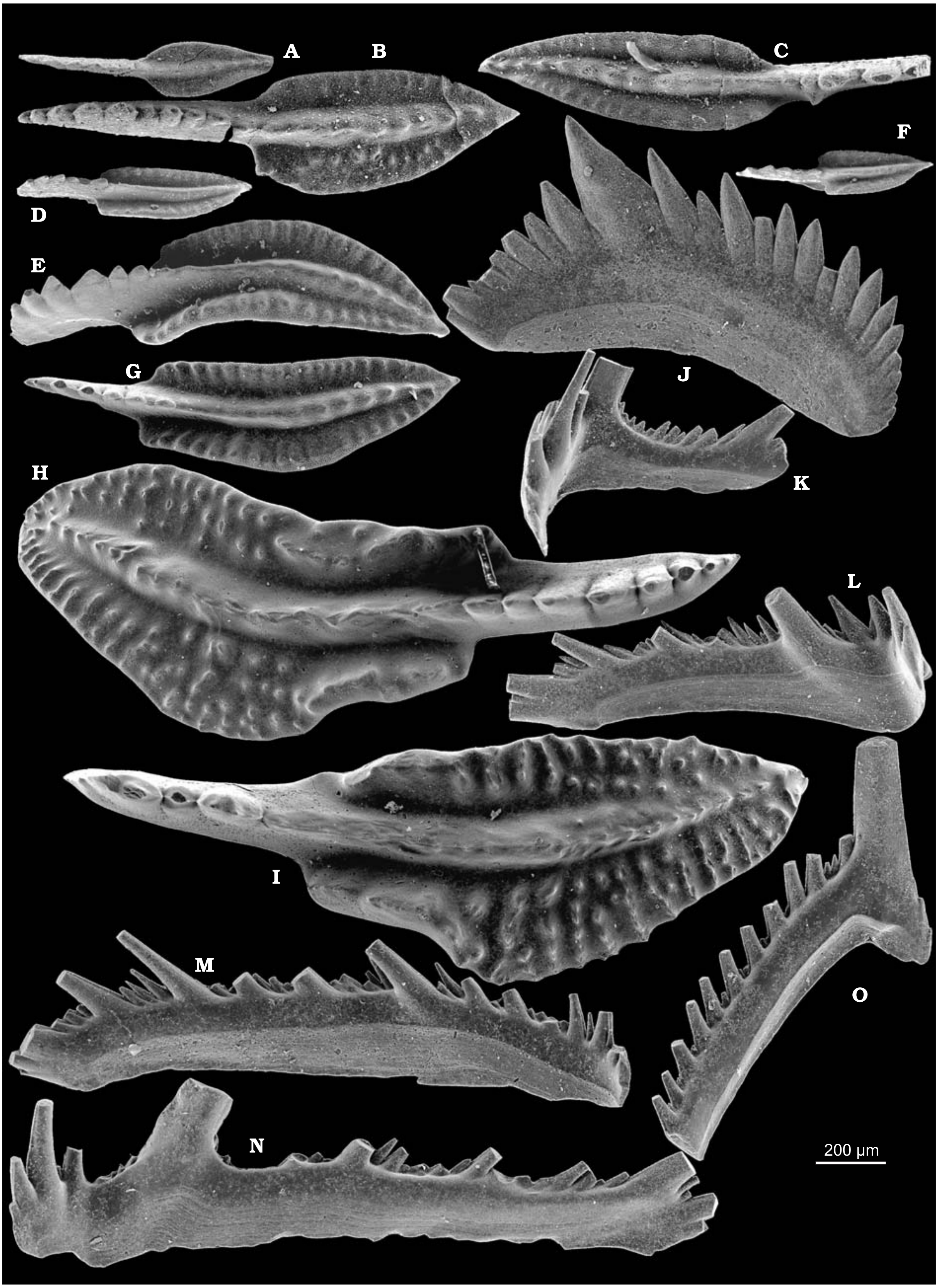


Fig. 65. Early Famennian narrow-platform polygnathids from *K. triangularis* Zone of the Holy Cross Mountains. **A**–**C**. *Polygnathus procerus* Sannemann, 1955 from Jabłonna (A, B, sample J-58; C, sample J-59). P_1 elements; specimens ZPAL cXVI/2450–2452. **D**–**O**. *Polygnathus volhynicus* Drygant, 1986 from Karczówka. P_1 (D–I), P_2 (J), S_0 (K), S_1 (L), S_2 (M), S_{3-4} (N), and M (O) elements; specimens ZPAL cXVI/2453–2464, respectively.

Polygnathus kadzielniae sp. n.
(Figs 66 and 131)

Holotype: Specimen ZPAL cXVI/2479 (Fig. 66O).

Type horizon and locality: Bed 8, early Famennian *K. crepida* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: The genitive case is applied for the name of the locality Kadzielnia, following the tradition initiated by Gürich (1896).

Material. — 1,458 specimens.

Diagnosis. — Margins of the main part of the platform in mature elements parallel, the ventral part of the platform occlusal surface gently concave, ornamented with weak transverse ribs and tubercles.

Remarks. — This is a late member of the *P. volhynicus* lineage, different in having the platform more widely expanded and in a more delicate and regular denticulation of P_2 elements. Identification of a so generalized *Polygnathus* species is a difficult task because of its great population variability and few diagnostic characters. Perhaps there is already a name for the species available in the literature, but I have not been able to identify it with confidence.

Occurrence. — The mid *K. crepida* Zone at Kadzielnia and Jabłonna.

Polygnathus? *pennatulus* Ulrich *et* Bassler, 1926
(Figs 58A, C and 129)

Type horizon and locality: Hardin Sandstone at Mount Pleasant, Tennessee (Klapper *in* Ziegler 1975).

Material. — 77 specimens.

Diagnosis. — Deeply concave platform occlusal surface with strong transverse ribs, outline of the platform triangular in juvenile specimens but its sides become parallel at later stages in the ventral half.

Remarks. — A few specimens of this species occuring without other platform-bearing polygnathids illustrated by Metzger (1989) from the Sheffield-Maple Mill Formation of Nebraska, support its separate status.

Although the P_1 elements are closely similar to those of *Immognathus rhabdotus* in the oral view, their bases are typical for *Polygnathus*. This makes relationship to the *Immognathus* lineage less likely than to *P. kadzielniae*, although aspects of the basal cavity are variable in these conodonts. The available material is too small to enable apparatus reconstruction, so I preserve the traditional location of the species provisionally.

Occurrence. — The *L. styriacus* and *P. jugosus* zones at Ostrówka, Kowala, Miedzianka, and Dzikowiec.

Genus ***Hemilistrona*** Chauff *et* Dombrowski, 1977

Type species: *Hemilistrona depkei* Chauff *et* Dombrowski, 1977 from the basal shale member of the Sulphur Springs Formation near Pevely, Missouri, lower costatus Zone.

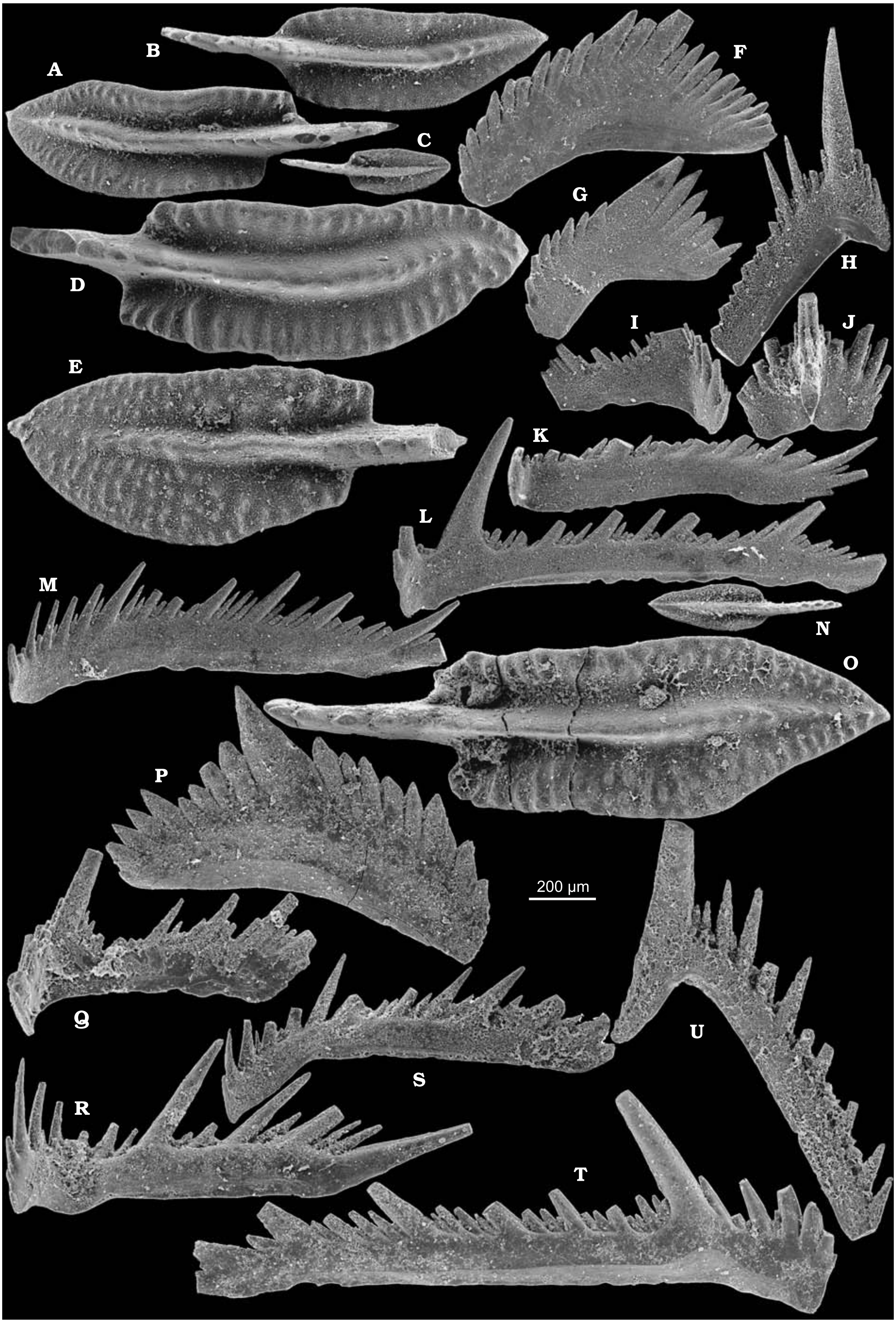
Diagnosis. — Polygnathids with elaborate platform developed also in P_2 elements; platform of P_1 elements with ridges parallel to blade in rostral ventral part and with tuberculated convex and strongly asymmetric dorsal part; remaining elements of the apparatus similar to *Polynodosus*.

Remarks. — The ancestry of *Hemilistrona* remains unsolved. The morphology of P_2 elements in its oldest species, *H. perplexa*, suggests relationship to the early Famennian *Polygnathus*. Prominent ridges backing the blade in the P_1 element are also similar to those in *P. webbi* group but, even if they are in asymmetric pairs, this is obscured by the tremendous population variability. Moreover, the ridges extend much farther dorsally than in *Polygnathus*, in smallest juveniles being rather like that of *Polynodosus*. Also the shape of M elements with transversely oriented processes speaks in favor of a relationship to the *Mehlina–Polynodosus* lineage, as suggested already with respect to *H. perplexa* by Vorontzova (1993). Her idea of *Polynodosus* as including all ornate Famennian polygnathids is, however, inconsistent with the diversity of their apparatus structure. A relationship to the Frasnian polygnathids of similar platform ornamentation remains to be tested by apparatus reconstructions.

Hemilistrona perplexa (Thomas, 1949)
(Figs 67 and 128)

Type horizon and locality: Maple Mill shale at roadcut (locality 14 of Thomas 1949) in Washington County, Iowa (same as for *Pelekysgnathus inclinatus*; see Klapper *in* Ziegler 1975).

Material. — 787 specimens.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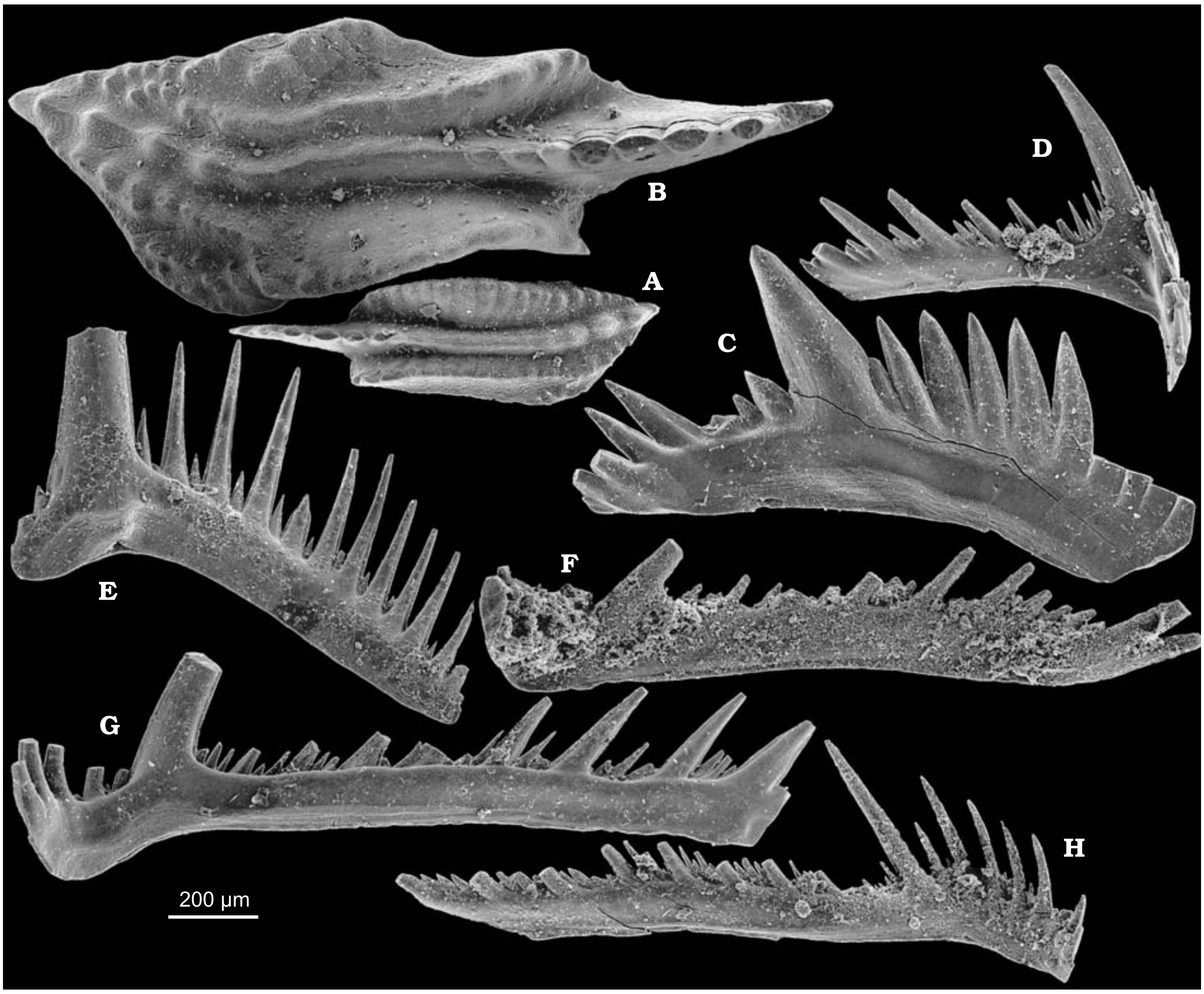

Fig. 67. *Hemilistrona perplexa* (Thomas, 1949), a ridged platform-bearing polygnathid, from the *C. marginifera* Zone at Ściegnia (Wzdół Plebański; sample Wzd-10) in the Holy Cross Mountains. P_1 (A, B), P_2 (C), S_0 (D), S_1 (E), S_2 (F), S_{3-4} (G), and M (H) elements; specimens ZPAL cXVI/2641–2644, 2648, 2645, 2647, and 2646, respectively.

Diagnosis. — Mature P_2 elements with incipient platform and straight processes, P_1 elements with the posterior tongue of the platform developed only in mature specimens.

Remarks. — The species actually does not show the wide platform in P_2 elements diagnostic for the genus but is also different from *Polynodosus* in not developing a peniculus (or at least the undulation of the process connected with it is not recognizable in larger specimens).

Ramiform elements of the apparatus may be indistinguishable from those of associated platform-bearing *Mehlina*. The holotype of the species is a juvenile P_1 element associated in the same sample (locality 14 of Thomas 1949) with apparently conspecific mature elements named *Palmatolepis*? *irregularis* and *Ancyrognathus irregularis*, robust P_2 elements named *Bryantodus*? sp., and low-arched robust M elements named *Euprioniodina iowaensis* and *E. lateralis*. Co-occurring *Branmehla inornata*, *Polygnathus semicostatus*, *Palmatolepis perlobata*, and *Conditolepis falcata* are suggestive of the *P. trachytera* Zone (unless this is a case of reworked material). Thomas (1949) illustrated also a P_2 element of advanced *Hemilistrona* from the same locality, but in Chauff and Dombrowski (1977) it is referred to as coming from another locality near

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← Fig. 66. *Polygnathus kadzielniae* sp. n. from the *K. crepida* Zone at Kadzielnia (A–D,F, G, sample Ka-2; E, H, I–M, sample Ka-13) and Jabłonna (N–U, bed 8) in the Holy Cross Mountains. P_1 (A–E, N, O), P_2 (F, G, P), S_0 (I, J, Q), S_1 (K, R), S_2 (M, S), S_{3-4} (L, T), and M (H, U) elements; specimens ZPAL cXVI/2466, 2467, 2465, 2468, 2471, 2469, 2470, 2477, 2473, 2472, 2474, 2476, 2475, and 2478–2485 (holotype, O), respectively.

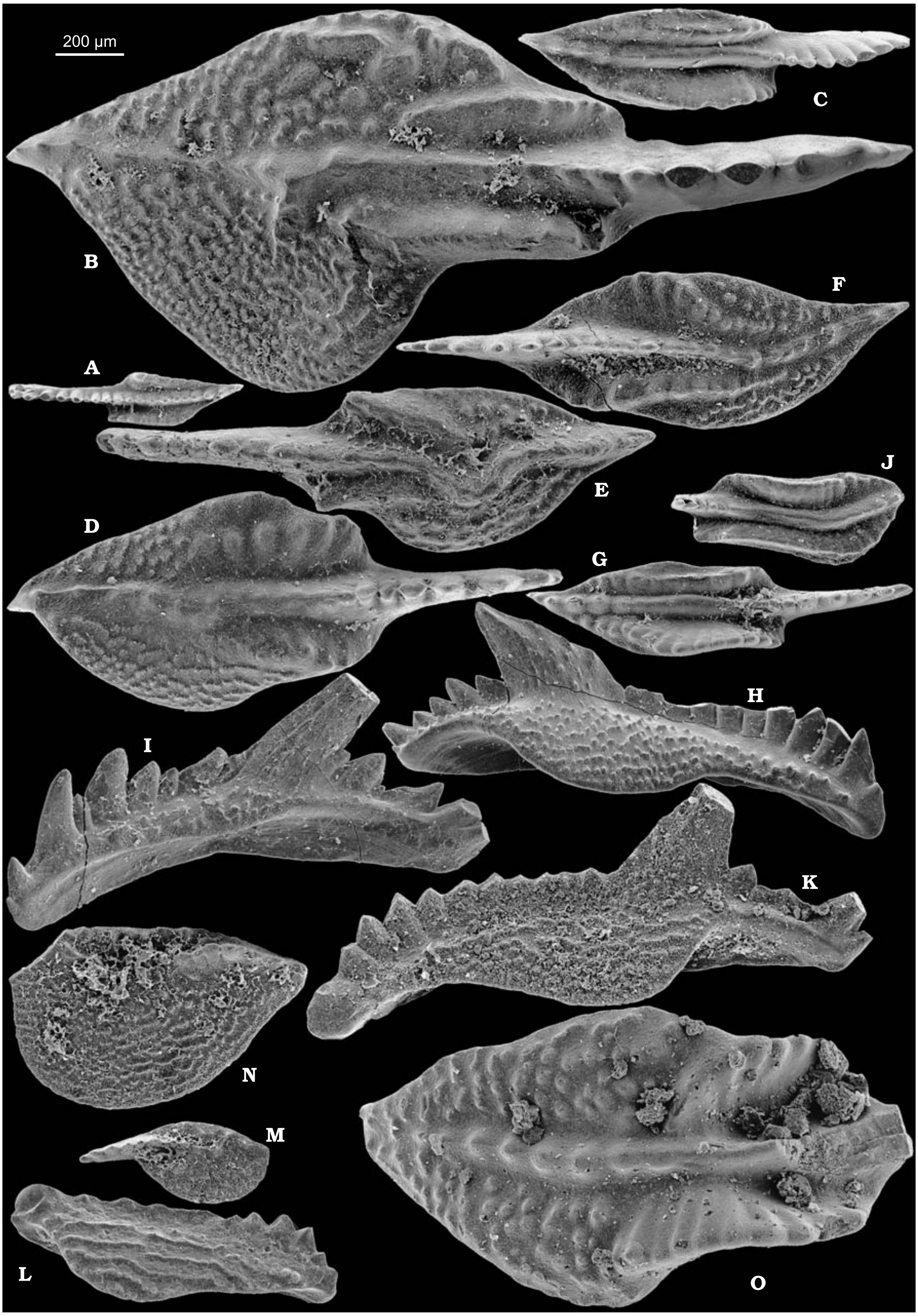


Fig. 68. Polygnathids with platform-bearing P_2 element. **A**–**K**, **O**. *Hemilistrona homoirregularis* (Ziegler, 1971) from the *L.styriacus* Zone at Ostrówka (A–K, sample Ost-12) in the Holy Cross Mountains and Gołogłowy (O, sample Goł-3) in the Sudetes. P_1 (A–G, J, O), P_2 (H, I, K), elements; specimens ZPAL cXVI/2649, 2652, 2657, 2658, 2659, 2660, 2659, 2662–2668, and 2716, respectively. **L**–**N**. *Hemilistrona pulchra* Chauff and Dombrowski, 1977 from the *L. styriacus* (M, N, sample Ko-6) and the *P. jugosus* (L, sample Ko-131) zones at Kowala. P_1 (M, N) and P_2 (L) elements, specimens ZPAL cXVI/2692 and 2678–2674, respectively.

Kalona. It is thus assumed here that also the early populations of the lineage from the *C. marginifera* Zone (velifer Zone) belong to this chronospecies.

Occurrence. — The *C. marginifera* to *L. styriacus* zones at Miedzianka, Kowala, Jabłonna, Ostrówka, and Gołogłowy.

Hemilistrona homoirregularis (Ziegler, 1971)
(Figs 68A–K, O and 128)

Type horizon and locality: Maple Mill Shale at road cut southeast of Kolona in Iowa (Ziegler 1975).

Material. — 810 specimens.

Diagnosis. — Mature P_1 and P_2 element with posterior platform tongue bent downward and ornamented with tubercles.

Remarks. — A relatively large collection of this species from sample Ost-12 contains elements of various ontogenetic ages. Except for the mature P_1 elements, they show a puzzling variability in virtually all aspects of the platform shape and ornamentation. This is probably the most variable population of polygnathids in the Famennian of the Holy Cross Mts. There is a transition to morphologies classified here as *Hemilistrona margaritata*, *Polygnathus*? *experplexus* and even *Neopolygnathus communis*. Until population and apparatus studies on much larger and taxonomically less diverse material are performed, this classification can be treated only as provisional.

Occurrence. — The *P. trachytera* to *L. jugosus* zones at Ostrówka, Miedzianka, Kowala and Jabłonna.

Hemilistrona pulchra Chauff *et* Dombrowski, 1977
(Figs 68L–N and 128)

Type horizon and locality: Basal shale member of the Sulphur Springs Formation near Pevely, Missouri, lower costatus Zone (reworked material).

Material. — 14 specimens.

Remarks. — Longitudinal ribs on the platform of P_2 elements characterize this species. Outside Missouri, it has been known from Thuringia (Helms 1961). In the Holy Cross Mountains only a few elements

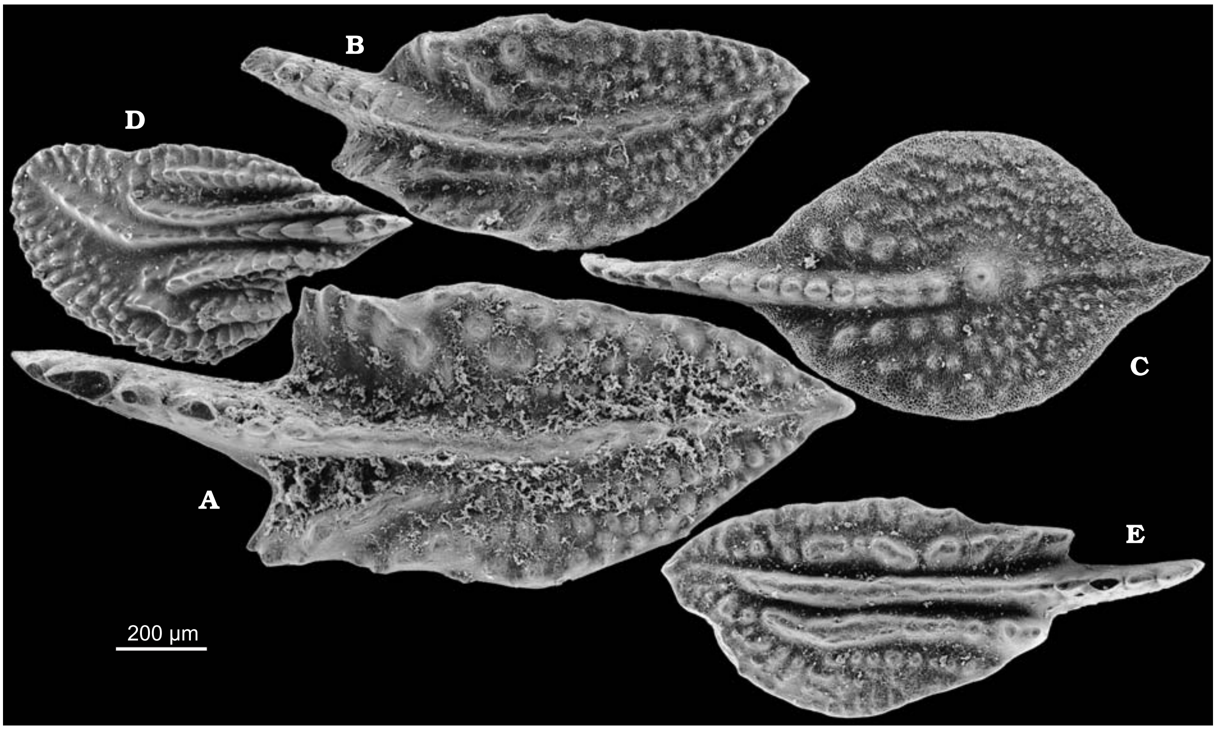


Fig. 69. *Hemilistrona margaritata* (Schäfer, 1976), a polygnathid with ornate platform, from the *L. styriacus* Zone at Ostrówka (A–C, sample Ost-12; D, E, sample Ost-293) in the Holy Cross Mountains; specimens ZPAL cXVI/2651, 2655, 2661, 2669, and 2674, respectively.

have been found and they hardly offer anything new regarding the apparatus composition. In sample Ko-6 two P_1 elements of different ontogenetic age are associated. Both show an unusually low and sinusoidal blade and are lacking a free carina (blade), suggesting that this is the end-member of the lineage, well represented in the material of Chauff and Dombrowski (1977).

Occurrence. — The *L. styriacus* and *P. jugosus* zones at Kowala.

Hemilistrona margaritata (Schäfer, 1976)
(Fig. 69)

Type horizon and locality: Bed 18 in trench dug at Dasberg near Hövel, Rhenish Slate Mountains (Schäfer 1976).

Material. — 14 specimens.

Remarks. — Longitudinal rows of tubercles on the platform of lanceolate P_1 elements are typical for the species. The morphology of this kind may be a part of population variability of *H. homoirregularis*. However, there seems to be a change in morphology of longitudinally ornamented P_1 elements of *Hemilistrona*. In geologically younger samples the tubercles are less prominent and the platform more regularly lanceolate, giving the P_1 elements aspects somewhat similar to *Dasbergina kayseri*.

Occurrence. — The *L. styriacus* Zone at Ostrówka.

Genus ***Neopolygnathus*** Vorontsova *in* Barskov *et al*., 1991

Type species: *Polygnathus communis* Branson *et* Mehl, 1934 from the Tournaisian Bushberg sandstone at Brickeys, Missouri.

Diagnosis. — Platform of P_1 elements smooth at least in its dorsal part, oval in outline, usually a distinctly separated juvenile basal cone located in a depression of the flat basal cavity; high arched M element.

Remarks. — The depression separating larval basal cone (interpreted here as a distinct larval stage preceding the development of platform) from the rest of the basal cavity is seems to appear several times in the evolution of various polygnathids and can hardly be used alone as the diagnostic character of the genus. It disappeared in some late species and is not characteristic of probable oldest populations of the main lineage. The same refers to the smooth, robust platform. The concept of the genus must thus remain provisional until its origin and evolution is elucidated. I suppose that *P. semicostatus* is ancestral and that a few paedomorphic lineages originated independently from it.

Advanced Tournaisian members of the genus are homeomorphic in the development of the platform of P_1 elements to some species of *Lagovignathus* gen. n.

Neopolygnathus communis (Branson *et* Mehl, 1934)
(Figs 9B, 70A–S, and 130)

Type horizon and locality: Tournaisian Bushberg sandstone at Brickeys, Missouri.

Material. — 1,447 specimens.

Diagnosis. — Margins of the platform of P_1 elements raised adorally, with more or less distinct longitudinal crests in its ventral area; only in extreme specimens tuberculation of various kinds may develop.

Remarks. — According to Vorontzova (1996) populations of a narrow-platform form of *N. communis* from the *K. crepida* Zone are ancestral to a clade of variously ornamented forms united only by their depressed basal pit. I am inclined rather to the alternative interpretation, that the separation of pre-platform stage from the fast growing platform marginally is rather a developmental aspect not requiring fundamental change in controlling mechanisms and thus appearing independently in unrelated lineages. This may be only an expansion of the larval stage (sinuosa larva), poorly controlled by developmental regulatory mechanisms, as suggested by great population variability in early populations. The range of variability includes forms with narrow and wide platforms, completely smooth and ornamented with transverse ridges, without any crests, bearing crests parallel to the blade or at an angle to it. This morphologic lability ceases in the latest Famennian, where a morphologic gap develops between *N. communis* and *N. vogesi*.

Occurrence. — The geologically oldest elements of *Neopolygnathus* morphology have been encountered in the Holy Cross Mountains in the *C. quadrantinodosa* Zone at Łagów (sample Ł-27) where they co-occur with *Polygnathus semicostatus* and may grade into its morphology, and in the *C. marginifera* Zone at Jabłonna. Unquestionable records of the species start from the *P. jugosus* Zone of all studied localities and continue into the Carboniferous.

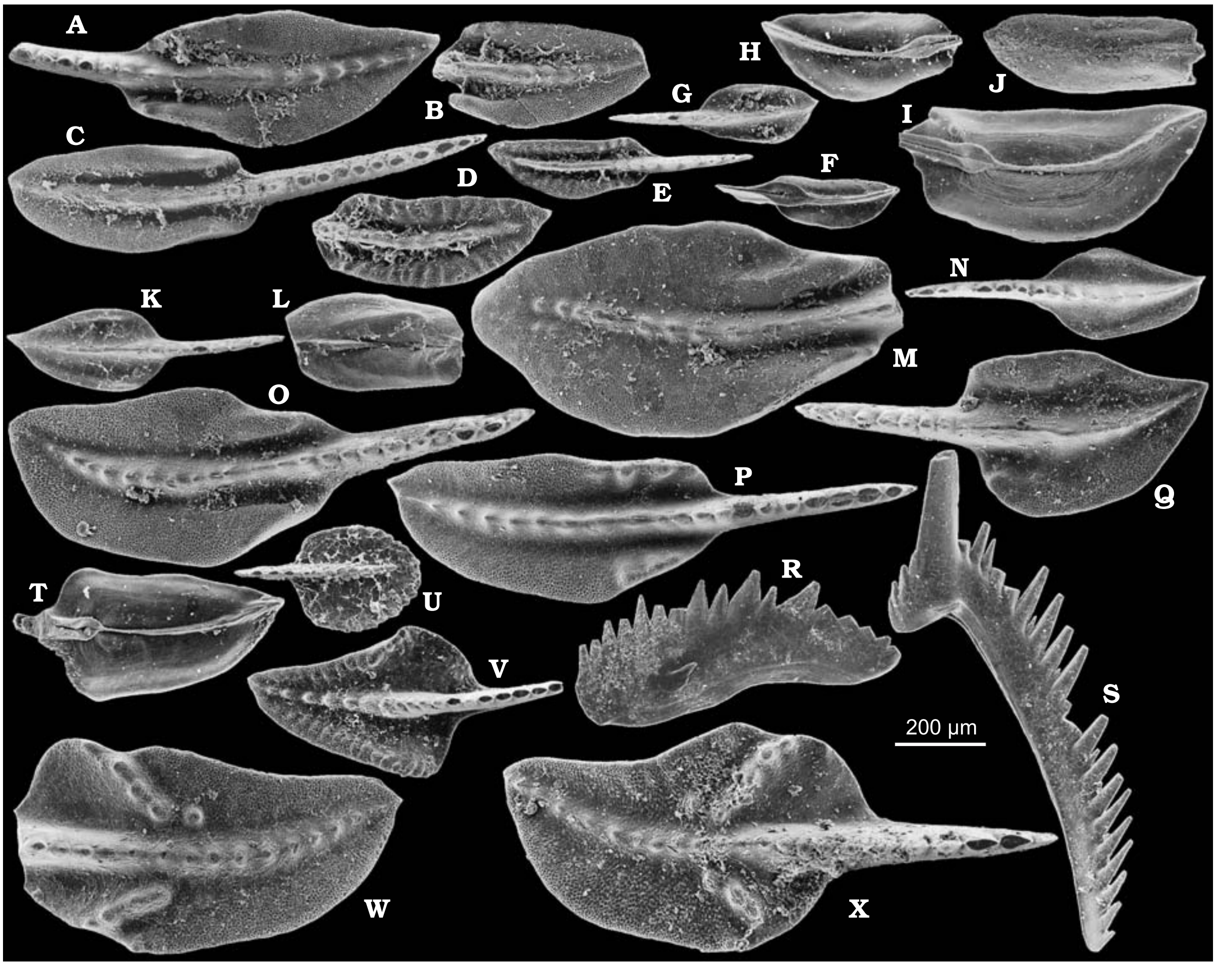


Fig. 70. Famennian populations of *Neopolygnathus*. **A**–**S**. *N. communis* (Branson *et* Mehl, 1934) from the *C. quadrantinodosa* Zone at Łagów (A, B, samples Ł-27), the early *L. styriacus* Zone (C–F, sample Ost-12) at Ostrówka, the *P. trachytera* Zone at Kowala (G–J, sample Ko-15), the late *L. styriacus* (sample Ost-293, K–N) and the *P. jugosus* (O–S, sample Ost-185) zones at Ostrówka in the Holy Cross Mountains. P_1 (A–Q), P_2 (R), and M (S) elements; specimens ZPAL cXVI/2527, 2528, 2693–2696, 2518, 2510, 2512, 2513, 2675–2677, 2674, 2703, 2704, 2706, 2708, respectively. **T**–**X**. *N. vogesi* (Ziegler, 1962) from the *P. jugosus* Zone at Ostrówka (T, X, sample Ost-185) and Kowala (U, V, sample Ko-191) in the Holy Cross Mountains and Dzikowiec (sample Dz 54, W) in the Sudetes. P_1 elements; specimens ZPAL cXVI/2701, 2994, 2993, 2707, and 2988.

Neopolygnathus vogesi (Ziegler, 1962)
(Figs 70T–X and 130)

Type horizon and locality: Sample 7 from the late Famennian middle costatus Zone at the Hönnetalstraße section in the Rhenish Slate Mountains (Ziegler 1962).

Material. — 595 specimens.

Diagnosis. — Platform of P_1 elements with prominent oblique crests in the ventral part.

Remarks. — Populations of this species show a rather stable morphology, similar to co-occurring *P. communis*, but unlike early populations of the latter.

In a few samples from the *P. jugosus* Zone at Kowala rare juvenile specimens of a polygnathid have been found (Fig. 70U, V) of the kind identified by Perri and Spaletta (1991) with the Tournaisian *Polygnathus margininvolutus* Gedik, 1969. In the triangular shape of the strongly concave thin platform these elements are similar to juveniles of *P. semicostatus*. Similar forms occur in the Tournaisian, where they probably represent juveniles of *Neopolygnathus vogesi* (Dzik 1997, fig. 12F). The available material is too small to be sure of their nature.

Occurrence. — The *P. jugosus* to *D. trigonica* zones at Ostrówka and probably Kowala in the Holy Cross Mountains and at Dzikowiec in the Sudetes. Continues into the Carboniferous.

Genus *Lagovignathus* gen. n.

Type species: *Polygnathus lagowiensis* Helms *et* Wolska 1967 from the Łagów Beds at Łagów, the Holy Cross Mountains.

Diagnosis. — Platform of P_1 elements thin, its surface ornamented with minute tubercles or smooth, lanceolate in outline, low arched M element.

Remarks. — The earliest species of the new genus, *L. glaber*, resembles some Carboniferous species of *Neopolygnathus* (e.g., *N. purus*) in having a flat and completely smooth platform. It is difficult to diagnose this genus in a way allowing its easy separation from such forms. The lineage apparently originated paedomorphically and the P_1 elements are secondarily simplified. This change took place much earlier than in the lineage of *N. communis* and it is unlikely that they are directly related. However, it has to be admitted that ancestry of both lineages remains to be supported with evidence.

Lagovignathus glaber (Ulrich *et* Bassler, 1926)
(Figs 71A–L and 131)

Type horizon and locality: Hardin Sandstone at Mount Pleasant, Tennessee.

Material. — 749 specimens.

Diagnosis. — Heart-shaped outline of flat, smooth platform with margins gently raised aborally.

Remarks. — The apparatus composition was restored by Metzger (1994). It is here assumed that the type specimens of *L. glaber* and *L. bilobatus* represent modal morphologies of their populations, which are successive parts of the same lineage. The platform outline, originally used to distinguish these species is highly variable and identification of the species should not be based on single specimens. Probably equally useful is the changing morphology of P_2 elements, which became more arched in *L. bilobatus*.

Occurrence. — The *K. crepida* Zone at Jabłonna, Kadzielnia, and Wietrznia.

Lagovignathus bilobatus (Ziegler, 1962)
(Figs 71M–T and 131)

Type horizon and locality: Bed 11 in trench II at Sessaker near Oberscheld.

Material. — 3,891 specimens.

Diagnosis. — Slight constriction in the middle of the heart-shaped outline of the flat, smooth platform.

Remarks. — This is clearly a successor of *L. glaber* and whether to distinguish them at the chronospecies or chronosubspecies rank is a matter of convenience. Differences are minor and ranges of population variability clearly overlap.

Occurrence. — The late *K. crepida* to *L. styriacus* zones at Kadzielnia, Jabłonna, Kowala, Miedzianka, and Ostrówka.

Lagovignathus fallax (Helms *et* Wolska, 1967)
(Figs 72J–Q and 131)

Type horizon and locality: Grey, bedded limestone of lower marginifera Zone from the old Geipelsch quarry in Schleiz, Thuringia (Helms and Wolska 1967).

Material. — 1,273 specimens.

Diagnosis. — Willow leaf-shaped platform ornamented with minute tubercles.

Remarks. — Rare specimens from the *C. quadrantinodosa* Zone at Łagów (samples Ł-27 and Ł-26), associated with *Polynodosus transitus* and probably belonging to that species (Fig. 50D), resemble *L. fallax* in the minute tuberculation of the platform. The regular denticulation and short dorsal process of P_2 elements make any relationships of this species to *Polynodosus* unlikely.

Basal cone of the platform-lacking larva is significantly larger in this species than in other coeval species of *Lagovignathus*, but in subsequent growth the boundary between conical and inverted basal cavity smoothened.

Occurrence. — The *C. marginifera* Zone at Łagów, Kowala, and Miedzianka.

Lagovignathus? *dissimilis* (Helms *et* Wolska 1967)
(Figs 73 and 131)

Type horizon and locality: Grey-purple, thin bedded limestone of the *Clymenia* Zone from Alte Heerstrasse near Oettersdorf, Thuringia (Helms and Wolska 1967).

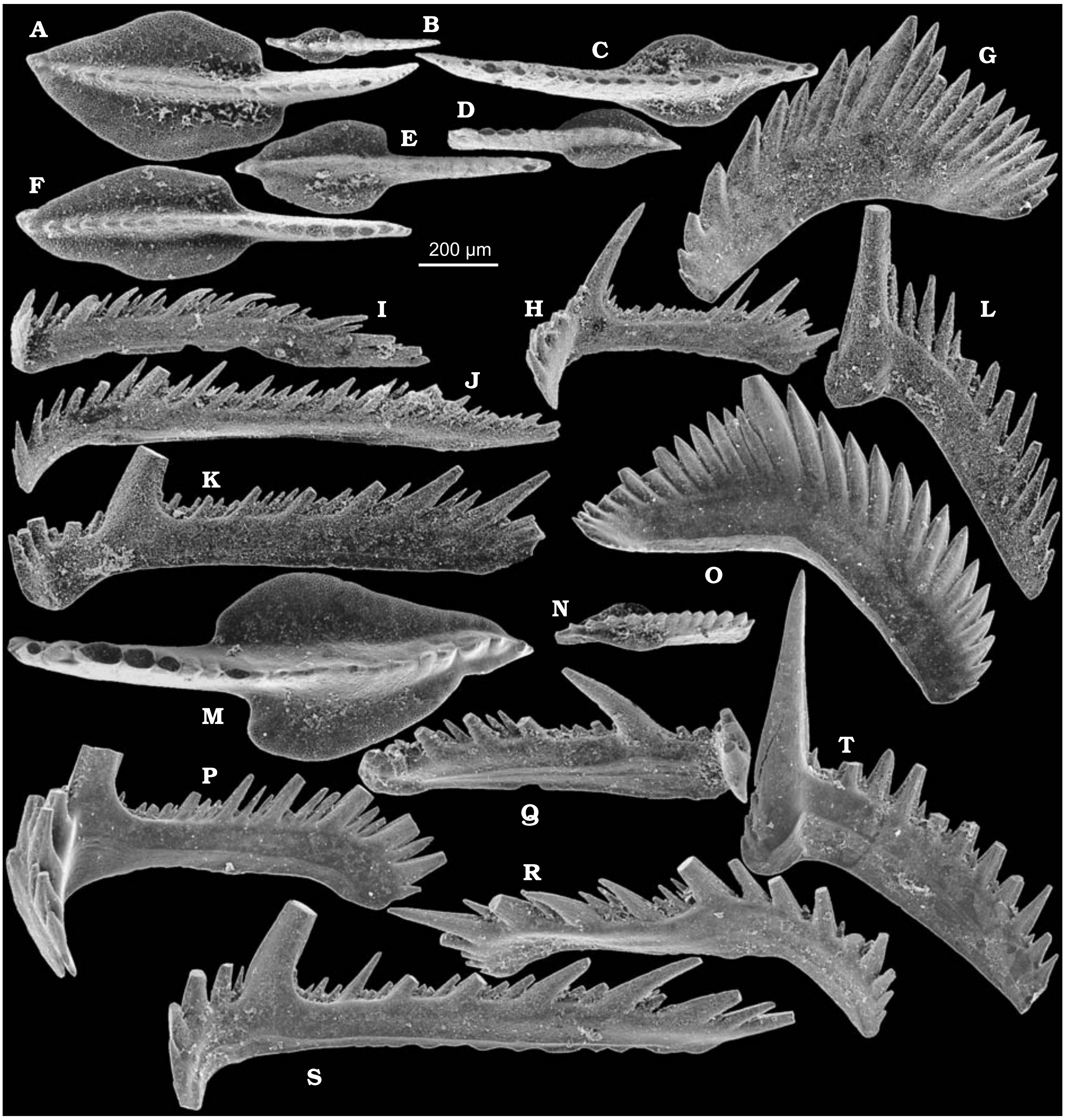


Fig. 71. Species of *Lagovignathus* with smooth platform from the Holy Cross Mountains. **A**–**L**. *Lagovignathus glaber* (Ulrich *et* Bassler, 1926) from the *K. crepida* Zone at Kadzielnia (A–C, E, sample Ka-14; D, F–L, sample Ka-4). P_1 (A–F), P_2 (G), S_0 (H), S_1 (I), S_2 (J), S_{3-4} (K), and M (L) elements; specimens ZPAL cXVI/2529, 2532, 2530, 2533, 2531, and 2534–2540, respectively. **M**–**T**. *Lagovignathus bilobatus* (Ziegler, 1962) from the *C. quadrantinodosa* Zone at Łagów (sample Ł-32). P_1 (M, N), P_2 (O), S_0 (P), S_1 (Q), S_2 (R), S_{3-4} (S), and M (T) elements; specimens ZPAL cXVI/2542, 2541, 2543, 2547, and 2549, respectively.

Material. — 513 specimens.

Diagnosis. — P_2 elements of robust appearance, with incipient platform, P_1 elements with usually narrow but robust platform and with extensive asymmetric basal cone.

Remarks. — Dense denticulation of juvenile P_1 elements somewhat resembles peniculus and together with the shape of the platform in P_1 elements may suggest affinities with *Polynodosus* (especially *P. lauriformis*). No transitional forms have been found, however. The basal cone, which corresponds to an expanded sinuosa larva, points to *Lagovignathus fallax* as the alternative ancestor. The shape of the platform and outline of mature P_1 elements fits this possibility even better. Probable M element is also unlike that of *Polynodosus*.

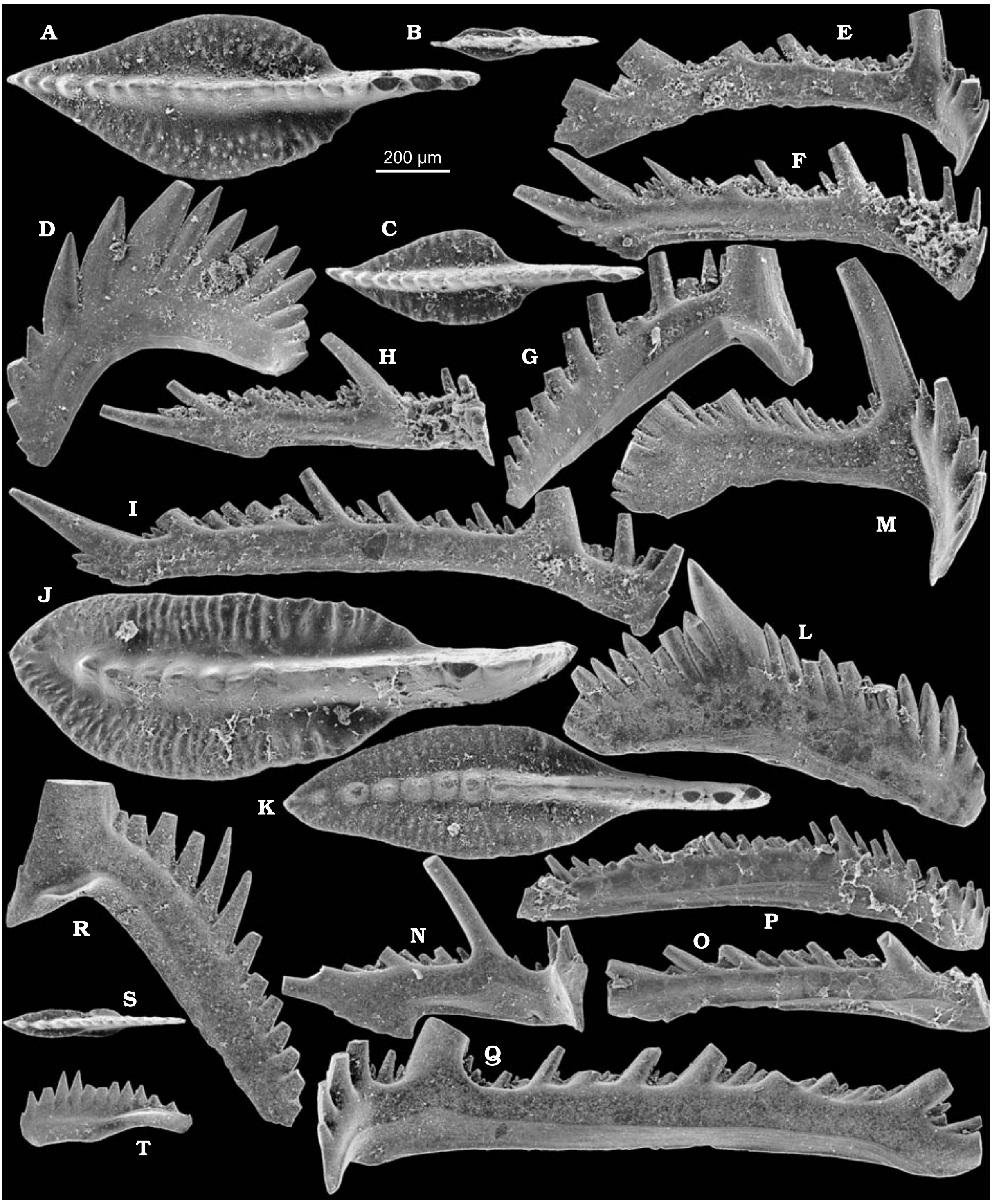


Fig. 72. Early species of *Lagovignathus* with tuberculated platform from the Holy Cross Mountains. **A–I**. *Lagovignathus lagowiensis* (Helms *et* Wolska, 1967) from the *C. quadrantinodosa* Zone at Łagów (sample ŁSł73-5). P_1 (A–C), P_2 (D), S_0 (E), S_1 (H), S_2 (F), $S_{3–4}$ (I), and M (G) elements; specimens ZPAL cXVI/2552, 2550, 2551, 2553, 2554, 2556, 2558, 2555, and 2557, respectively. **J–Q**. *Lagovignathus fallax* (Helms *et* Wolska, 1967) from slightly older part of the same zone at the same locality (sample ŁSł73-2). P_1 (J, K, S, T), P_2 (L), S_0 (M), S_1 (N, O), S_2 (P), $S_{3–4}$ (Q), and M (R) elements; specimens ZPAL cXVI/2562, 2561, 2563, 2564, 2566, 2565, 2568, 2569, 2560, and 2559, respectively.

The evolutionary change with respect to *L. fallax* was the probable further extension of the sinuosa larva stage and development of strong asymmetry of the basal cone in its P_1 element. As a result, a situation developed closely similar to that in advanced species of the palmatolepidid *Tripodellus* lineage.

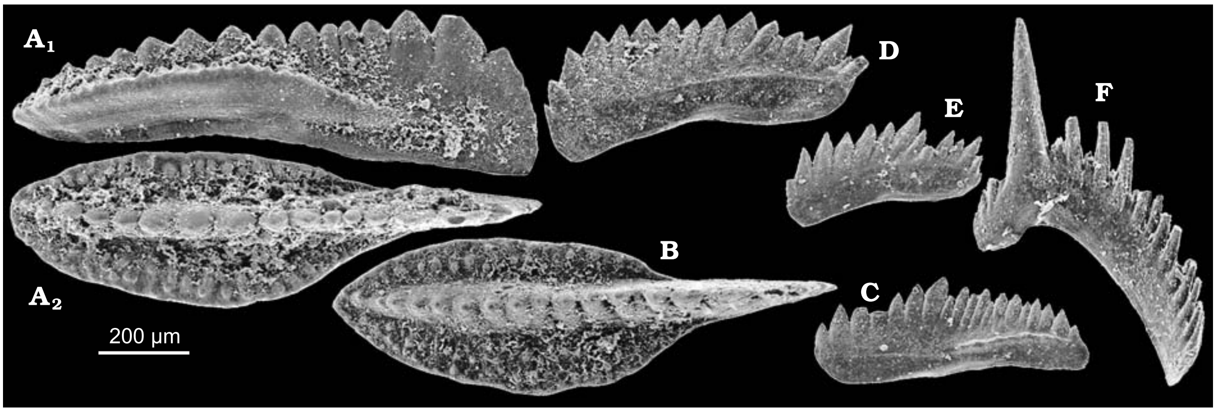


Fig. 73. *Lagovignathus? dissimilis* (Helms *et* Wolska 1967) from the *P. jugosus* Zone at Jabłonna (sample J-51) in the Holy Cross Mountains. P_1 (A–C), P_2 (D, E), and M (F) elements; specimens ZPAL cXVI/2172–2177, respectively.

Occurrence. — The *L. styriacus* to *P. jugosus* zones at Kowala, Ostrówka, Jabłonna and Dzikowiec.

Lagovignathus lagowiensis (Helms *et* Wolska, 1967)
(Figs 72A–I and 131)

Type horizon and locality: Sacculus bank with *Cheiloceras lagowiense* and *Dimeroceras lentiforme*, mixed uppermost rhomboidea and upper marginifera zones according to Helms and Wolska (1967).

Material. — 3,379 specimens.

Diagnosis. — Leaf-like, relatively wide platform of P_1 elements ornamented with small tubercles.

Remarks. — The species is preceded in the Łagów section by the somewhat similar *L. fallax* but transition between these species has not been demonstrated. A much more probable origin from *L. glaber* would require only development of tuberculation of the platform. This is actually the only apparent difference between these species.

Occurrence. — The late *C. marginifera* Zone at Łagów, Kowala, and Miedzianka.

Lagovignathus granulosus (Branson *et* Mehl, 1934)
(Figs 74A–C and 131)

Type horizon and locality: Famennian shale at Noel, Missouri (G. Klapper personal communication 2005).

Material. — 39 specimens.

Diagnosis. — Leaf-like, relatively wide platform of P_1 elements densely ornamented with relatively large tubercles.

Remarks. — The species is so similar to the significantly older *L. lagowiensis* that, despite the discontinuous fossil record at Łagów, the ancestor-descendant relationship seems almost certain. Specimens with smooth concave areas near the ventral end of the platform are transitional to *L. styriacus*, the successor of *L. granulosus* in the same lineage.

Occurrence. — The *P. trachytera* Zone at Łagów, Miedzianka, Jabłonna, Kowala, and Wzdół.

Lagovignathus styriacus (Ziegler, 1957)
(Figs 74D–F and 131)

Type horizon and locality: Sample 73 from a nodular goniatite limestone collected in a quarry between Steinberg and Hitzendorf near Graz, Austria.

Material. — 287 specimens.

Diagnosis. — Wide and asymmetric platform of P_1 element with densely tuberculated dorsal part separated from smooth ventral areas by a transverse row of larger tubercles.

Remarks. — Early populations of *L. styriacus* show great variability in their platform outline, some specimens being narrower even than in the ancestral *L. granulosus*. The transition apparently took a significant time span, the zonal boundary is thus hardly clear-cut. It is possible that some populations from Ostrówka

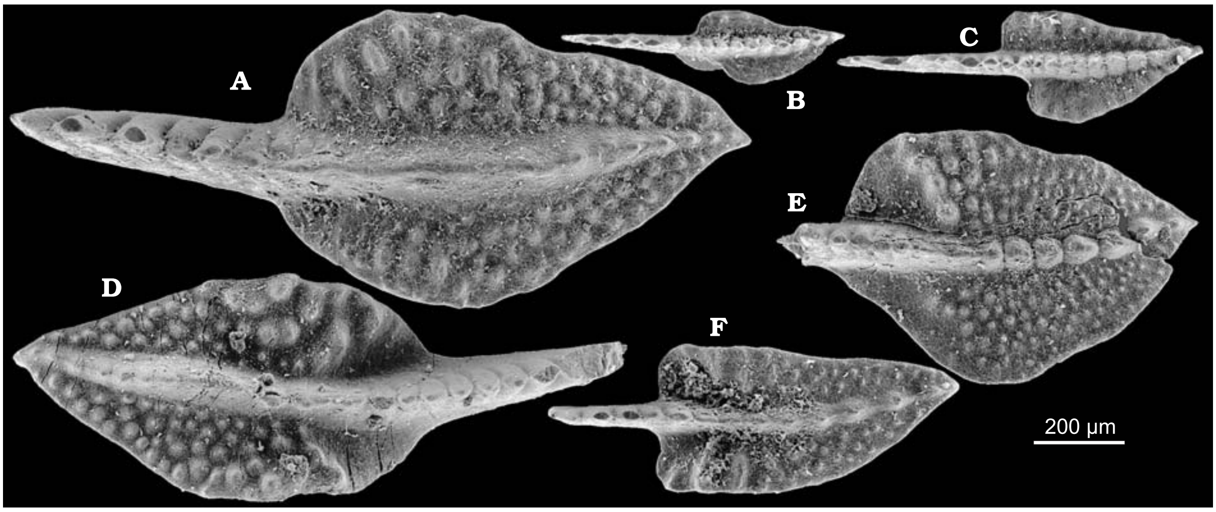


Fig. 74. Late species of *Lagovignathus* with tuberculated platform from the Holy Cross Mountains. **A–C**. *Lagovignathus granulosus* (Branson *et* Mehl, 1934) from the *P. trachytera* Zone at Jabłonna (bed 24). P_1 elements; specimens ZPAL cXVI/2709, 2711, and 2710, respectively. **D–F**. *Lagovignathus styriacus* (Ziegler, 1957) from its nominal Zone at Miedzianka (D, sample Md-6) and Ostrówka (E, F, sample Ost-265). P_1 elements; specimens ZPAL cXVI/2714, and 2712, 2713, respectively.

co-occurring with *P. trachytera* actually represent *L. granulosus*, not *L. styriacus* as suggested by their variable morphology.

Occurrence. — The nominal zone at Jabłonna, Ostrówka, Kowala, and Miedzianka.

Family **Ancyrognathidae** fam. n.

Diagnosis. — Robust and sharply denticulated elements with clearly terminal growth, P_1 element with reduced free blade in adult specimens, S_{1-2} elements bear short processes, M element with prominent and well denticulated external process.

Remarks. — The morphology of the ancyrognathid apparatus elements is in many respects transitional between that of the Polygnathidae and Palmatolepididae. Like the palmatolepidids, processes of elements of *Ancyrognathus* are relatively short and with the clearly terminal growth. *Mesotaxis* is apparently the ancestor of the palmatolepidids although, except for the M element, it has not developed all their diagnostic characters (symmetrical element lacking medial process, lobate platform of P_1 elements).

Genera included. — *Mesotaxis* Klapper and Philip, 1972; *Ancyrognathus* Branson *et* Mehl, 1934; *Ancyrolepis* Ziegler, 1959; *Polylophodonta* Branson *et* Mehl, 1934.

Genus ***Ancyrognathus*** Branson *et* Mehl, 1934

Type species: *Ancyrognathus symmetricus* Branson *et* Mehl, 1934 from the Famennian Saverton Shale at Sees Creek in Monroe County, Missouri (Ziegler 1975).

Diagnosis. —Elongated platform in P_1 elements, tending to develop a prominently tuberculation; triramous in early species; other elements of the apparatus tend to develop a rudimentary platform but still of a generalized polygnathid morphology.

Ancyrognathus sinelamina (Branson *et* Mehl, 1934)
(Figs 75A–H and 132)

Type horizon and locality: Famennian shale at Dixie, Missouri (Ziegler 1977, p. 313).

Material. — 22 specimens.

Diagnosis. — Slender P_1 elements virtually without free blade and any flank lobe of the platform; minute basal cone (pit).

Remarks. — The transition from the biramous latest Frasnian ancyrognathids to this species has been documented by Schülke (1996); probably the early Famennian type species of the genus derived at the transi-

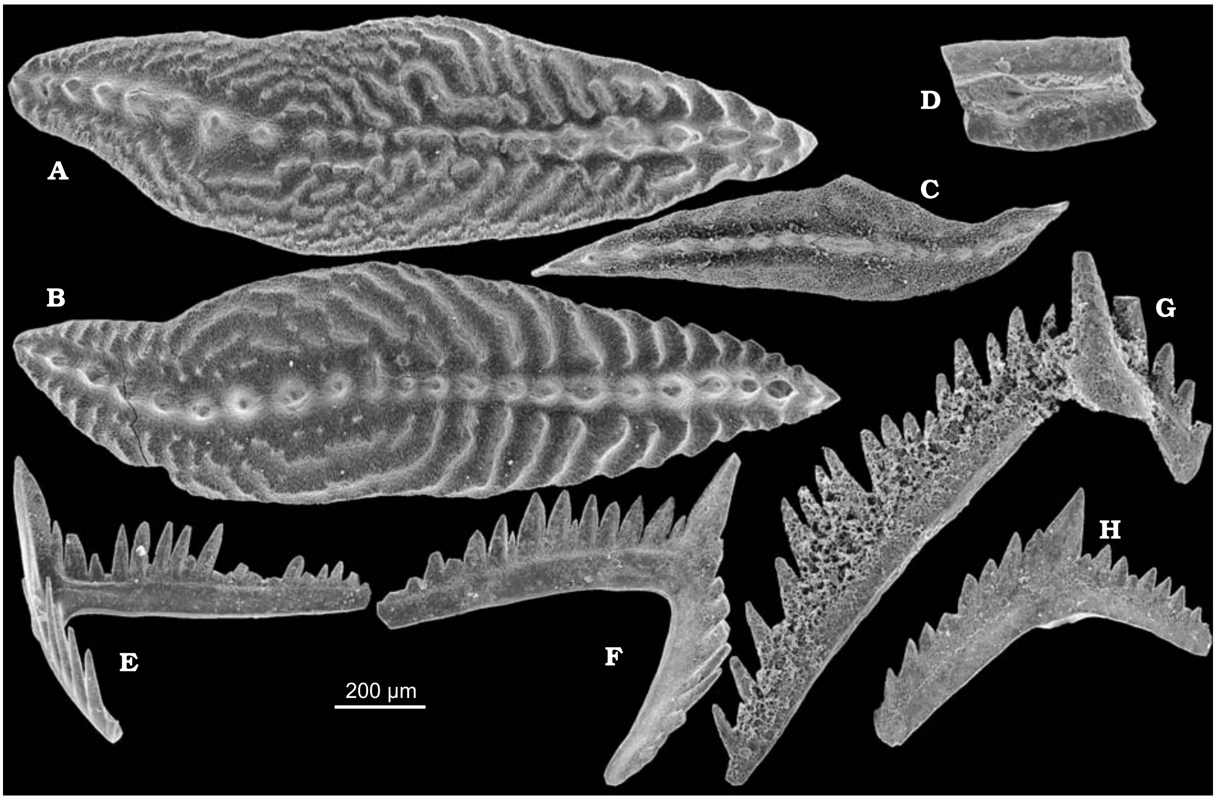


Fig. 75. Typical ancyrognathids from the Holy Cross Mountains, *Ancyrognathus sinelamina* (Branson *et* Mehl, 1934) from the late *K. triangularis* Zone at Karczówka (A, B), the *K. crepida* Zone at Jabłonna (C–F, H, I, bed 3) and Kadzielnia (G, sample Ka-2). P_1 (A–D), P_2 (H), S_0 (E), S_{3-4} (F), and M (G, I) elements; specimens ZPAL cXVI/2604–2607, 2609, 2610, 2612, 2608, and 2611, respectively.

tion. Schülke (1999) attempted restoration of the apparatus but only identification of P_1 elements is supported here. Ramiform elements similar to those associated with Frasnian species of *Ancyrognathus* (Dzik 2002) co-occur with platform elements of *A. sinelamina* in the Holy Cross Mountains.

Occurrence. — The late *K. triangularis* and early *K. crepida* zones at Jabłonna, Wietrznia, Kadzielnia, and Miedzianka. The species occurs also in the Dębnik area (Baliński 1995).

Ancyrognathus sp. n.
(Figs 9E, 76, and 132)

Material. — 28 specimens.

Remarks. — In the early Famennian of the Holy Cross Mountains rare platform elements similar to those of *Dasbergina kayseri* occur, different from those from their late Famennian type horizon in a less regular outline and coarser tuberculation of the platform. However, rare associated ramiform elements probably belonging to the species support its affinities with *Polylophodonta* and *Ancyrognathus*. Perhaps this is a successor of *A. sinelamina*.

Occurrence. — The *K. crepida* Zone at Jabłonna and Kadzielnia.

Genus ***Polylophodonta*** Branson *et* Mehl, 1934

Type species: *Polygnathus gyratilineatus* Holmes, 1928 from the Gassaway Member of the Chattanooga Shale, Alabama.

Diagnosis. — Wide oval platform in P_1 elements; M element preserves generalized polygnathid morphology.

Remarks. — There are some difficulties with delineating the boundary between early species of the ancyrognathid *Polylophodonta* and homeomorphic advanced platform-bering members of the *Mehlina* lineage (*Polynodosus*) if only platform elements are considered.

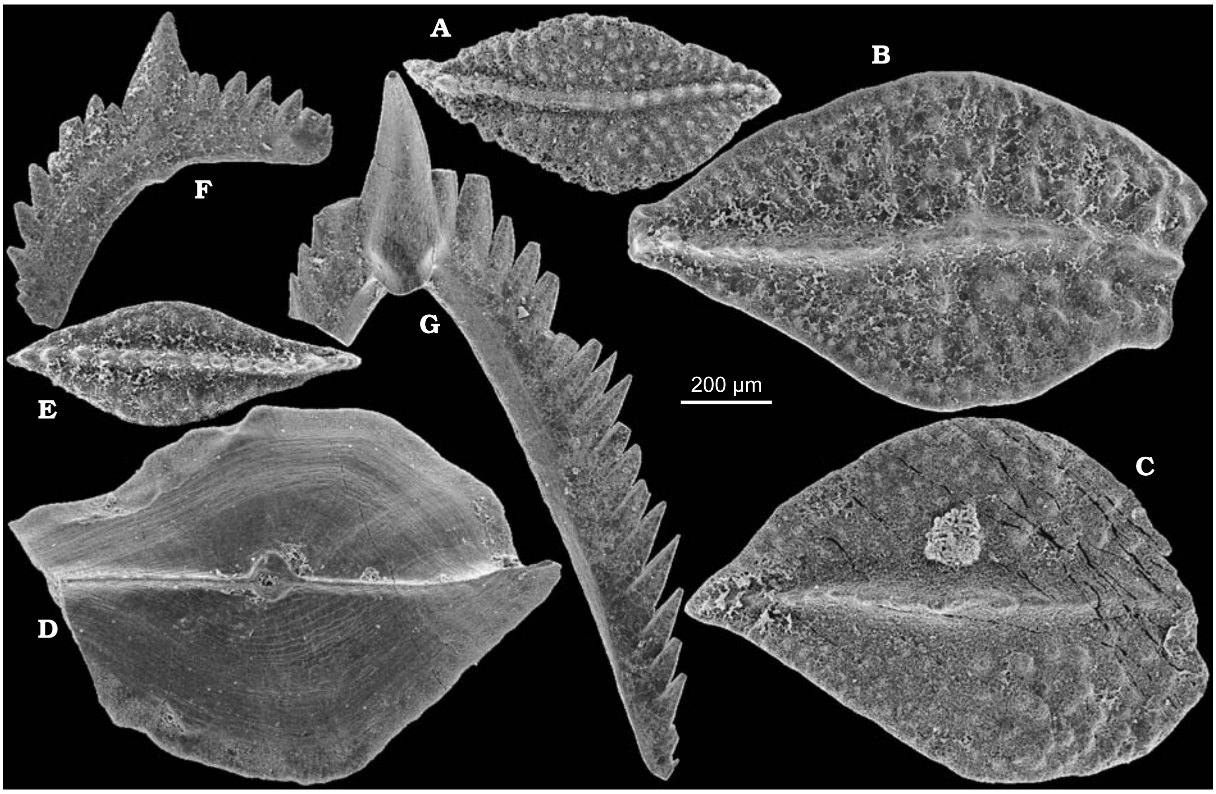


Fig. 76. *Ancyrognathus* sp. n. a relict ancyrognathid from the *K. crepida* Zone at Jabłonna (A–D, sample J-65) and Kadzielnia (E–G, sample Ka-5) in the Holy Cross Mountains.

Polylophodonta ovata (Helms, 1961)
(Figs 77 and 132)

Type horizon and locality: Lower bed of red limestone, lower *Cheiloceras* Zone, in western quarry on Kahlleithe near Rödersdorf, Thuringia (Helms 1961).

Material. — 289 specimens.

Diagnosis. — Row of denticles of the blade of recognizable to the dorsal end of the platform in P_1 elements even in mature specimens.

Remarks. — The oldest occurrence of the species is in bed 4 at Jabłonna, where it occurs together with *Klapperilepis crepida* prior to the entrance of *Conditolepis tenuipunctata*. Elements from there are of a rather robust and irregular appearance. The typical form occurs in the somewhat younger samples J-45a and Wtr-32.

Occurrence. — The late *K. triangularis* and early *K. crepida* Zone at Jabłonna, Wietrznia, and Miedzianka. The species occurs also in the Dębnik area, identified there as *P. confluens* by Baliński (1995).

Polylophodonta pergyrata (Holmes *in* Butts, 1926)
(Figs 78 and 132)

Type horizon and locality: Gassaway Member of the Chattanooga Shale at Quicks Mill, Alabama (Huddle 1968).

Material. — 559 specimens.

Diagnosis. — Concentric ridges forming a fingerprint-like appearance of the mature platform of P_1 elements.

Remarks. — Many species names are available for advanced *Polylophodonta*. Although it cannot be excluded that several biological species are represented in the studied material, I am not able to find any discontinuity in the observed population variability.

Occurrence. — The mid *K. crepida* to *P. trachytera* zones at Jabłonna, Kowala, Kadzielnia, Łagów, Miedzianka, and Ostrówka.

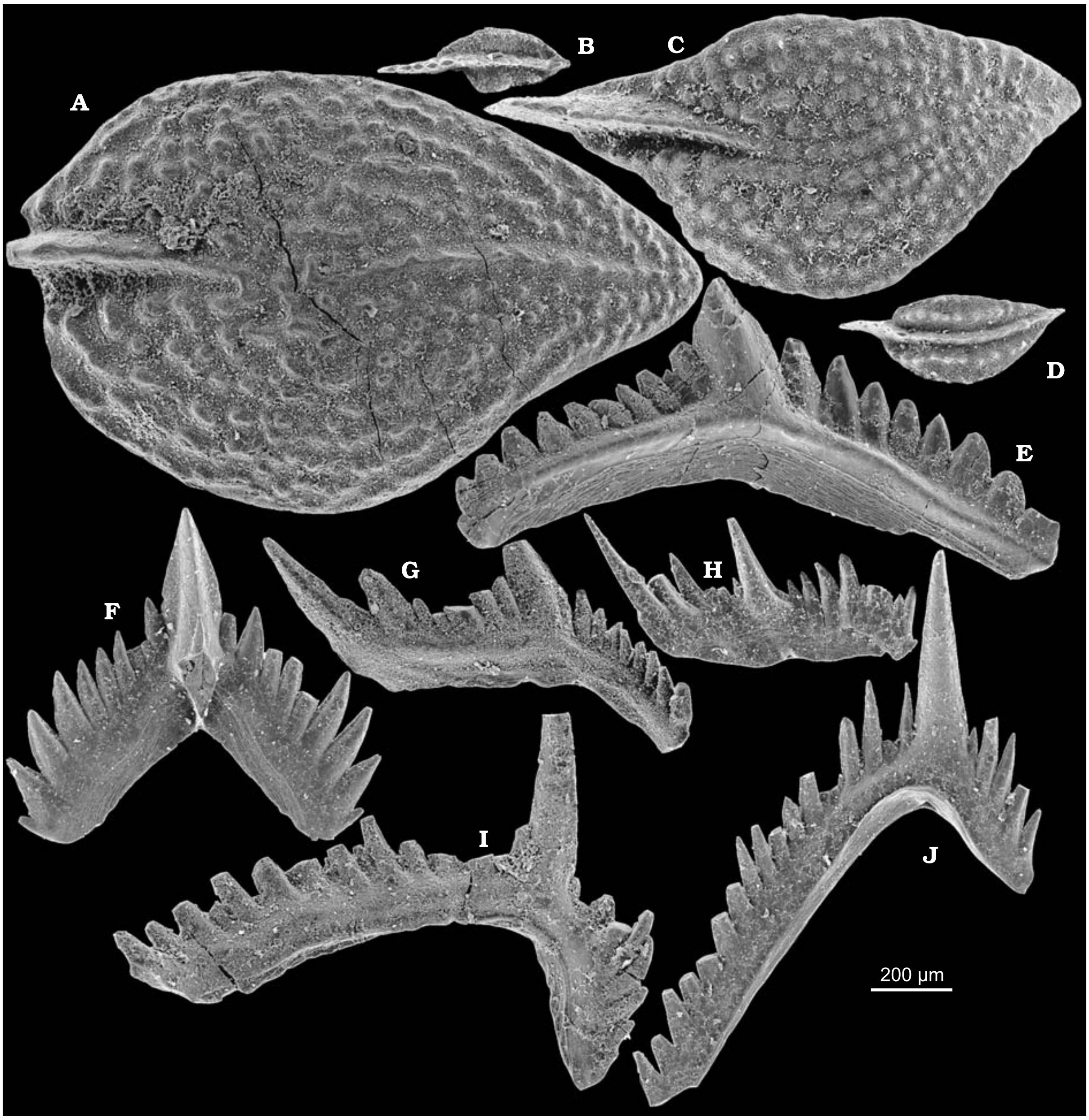


Fig. 77. Derived ancyrognathid *Polylophodonta ovata* (Helms, 1961) from the early *K. crepida* Zone at Wietrznia (A, D, sample Wtr-32) and the *K. triangularis* Zone at Jabłonna (B, E, H, I, J, sample J-45a; F, G, sample J-44) in the Holy Cross Mountains. P_1 (A–D), P_2 (E), S_0 (F), S_1 (H), S_2 (G), S_{3-4} (I), and M (J) elements; specimens ZPAL cXVI/2579, 2582, 2580, 2581, 2583, 2584–2588, respectively.

Family **Palmatolepididae** Sweet, 1988

Diagnosis. — Apparatus with M element having straight processes and S_0 element with more or less reduced medial process; usually lobate platform-bearing P_1 and P_2 elements.

Genus ***Klapperilepis*** Dzik, 2002

Type species: *Palmatolepis triangularis* Sannemann, 1955 from the early Famennian of Frankenwald.

Diagnosis. — P_1 elements with raised tip of the dorsal process and underived appearance of the remaining elements of the apparatus.

Remarks. — Discrimination of early sympatric species of *Klapperilepis* is a difficult task and while discussing their taxonomy in the context of the end-Frasnian events I failed to find a satisfactory solution (Dzik

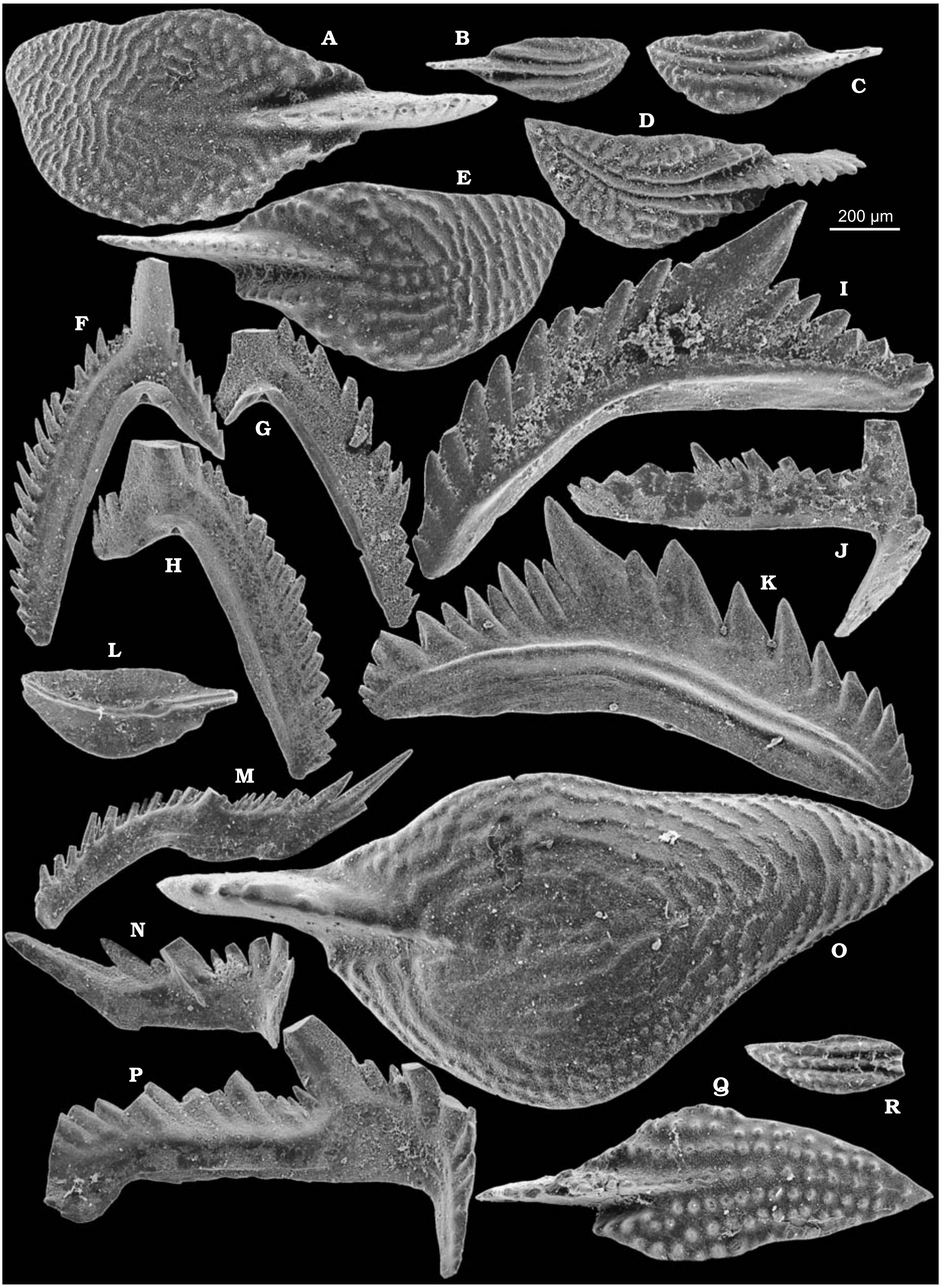


Fig. 78. Derived ancyrognathid *Polylophodonta pergyrata* (Holmes *in* Butts, 1926) from the *K. crepida* Zone at Kadzielnia (A, H, sample Ka-12; B, D, K, sample Ka-5; G, J, and M–R, sample Ka-2) and Jabłonna (C, E, F, and L, bed 7), and the *C. quadrantinodosa* Zone at Łagów (I, sample Ł-26) in the Holy Cross Mountains. P_1 (A–E, L, O, Q, R), P_2 (I, K), S_1 (N), S_2 (M), S_{3-4} (P), and M (F–H) elements; specimens ZPAL cXVI/2596, 2594, 2573, 2595, 2574, 2575, 2613, 2597, 2159, 2617, 2591, 2572, 2619, 2614, 2618, 2620, and 2615, 2616, respectively.

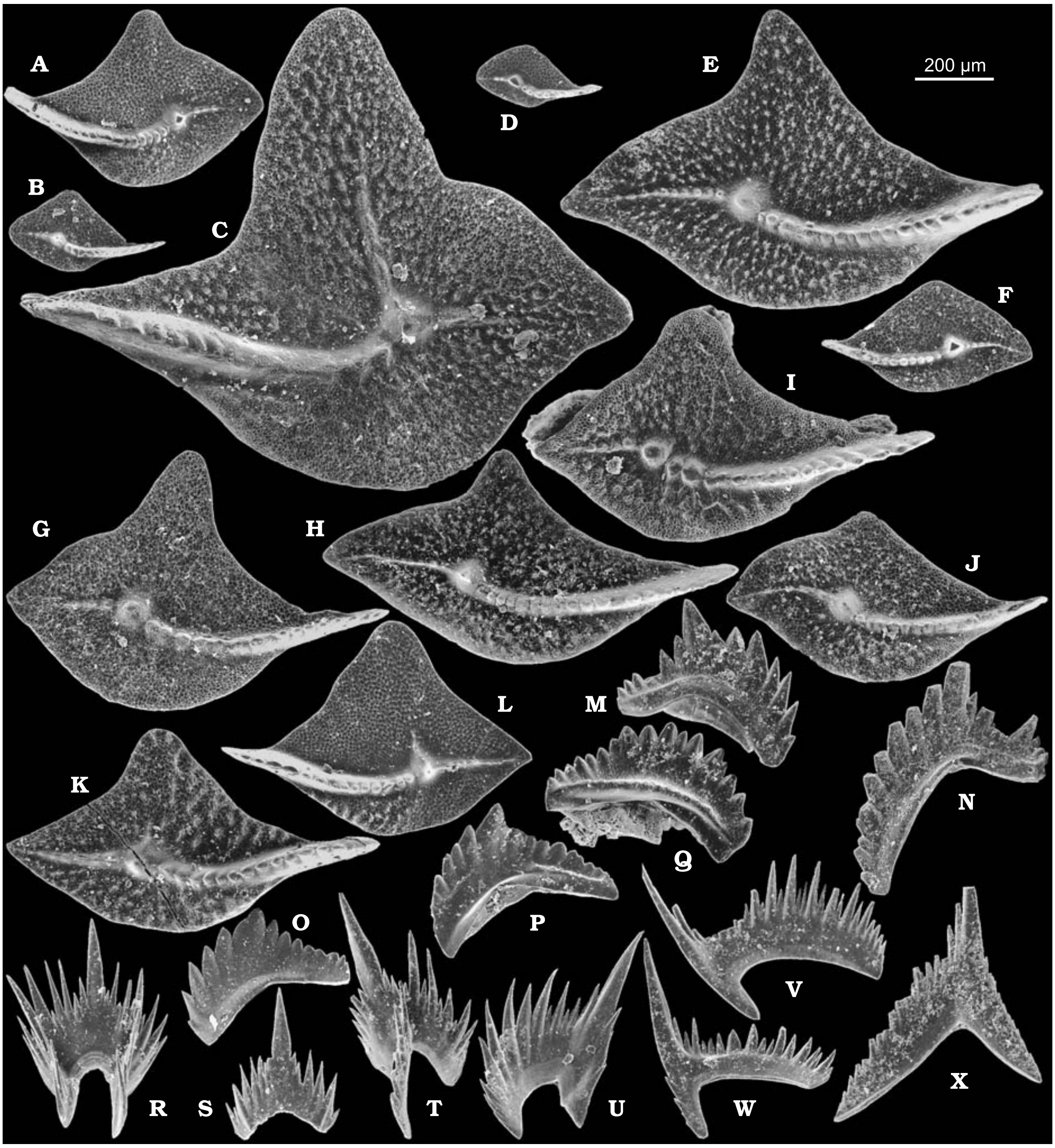


Fig. 79. Ancestor of Famennian palmatolepidids, *Klapperilepis ultima* (Ziegler, 1958) from the pre-*K. triangularis* Zone strata at Płucki (sample Pł-36) in the Holy Cross Mountains. P_1 (A–L), P_2 (M–Q), S_0 (R, S), S_1 (T), S_2 (U), S_{3-4} (V, W), and M (X) elements; specimens ZPAL cXVI/1512, 1503, 1506, 1513, 1509, 1505, 1502, 1510, 1508, 1511, 1507, 1504, 1514, 1518, 1516, 1517, 1515, and 1519–1525, respectively.

2002). No doubt that several new lineages emerged soon after the taxonomic diversity of the palmatolepidids was reduced to the single species, *K. ultima*.

This is proven by the occurrence of two distinct types of M elements in sample Pł-42: one of the primitive latest Frasnian morphology, the other of an appearance similar to that of *K. quadrantinodosolobata*. Other ramiform elements of the *Klapperilepis* apparatus do not form any discrete classes and are probably indistinguishable at the species level. It seems reasonable to assume that the P_1 elements morphologically closest to *K. ultima* belong to the same apparatus as the associated primitive M elements. Platform elements of this kind show a relatively sinuous course of the blade. Juveniles may resemble *Conditolepis tenuipunctata* or *Klapperilepis circularis* (in Dzik 2002, table 2 they were provisionally listed under these names). Somewhat arbitrarily this population is here considered to be the oldest *K. triangularis*.

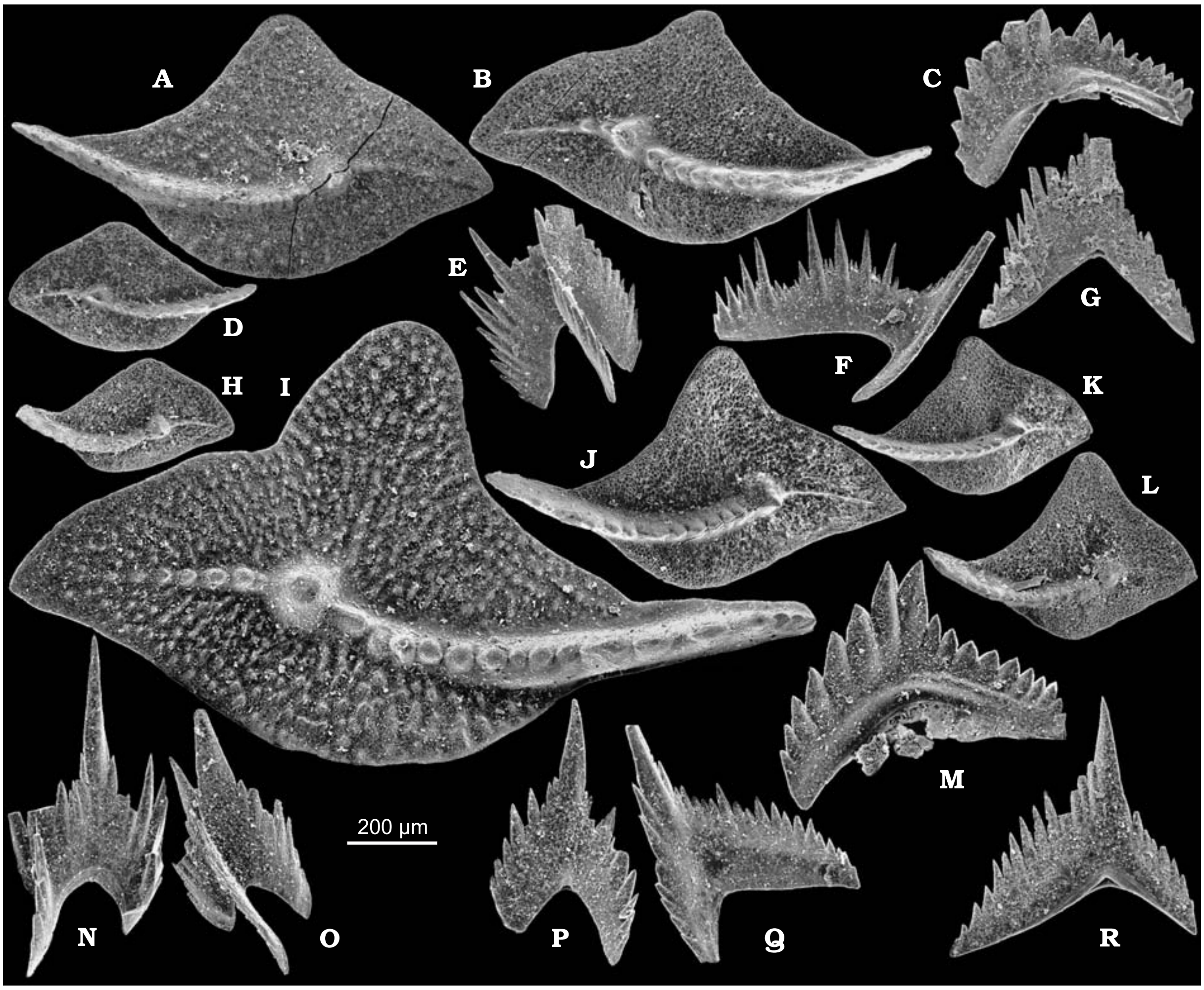


Fig. 80. Palmatolepidids of the *Klapperilepis triangularis* (Sannemann, 1955) lineage from its nominal zone strata at Płucki in the Holy Cross Mountains. **A**–**G**. *K. triangularis* from sample Pł-42. **H**–**R**. Probable ancestral population of *Palmatolepis initialis* sp. n. (sample Pł-1). P_1 (A, B, D, H–L), P_2 (C and M), S_0 (N), S_1 (E and O), S_2 (P), S_{3-4} (F and Q), and M (G and R) elements; specimens ZPAL cXVI/1232, 1233, 1235, 1234, 1237–1239, 1344, 1339, 1340, 1341, 1343, 1345, 1346–1348, and 1350, 11351, respectively.

Using the same line of reasoning one would expect that P_1 elements resembling those of *K. spathula* in sample Pł-42 are conspecific with the advanced M elements. Although there is no apparent gap between the range of its morphologic variability and that of associated *K. triangularis*, such an interpretation is consistent with the apparatus reconstruction proposed by Schülke (1999) for the species here named *K. schuelkei* sp. n.

The remaining morphotype of platform elements in sample Pł-42 is much more clearly delimited. In having a rhomboidal outline of the smooth platform with raised margins and a straight blade it closely resembles *Tripodellus clarki* and probably represents its early population. There is a gradual transition towards morphologies with a wide platform resembling *K. delicatula*.

Klapperilepis ultima (Ziegler, 1958)
(Figs 8C, 79, and 135)

Type horizon and locality: Latest Frasnian sample 27 from Sessacker II trench (Ziegler 1958).

Material. — 2,084 specimens (1,207 from the Famennian).

Diagnosis. — Relatively wide and short platform of P_1 elements, underived appearance of A-shaped M elements.

Remarks. — There is a gradual evolutionary change in the morphology of P_1 elements obscured by a wide population variability (Dzik 2002). This variability makes the lineage to be of little correlative value. The apparatus of the species is documented with clusters of elements from the earliest Famennian at Płucki (samples Pł-20 and Pł-16), some representing significant portions of the apparatus (Dzik 2002). *Palmatolepis praetriangularis* Ziegler and Sandberg, 1988 has been pointed out by Klapper *et al.* (2004) to be a junior subjective synonym of *P. ultima*.

Occurrence. — The origin of the lineage remains cryptic. Populations from the latest Frasnian do not seem to differ from those from the beginning of the Famennian. At Płucki specimens with somewhat elongated platform classified within the succeeding *K. triangularis* appear in a greater number in sample Pł-42 (note, however that this character is size-dependent), at Kowala in sample Ko-155.

Klapperilepis triangularis (Sannemann, 1955)
(Figs 80A–G, 81A–J, and 135)

Type horizon and locality: Nodular limestone at Schübelebene in Frankenwald (Sannemann 1955b; Ziegler 1975).

Material. — 422 specimens.

Diagnosis. — P_1 elements relatively elongated and M elements usually with relatively wide angle between processes.

Remarks. — P_2 elements of the apparatus were identified by van den Boogaard and Kuhry (1979); the complete apparatus was restored by Schülke (1999).

This is a variable species, both in respect to the outline of platform in P_1 elements, which ranges from that typical to *K. ultima* to that of early species of *Palmatolepis*, but also in the prominence of the cusp and curvature of P_2 elements. The mean value of elongation index of the P_1 elements is, however, distinctly higher than in *K. ultima* (Dzik 2002, 2004), remaining elements of the apparatus being hardly distinguishable. In fact, to distinguish these chronospecies a large sample is needed and singler elements are of little taxonomic value.

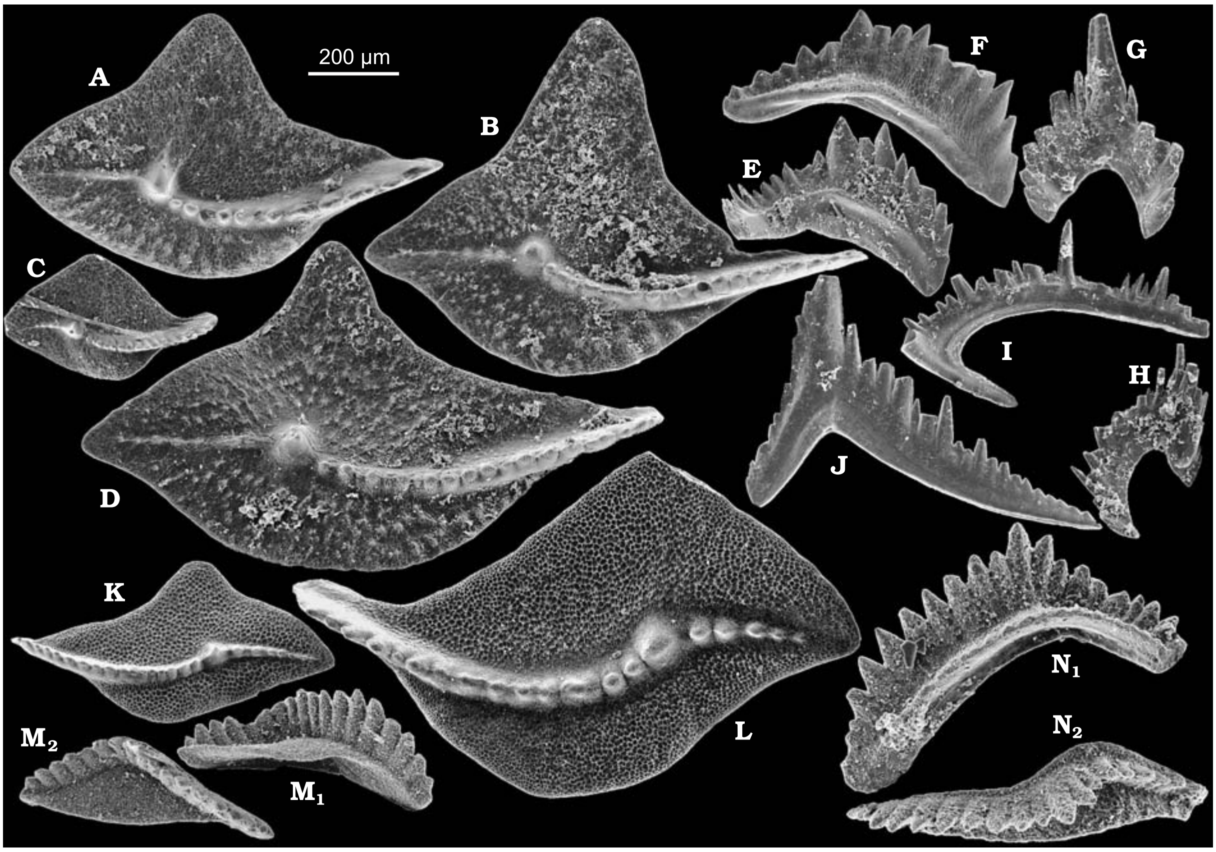


Fig. 81. Species of the palmatolepidid *Klapperilepis* from the early Famennian of the Holy Cross Mountains. **A**–**J**. *K. triangularis* (Sannemann, 1955) from its nominal Zone strata at Kowala (A, B, H–J, sample Ko-153; C–G, sample Ko-154). P_1 (A–D), P_2 (E, F), S_0 (G), S_1 (H), $S_{3–4}$ (I), and M (J) elements; specimens ZPAL cXVI/2732, 2733, 2727, 2728, 2729–2731, and 2734–2736, respectively. **K**–**N**. *Klapperilepis regularis* (Cooper, 1931) from the late *K. triangularis* Zone at Karczówka (K, L) and the *K. crepida* Zone at Kadzielnia (M, Ka-12) and Miedzianka (N, sample Md-1). P_1 (K, L) and P_2 (M, N) elements; specimens ZPAL cXVI/2919, 2820, 2818, and 2955.

Some late populations (e.g., Pł-1; Fig. 80H–R) show robust denticulation of ramiform elements and widely angular processes of the M element typical of *Palmatolepis initialis* sp. n.

Occurrence. — Zone of its own at Płucki, Karczówka, Kowala, and Wietrznia.

Klapperilepis regularis (Cooper, 1931)
(Figs 81K–N and 134)

Type horizon and locality: Woodford Shale of the Arbuckle Mountains, Oklahoma (Cooper 1931).

Material. — 222 specimens.

Diagnosis. — Sinuously curved P_1 elements with subparallel margins of wide platform; angularly bent P_2 elements with low denticles and posteriorly wide platform.

Remarks. — Apparatus was partially restored by Schülke (1999) with the M element indicating a relationship to *Klapperilepis triangularis*. P_2 elements of the same morphology as those from the Montagne Noire occur in the Holy Cross Mountains.

Occurrence. — The late *K. triangularis* and *K. crepida* zones at Jabłonna, Karczówka, Kadzielnia and Kowala.

Klapperilepis protorhomboidea (Sandberg *et* Ziegler, 1973)
(Figs 82A–C and 134)

Type horizon and locality: 7.5–8.5 m above the base of the West Range Limestone at Bactrian Mountain, Nevada.

Material. — 32 specimens.

Diagnosis. — Platform in minute P_1 element of variable, more or less rhomboidal outline and with irregularly distributed tubercles, mostly on the ventral anterior quadrant.

Remarks. — Apparatus was restored by Schülke (1995). The species changes into *K. rhomboidea* but the transition is rather unclear because of the great population variability and generally low number of elements in studied samples.

Occurrence. — The *K. triangularis* Zone at Płucki, Kowala, Wietrznia and Jabłonna.

Klapperilepis rhomboidea (Sannemann, 1955)
(Figs 82D–H and 134)

Type horizon and locality: Nodular limestone of upper *Cheiloceras* Stufe at Kirchgattendorf in Frankenwald (Sannemann 1955b; Ziegler 1975).

Material. — 557 specimens.

Diagnosis. — Platform in minute P_1 element of angularly oval outline, without posterior lobe, smooth.

Remarks. — Metzger (1994) proposed a P_2 element identification that seems unlikely to be correct. The species is well represented in some samples by P_1 elements but other elements of the apparatus are difficult to collect because of their small size. They are identified as belonging to this species mostly on the basis of their unusually primitive morphology compared with the age of the sample.

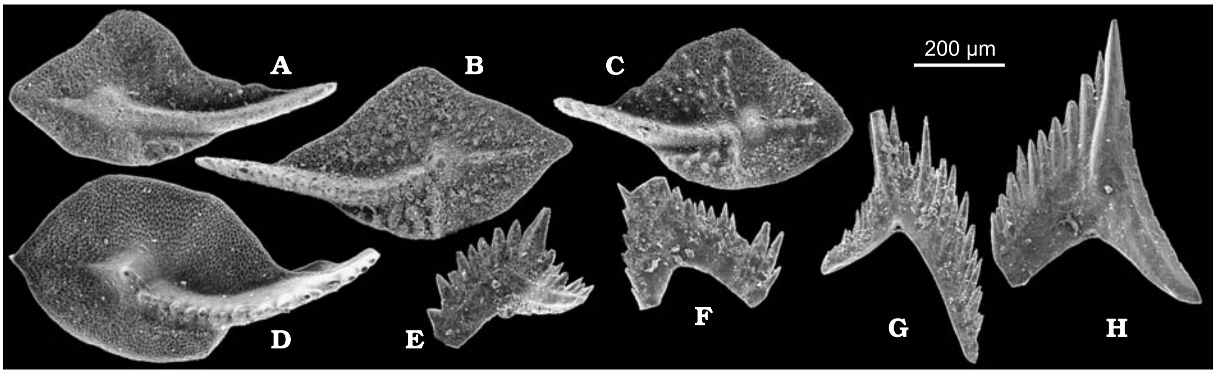


Fig. 82. Palmatolepidids of the *K. rhomboidea* lineage from the Holy Cross Mountains. **A**–**C**. *Klapperilepis protorhomboidea* (Sandberg *et* Ziegler, 1973) from the mid *K. triangularis* Zone at Jabłonna (sample J-54). P_1 elements; specimens ZPAL cXVI/2737–2739. **D**–**H**. *Klapperilepis rhomboidea* (Sannemann, 1955) from the *C. quadrantinodosa* Zone at Łagów (sample Ł-32). P_1 (D), P_2 (E), S_2 (F), and M (G, H) elements; specimens ZPAL cXVI/1370–1375, respectively.

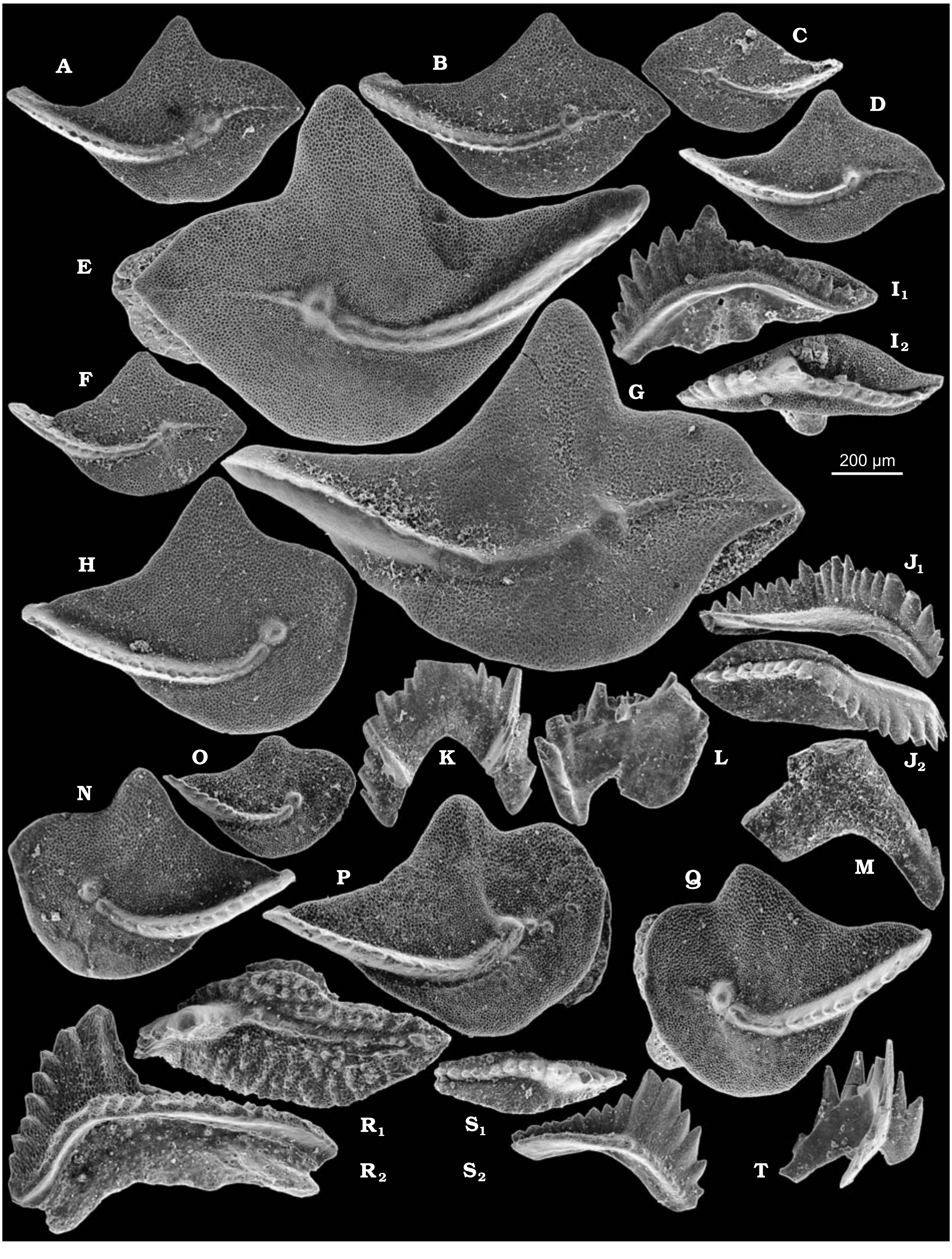


Fig. 83. Palmatolepidids of the *K. circularis* lineage. **A**–**M**. *Klapperilepis wolskae* (Ovnatanova, 1969) from the late *K. triangularis* Zone at Wietrznia (A–D, F–H, J, K, and M, sample Wtr-27) and Karczówka (E, I, and L) in the Holy Cross Mountains. P_1 (A–H), P_2 (I, J), S_2 (K), and M (M) elements; specimens ZPAL cXVI/1449, 2795, 1450, 2949, 1451, 2948, 2806, 2796, 2950, 1452, 1453, 2951, 1454, and respectively. **N**–**T**. *Klapperilepis circularis* (Szulczewski, 1971) from the *K. crepida* Zone at Miedzianka (N, S, T, sample Md-1), Jabłonna (O, P, bed 7), and Łagów? (S, T, sample Ł-Mec). P_1 (N–Q), P_2 (R, S), and S_1 (T) elements; specimens ZPAL cXVI/2952, 2958, 2959, 2956, 2957, and 2953, 2954, respectively.

Occurrence. — The late *K. crepida* Zone (with *C. klapperi*) at Kadzielnia and the *C. quadrantinodosa* Zone at Kowala, Łagów, and Miedzianka. The species occurs also in the Dębnik area (Baliński 1995).

Klapperilepis wolskae (Ovnatanova, 1969)
(Figs 83A–M and 133)

Type horizon and locality: Sandonsk stage at depth 375.4–377.8 m of borehole Ilmen in Woronezh region, Russia; crepida Zone (Ziegler 1975).

Material. — 236 specimens.

Diagnosis. — Oval platform of P_1 elements with prominent narrow extension of the posterior lobe.

Remarks. — Elements of the kind attributed to the apparatus of this species by Metzger (1994) do not occur in the Holy Cross Mountains (perhaps this is a partial apparatus of a new species of *Syncladognathus*) and a different composition is suggested here, although the evidence remains very weak. P_1 elements are extremely variable in Wietrznia (Wtr-27), ranging from an outline resembling that of *K. triangularis* to that of *K. circularis* (Fig. 83D, H).

Occurrence. — The late *K. triangularis* and the early *K. crepida* zones at Płucki, Wietrznia, Karczówka, and Jabłonna.

Klapperilepis circularis (Szulczewski, 1971)
(Figs 83N–T and 133)

Type horizon and locality: Sample X.4 from a bed of cephalopod limestone at the Kadzielnia quarry with early *K. termini*, the *K. crepida* Zone, Holy Cross Mountains.

Material. — 312 specimens.

Diagnosis. — Subcircular outline of platform of P_1 elements with short and wide extension of the posterior lobe and blunt dorsal tip.

Remarks. — Elements of the species are generally much smaller than those of the ancestral *K. wolskae*, even at a stage of apparent maturity. The main distinguishing character is the rounded dorsal tip of the platform and strongly curved blade. No other apparatus elements have been identified with reasonable confidence.

Occurrence. — The *K. crepida* Zone at Kadzielnia, Jabłonna, Wietrznia, Miedzianka, and Kowala. The species occurs also in the Dębnik area (Baliński 1995).

Klapperilepis schuelkei sp. n.
(Figs 84A–H and 133)

Holotype: Specimen ZPAL cXVI/1240 (Fig. 84A).

Type horizon and locality: Sample Pł-42, early Famennian earliest *K. triangularis* Zone at Płucki, Holy Cross Mountains.

Derivation of name: To honour the contribution of Immo Schülke to understanding this species.

Material. — 25 specimens.

Diagnosis. — Smooth platform of P_1 elements with pointed lobe, M element with fan-like arrangement of denticles, P_2 elements with weakly developed platform and regular denticulation.

Remarks. — The apparatus of this species was restored by Schülke (1999) as *Palmatolepis arcuata*, but as I already pointed out elsewhere (Dzik 2002, p. 624), the type horizon of the holotype of *Palmatolepis arcuata* of Schülke (1995) is of significantly younger age and cannot serve as the name-bearer for it. Instead, I suggested *Palmatolepis marginata clarki* Ziegler, 1962 as possibly conspecific with this early member of the *Klapperilepis* lineage, although the latter species has been synonimized with *Tripodellus variabilis* by Schülke (1999). Without additional topotype material large enough to enable apparatus reconstruction it is hard to decide on such subjects and the only basis for this decision was that the type specimen of *K. clarki* shows a more rounded appearance of the lobe and its more transverse direction that is typical for *T. variabilis*. Admittedly, the three specimens from the type horizon illustrated by Ziegler (1962, pl. 2: 20–25) show a robust platform margin typical of early *Tripodellus*. Moreover, the co-occurrence of the type material with the rather advanced member of the *Klapperilepis* lineage, *K. quadrantinodosolobata*, supports the Schülke's (1999) idea that *P. clarki* is a member of another lineage, thus belonging rather to *Tripodellus*. To clarify these nomenclatorial uncertainties, I propose a new name for this species, based on the material from the earliest Famennian and accept Schülke's (1999) interpretation of *T. clarki*.

Occurrence. — The earliest *K. triangularis* Zone at Płucki.

Klapperilepis spathula (Schülke, 1995)
(Figs 84I–L and 133)

Type horizon and locality: Bed 14 at the Upper Coumiac quarry near Cessenon, Montagne Noire (Schülke, 1995).

Material. — 49 specimens.

Diagnosis. — P_1 element with long and narrow extension of the posterior lobe, its surface ornamented with irregular tuberculation, P_2 elements flat, without platform, regularly denticulated and with posteriorly bent dorsal process.

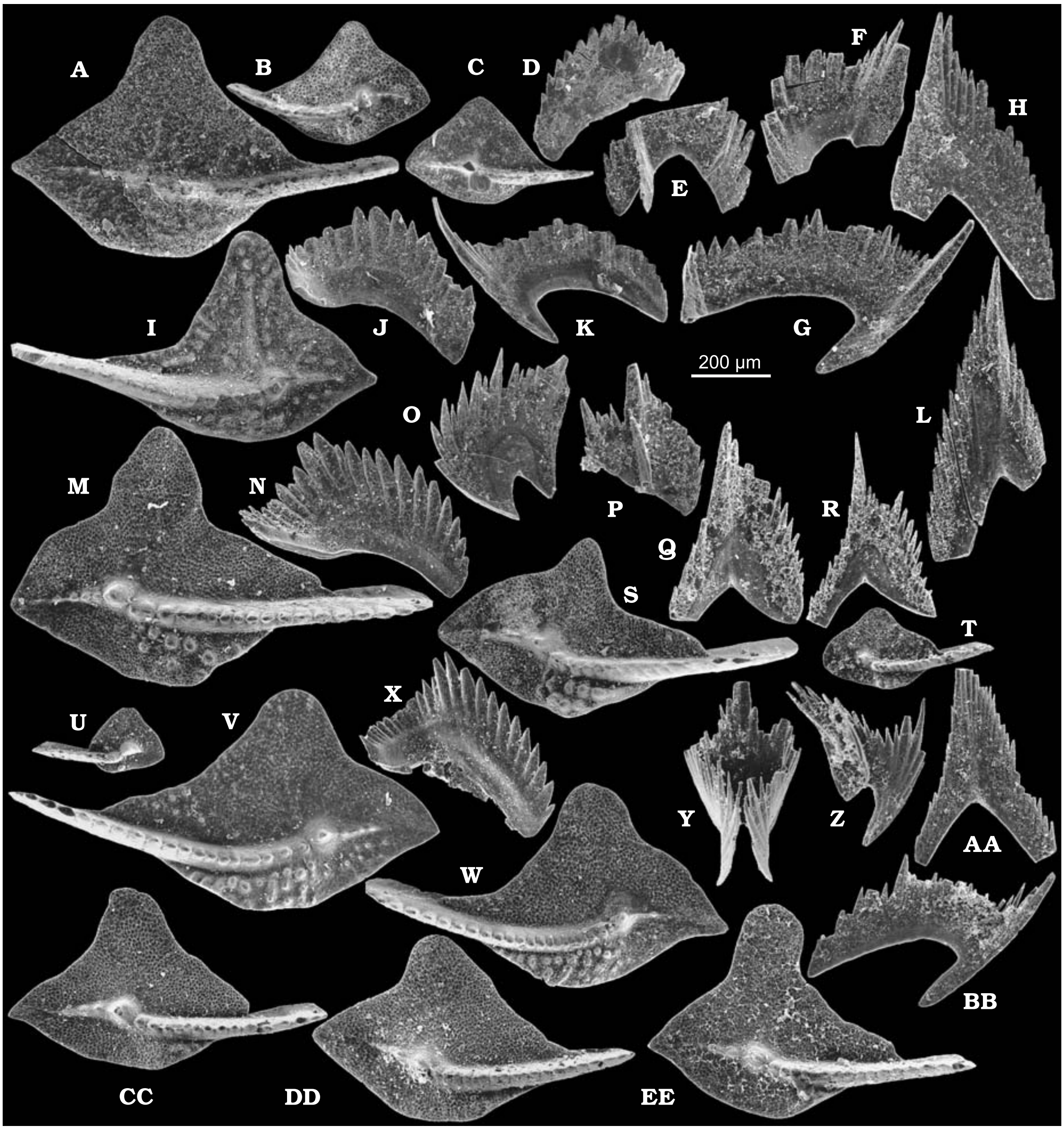


Fig. 84. Early Famennian lobate palmatolepidids from the Holy Cross Mountains. **A–H**. *Klapperilepis schuelkei* sp. n. from the *K. triangularis* Zone strata at Płucki (sample Pł-42; for location and details see Dzik 2002). P_1 (A–C), P_2 (D), S_0 (E), S_1 (F), S_2 (P), S_{3-4} (G), and M (H) elements; specimens ZPAL cXVI/1240 (holotype, A), 1242, 1241, and 1243–1247, respectively. **I–L**. *Klapperilepis spathula* (Schülke, 1995) from the mid *K. triangularis* Zone at Jabłonna (samples J-53, I, J, L and J-53a, K). P_1 (I), P_2 (J), S_{3-4} (K), and M (L) elements; specimens ZPAL cXVI/1262, 1263, 1227 and 1264, respectively. **M–BB**, **CC–EE**?. *Klapperilepis quadrantinodosolobata* (Sannemann, 1955) from the late *K. triangularis* Zone at Jabłonna (M, N, sample J-42; O–S, sample J-45a) and Wietrznia (T–DD, sample Wtr-27). P_1 (M, S–W, possibly CC–EE), P_2 (N and X), S_0 (Y), S_1 (P and Z), S_2 (O), S_{3-4} (BB), and M (Q, R, AA) elements; specimens ZPAL cXVI/1412, 1413, 1330, 1329, 1332, 1331, 1327, 1328, 1433, 1441, 1431, 1434, 1435, 1436, 1439, 1438, 1429, 1432, and 1430, respectively.

Remarks. — Apparatus restoration of Schülke (1995) is confirmed by data from the Holy Cross Mountains. Apart from the platform shape, the most characteristic aspect of this and successive species of the lineage is the stepping arrangement of alternating denticles of S_0 to S_2 elements giving them a highly ordered appearance unknown in any other Famennian conodonts. Also P_2 elements, lacking platform and strongly bent, are of much diagnostic value in this lineage.

Occurrence. — The late *K. triangularis* Zone at Płucki, Wietrznia, Karczówka, Jabłonna, and Kowala.

Klapperilepis quadrantinodosolobata (Sannemann, 1955)
(Figs 84M–BB, CC–EE?, and 133)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955a; Ziegler 1975).

Material. — 4,256 specimens.

Diagnosis. — P_1 element with prominently tuberculated anterior lobe and a tongue-like extension of the smooth posterior lobe, flat P_2 elements with strongly bent dorsal process.

Remarks. — Apparatus composition was restored by Metzger (1994) and confirmed by Schülke (1995). This is the end-member of its lineage sharing with its older relatives the highly regular appearance of ramiform elements.

Occurrence. — The *K. crepida* Zone at Jabłonna, Kadzielnia, Wietrznia, Łagów, Miedzianka, and Kowala.

Klapperilepis delicatula (Branson *et* Mehl, 1934)
(Figs 85 and 133)

Type horizon and locality: Base of the Saverton Shale at Sees Creek in Monroe County, Missouri (Ziegler 1975).

Material. — 208 specimens.

Diagnosis. — P_1 element with triangular outline of the platform extending into an extremely wide posterior lobe.

Remarks. — This is the first, and probably only up to the present Famennian conodont with the apparatus confirmed by a natural assemblage (Puchkov *et al*. 1981). Its preservation is not good enough to offer details on morphology of individual elements but the relatively wide angle between processes of the M element resembles early species of *Klapperilepis*. In sample Pł-1 relatively numerous P_1 elements are associated with those of *Palmatolepis sandbergi* and *Tripodellus clarki* and M elements of *K. quadrantinodosolobata* type. This leaves little choice and most probably *K. delicatula* belongs to an advanced lineage of *Klapperilepis*. Perhaps the Russian apparatus represents an early stage in its evolution with characters of the ancestral *K. ultima* still preserved.

Occurrence. — The *K. triangularis* Zone at Płucki, Wietrznia, Miedzianka, Jabłonna, and Kowala.

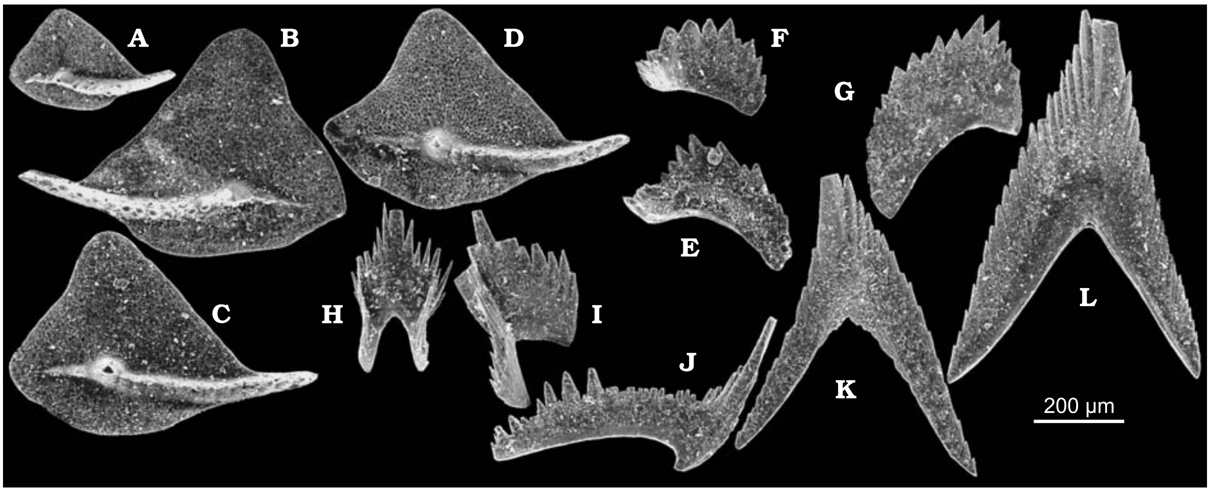


Fig. 85. Palmatolepidid *Klapperilepis delicatula* (Branson *et* Mehl, 1934) from the *K. triangularis* Zone at Płucki (A–G, sample Pł-1) in the Holy Cross Mountains. P_1 (A–D), P_2 (E–G), S_0 (H), S_1 (I), S_2 (O), S_{3-4} (J), and M (K, L) elements; specimens ZPAL cXVI/1359, 1361, 1342, 1360, 1367, 1368, 1362–1366, and 1369, respectively.

Klapperilepis robusta (Schülke, 1995)
(Figs 86A–D and 133)

Type horizon and locality: Bed 72 in Schmidt's quarry in the Kellerwald in the Rhenish Slate Mountains, together with *K. regularis* (Schülke 1995).

Material. — 59 specimens.

Diagnosis. — Platform of P_1 element with small but distinct posterior lobe and pointed dorsal end; juveniles obliquely rhomboidal in outline.

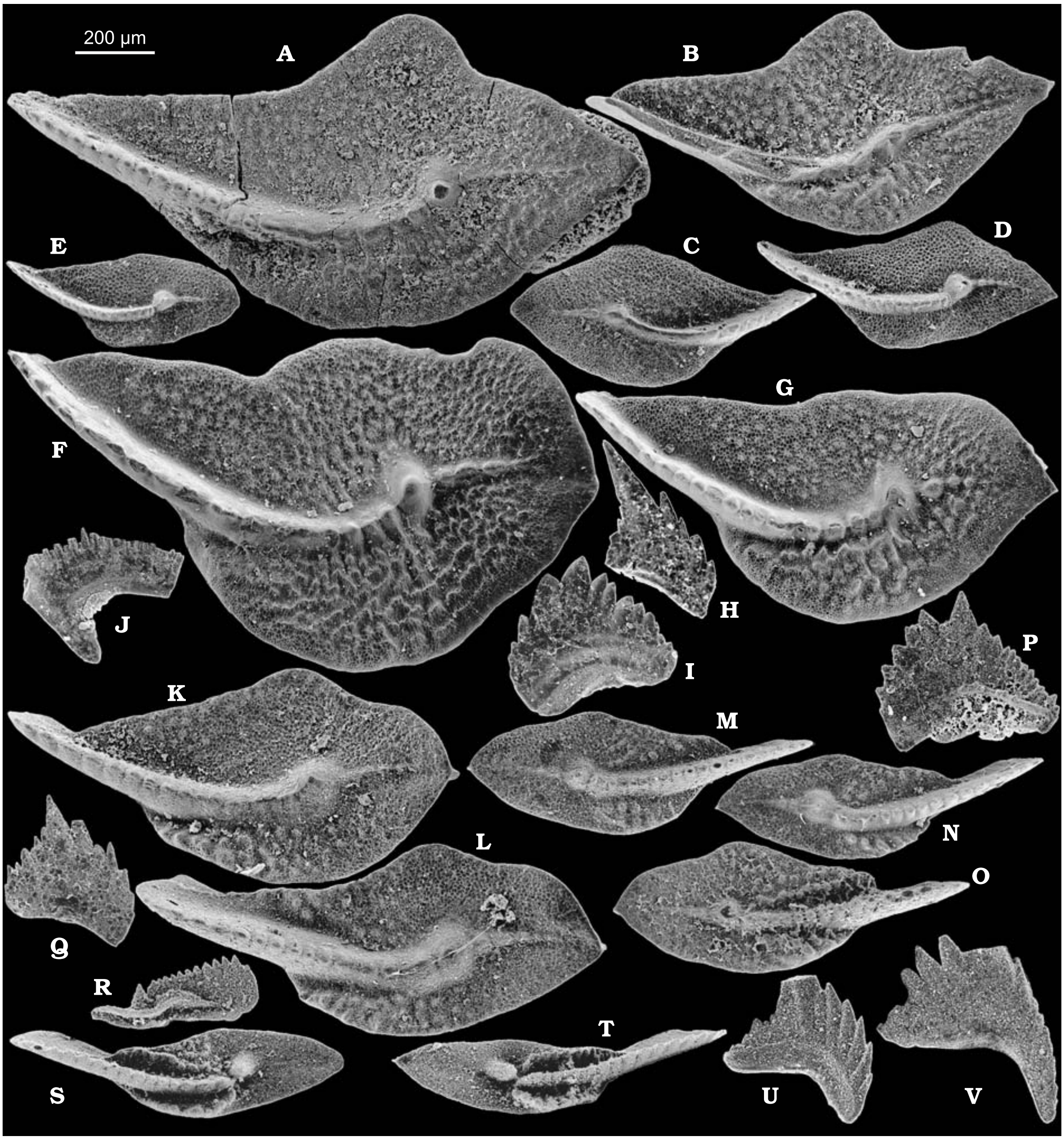


Fig. 86. Robust palmatolepidids of the *K. crepida* group from the Holy Cross Mountains. **A**–**D**. *Klapperilepis robusta* (Schülke, 1995) from the late *K. triangularis* Zone at Wietrznia (A, sample Wtr-26; B–D, sample Wtr-27). P_1 elements; specimens ZPAL cXVI/2797–2800. **E**–**J**. Typical *Klapperilepis crepida* (Sannemann, 1955) from its nominal zone at Wietrznia (sample Wtr-21). P_1 (F, G), P_2 (H, I), and S_{3-4} (J) elements; specimens ZPAL cXVI/2808, 2809, 1962, 2812, and 2811, respectively. **K**–**Q**. Transition series encompassing *K. crepida* and early *K. termini* (Sannemann, 1955) morphologies from Kadzielnia (K–O, Q, sample Ka-14) and Jabłonna (P, sample J-65). P_1 (K–O) and P_2 (P, Q) elements; specimens ZPAL cXVI/2923–2927, 2876, and 2928, respectively. **R**–**V**. Late *K. termini* (Sannemann, 1955) from the *K. crepida* Zone at Kadzielnia (sample Ka-12). P_1 (R–T), P_2 (U), and M (V) elements; specimens ZPAL cXVI/2815, 2813, 2814, and 2816, 2817, respectively.

Remarks. — P_2 elements were identified by van den Boogaard and Kuhry (1979, fig. 18), the complete apparatus by Schülke (1999). The primitive appearance of the M elements indicates a relationship to *Klapperilepis triangularis*. Platform of P_1 element extending almost to the end of the free blade is shared by this species with its successor, *K. crepida*.

Occurrence. — The latest *K. triangularis* Zone at Płucki and Wietrznia.

Klapperilepis crepida (Sannemann, 1955)
(Figs 86E–L and 133)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955*a*; Ziegler 1975).

Material. — 840 specimens.

Diagnosis. — Platform of P_1 element almost lacking the posterior lobe and with blunt dorsal apex, ornamented with irregularly distributed tubercles.

Remarks. — P_2 elements of the apparatus were identified by Schülke (1999). This is a highly characteristic species owing to the robust and somewhat irregular appearance of the platform. The transition from *K. robusta* to *K. crepida* seems to be gradual and identification of some samples may be difficult because of the great variability of both species.

Occurrence. — Zone of its own at Jabłonna, Kadzielnia, Wietrznia, Kowala, and Miedzianka.

Klapperilepis termini (Sannemann, 1955)
(Figs 86M–V and 133)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955a; Ziegler 1975).

Material. — 931 specimens.

Diagnosis. — Platform of P_1 element with rows of high tubercles on both sides of the ventral blade and prominent, isolated cusp.

Remarks. — The P_2 element of the apparatus was identified by Schülke (1999) and such elements also occur in the Holy Cross Mountains.

As already shown by Schülke (1995), early populations of the species (in my material samples J-65, Ka-14, Wtr-25, and Md-27) are morphologically transitional to *K. crepida* and *K. robusta*, with some elements having only one row of relatively low denticles posterior to the blade, others lacking them completely and differing from associsted *K. crepida* only in a narrower platform. There is an apparent change within the lineage towards a more and more narrower platform with a stronger separation of its smooth and flat dorsal area and extremely high ridges on both sides of the blade. The ridges do not reach the cusp, which forms an isolated high conical structure in the middle of the element. This change seems to be of much correlative value.

Occurrence. — The *K. crepida* Zone at Jabłonna, Kadzielnia, Wietrznia, Kowala, and Miedzianka.

Genus ***Tripodellus*** Sannemann, 1955

Type species: *Tripodellus flexuosus* Sannemann 1955a (P_2 element of *T. minutus*) from the Famennian of Frankenwald.

Diagnosis. — Apparatus with triramous or at least angularly bent P_2 elements, lacking platform in underived species.

Fig. 87. Earliest species of the palmatolepidid *Tripodellus*, *T. clarki* (Ziegler, 1962) with biramous P_2 elements from *K. triangularis* Zone strata at Płucki (sample Pł-42) in the Holy Cross Mountains. P_1 (A–C) and M (D) elements; specimens ZPAL cXVI/1250, 1249, 1248, and 1251, respectively.

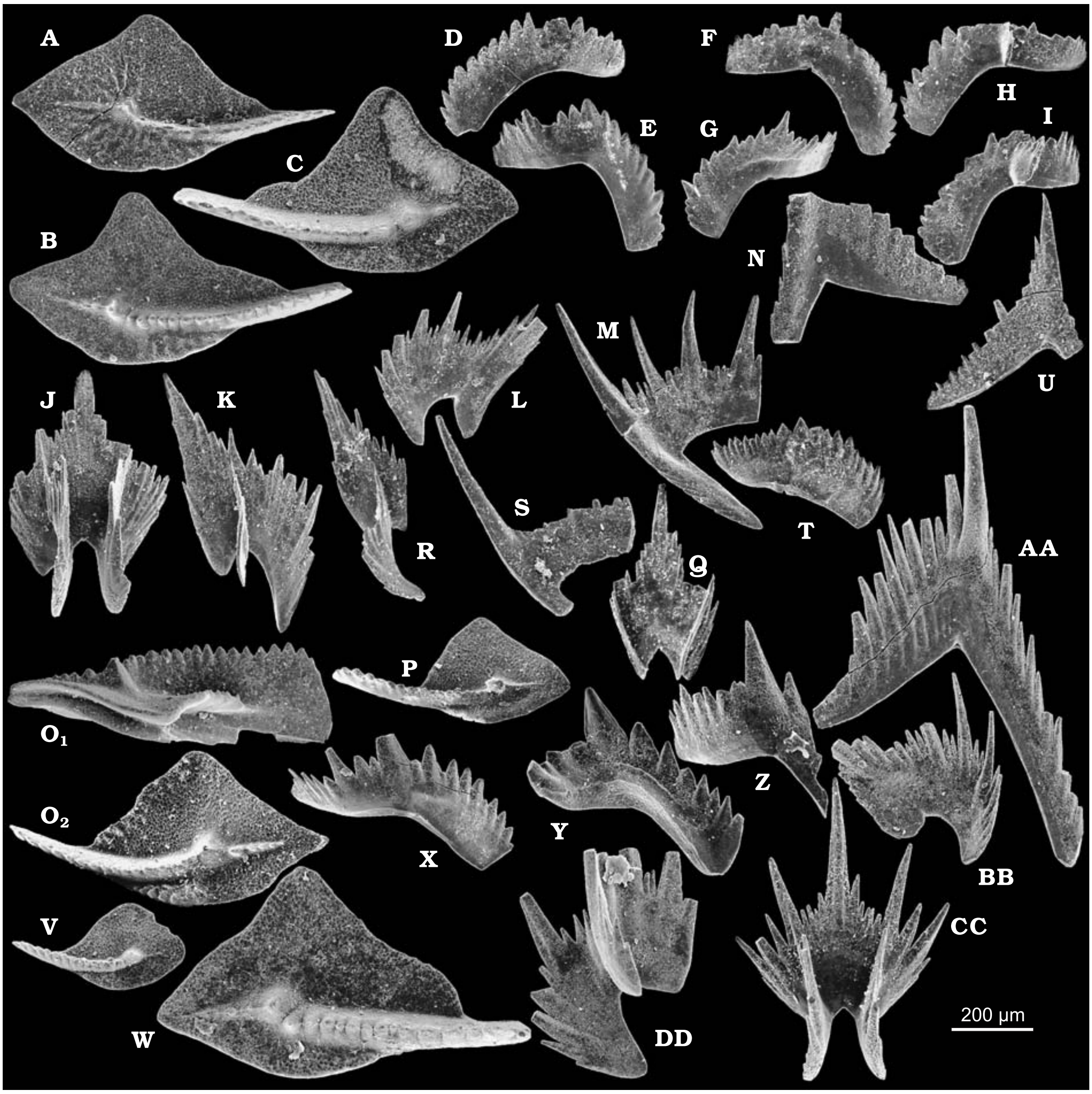


Fig. 88. Typical *Tripodellus clarki* (Ziegler, 1962) from *K. triangularis* Zone strata at Jabłonna (A, C, D, F–H, sample J-53; B, C, E, G, J–N, sample J-53a; V–CC, sample J-58) and Płucki (O–U, sample Pł-1) in the Holy Cross Mountains. P_1 (A–C, O, P, V, W), P_2 (D–I, T, X–Z), S_0 (J, Q, and CC), S_1 (K, R, DD), S_2 (L, BB), S_{3-4} (M, S), and M (N, U, and AA) elements; specimens ZPAL cXVI/1250, 1249, 1248, and 1251, respectively.

Tripodellus clarki (Ziegler, 1962)
(Figs 87, 88, and 134)

Type horizon and locality: Bed 23 in trench II at Seßacker near Oberscheld, Rhenish Slate Mountains (Ziegler 1975).

Material. — 623 specimens.

Diagnosis. — Gently bent P_2 element without platform, rhomboidal outline of relatively wide platform in P_1 element, short processes of M element.

Remarks. — The apparatus was restored by Schülke (1995) as *Palmatolepis variabilis* and *P. delicatula postdelicatula*. I failed to distinguish between these morphologies in my highly variable material from the earliest Famennian. Populations from the late *K. triangularis* Zone are much more advanced towards the morphologies typical of *Tripodellus* and they deserve taxonomic separation as *T. variabilis*.

Occurrence. — The *K. triangularis* Zone at Płucki, Wietrznia, and Jabłonna.

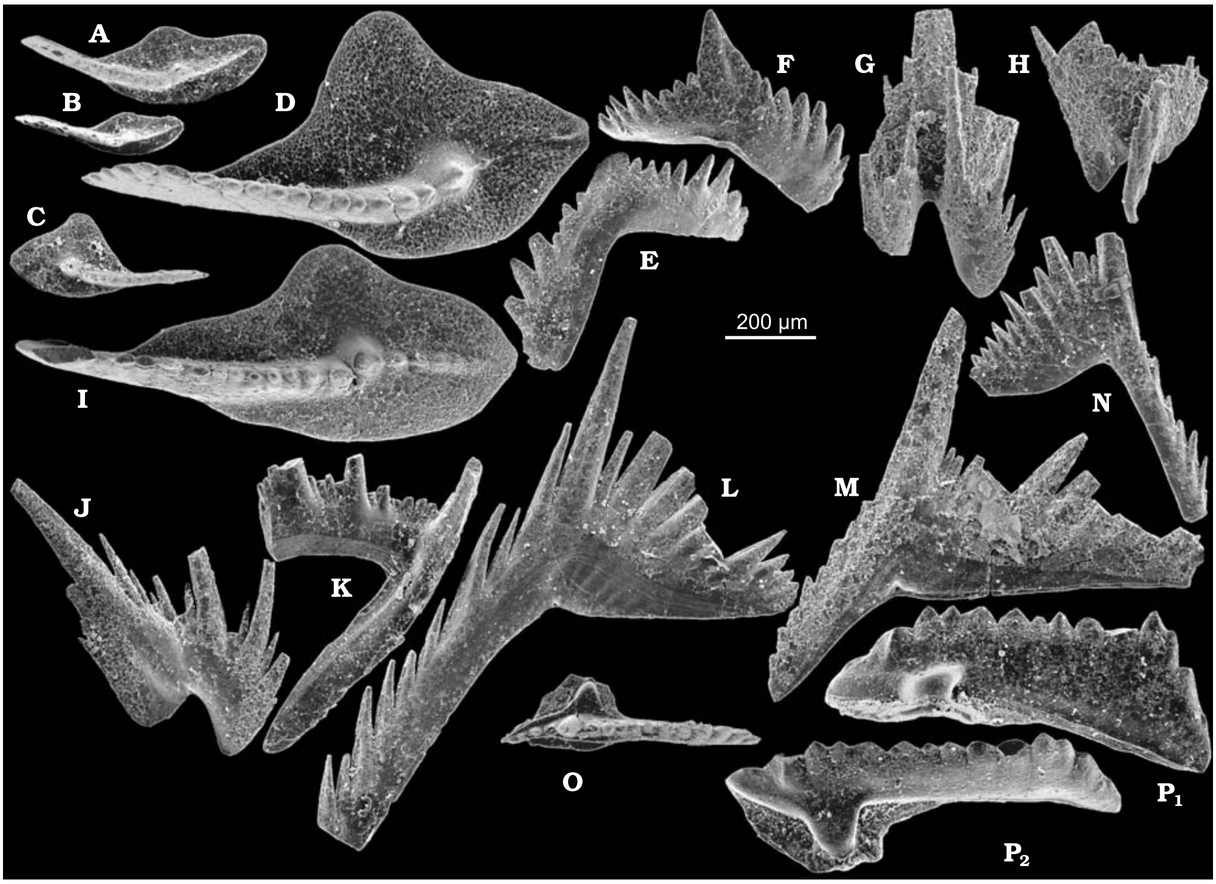


Fig. 89. Species of the palmatolepidid *Tripodellus* with biramous P_2 elements from the *K. crepida* Zone at Jabłonna (A–O, sample J-45a) and Wietrznia (P, sample Wtr-21) in the Holy Cross Mountains. **A**–**N**. *T. variabilis* (Sannemann, 1955). P_1 (A–D, I), P_2 (E, F), S_0 (G), S_1 (H), S_2 (J), $S_{3–4}$ (K), and M (L–N) elements; specimens ZPAL cXVI/1315–1322, 2757, 1338, 1323, 1325, 1326, and 1324, respectively. **O**–**P**. *T. subgracilis* (Bischoff, 1956). P_1 elements; specimens ZPAL cXVI/2834 and 1967.

Tripodellus variabilis (Sannemann, 1955)
(Figs 89A–N and 134)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955a; Ziegler 1975).

Material. — 22,931 specimens.

Diagnosis. — Angularly bent P_2 element, elongated platform in P_1 element with short, rounded posterior lobe, elongate external process of M element.

Remarks. — It is convenient to separate the early part of the *Tripodellus* lineage into at least three chronospecies (*T. clarki*, *T. variabilis*, and *T. minutus*). *T. variabilis* has been chosen by Schülke (1999) as the name for the first species of the lineage, but there is hardly any evidence that the material of Sannemenn (1955a) truly represents this species as long as advanced *K. termini* and *K. crepida* co-occur in the same bed. The P_2 elements of the palmatolepidids are highly variable and at this stage of the evolution they are hardly of much diagnostic value.

P. variabilis is a senior synonym of *Palmatolepis minuta wolskae* of Szulczewski (1971), on the evidence of material from a bed at Kadzielnia with early *P. termini*.

Occurrence. — The late *K. triangularis* and *K. crepida* zones at Jabłonna, Kadzielnia, Wietrznia, Kowala, and Miedzianka.

Tripodellus subtilis (Khalymbadzha *et* Chernysheva, 1978)
(Figs 90 and 134)

Type horizon and locality: Famennian of the Urals.

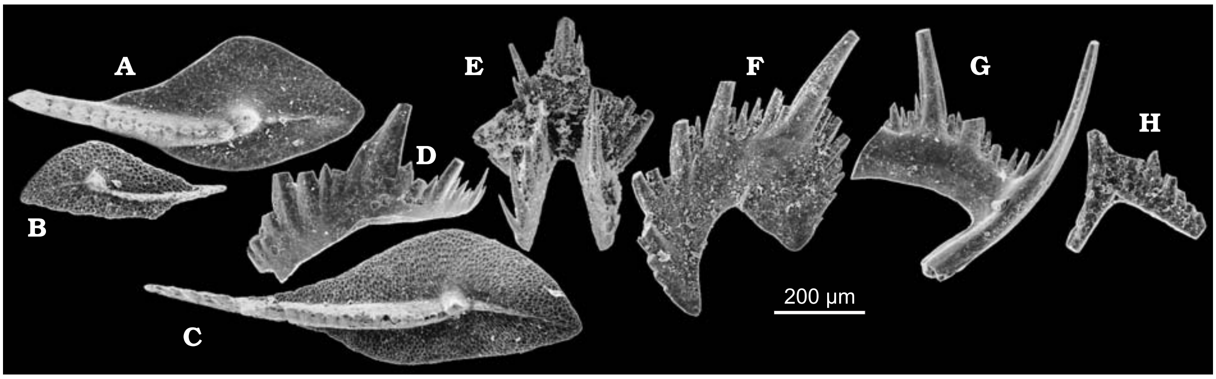


Fig. 90. Palmatolepidid *Tripodellus subtilis* (Khalymbadzha *et* Chernysheva, 1978) with biramous P_2 elements from the late *K. triangularis* Zone at Wietrznia (A, D–H, sample Wtr-27) and the *K. crepida* Zone at Jabłonna (B, C, sample J-45a) in the Holy Cross Mountains. P_1 (A–C), P_2 (D), S_0 (E), S_2 (F), $S_{3–4}$ (G), and M (H) elements; specimens ZPAL cXVI/1422, 1314, 1313, and 1424–1428, respectively.

Material. — 24 specimens.

Diagnosis. — P_1 element with narrow, convex platform of asymmetric lanceolate outline, extending ventrally to half length of the blade.

Remarks. — Taxonomic identification of the species is based on Metzger (1994). Rare elements associated with P_1 elements of the species include biramous P_2 elements, which suggests its origin from *T. variabilis*. If true, this would then be a relict lineage evolving towards reduction of the platform in P_1 elements.

Occurrence. — The *K. crepida* Zone at Wietrznia and Jabłonna.

Tripodellus lobus (Helms, 1963)
(Figs 91 and 134)

Type horizon and locality: A block of *Cheiloceras* Stufe limestone from a Carboniferous breccia at Langenaubach, Rhenish Slate Mountains (Ziegler 1975).

Material. — 653 specimens.

Diagnosis. — Platform in P_1 element with prominent, narrow posterior lobe, in juvenile specimens oriented somewhat ventrally; angularly bent biramous P_2 element.

Remarks. — Apparatus of the species was reconstructed by Metzger (1994).

Specimens of juvenile morphology typical of this species co-occur with late populations of *T. minutus* and there seems to be no transition between them. This is apparently a successor of *T. variabilis* that became separated from the main lineage represented by *T. minutus* as a result of an allopatric speciation process and subsequent merging of their populations.

Occurrence. — The *K. crepida* Zone at Kadzielnia, Jabłonna, Wietrznia, and Miedzianka.

Tripodellus subgracilis (Bischoff, 1956)
(Figs 89O, P and 134)

Type horizon and locality: *K. crepida* Zone at Bicken quarry (Bischoff 1956).

Material. — Three specimens.

Diagnosis. — P_1 element with very narrow platform bearing sharply triangular small posterior lobe.

Remarks. — Apparatus was restored by Metzger (1994) for a more advanced population with well denticulated posterior process. Biramous P_2 element indicates a close relationship to *T. lobus* and the Polish specimens, lacking denticulation of the posterior process, are transitional to those illustrated by Metzger (1994). *Palmatolepis parva* Klapper *et al*., 2004 may be ancestral to this species.

Occurrence. — The *K. crepida* Zone at Jabłonna.

Tripodellus minutus (Branson *et* Mehl, 1934)
(Figs 9D, 92A–J, and 134)

Type horizon and locality: Famennian at Dixie, Missouri (Ziegler 1977, p. 313).

Material. — 2,504 specimens.

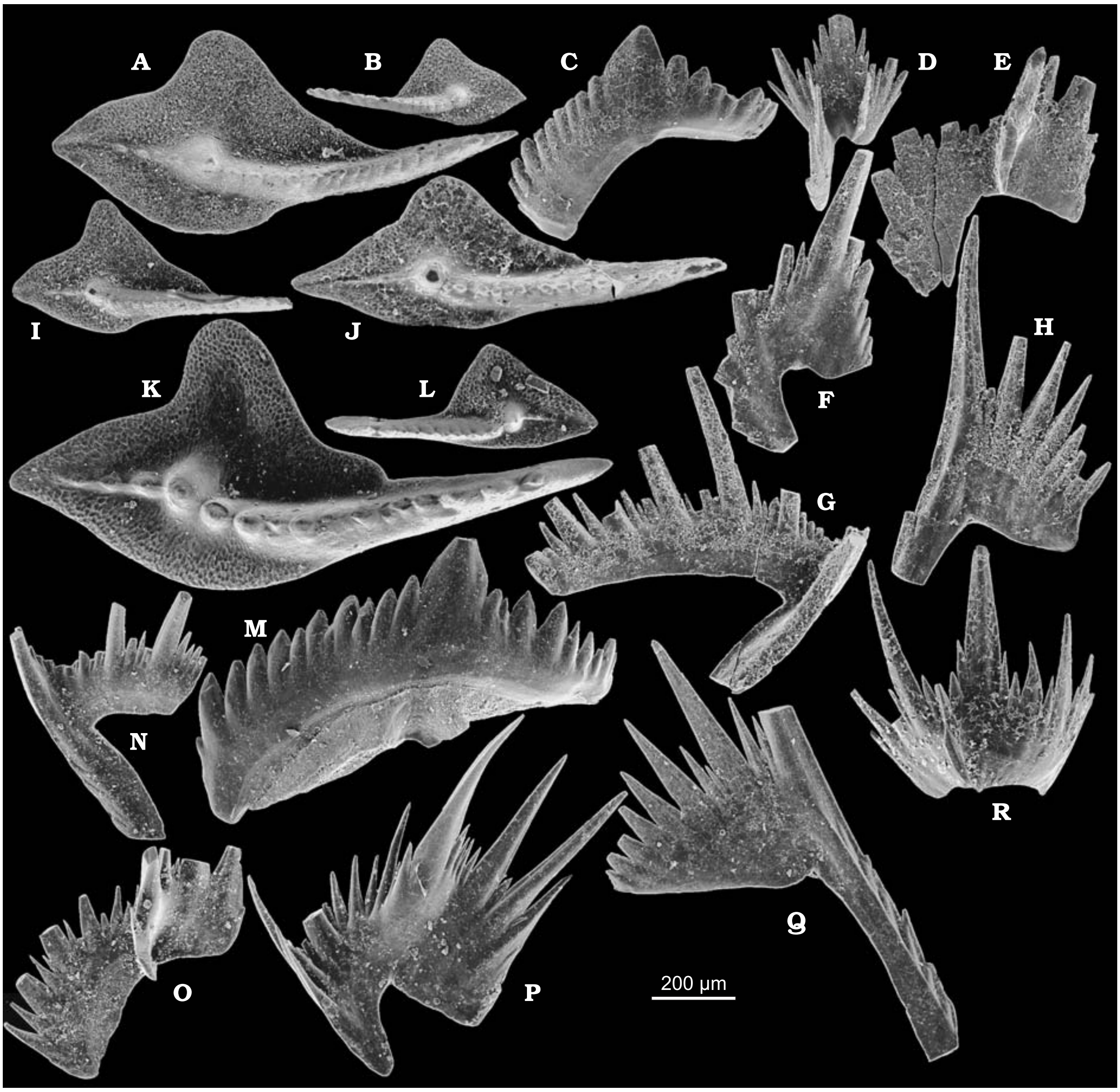


Fig. 91. Late palmatolepidid *Tripodellus lobus* (Helms, 1963) with biramous P_2 elements from the late *K. triangularis* Zone at Wietrznia (I, J, sample Wtr-27), the *K. crepida* Zone at Jabłonna (A–H,) sample J-44, and the late *K. crepida* (with *K. rhomboidea*) Zone at Łagów (K–R, sample Mak-3-4) in the Holy Cross Mountains. P_1 (A, B, I, J, K, L), P_2 (C, M), S_0 (D, R), S_1 (E, O), S_2 (F, P), $S_{3–4}$ (G, N), and M (H, Q) elements; specimens ZPAL cXVI/2742, 2741, 2743–2748, 1423, 1421, 2750, 2749, 2751, 2755, 2753, 2754, 2756, and 2752, respectively.

Diagnosis. — Triramous P_2 element, rhomboidal outline of platform of P_1 almost without any lobe; straight or slightly asymmetric juvenile specimens.

Remarks. — The P_2 element was identified by van den Boogaard and Kuhry (1979). Apparatus was restored by Metzger (1994). P_2 elements with additional process occur rarely but consistently in samples with *T. variabilis*, being probably end-members of population variability expressed mostly in bending of the element. They start to dominate the sample in the Kadzielnia section between samples Ka-3 and Ka-5.

Occurrence. — The *K. crepida* Zone to the earliest *C. quadrantinodosa* Zone at Kadzielnia, Łagów, Jabłonna, Wietrznia, Miedzianka, and Kowala.

Tripodellus donoghuei sp. n.
(Figs 92K–Q and 134)

Holotype: Specimen ZPAL cXVI/2763 (Fig. 92N).

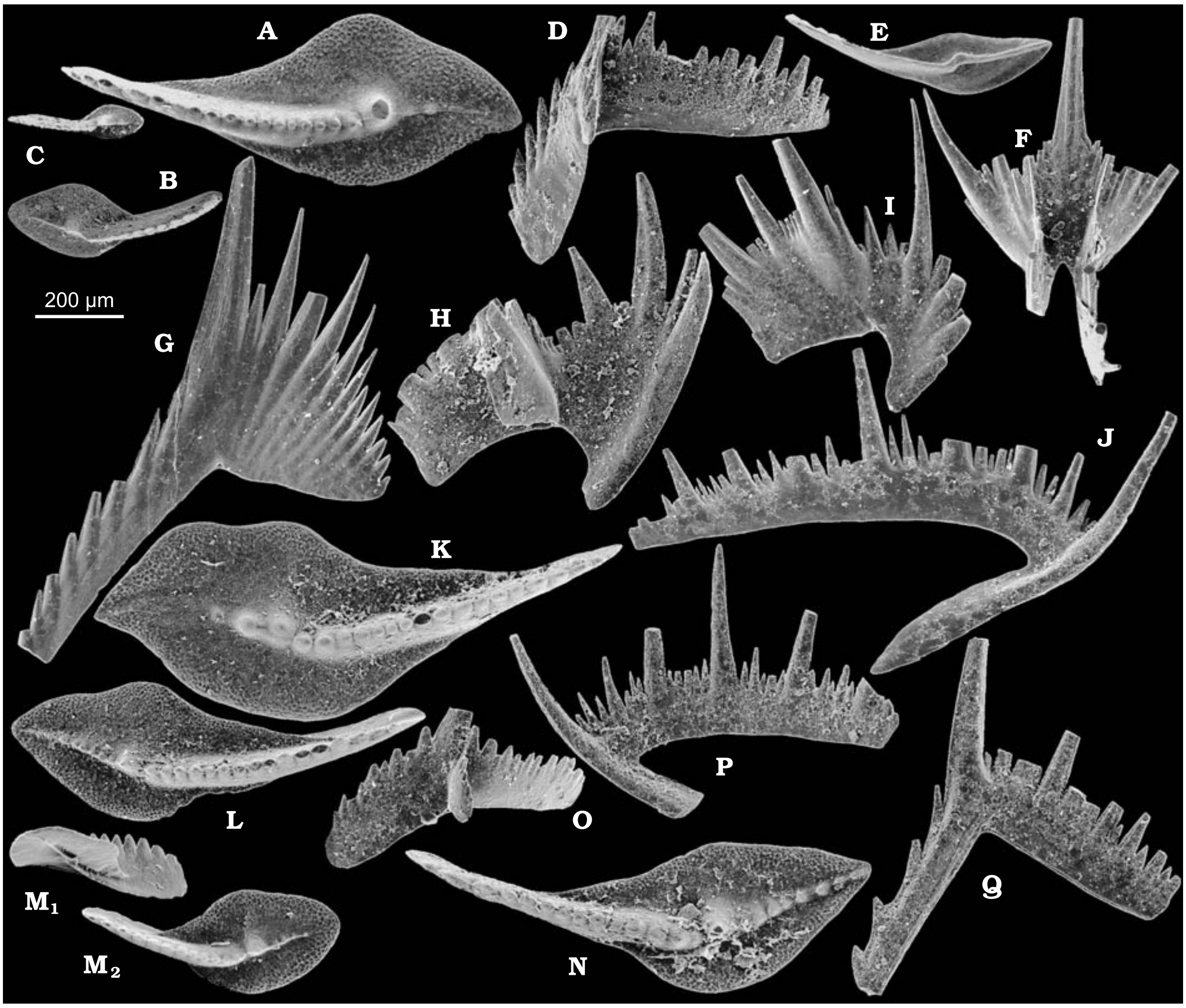


Fig. 92. Species of the palmatolepidid *Tripodellus* with triramous P_2 elements from the Holy Cross Mountains. **A**–**J**. *T. minutus* (Branson *et* Mehl, 1934) from the *C. quadrantinodosa* Zone at Łagów (sample Ł-28). P_1 (A–C, E), P_2 (D), S_0 (F), S_1 (H), S_2 (I), $S_{3–4}$ (J), and M (G) elements; specimens ZPAL cXVI/1402–1405, 2940, 1406, 1410, 1408, 1407, and 1409, respectively. **K**–**Q**. *T. donoghuei* sp. n. from the early *L. styriacus* Zone at Ostrówka (K, M, N, sample Ost-12) and the *P. trachytera* Zone at Jabłonna (L, O–Q, bed 24). P_1 (K–N), P_2 (O), $S_{3–4}$ (P), and M (Q) elements; specimens ZPAL cXVI/2764, 2758, 2762, 2763 (holotype, N), and 2759–2761, respectively.

Type horizon and locality: Sample Ost-12, late Famennian *L. styriacus* Zone at Ostrówka, Holy Cross Mountains.

Derivation of name: To honour Philip Donoghue for his contribution to understanding the architecture of conodont apparatuses.

Material. — 391 specimens.

Diagnosis. — Twisted P_1 element with wide, lanceolate platform and minute larval basal cone (pit).

Remarks. — The apparatus of this species was already restored by Schülke (1999) as *Palmatolepis* aff. *Pal. gracilis*. Specimens of similar morphology occur in samples with *T. minutus* but there is no gap in variability separating them from the modal morphology of that species. Such a gap can be identified only in samples with *T. schleizius* and *T. lobus* as associated species, although rarely juvenile specimens of *T. schleizius* of comparable size are associated with *T. donoghuei* in its early populations. The oldest sample with juveniles of *T. schleizius* showing a virtually straight blade have been found in Kadzielnia in sample Ka-7, where *T. donoghuei* is missing.

In the outline of the platform *T. donoghuei* resembles members of the *T. gonioclymeniae* lineage but it lacks the stage of “sinuosa” larva with strongly asymmetric basal cone in P_1 elements. It seems to be a successor of *T. minutus*, which originated allopatrically in respect to *T. schleizius*.

Occurrence. — The late *K. crepida* (with *C. klapperi*) to *L. styriacus* zones at Kadzielnia, Jabłonna, Kowala, and Ostrówka.

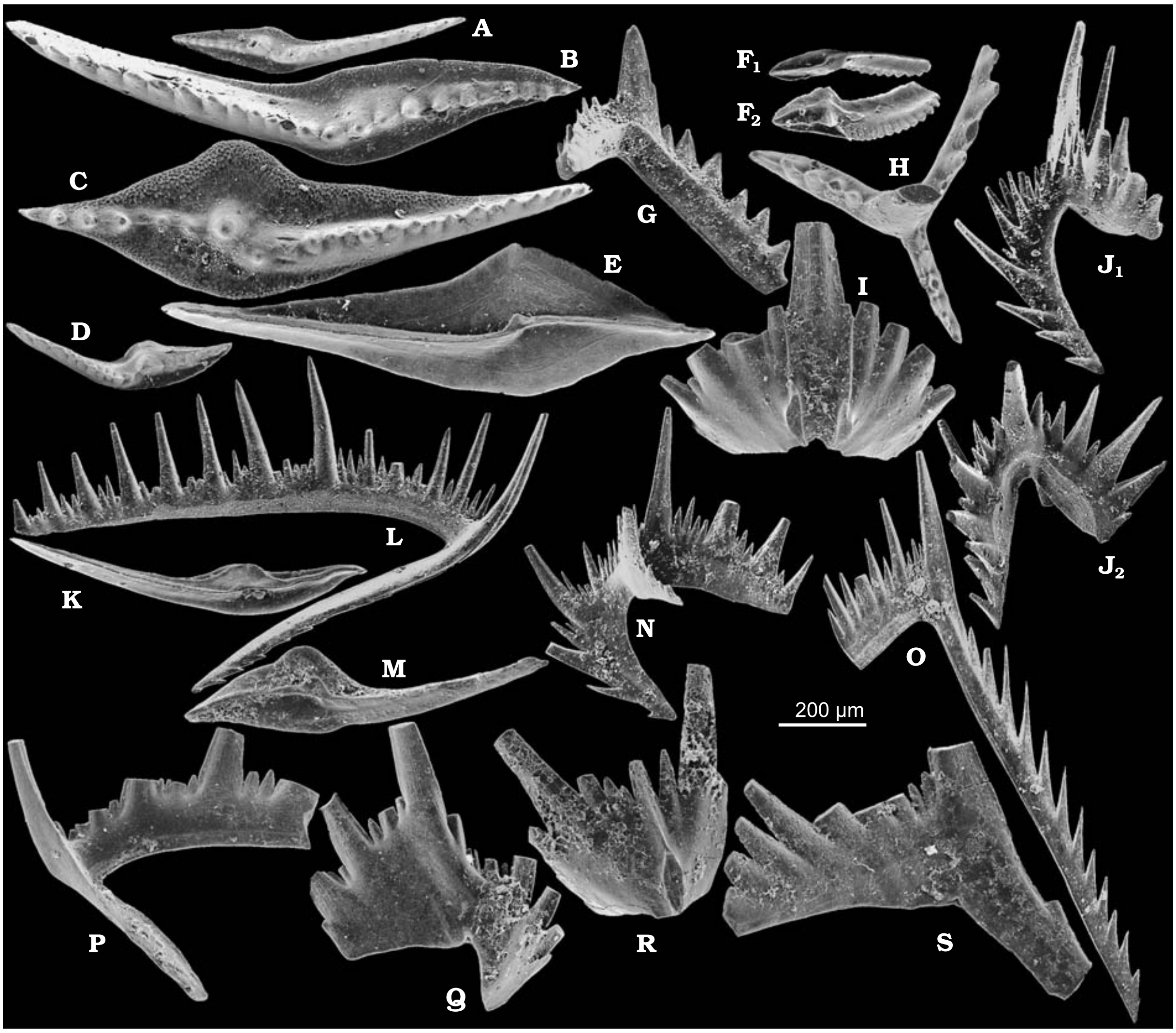


Fig. 93. Palmatolepidid *Tripodellus schleizius* (Helms, 1963) with triramous P_2 elements from the *P. trachytera* Zone at Kowala (B, F, G, J–L, N, O, sample Ko-8a; M, sample Ko-9a) and the early *Lagovignathus styriacus* Zone at Ostrówka (A, C–H, I, P–S, sample Ost-12) in the Holy Cross Mountains. P_1 (A–F, K, M), P_2 (G, H), S_0 (I, J), S_1 (N, R), S_2 (Q), $S_{3–4}$ (L, P), and M (O, S) elements; specimens ZPAL cXVI/2768, 391, 2769, 2766, 2765, 392, 2770, 2771, 393, 2937, 395, 2944, 394, 396, 2774, 2773, 2772, and 2775, respectively.

Tripodellus schleizius (Helms, 1963)
(Figs 9C, 93, and 134)

Type horizon and locality: 6.5 m below the top of the Famennian at Großen Buschteich near Rödersdorf, Thuringia, upper part of the *Platyclymenia* Stufe (Ziegler 1975).

Material. — 5,112 specimens.

Diagnosis. — Clearly separate asymmetric basal cone (pit) and sinuous blade in juvenile P_1 element, platform sometimes disappearing in front of the tip in adults with an angular posterior lobe near the cusp, triramous P_2 element.

Remarks. — The transition from *T. minutus* to *T. schleizius* can be traced through the Łagów section near the base of the *C. quadrantinodosa* Zone. In samples from the Lower Łagów Beds minute specimens of *Tripodellus* are laterally arched and their basal cone remains very small. At the base of the Upper Łagów Beds sigmoidally bent juvenile elements appear with a wide asymmetric basal cone. From some reason in these transitional samples there is a distinct bimodality in size frequency distribution and no intermediate specimens have been found. It looks as if sinuous morphologies had a higher rate of juvenile mortality, perhaps related to metamorphosis at the end of the sinuosa larva stage. The blade is usually more sinuous in adults than it was in older samples but they do not show clear separation of the larval basal cavity. Either it was resorbed, specimens with asymmetry rarely survived to adult stages, or species of two separate lineages co-occurred. The latter possibility seems unlikely, as in samples from somewhat higher beds (e.g., Ł-40) intermediate specimens occur showing continuity between extreme stages of ontogeny. This is the case also with late Famennian samples with *T. gracilis*. They show, however, increased juvenile mortality and are in this respect different from co-occurring conodont species. Perhaps this was an ecologically opportunistic species. In the course of evolution of the lineage within the mid Famennian the basal cavity became wider and wider, as documented in the Kowala section.

The boundary between this chronospecies and its successor *T. gracilis* is difficult to define as the diagnostic characters are very variable in populations and seem to spread gradually in the course of evolution. The type population of *T. schleizius* is uncomfortably close to the end of its range.

Occurrence. — The *C. quadrantinodosa* to *P. trachytera* zones at Łagów, Jabłonna, Miedzianka, Kowala, and Ostrówka.

Tripodellus gracilis (Branson *et* Mehl, 1934)
(Figs 94A–K and 134)

Type horizon and locality: Famennian at Dixie, Missouri (Ziegler 1977, p. 313).

Material. — 11,928 specimens.

Diagnosis. — Wide and strongly asymmetric basal cone (pit) of P_1 element, its tip bent posteriorly, rounded lobe near the cusp even in large specimens.

Remarks. — Apparatus was restored by van den Boogaard and Kuhry (1979), and confirmed by myself (Dzik 1991). No specimens of the morphology proposed to be typical for *Tripodellus expansus* (Sandberg *et* Ziegler, 1979) are known from the Holy Cross Mountains but some mature elements with an extremely wide platform approach that morphology (e.g., in sample Ost-5). They share with those from Montana their asymmetric larval basal cavity, which places them in the *T. gonioclymeniae* lineage, but they do not show so strong a widening of the platform and in occlusal view do not differ form *T. gracilis*. In sample Ost-7 the dominant elements with asymmetric larval basal cavity are associated with rare specimens having a wider platform, which do not show a separation of the basal cavity at all, thus being similar in those respects to older populations of *T. gracilis*. In fact, such asymmetry and incipient separation of the basal cone is observable in the population of *T. gracilis* from sample Ost-12, but the basal cone is small and well visible only in juvenile and strongly asymmetric specimens. It seems thus that this stage in the evolution of the *Tripodellus* branch is marked by expansion of juvenile characters to later ontogenetic stages. *Palmatolepis deflectens sigmoidalis* of Ziegler (1962) seems to be based on a juvenile *T. gracilis*.

Possibly, "*Palmatolepis expansa*" is a morphotype within the range of population variability of *T. gracilis*. Perri and Spaletta (1991) classified within "*P. expansa*" specimens that do not show asymmetry of the basal cavity. This indicates how misleading may be the concept of that species and that stratigraphic decisions based on it are of questionable value.

Occurrence. — The *L. styriacus* to *D. trigonica* zones at Jabłonna, Ostrówka, Miedzianka, Kowala, Gołogłowy, and Dzikowiec.

Tripodellus mancus (Helms, 1963)
(Figs 94S and 134)

Type horizon and locality: 3 m below the top of the red limestone of the *Platyclymenia* Stufe at Alte Heerstrasse near Oettersdorf, Thuringia (Helms, 1963).

Material. — 12 specimens.

Diagnosis. — Strongly bent P_1 element with obtuse tip of the platform and strongly asymmetric juvenile basal cavity; apparatus unknown.

Remarks. — This is a poorly known species, represented by a few specimens of minute size in all published localities. Perhaps they represent marginal populations of the *T. gonioclymeniae* lineage at the stage of its allopatric separation from the main lineage of *Tripodellus*. Small size of elements seems consistent with apparently paedomorphic evolution of the lineage, marked by expansion of the sinuosa larva stage to the end of ontogeny. The platform of some specimens from Kowala show a pointed dorsal tip, which makes them similar to *T. gonioclymeniae*.

Occurrence. — The early *P. jugosus* Zone at Ostrówka and Kowala.

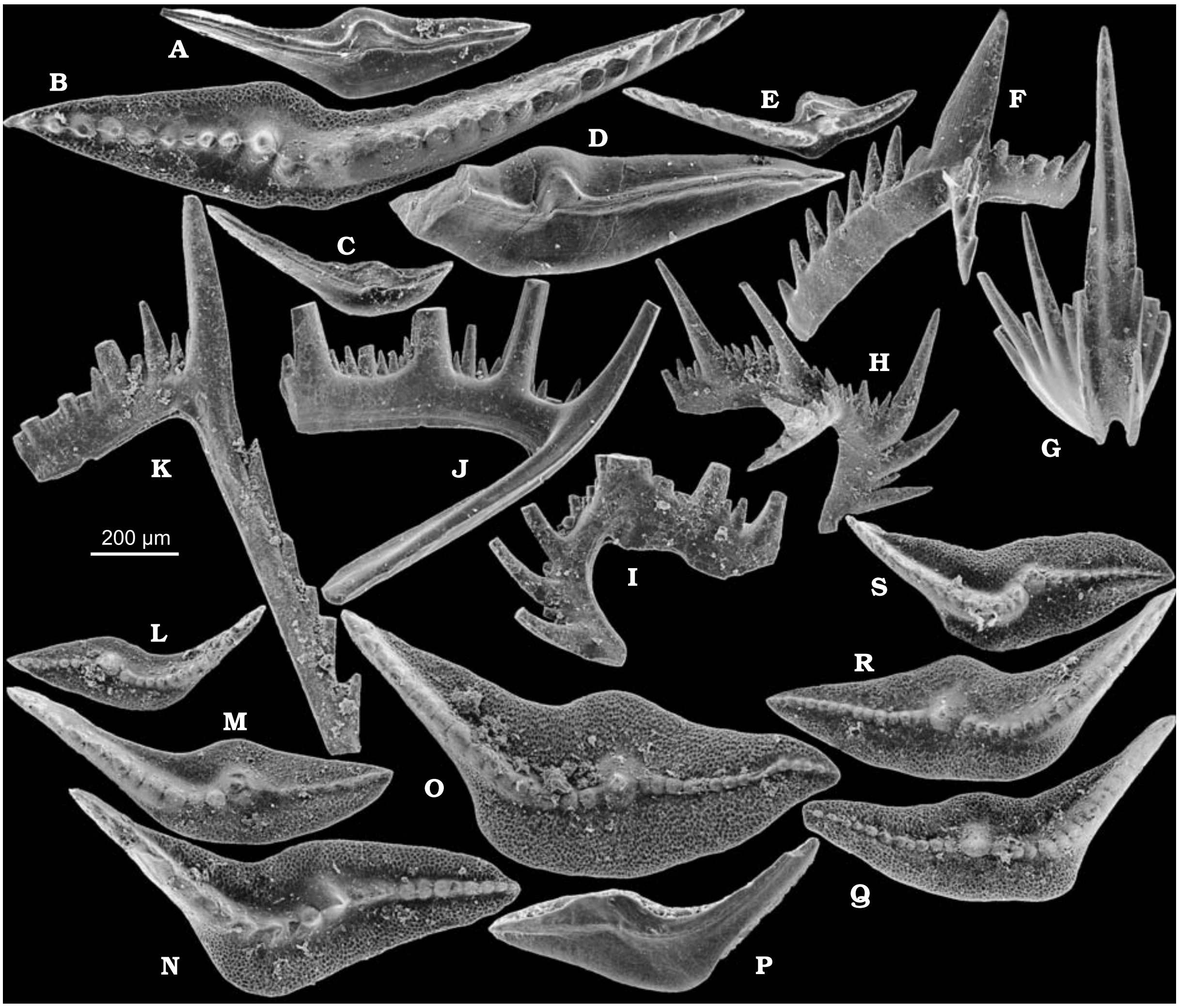


Fig. 94. Late species of the palmatolepidid *Tripodellus* with triramous P_2 elements. **A**–**K**. *T. gracilis* (Branson *et* Mehl, 1934) from the *D. trigonica* (A, sample Ko-166) and *P. jugosus* (C, sample Ko-3) zones at Kowala and the *P. jugosus* Zone at Ostrówka (B, D–K, sample Ost-2). P_1 (A–E), P_2 (F), S_0 (G), S_1 (H), S_2 (I), S_{3-4} (J), and M (K) elements; specimens ZPAL cXVI/2931, 2780, 2934, 2781, 2779, 2782–2787, respectively. **L**–**R**. *T. gonioclymeniae* (Müller, 1956) from the *P. jugosus* Zone at Ostrówka (L, M, Q, sample Ost-2) and Kowala (P, sample Ko-62) in the Holy Cross Mountains and the *P. jugosus* (N, R, sample Dz-8) and the *D. trigonica* (O, sample Dz-7) zones at Dzikowiec in the Sudetes. P_1 elements; specimens ZPAL cXVI/2790, 2777, 2792, 2789, 2788, 2778 an 2791, respectively. **S**. *T. mancus* (Helms, 1963) from the *L. styriacus* Zone at Ostrówka (sample Ost-5). P_1 element; specimens ZPAL cXVI/2776.

Tripodellus gonioclymeniae (Müller, 1956)
(Figs 94L–R and 134)

Type horizon and locality: Grayish brown limestone from the top of Effenberg near Hachen, Rhenish Slate Mountains (Ziegler 1975).

Material. — 243 specimens.

Diagnosis. — Strongly bent P_1 element with platform narrowing to the tip, with its greatest width in the middle length of the element, the asymmetric basal cone continues throughout ontogeny, other elements of the apparatus probably indistinguishable from *T. gracilis*.

Remarks. — No doubt that the lineage *T. mancus* → *T. gonioclymeniae* originated from *T. gracilis*. Sandberg and Ziegler (1979) proposed "*Palmatolepis expansa*" to be the connecting link. As noted above, this morphology is not represented in the Holy Cross Mountains and probably the evolution took place elsewhere, with *T. manca* and *T. gonioclymeniae* being successive immigrants from that source area.

Occurrence. — The late *P. jugosus* to *D. trigonica* zones at Ostrówka, Kowala, aned Dzikowiec.

Genus **Palmatolepis** Ulrich *et* Bassler, 1926

Type species: *Palmatolepis perlobata* Ulrich *et* Bassler, 1926 from the "Hardin sandstone" of Tennessee.

Diagnosis. — Apparatus with the symmetry transition series elements bearing weakly developed cusps and irregularly arranged denticles, M element processes in linear arrangement, large P_1 elements with elaborate, usually prominently tuberculated platform.

Palmatolepis initialis sp. n.
(Figs 80H–R, 95, and 135)

Holotype: M element ZPAL cXVI/1261 (Fig. 95Q).

Type horizon and locality: Sample J-53, early Famennian *K. triangularis* Zone at Jabłonna, Holy Cross Mountains, Poland.

Derivation of name: From the initial position of the species in the *Palmatolepis* lineage.

Material. — 2,041 specimens.

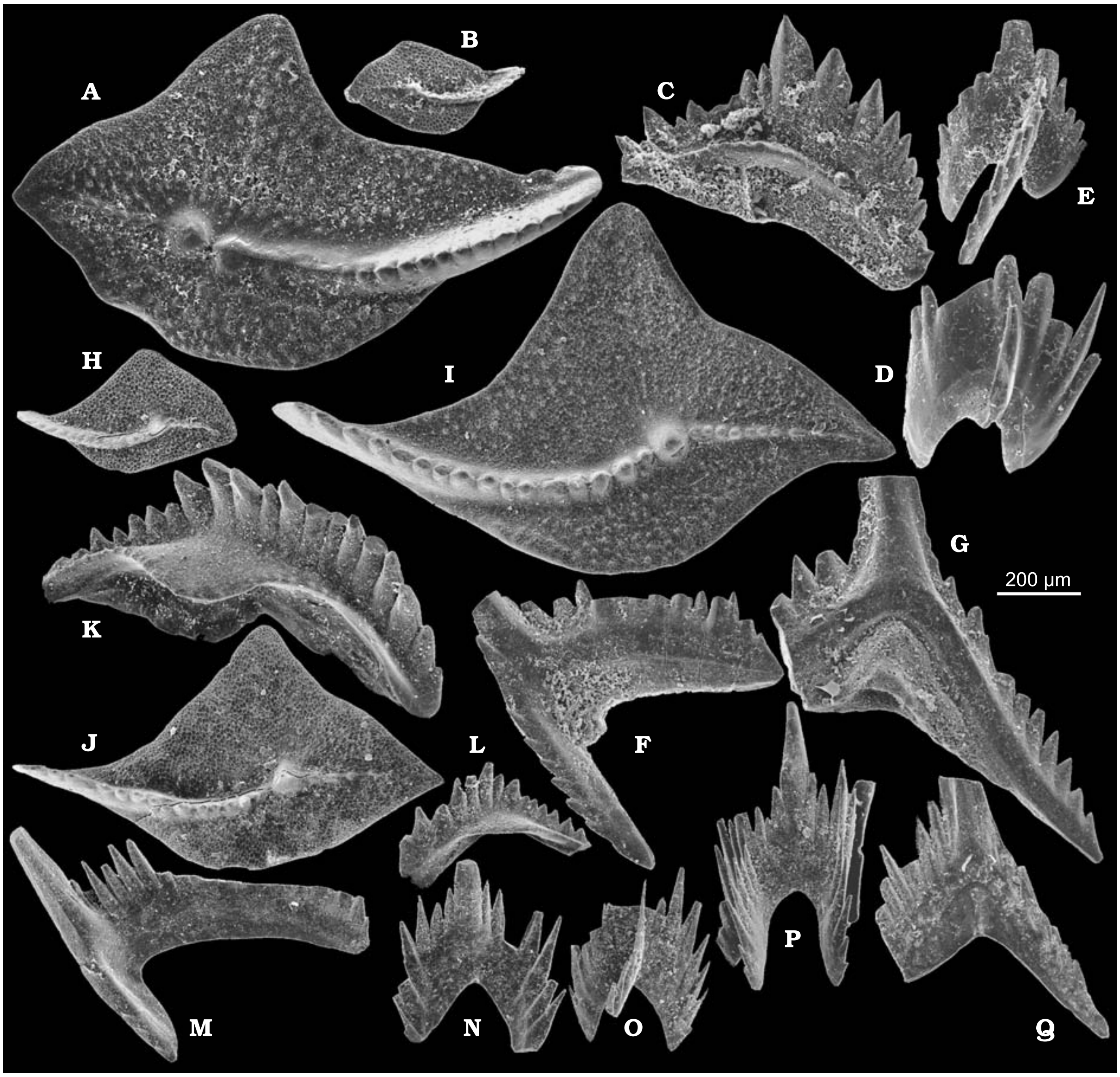


Fig. 95. *Palmatolepis initialis* sp. n. from the late *K. triangularis* Zone at Wietrznia (A–G, sample Wtr-27) and Jabłonna (H–Q, sample J-53) in the Holy Cross Mountains. P_1 (A, B, H–J), P_2 (C, K, L), S_0 (P), S_1 (D, E, O), S_2 (N), $S_{3–4}$ (F, M), and M (G, Q) elements; specimens ZPAL cXVI/1440, 1442–1447, 1252, 1254, 1253, 1256, 1255, 1260, 1259, 1258, a257, and 1261 (holotype), respectively.

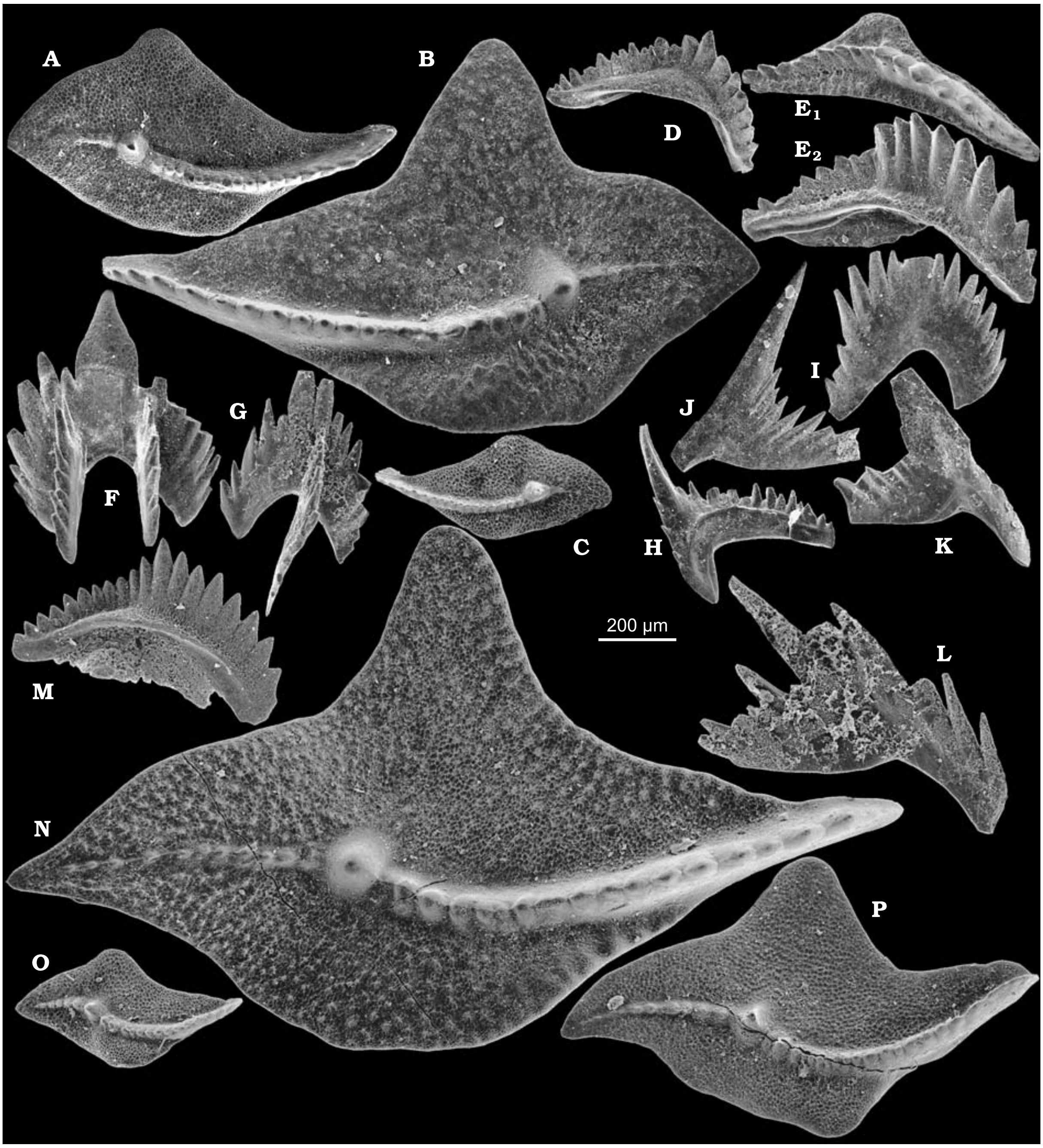


Fig. 96. *Palmatolepis sandbergi* Ji *et* Ziegler, 1993 from the late *K. triangularis* (A–K, sample J-53a) and early *K. crepida* (L, sample J-43; M, O, P, bed 3; N, bed 5) zones at Jabłonna in the Holy Cross Mountains. P_1 (A–C, N–P), P_2 (D, E, M), S_0 (F), S_1 (G), S_2 (I), $S_{3–4}$ (H), and M (J-L) elements; specimens ZPAL cXVI/1280-1284, 1286, 1288, 1285, 1289, 1290, 2884, 2883, 2882, and 2880, 2881, respectively.

Diagnosis. — M element with almost straight cusp and short but well denticulated ventral process forming a wide angle with the prominently denticulated dorsal process.

Remarks. — Schülke (1999) proposed to use the name *Palmatolepis abnormis* (Branson et Mehl, 1934) for this species. However, as pointed out by Klapper *et al.* (2004, p. 382) the P_2 element from the Saverton Shale chosen to be the holotype of this species is undiagnostic and indistinguishable from ones that occur in different apparatus reconstructions (according to Branson and Mehl 1934 there is a “fairy complete gradation” to other P_2 specimens in the sample) and the species is invalid (a *nomen dubium*). It is rather the M element that bears characters diagnostic for the species. In its shape, with slightly reclined cusp, it is transitional between the ancestral morphology of *Klapperilepis* and that of *Palmatolepis* and *Conditolepis*. The population from sample Pł-1 (Fig. 80H–R) is probably the oldest one in my material showing features of *P. initialis* sp. n., but the generally small size of elements makes it similar rather to *Klapperilepis triangularis*. P_1 elements of these two species seem to be indistinguishable.

Occurrence. — The mid *K. triangularis* Zone at Płucki and Jabłonna.

Palmatolepis sandbergi Ji *et* Ziegler, 1993
(Figs 96 and 135)

Type horizon and locality: Lali section, southern China.

Material. — 803 specimens.

Diagnosis. — M element with proclined cusp and short finely denticulated ventral process forming a wide angle with the prominently denticulated dorsal process.

Remarks. — The apparatus was restored by Schülke (1999). Except for the apparent trend towards typical *Palmatolepis* in the morphology of M elements, the apparatus is similar to *Klapperilepis triangularis*.

In bed 3 at Jabłonna P_1 elements somewhat resembling those of *Conditolepis lobicornis*, but with the posterior lobe of the platform differently oriented, co-occur with P_2 and M elements closely similar to those of *P. sandbergi* (Fig. 96M, O, P). Whether the proposed apparatus composition is correct, and then this is possibly a new species of *Palmatolepis*, or the platform elements belong to another genus, has to be tested with a material from another locality.

Occurrence. — The late *K. triangularis* and early *K. crepida* zones at Płucki, Wietrznia, Kowala, Miedzianka, and Jabłonna.

Palmatolepis perlobata Ulrich *et* Bassler, 1926
(Figs 97, 98, and 135)

Type horizon and locality: "Hardin sandstone" near Mount Pleasant, Tennessee (Huddle 1968).

Material. — 320 specimens.

Diagnosis. — Relatively low population variability in P_1 elements with sinuous outline and small posterior lobe of almost smooth platform, sharply denticulated P_2 elements with prominent cusp.

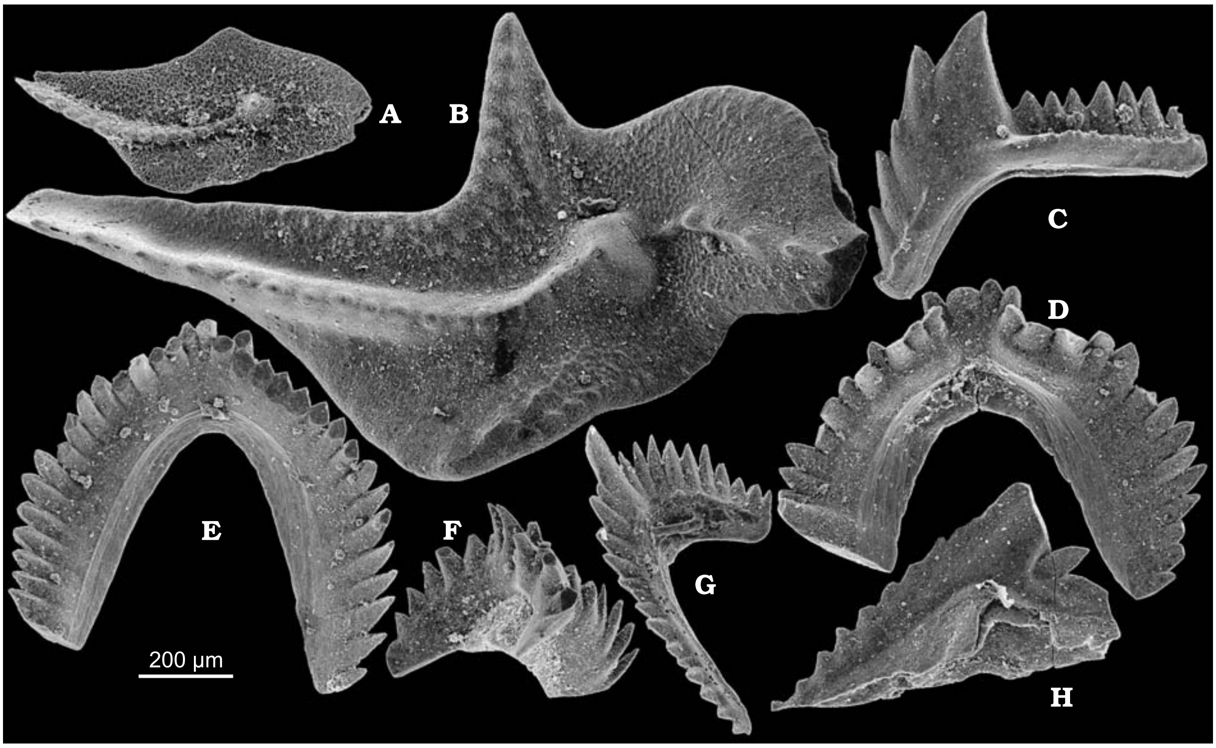


Fig. 97. *Palmatolepis perlobata* Ulrich *et* Bassler, 1926 from the *K. crepida* Zone at Kadzielnia (sample Ka-7) in the Holy Cross Mountains. P_1 (A, B), P_2 (C), S_0 (D), S_1 (E), S_2 (F), S_{3-4} (G), and M (H) elements; specimens ZPAL cXVI/2885–2892, respectively.

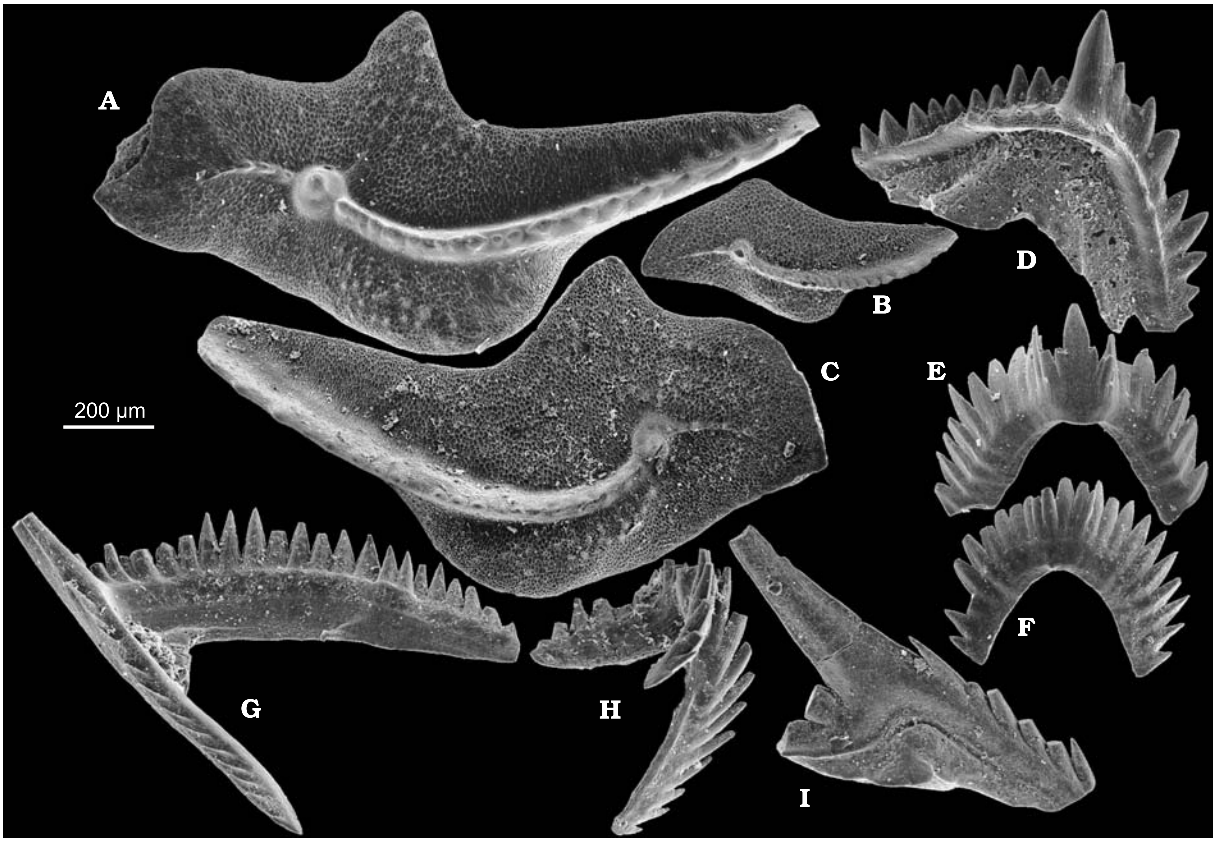


Fig. 98. *Palmatolepis perlobata* Ulrich *et* Bassler, 1926 from the *C. quadrantinodosa* Zone at Łagów (A–D, F–I, sample Ł-28; E, sample Ł-38) in the Holy Cross Mountains. P_1 (A–C), P_2 (D), S_0 (E, F), S_1 (H), S_{3-4} (G), and M (I) elements; specimens ZPAL cXVI/2893, 2894, 1376, 1377, 1414, 1378, 1380, 1379, and 1381, respectively.

Remarks. — Apparatus of the species was restored by Metzger (1994) and the Holy Cross Mountains material supports his interpretation. P_2 elements in samples from Miedzianka frequently show bifurcation of the external process. Their platform may be very wide and broken pieces superficially resemble ancyrognathid P_1 elements.

Occurrence. — The late *K. crepida* to *C. marginifera* zones at Jabłonna, Wietrznia, Łagów, Kowala, and Kadzielnia.

Palmatolepis schindewolfi Müller, 1956
(Figs 99 and 135)

Type horizon and locality: Gray limestone from a breccia with ?*Platyclymenia* from a quarry at Langenaubach near Haiger, Rhenish Slate Mountains (Ziegler 1975).

Material. — 6,378 specimens.

Diagnosis. — Variable shape of P_1 elements with mature elements showing frequently very narrow and sharp lobes of the platform, while juveniles may lack any posterior processes having instead a large rounded anterior lobe.

Remarks. — P_2 elements were identified by van den Boogaard and Kuhry (1979), complete apparatus was restored by Metzger (1994) but with incorrectly attributed M element (actually belonging to *Conditolepis*).

P. schindewolfi is a variable species. Even the very large sample Ost-12, with almost eight hundred P_1 elements has not helped much in identification of possible cryptic species within the observed range of variability. The anterior lobe is semicircular in outline and gently convex in the dominant morphotype (usually classified as *P. maxima*, e.g., Metzger 1994), whereas the posterior lobe is well developed and sharply pointed. The variability extends in three main directions. One of the extreme morphotypes develops a crenulated marginal ridge of the anterior lobe. It is transitional to *P. trachytera* but just a couple of such specimens (*P. perlobata sigmoidea* Ziegler, 1962) have been found and the demarcation of *P. schindewolfi* and *P.*

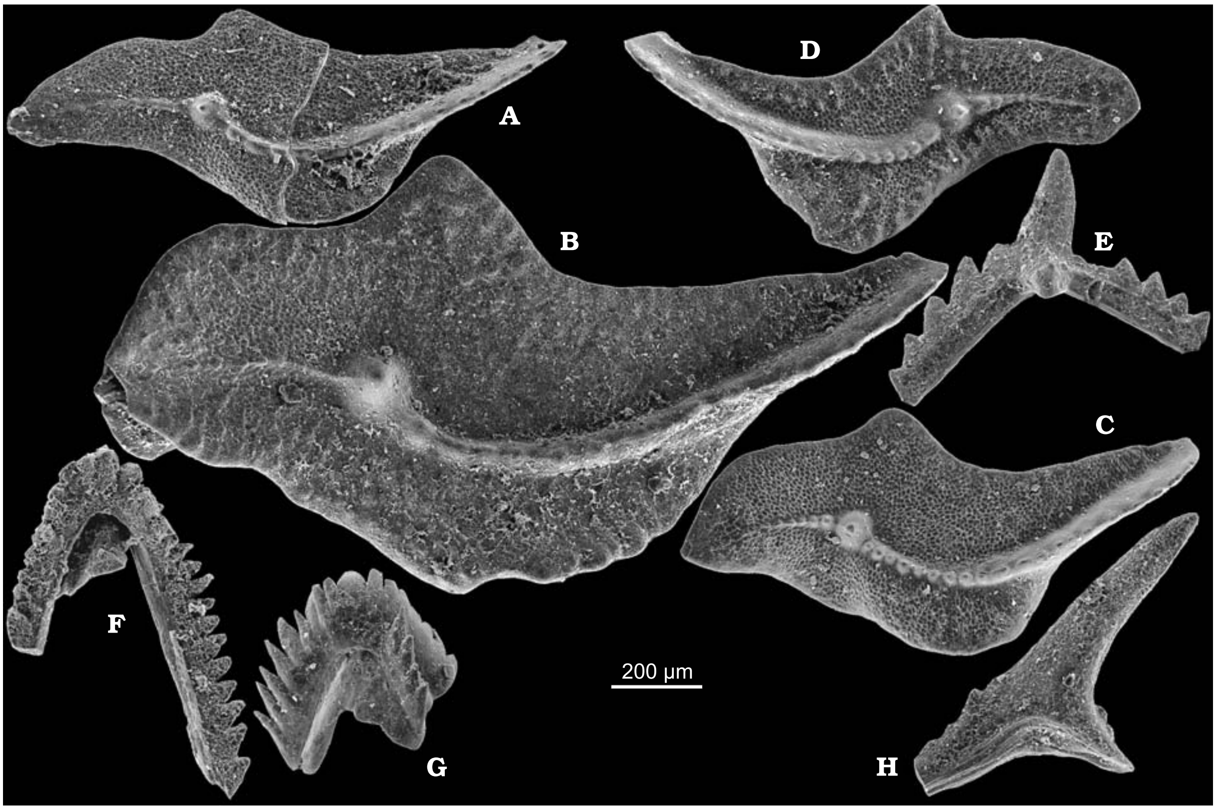


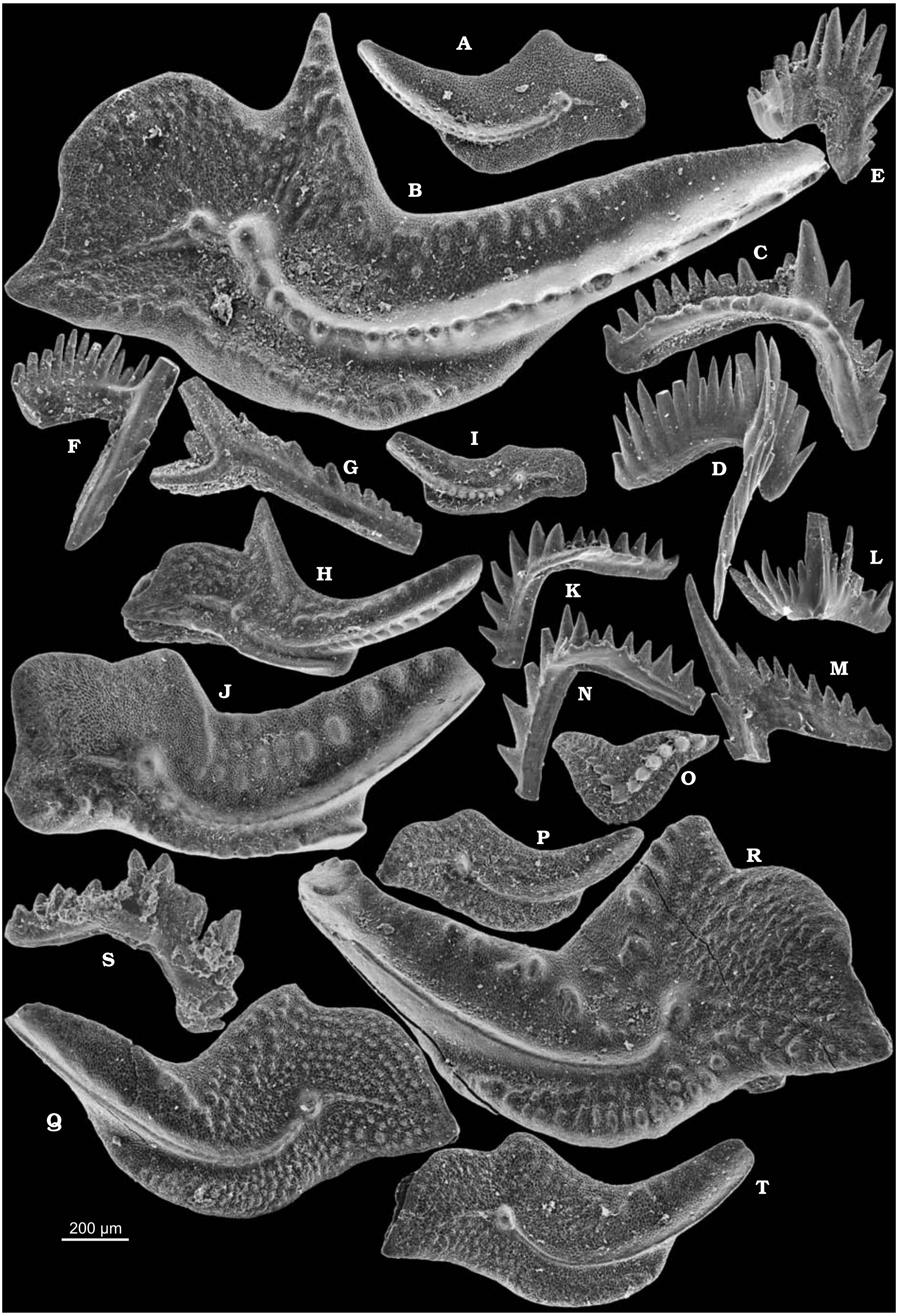
Fig. 99. *Palmatolepis schindewolfi* Müller, 1956 from the *P. trachytera* Zone at Kowala (A, sample Ko-6) and the *P. jugosus* Zone at Ostrówka (B–H, sample Ost-5) in the Holy Cross Mountains. P_1 (A–D), P_2 (E), S_1 (F), S_2 (G), and M (H) elements; specimens ZPAL cXVI/291–298, respectively.

trachytera seems rather objective. A possibility remains, however, that some cross-breeding between them took place. The second extreme morphotype lacks the posterior lobe and the whole platform is triangular in outline (*Palmatolepis perlobata helmsi* Ziegler, 1962). There is a complete gradation connecting it with the modal morphology of the population. No morphologic gap or even a lowering of frequency that would substantiate species distinction has been observed. The third extreme morphotype is the most troublesome. These are also specimens with reduced posterior lobe but the platform margins are roughly parallel and the whole robust element is strongly twisted (*P. perlobata postera* Ziegler, 1960). Their most striking feature is the anterior lobe with its ventral end protruding far from the blade. There is also a complete gradation between this morphology and the modal one but the transitional specimens may not be numerous enough to give a normal distribution of morphologic classes. As the evidence is equivocal, no separate taxon is here recognized.

The P_2 elements are equally variable. They are always highly arched with a dominant cusp. The platform may form a wide asymmetric leaf-like shelf but may be almost lacking in other morphotypes, with robust appearence of denticulation. There is no clear correspondence between these morphologies and size so they probably correspond to ranges of variability in platform extent and robustness in P_1 elements.The external process tends to be bifurcated in late populations.

Elements of the symmetry transition series are very irregular in appearance and variable, which obscures distinctions between locations. Their denticulation is rather robust, with somewhat irregularly sinuous distribution and no dominant cusp. Those virtually symmetrical with subquadrate apical part and arched processes, apparently represent S_0 elements. Similar in shape but somewhat asymmetrical elements with additional process of variable length represent the S_1 location. The process may be incipient and rarely the additional second process developed, which suggests that this morphology overlaps with the neighboring S_0 and S_2 locations. Similarly arched elements without processes are probably typical for the S_2 location.

$S_{3–4}$ elements are strongly asymmetric, with one process almost straight or gently curved, the other sinuous and they diverge at the apex at a narrow angle.


A
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200 μm

M elements differ from those of *Conditolepis* in the presence of a dominant cusp, weak dorsal denticles and somewhat angular disposition of processes as seen in profile.

Occurrence. — The *P. trachytera* to *P. jugosus* zones at Łagów, Ostrówka, Kowala, and Miedzianka.

Palmatolepis ampla Müller, 1956
(Figs 100A–G and 135)

Type horizon and locality: Sample 217 of *Platyclymenia* or *Clymenia* Stufe from Seßacker near Oberscheld in the Rhenish Slate Mountains (Ziegler 1975).

Material. — 562 specimens.

Diagnosis. — Platform of strongly sinuous P_1 elements ornamented with randomly distributed tubercles on its posterior part and transverse rows of small tubercles on the anterior lobe, P_2 elements with low cusp and wide posterior platform.

Remarks. — Apparatus was restored by myself under the name *P. rugosa* (Dzik 1991). The P_1 elements show a relatively narrow range of variability for a *Palmatolepis* species and are easily distinguishable from associated *P. perlobata*.

Occurrence. — The *C. quadrantinodosa* and *C. marginifera* zones at Łagów, Kowala, and Miedzianka.

Palmatolepis trachytera Ziegler, 1960
(Figs 100H–O and 135)

Type horizon and locality: Sample 10 of gray cephalopod limestone 0.3 m above layer with *Prolobites delphinus* and *Platyclymenia involuta* (Ziegler 1975).

Material. — 989 specimens.

Diagnosis. — Platform of P_1 elements with sharp ridge or a row of tubercles along its anterior margin.

Remarks. — P_1 elements are flat and sinous in appearance. They vary much in development of the posterior pointed lobe. In early populations the posterior lobe is sharply pointed and elongate (Fig. 100H), whereas in later populations it may be virtually missing.

The P_2 elements bear a minute cusp and denticles in proximity of it are lower than others. The processes meet at an angle in the plane of the platform, which results in its boomerang-like shape. Width and ornamentation of the platform vary and extremely smooth, wide-platform elements resemble somewhat elements of *Conditolepis*.

The symmetry transistion series elements differ from those of *P. schindewolfi* in a more generalized appearance, that is, in usual domination of the cusp, sharp denticulation and their less sinuous arrangement. Otherwise they are similar to those of other *Palmatolepis* species.

Occurrence. — Zone of its own at Łagów, Ostrówka, Miedzianka, Kowala, and Jabłonna.

Palmatolepis rugosa Branson *et* Mehl, 1934
(Figs 100PO–S and 135)

Type horizon and locality: Saverton Shale seven miles north of Monroe City, Missouri (Ziegler 1975).

Material. — 664 specimens.

Diagnosis. — P_1 elements with transversely ribbed anterior lobe.

Remarks. — There is a gap in occurrence between *P. trachytera* and *P. rugosa* in the Holy Cross Mountains but the laterally sinuous shape of P_2 elements suggests a close relationship between these species. In some specimens of late *P. trachytera* the anterior ridge splits into a row of tubercles. There would not be much to change this into the tuberculated anterior field of *P. rugosa*, but the change remains to be domonstrated.

Occurrence. — The *P. styriacus* and *P. jugosus* zones at Ostrówka, Miedzianka, Kowala, and Jabłonna.

← Fig. 100. Advanced species of *Palmatolepis* from the Holy Cross Mountains. **A–G**. *Palmatolepis ampla* Müller, 1956 from the *C. marginifera* Zone at Łagów (sample Ł-5). P_1 (A, B), P_2 (C), S_1 (D), S_2 (E), S_{3-4} (F), and M (G) elements; specimens ZPAL cXVI/2895–2901, respectively. **H–O**. *Palmatolepis trachytera* Ziegler, 1960 from its nominal zone at Łagów (H, sample Ł-40) and Jabłonna (N, bed 24) and the *L. styriacus* Zone at Ostrówka (I–O, sample Ost-12). P_1 (H–J), P_2 (K, N, O), S_1 (L), and M (M) elements; specimens ZPAL cXVI/2902–2909, respectively. **P–T**. *Palmatolepis rugosa* Branson *et* Mehl, 1934 from the *P. jugosus* Zone at Ostrówka (P–S, sample Ost-5) and the late *L. styriacus* zone at Kowala (T, sample Ko-6). P_1 (P–R, T), and P_2 (S) elements; specimens ZPAL cXVI/2919–2922, and 2910, respectively.

Genus ***Conditolepis*** van den Boogaard *et* Kuhry, 1979

Type species: *Palmatolepis marginifera* Helms, 1959 from the *Cheiloceras* Stufe of the Rhenish Slate Mountains.

Diagnosis. — Apparatus with biramous S_0 elements, laterally sinuous P_2 elements with low cusp and usually uniform distribution of denticles, M element having proclined cusp, linearly arranged processes with radiating denticles of the dorsal process.

Remarks. — *Panderolepis* Helms, 1963 has a priority over *Conditolepis* van den Boogard and Kuhry, 1979 but it was based on the type species *Polygnathus*? *serratus* Hinde, 1879, which was found to be a *nomen dubium* by Huddle (1968).

Conditolepis lobicornis (Schülke, 1995)
(Figs 101A–M and 136)

Type horizon and locality: Bed 29 of Seßacker trench near Dillenburg in the Rhenisch Slate Mountains (Schülke 1995).

Material. — 403 specimens.

Diagnosis. — Smooth P_1 element with a narrow extension of the posterior lobe and gently bent P_2 element with incipient platform and denticles of almost uniform height and size.

Remarks. — Apparatus was restored by Schülke (1999) who identified it as the first member of the branch of palmatolepidids with reduced additional processes in S_0 elements, indicating also its proximity to *K. linguiloba* sp. n. representing a continuation of its lineage. As shown by Schülke (1999) *Klapperilepis subperlobata* (Branson *et* Mehl, 1934 *sensu* Schülke 1999) is ancestral to *C. lobicornis*. Its relationship to, and possible identity with, *K. triangularis* remains to be clarified.

The shape of the platform of P_1 elements is very variable in each of the studied samples, with end-members of transition series approaching *Palmatolepis initialis* sp. n. (Fig. 101 C–E), *C. tenuipunctata* (Fig. 101O), and *C. linguiloba* sp. n. (Fig. 101E). This apparent similarity is the result of a phylogenetic proximity to all these species, in the first case the shared features of the apparatus morphology are plesiomorphic, in two others these could be considered apomorphic for the genus. There is a clear morphologic gap between the ranges of the platform shape variability of the type populations of *C. lobicornis*, *C. linguiloba* sp. n., and *C. tenuipunctata*.

Klapper *et al*. (2004) considered *C. lobicornis* conspecific with *Palmatolepis subperlobata helmsi* Ovnatanova, 1976, here renamed *C. linguiloba* sp. n. However, the holotype of *C. lobicornis* with its narrow posterior lobe is unsimilar to specimens of *C. linguiloba*, and no specimen in the type series (Schülke 1995, pl. 40) fits its morphology. Instead, they tend to be similar in the shape of the platform to underived species of *Palmatolepis*.

Occurrence. — The *K. triangularis* Zone at Płucki, Wietrznia, and Jabłonna.

Conditolepis linguiloba sp. n.
(Figs 101N, O and 136)

Holotype: Specimen ZPAL cXVI/2794 (Fig. 101N).

Type horizon and locality: Sample J-48, early Famennian *K. crepida* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: Referring to the tongue-like shape of the platform lobe.

Material. — 125 specimens.

Diagnosis. — Smooth P_1 element with a wide tongue-like extension of the posterior lobe.

Remarks. —Although no other element of the apparatus of this species was identified with confidence, co-occurrence of its relatively numerous P_1 elements with species of *Conditolepis* suggests that the P_1 and other elements of their apparatuses were indistinguishable, thus more advanced than those of *C. lobicornis*. *C. lobicornis* probably represents the same lineage but differs in the more pointed tip of the platform lobe in the P_1 elements, its P_2 elements virtually lack a platform, and occur in older strata.

This species has been referred to as *Palmatolepis subperlobata* by i.a., Wolska (1967), Dreesen and Dusar (1974), Helms and Ziegler in Clark (1981, fig. 52), Wang (1989), and Metzger (1994), but it definitely represents a different lineage, as shown both by the morphology of P_1 elements and apparatus composition (Schülke 1999). Klapper *et al*. (2004) used the name *C. lobicornis* for this species as a replacement for *Palmatolepis subperlobata helmsi* Ovnatanova, 1976, a homonym of *Palmatolepis helmsi* Ziegler, 1962.

Occurrence. — The *K. crepida* and *C. quadrantinodosa* zones at Jabłonna, Kowala, Miedzianka, and Łagów.

Fig. 101. Early species of the palmatolepidid *Conditolepis*. **A–M**. *Conditolepis lobicornis* (Schülke, 1995) from the late *K. triangularis* Zone at Jabłonna (A, B, F, sample J-65) and Wietrznia (C–E, G–L, sample Wtr-27). P_1 (A–E), P_2 (F–J), S_1 (K), $S_{3–4}$ (L), and M (M) elements; specimens ZPAL cXVI/2875, 2878, 2803, 2804, 2879, 1417, 2801, 2805, 2802, 1418–1420, respectively. **N**, **O**. *C. linguiloba* sp. n. from the *K. crepida* Zone at Jabłonna (sample J-48). P_1 elements; specimens ZPAL cXVI/2794 (holotype) and 2793. **P**–**BB**. *Conditolepis tenuipunctata* (Sannemann, 1955) from the *K. crepida* Zone at Jabłonna (sample J-45a). P_1 (P–R), P_2 (S, T), S_0 (U, V), S_1 (W), S_2 (X, Y), $S_{3–4}$ (Z), and M (AA, BB) elements; specimens ZPAL cXVI/1303, 1301, 1302, 1304–1306, 1311, 1308, 1307, 1309, 1310, and 2829, respectively.

Conditolepis tenuipunctata (Sannemann, 1955)
(Figs 101P–CC and 136)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955a).

Material. — 3,535 specimens.

Diagnosis. — P_1 elements elongate and sinuous, with wide smooth platform bearing rounded triangular extension in the middle.

Remarks. — The species may be related to stratigraphically older *C. lobicornis*, from which it differs in the reduced lobe of the platform. At Wietrznia in sample Wtr-27 an early population of this species occurs with P_2 elements virtually lacking the platform, similar to those of *C. falcata*, that is without a recognizable cusp. Such an element was already attributed to the species by den Boogaard and Kuhry (1979, fig. 8; the specimen on Fig. 7 belongs to *Klapperilepis quadrantinodosolobata*, as pointed out by Schülke 1999). Younger samples with P_1 elements typical for the species contain P_2 elements with very wide, oval platform, closely similar to that in more advanced *Conditolepis* species. I suggest to distinguish early and late forms of the species on this basis. A robust appearance of P_1 elements characterizes populations with the platform of P_2 elements already well developed but not reaching the tip of the inner process (sample Md-27).

Occurrence. — The *K. crepida* Zone at Jabłonna, Wietrznia, Kowala, and Miedzianka.

Conditolepis prima (Ziegler *et* Huddle, 1969)
(Figs 102 and 136)

Type horizon and locality: Reddish limestone at the base of the upper *Cheiloceras* Stufe at Amönau near Marburg, Rhenish Slate Mountains (Ziegler 1975).

Material. — 7,165 specimens.

Diagnosis. — Narrow P_1 elements with short anterior lobe having elevated rounded margin and no posterior lobe.

Remarks. — P_2 elements of the apparatus were identified by van den Boogaard and Kuhry (1979) and Metzger (1994) and its complete restoration was offered by Schülke (1999).

The species is transitional between *C. tenuipunctata* and *C. glabra* but usually is understood in a typological sense. Schülke (1999) synonymized it with *Palmatodella unca* of Sannemann (1955a). However, *C. tenuipunctata* and *P. unca* share the same type locality and there is nothing in the text of their original description (Sannemann 1955a) that would suggest that they occur in different horizons. Moreover, Sanemmann (1955a) illustrated typical *C. glabra* from the same locality. Perhaps Schülke (1999) was in possession

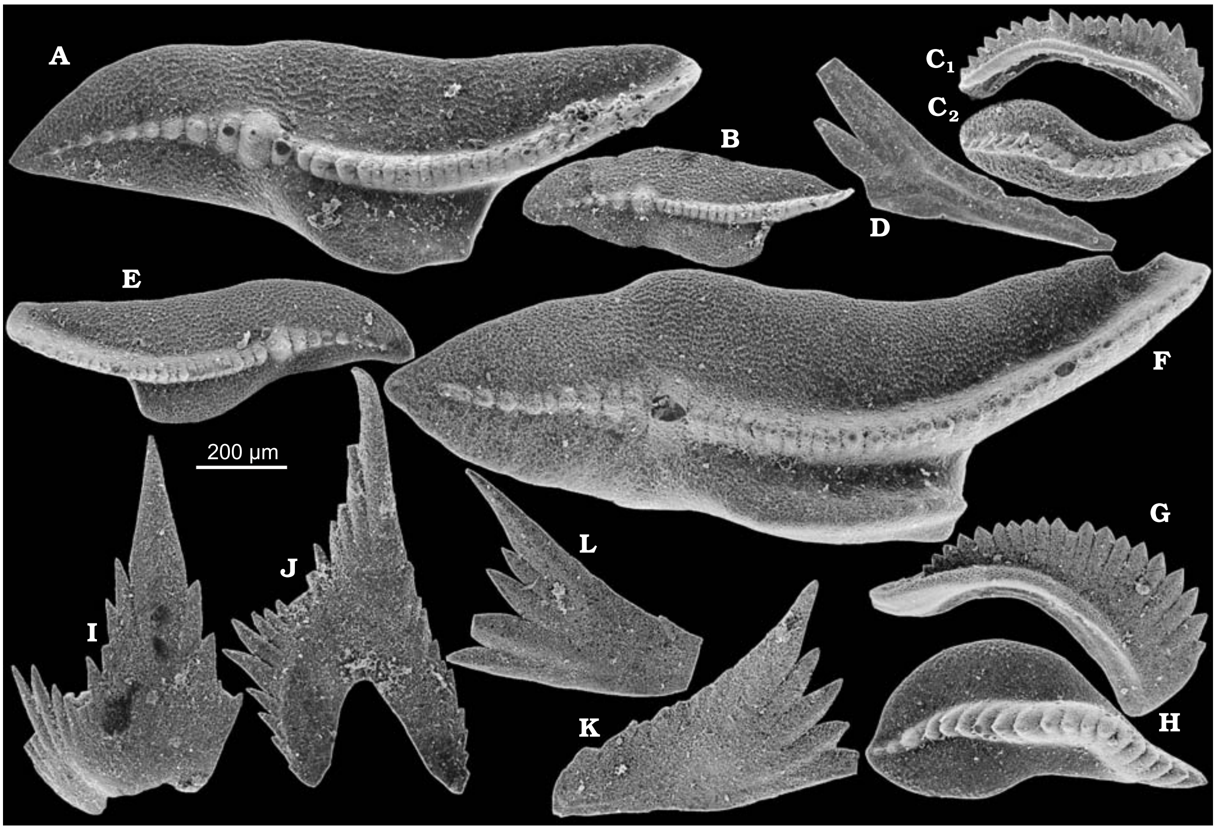

Fig. 102. *Conditolepis prima* (Ziegler *et* Huddle, 1969), an early member of the *C. glabra* lineage, from the *K. crepida* Zone at Jabłonna (I–L, sample J-50) and Kadzielnia (E, F, and H, samples Ka-3; G, I–K, sample Ka-4) in the Holy Cross Mountains. P_1 (A, B, E, F), P_2 (C, G, H), S_0 (I), S_2 (J), and M (K, L) elements; specimens ZPAL cXVI/2831, 2830, 2832, 2833, 2867, 2868, 2871, 2869, 2872–2874, and 2870, respectively.

of additional information that the third species is represented in the same assemblage. In my material apparatuses of *C. tenuipunctata* and *C. glabra*, as well as populations possibly transitional between them, do not differ in their apparatus composition. This refers also to the M elements and the specimen illustrated by Schülke (1999, pl. 3: 18) as belonging to *C. tenuipunctata* may be atypical. Narrow-platform elements classified by Schülke (1999) in *P. unca* co-occur with typical elements of *C. tenuipunctata* in its late samples and the same

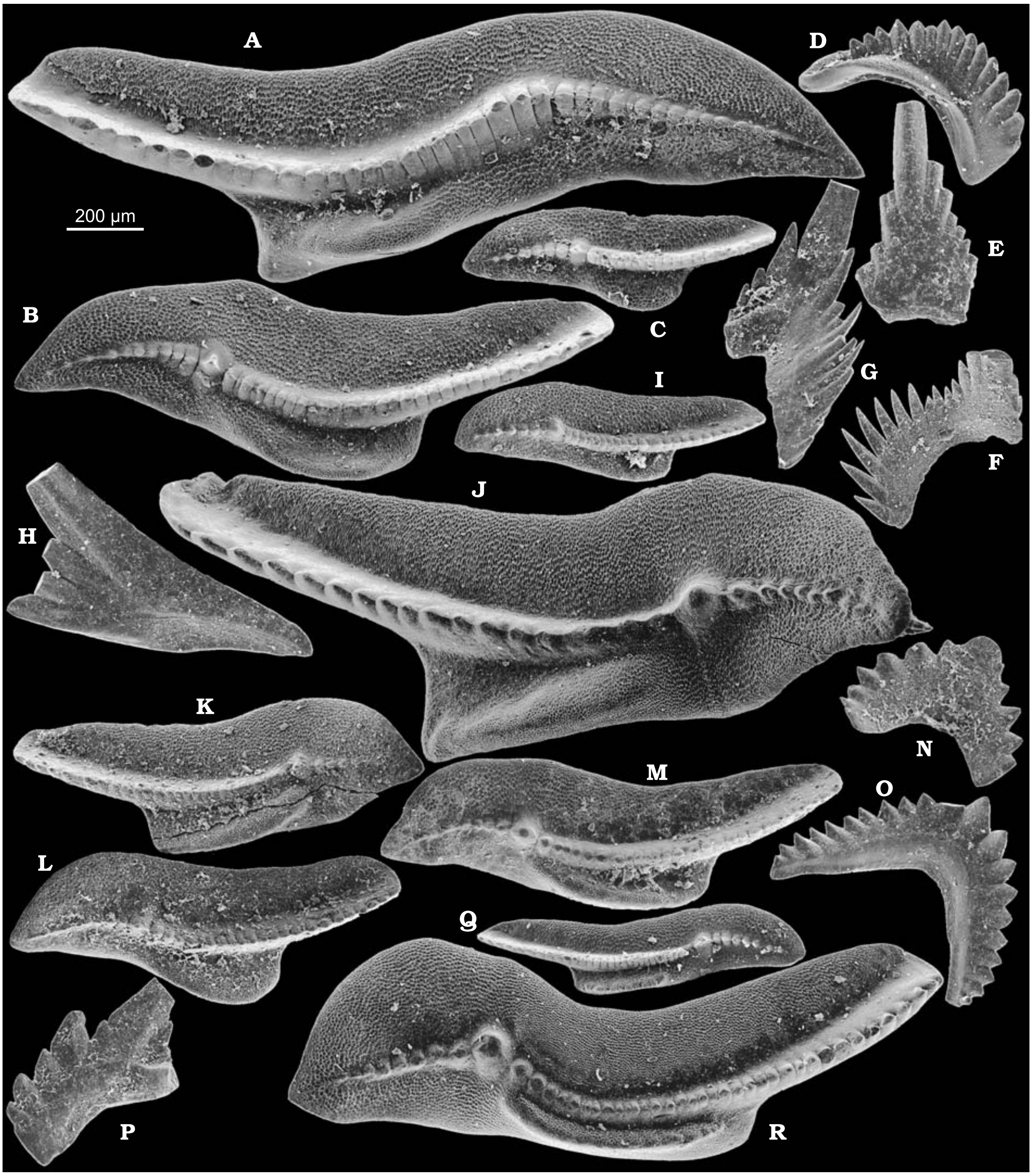

Fig. 103. Advanced species of the palmatolepidid *Conditolepis glabra* lineage from the Holy Cross Mountains. **A**–**P**. *Conditolepis glabra* Ulrich *et* Bassler, 1926 from the *C. quadrantinodosa* Zone at Łagów (A–H, sample Mak-3-4; I, J, sample Ł-26; L–N, sample Ł-28) and Miedzianka (O, P, sample Md-2). P$_1$ (A–C, I–M), P$_2$ (D, N, O), S$_0$ (E), S$_2$ (F), S$_{3–4}$ (G, P?), and M (H) elements; specimens ZPAL cXVI/2837, 2836, 2835, 2838–2842, 2864, 2863, 1394, 1393, 1395, 1397, 2865, 1393, and 2866, respectively. **Q**, **R**. *Conditolepis distorta* (Branson *et* Mehl, 1934) from the *C. marginifera* Zone at Łagów (sample Ł-9). P$_1$ elements; specimens ZPAL cXVI/2850 and 2851.

is in the Montagne Noire material of Schülke (1999, p. 91). This suggests that these are just morphologies within monospecific populations instead of distinct species and that in the course of evolution narrow-platform elements became more and more numerous.

Occurrence. — The *K. crepida* Zone at Kadzielnia, Jabłonna, Wietrznia, Łagów, Kowala, and Miedzianka.

Conditolepis glabra Ulrich *et* Bassler, 1926

(Figs 103A–P and 136)

Type horizon and locality: "Hardin sandstone" near Mount Pleasant, Tennessee (Huddle 1968).

Material. — 2,230 specimens.

Diagnosis. — P_1 elements with a ridge along the anterior margin of the platform, ventrally departing from the blade and truncated with an angulation perpendicular to it.

Remarks. — In several large samples studied there is a complete gradation between morphologies traditionally believed to characterize separate species, including "*Palmatolepis*" *prima* (Fig. 103L), "*P.*" *pectinata* (Fig. 103K–M) or "*P.*" *acuta* (Fig. 103J). I consider them variants within population variability, although the type populations of some of them may truly be distinct from *C. glabra*.

Elements of the apparatus of this species are closely similar to those of *C. quadrantinodosa* and it is difficult to separate them in samples. The difference is that in *C. glabra* P_2 elements are more arched and M elements more elongated than in the other lineage.

The species is apparently ancestral to *C. distorta* and probably to *C. falcata*. Evolution from *C. prima* to *C. glabra* and from *C. glabra* to *C. distorta* is connected with increased variability and transitional populations are polymorphic in respect to morphology of P_1 elements. Delimitation of these probable chronospecies is thus rather conventional.

Occurrence. — The *C. quadrantinodosa* Zone at Łagów, Kowala, Jabłonna, and Miedzianka; also in the Dębnik area (Baliński 1995).

Conditolepis distorta (Branson *et* Mehl, 1934)

(Figs 103Q, R and 136)

Type horizon and locality: Famennian at Dixie, Missouri (Ziegler 1977, p. 313).

Material. — 890 specimens.

Diagnosis. — P_1 elements elongate and sinusoidal, with narrow platform bearing a prominent anterior ridge, close to the blade along its whole length.

Remarks. — Transition from *C. glabra* to *C. distorta* took place early in the *C. marginifera* Zone. As already shown in the Canning Basin succession in Australia by Glenister and Klapper (1966, text-fig. 3), the change is gradual. Populations intermediate in age show more and more common elements having the narrow furrow between the ridge on the anterior lobe and the blade, including those usually classified as *C. pectinata*.

Occurrence. — Typical populations are common in the *C. marginifera* Zone at Łagów, Kowala, and Miedzianka. Rare specimens from higher horizons at Ostrówka and Miedzianka may be reworked.

Conditolepis falcata (Helms, 1959)

(Figs 104 and 136)

Type horizon and locality: Upper part of bed 5 at Bohlen near Saalfeld, Thuringia (Helms, 1959).

Material. — 41,366 specimens.

Diagnosis. — P_1 elements very elongate and narrow, with triangular, aborally pointing anterior lobe; P_2 elements sinuous, with rudimentary platform, S_0 elements with prominent processes.

Remarks. — P_2 elements of the apparatus were identified by van den Boogaard and Kuhry (1979), the complete apparatus by myself (Dzik 1991). Metzger (1994) confirmed identification of the symmetry transition series but questioned the identification of the M element, transfering it incorrectly to *P. schindewolfi* (this would be the only element of that species different from the apparatus of related *P. perlobata*). *C. falcata* is the most abundant palmatolepidid species in the Holy Cross Mountains and its apparatus reconstruction leaves little doubt. Sample Ost-12 offers the largest material of this species being devoid of any other *Conditolepis* species.

Fig. 104. Palmatolepidid *Conditolepis falcata* (Helms, 1959) from the *C. quadrantinodosa* Zone at Łagów (C, F, I, J, M, and P, sample Ł-28) and the early *Lagovignathus styriacus* Zone at Ostrówka (A, B, D, E, G, H, K, L, N, O, and Q, sample Ost-12) in the Holy Cross Mountains. P_1 (A–C), P_2 (D–F), S_0 (G–I), S_{1-2} (J, K), S_{3-4} (L–N), and M (O–Q) elements; specimens ZPAL cXVI/2852, 2853, 1392, 2854, 2855, 1396, 2857, 2856, 1398, 1399, 2858, 2859, 1400, 2860, 2862, 1401, and 2861, respectively.

The origin of this species remains in doubt. The species emerged from an unknown source in the late *K. crepida* Zone at Kadzielnia together with equally cryptic *C. klapperi*. Although relatively little change is necessary in the morphology of the P_1 element to derive it from that of *C. glabra*, the whole apparatus is quite different. It cannot be excluded that the lack of a platform in P_2 elements is an ancestral feature inherited from *C. lobicornis* and early *C. tenuipunctata* and that the lineage of *C. falcata* is independent of that of *C. glabra*.

Occurrence. — Common from the *C. quadrantinodosa* Zone, most abundant in the *P. trachytera* and *L. styriacus* zones of all studied localities. Rare specimens found together with *P. jugosus* at Ostrówka and Miedzianka may be reworked.

Conditolepis klapperi (Sandberg *et* Ziegler, 1973)
(Figs 105A–G and 136)

Type horizon and locality: 42 m above the base of the West Range Limestone at the Bactrian Mountains, Nevada (Ziegler 1975).

Material. — 2,846 specimens.

Diagnosis. — Anterior margin of the P_1 element with a massive ramp-like ridge, posterior margin of the platform non-lobate, strongly sinuous.

Remarks. — This is the first species of the *C. marginifera* lineage as indicated by its robust appearance with massive anterior ridge of the platform. Similarly to the P_1 element, other elements of the apparatus are of large size, massive appearance and regular distribution of sharp denticles, otherwise they resemble those of other typical *Conditolepis* species.

Occurrence. — The late *K. crepida* Zone at Kadzielnia and Jabłonna.

Conditolepis quadrantinodosa (Branson *et* Mehl, 1934)
(Figs 105H–N and 136)

Type horizon and locality: Saverton Shale seven miles north of Monroe City, Missouri (Ziegler 1977, p. 367).

Material. — 139 specimens.

Diagnosis. — Very variable P_1 element, oval in outline with gently convex anterior lobe covered with tubercles or forming a ridge.

Remarks. — The range of population variability of this species encompasses, with completely smooth gradation, morphologies typical of *C. inflexa* (see Dreesen and Dusar 1974; Dreesen 1976) but also *C. marginifera* and *C. inflexoidea*. They separated into distinct biological species somewhat later in their evolution.

Occurrence. — Zone of its own at Łagów, Kowala, and Miedzianka.

Conditolepis marginifera (Helms, 1959)
(Figs 105O, P, S–V and 136)

Type horizon and locality: Bed 13 of reddish limestone with *Cheiloceras enkebergense* in trench II at Seßacker near Oberscheld, Rhenisch Slate Mountains (Ziegler 1977, p. 325).

Material. — 1,430 specimens.

Diagnosis. — Short P_1 element with subcircular dorsal end, bearing a sharp ridge or row of tubercles along the anterior margin in proximity to the blade.

Remarks. — Because of the tremendous morphological variability of the P_1 elements of this species it is difficult to determine it reliably based on single specimens. In fact, the co-occurrence of *C. inflexoidea*, separated by a gap in morphologic variability, gives a helpful hint that one is dealing with a separate species and not with an extreme morphology of the stratigraphically preceding *C. quadrantinodosa*.

Occurrence. — Zone of its own at Łagów, Kowala, Ostrówka, and Miedzianka.

Conditolepis inflexoidea (Ziegler, 1962)
(Figs 105Q, R and 136)

Type horizon and locality: Bed 13 of reddish limestone with *Cheiloceras enkebergense* in trench II at Seßacker near Oberscheld, Rhenish Slate Mountains (Ziegler 1975).

Material. — 145 specimens.

Diagnosis. — Elongate P_1 element with gently convex smooth anterior lobe.

Remarks. — The problem of the evolutionary origin of this species remains to be solved. As shown by Dreesen and Dusar (1974) and Dreesen (1976) there is a tremendous polymorphism in the populations transitional between those with dominant *C. quadrantinodosa* and *C. marginifera* morphologies, which obliterates the true nature of evolutionary change. Whether the genetic barrier developed sympatrically in the whole area of occurrence of the species or, alternatively, an allopatric speciation event not expressed in morphology preceded spatial reunification of the lineage, remains unknown. Perhaps detailed biometrical studies in successions from different places in the world may help in finding an answer to this question.

Occurrence. — The *C. marginifera* Zone at Łagów, Kowala, and Miedzianka.

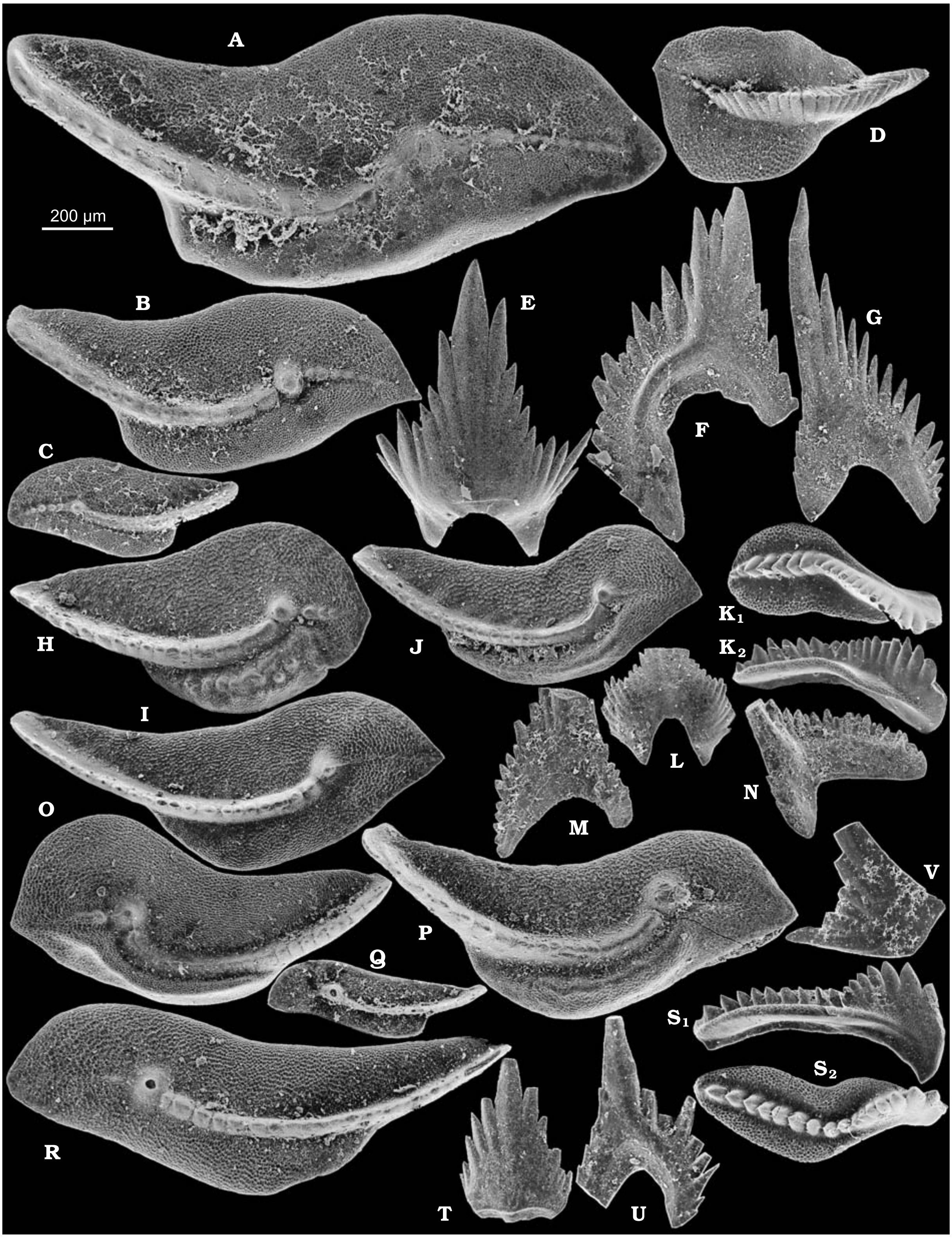

Fig. 105. Palmatolepidids of the *Conditolepis marginifera* lineage from the Holy Cross Mountains. **A**–**G**. *C. klapperi* (Sandberg *et* Ziegler, 1973) from the *K. crepida* Zone at Kadzielnia (sample Ka-10). P_1 (A–C), P_2 (D), S_0 (E), $S_{1–2}$ (F), and $S_{3–4}$ (G) elements; specimens ZPAL cXVI/2845, 2844, 2846, 2847, 2849, and 2848, respectively. **H**–**N**. *C. quadrantinodosa* (Branson *et* Mehl, 1934) from its nominal zone at Łagów (sample Ł-28). P_1 (H–J), P_2 (K), S_0 (L), $S_{1–2}$ (M), and $S_{3–4}$ (N) elements; specimens ZPAL cXVI/1382–1386, 1389, and 1390, respectively. **O**, **P**, **S**–**V**. *C. marginifera* (Helms, 1959) from its nominal zone at Łagów (sample ŁSł73-3). P_1 (O, P), P_2 (S), S_0 (T), $S_{1–2}$ (U), and M (V) elements; specimens ZPAL cXVI/2821, 2825, 2826, 2823, 2827, and 2828, respectively. **R**. *C. inflexoidea* (Ziegler, 1962) from the same sample. P_1 elements; specimens ZPAL cXVI/2825 and 2824.

Family **Cavusgnathidae** Austin *et* Rhodes, 1981

Diagnosis. — P_1 elements with axial symmetry, bearing elaborate icrion or high-positioned platform.

Remarks. — The three Famennian conodont lineages with more or less developed axial symmetry in their platform elements discussed below, probably share their common ancestry in a *Pandorinellina*-like form of early Famennian age. The *Pseudopolygnathus* lineage continued without any drastic morphological changes from the Famennian to the Tournaisian when it diversified significantly (Dzik 1997). *Alternognathus* is apparently only a homeomorph of *Pinacognathus* (sensu Dzik 1994) and early *Siphonodella* (Ziegler and Sandberg 1984; Sweet 1988). *Omolonognathus*, known from the late Famennian of the Cracow area (Baliński 1995) may be an extremely shallow-water offshoot of the *Alternognathus* lineage. As shown by Beinert *et al.* (1971) there is a continuity between the mid Famennian *Scaphignathus* and Tournaisian *Clydagnathus* lineages. It has to be admitted that there is some uncertainty whether the axial symmetry originated only once at the base of the whole clade. Whereas *Pandorinellina* seems to be truly the best root for the *Alternognathus* branch, the oldest member of the *Pseudopolygnathus* lineage (*P. jugosus*) shows expanded basal cone similar rather to *Dasbergina stabilis*, the species stratigraphically preceding the lineage of *Pseudopolygnathus* but not *Alternognathus*. The family defined as above may thus be polyphyletic.

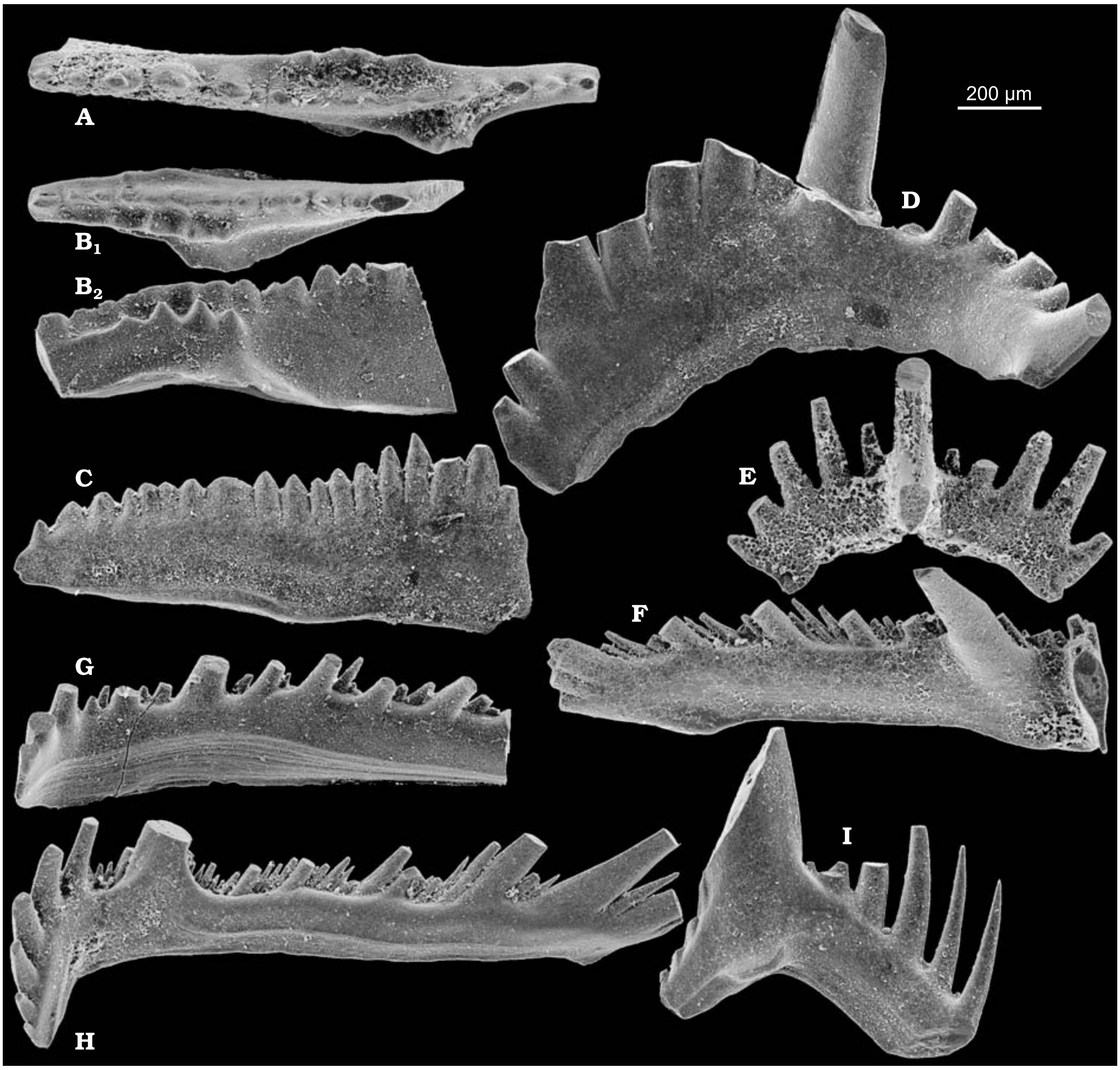

Fig. 106. *Alternognathus pseudostrigosus* (Dreesen *et* Dusar, 1974), probably the earliest cavusgnathid, from the *K. crepida* Zone at Kadzielnia (sample Ka-10) in the Holy Cross Mountains. P_1 (A–C), P_2 (D), S_0 (E), S_1 (F), S_2 (G), S_{3-4} (H), and M (I) elements; specimens ZPAL cXVI/2236–2244 (holotype B), respectively.

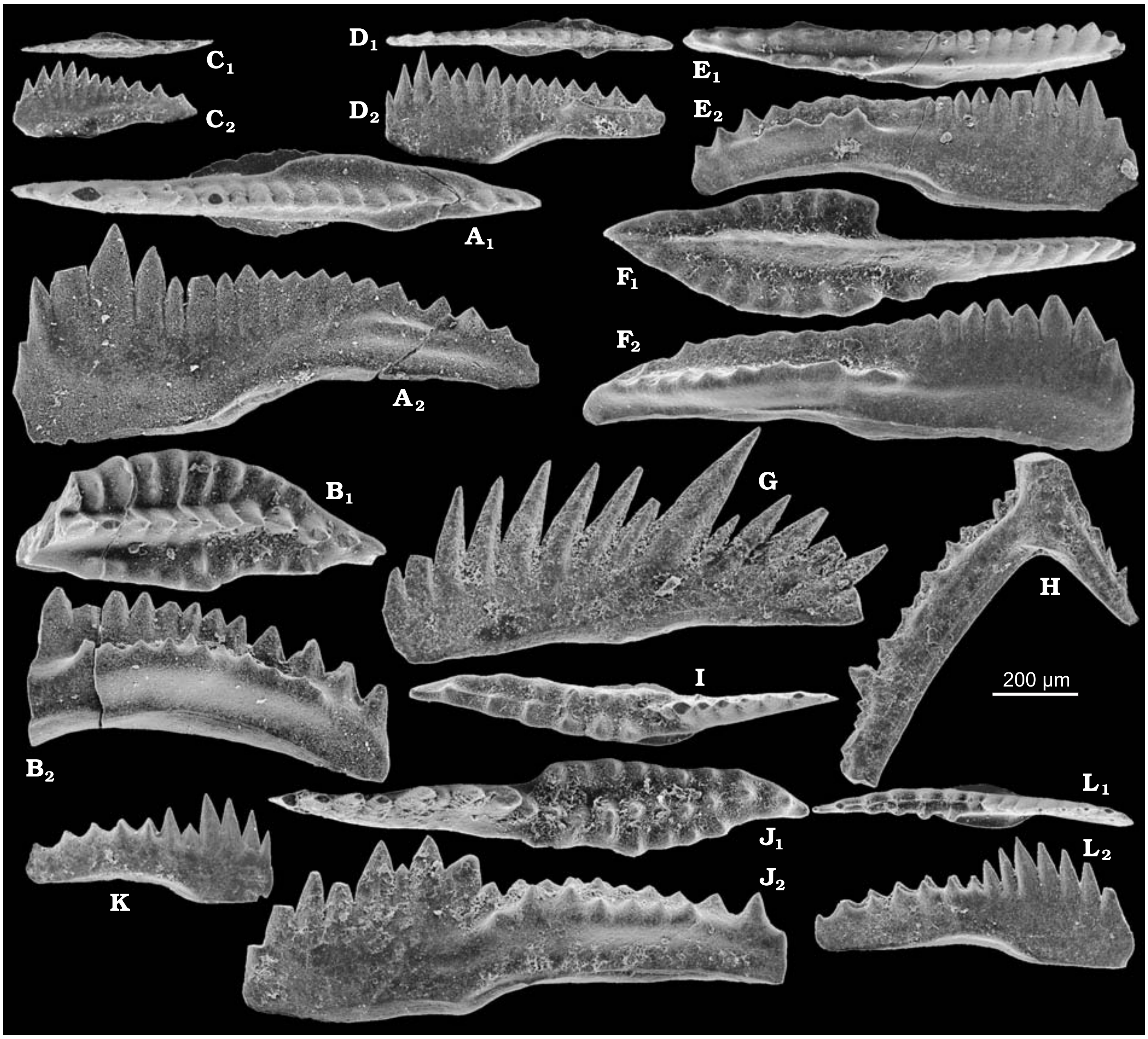

Fig. 107. Early cavusgnathids from the Holy Cross Mountains. **A**, **B**. *Alternognathus pseudostrigosus* (Dreesen *et* Dusar, 1974) from the *C. quadrantinodosa* Zone at Miedzianka (sample Md-2). P_1 elements; specimens ZPAL cXVI/2346, 2347. **C**–**H**. *Alternognathus regularis* Ziegler *et* Sandberg, 1984 from the *P. trachytera* Zone at Jabłonna (bed 24). P_1 (A–F), P_2 (G), and M (H) elements; specimens ZPAL cXVI/2351, 2350, 2349, 2348, 2352, and 2353, respectively. **I**–**L**. *Scaphignathus velifer* Helms, 1959 from the same sample. P_1 elements; specimens ZPAL cXVI/2355–2357 and 2354.

Genus *Alternognathus* Ziegler *et* Sandberg, 1984

Type species: *Alternognathus regularis* Ziegler *et* Sandberg, 1984 from the Famennian Three Forks Formation of Montana.

Diagnosis. — P_1 element with platform developing transverse ridges almost at the same level as the tips of nearby denticles of the blade, distinct shallow larval basal cavity of fusiform outline.

Remarks. — The oldest occurrence of the *Alternognathus* lineage in the Holy Cross Mountains is sample Md-2 from Miedzianka, where it co-occurs with *C.* (*C.*) *inflexoidea*, thus older than the entry of *P. trachytera*. P_1 elements in this sample usually show very weak development of the platform, which remains incipient even in large specimens. A platform-icrion developed stronger on one side of the blade and axial symmetry may be involved there. In bed 24 at Jabłonna the lineage co-occurs with *P. trachytera*, but the platform remains relatively narrow. Mature elements with very wide platform occur abundantly in sample Wzd-10 at Ściegnia. Juveniles are virtually missing there. It remains thus undecided whether the difference in width of the platform between samples results from evolution or only expresses differences in population dynamics.

The P_2 elements of *Alternognathus* differ from those of associated *Pseudopolygnathus*, *Dasbergina* and *Pandorinellina* in a significantly more prominent dorsal process. The differences between these genera in the rest of the apparatus are minor and it is hardly possible to separate them in samples where they occur in similar numbers.

Alternognathus pseudostrigosus (Dreesen *et* Dusar, 1974)
(Figs 106, 107A, B, and 137)

Type horizon and locality: Sample 4 from the Hamoir-Fairon section near Liege, Belgium.

Material. — 114 specimens.

Diagnosis. — Irregular, strongly asymmetric incipient platform located high on the blade slightly below the tips of its denticles in mature P_1 elements; elements of the apparatus robust of *Pandorinellina* type.

Remarks. — This is the earliest of the more or less certain members of the *Alternognathus* lineage. In its stratigraphic occurrence it significantly predates other species of *Alternognathus* and species of *Pseudopolygnathus* with robust icrion. The structure referred to as an incipient platform may approach icrion in some elements and is so irregularly developed that it is hard to say whether axial symmetry is already developed in P_1 elements of this species, or not. There seems to be an evolutionary change in the Holy Cross Mountains material; the stratigraphically younger specimens show a better developed platform originating earlier in the ontogeny and not so high on the blade. The elements are also less robust and somewhat "arthritic" in appearance.

Occurrence. — The late *K. crepida* Zone at Kadzielnia and the *C. quadrantinodosa* Zone at Miedzianka (Md-2).

Alternognathus regularis Ziegler *et* Sandberg, 1984
(Figs 107C–H, 108, and 137)

Type horizon and locality: Top of the Trident Member of Three Forks Formation at Sheep Mountain in Centennian Range of Montana (Ziegler and Sandberg 1984).

Material. — 1,390 specimens.

Diagnosis. — Well developed but rather narrow platform of P_1 element with large nodes along the margin.

Remarks. — The species was referred to as *Scaphignathus subserratus* until Ziegler and Sandberg (1984) questioned the species identity of the lectotype. The incipient axial symmetry of the elements refers only to the shape of the platform and is more clearly visible on juveniles than on large specimens with a wider platform. The blade remains curved in mirror-image pairs.

Occurrence. — The *C. quadrantinodosa* to early *P. jugosus* zones at Łagów, Kowala, Ostrówka, and Miedzianka.

Alternognathus? sp.
(Fig. 110H–L)

Material. — Seven specimens.

Remarks. — Rare P_1 elements from Dzikowiec are of juvenile *A. regularis* size and morphology but their free blade is shorter, resembling thus much more ontogenetically advanced and larger specimens of that species. They may thus represent adults of a separate species.

Occurrence. — The late *P. jugosus* Zone at Dzikowiec in the Sudetes.

Alternognathus beulensis Ziegler *et* Sandberg, 1984
(Figs 9A, 109, and 137)

Type horizon and locality: Top of the Hemberg Limestone at the top of Beul Mountain near Balve in the Rhenish Slate Mountains (Ziegler and Sandberg 1984; Beinert *et al*. 1971).

Material. — 202 specimens.

Diagnosis. — Wide platform ornamented with ridges and nodes.

Remarks. — This is the most advanced species of the *Alternognathus* lineage, probable a successor of *A. regularis* and this is consistent with the stratigraphic succession of these species in the Holy Cross Mountains.

Although the non-platform elements of the *Alternognathus* apparatus are of a rather generalized morphology, P_2 elements with their straight long processes may be of some use in determining the generic affinity.

Occurrence. — The *P. trachytera* to *L. styriacus* zones at Jabłonna, Ściegnia, Miedzianka, and Ostrówka.

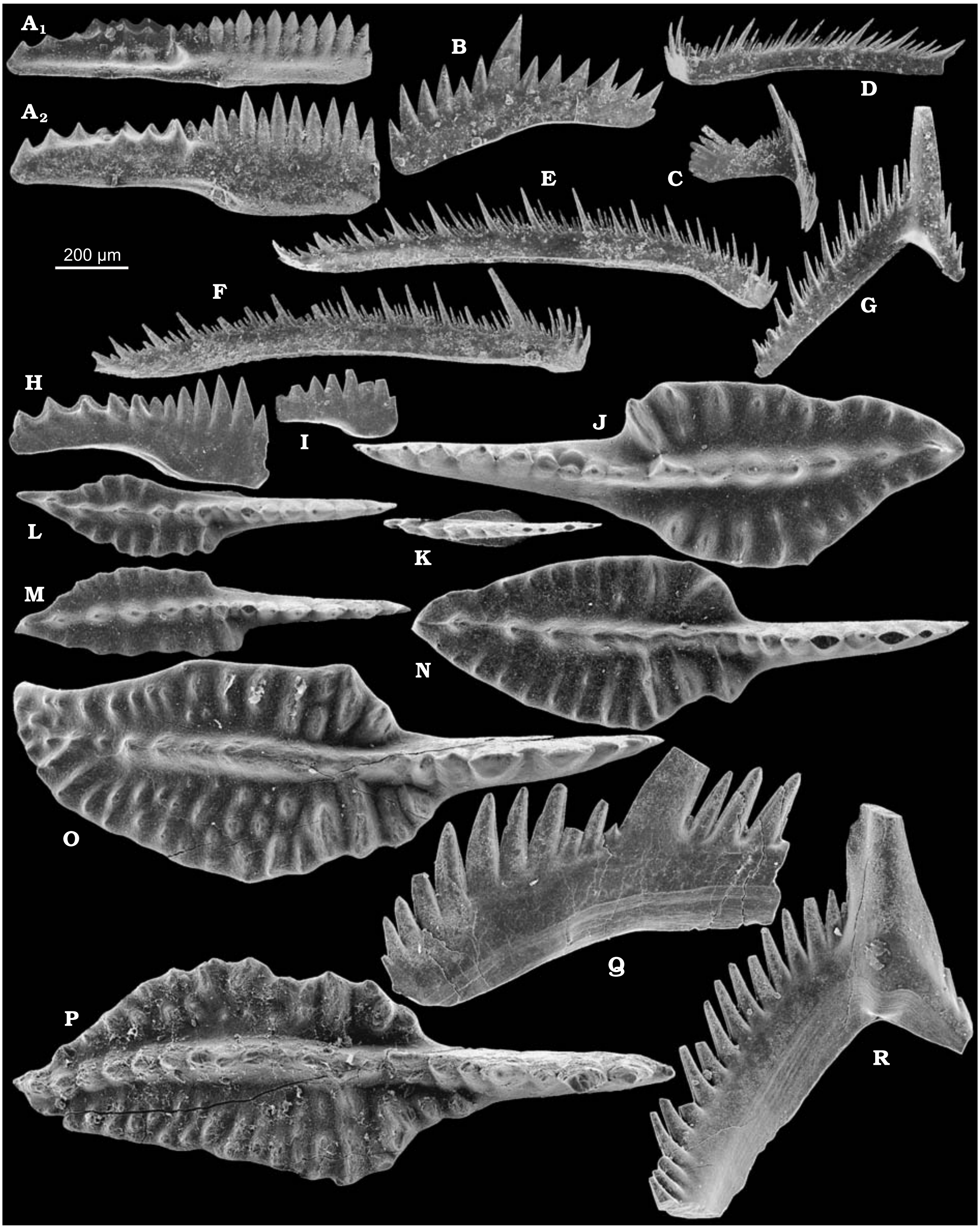

Fig. 108. Cavusgnathid *Alternognathus regularis* Ziegler *et* Sandberg, 1984 from the early *P. trachytera* Zone at Kowala (A–G, sample Ko-8a) and the *L. styriacus* Zone at Miedzianka (H–R, sample Md-14) in the Holy Cross Mountains. P_1 (A, H–P), P_2 (Q), and M (R) elements; specimens ZPAL cXVI/527, 528, 531–533, 535, 534, 2358, 2360, 2365, 2359, 2367, 2368, 2366, 2364, 2361, 2363, and 2362, respectively.

Genus *Scaphignathus* Helms, 1959

Type species: *Scaphignathus velifera* Helms, 1959 from the mid Famennian of the Saalfeld area.

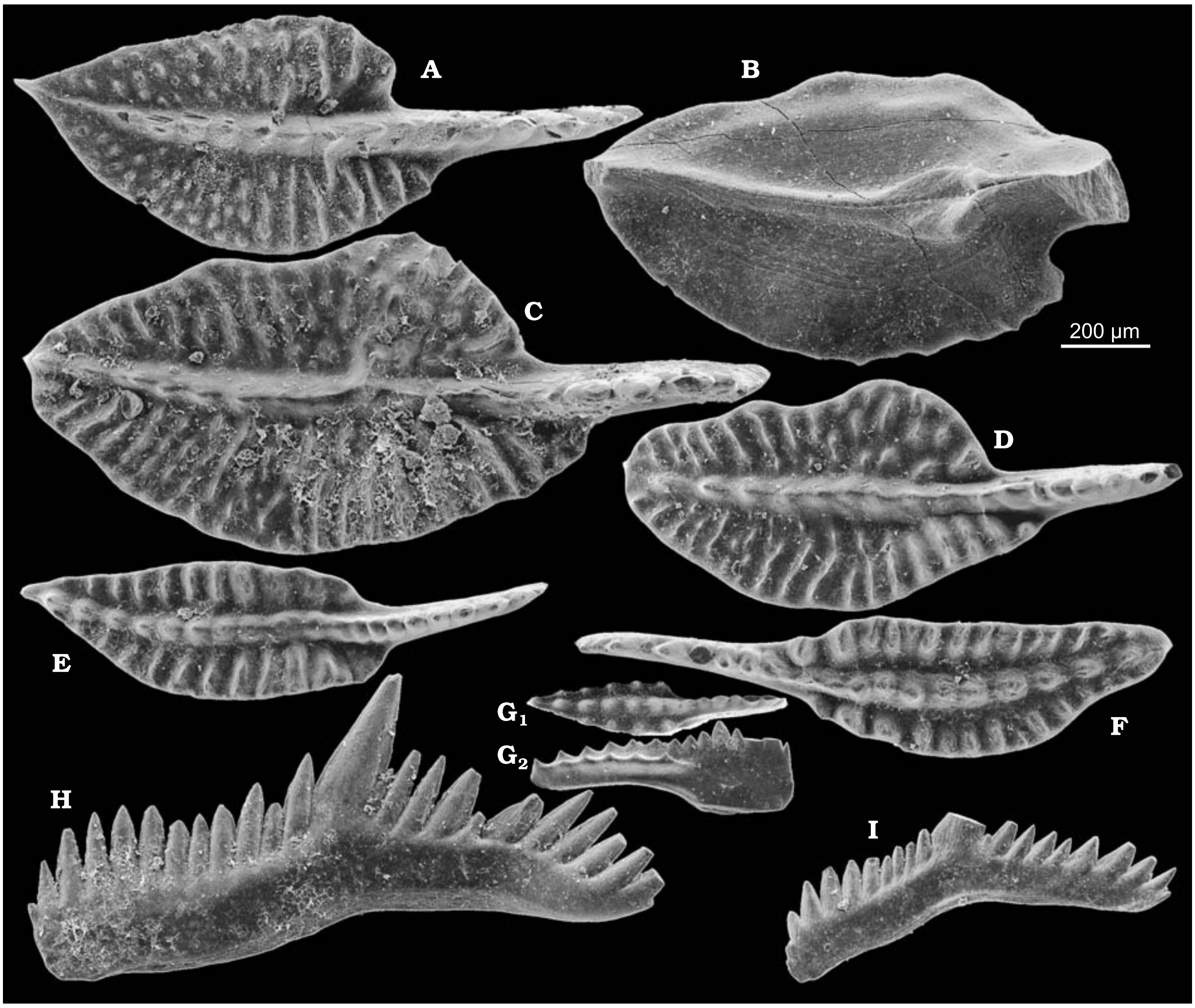

Fig. 109. Cavusgnathid *Alternognathus beulensis* Ziegler *et* Sandberg, 1984 from from the *P. trachytera* Zone at Ściegnia (Wzdół Plebański; sample Wzd-10; homeomorph of the species?) and the *L. styriacus* Zone at Miedzianka (A, B, sample Md-14) and Ostrówka (C–I, sample Ost-15) in the Holy Cross Mountains. P_1 (A–G) and P_2 (H, I) elements; specimens ZPAL cXVI/2370–2376, 2378, and 2377, respectively.

Diagnosis. — Strongly asymmetric icrion in P_1 elements, with tubercles of lateral and middle rows at approximately the same level, high free blade.

Remarks. — *Scaphignathus* differs from *Alternognathus* mainly in virtually equal height of tubercles of the platform and those of the corresponding part of the blade. In fact, at early stages of the ontogeny this is not a true platform but rather an icrion. This difference is apparent even in the geologically oldest samples with species of those genera co-occurring (e.g., J-24), although some specimens remain difficult to tell apart. There was probably no difference in the apparatus structure between those erliest members of the lineage. In geologically younger samples two kinds of P_2 elements seem to occur, one with a rather generalized morphology belonging to *Alternognathus* and the other with a very regular and low denticulation, probably representing *Scaphignathus*. Early occurrences of *Scaphignathus* in the Holy Cross Mountains differ from those from younger strata in a much narrower icrion. In the icrion being developed dorsally mostly on one side, the P_1 elements exhibit an axial symmetry, although some bending of the blade allows recognition of particular members of the mirror image pair.

Scaphignathus velifer Helms, 1959
(Figs 110G and 137)

Type horizon and locality: 4.5 m below the top of the finely nodular limestone Unit 5 at Bohlen, assemblage dominated by *Palmatolepis schindewolfi* and *Conditolepis falcata* (Helms 1959).

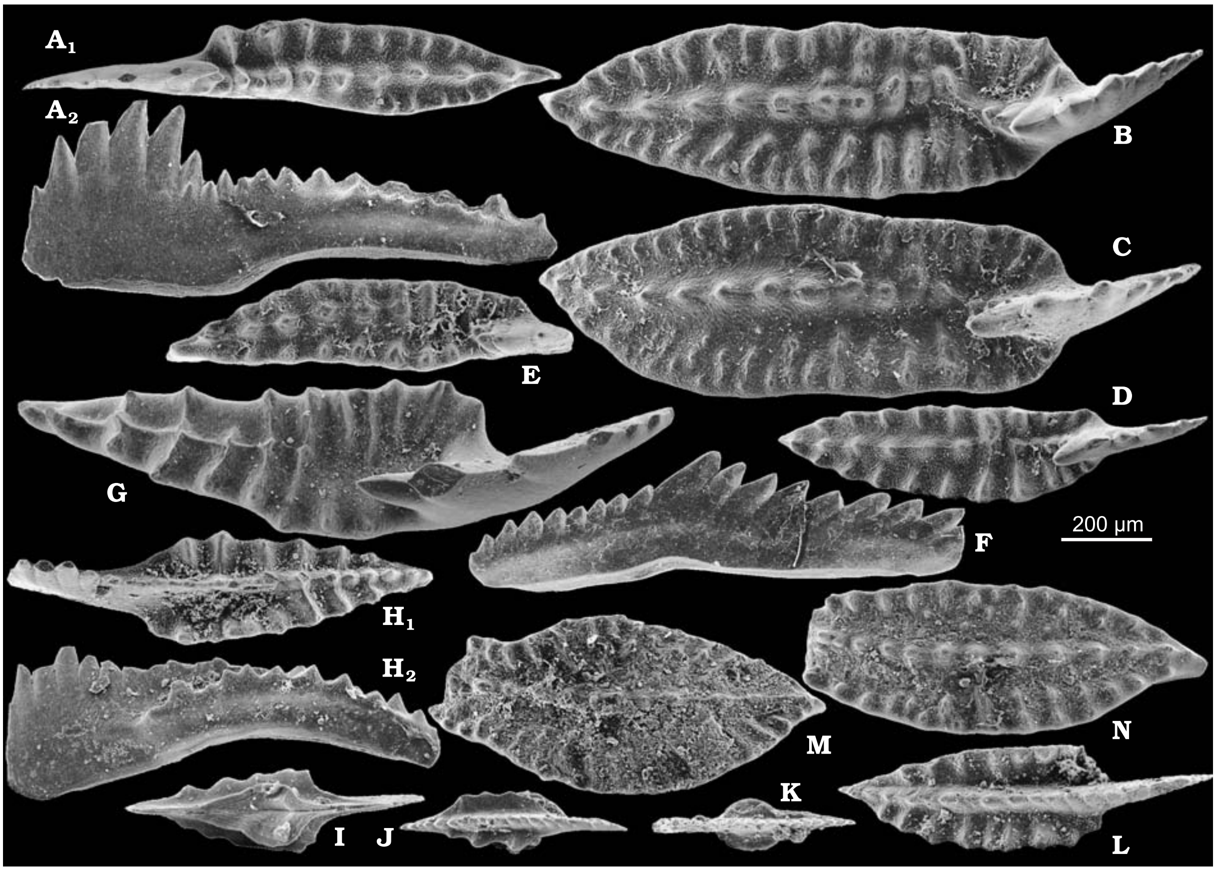

Fig. 110. Cavusgnathids. **A**–**F**. *Scaphignathus leptus* (Ziegler *et* Sandberg, 1984) from the *L. styriacus* Zone at Miedzianka (sample Md-14, A) and Ostrówka (B, D–F, sample Ost-12; C, sample Ost-1a) in the Holy Cross Mountains. P_1 (A–E) and P_2 (F) elements; specimens ZPAL cXVI/2369, 2379, 2504, and 2380–2382, respectively. **G**. *Scaphignathus velifer* Helms, 1959 from the *C. marginifera* Zone at Łagów (G, sample Ł-5) in the Holy Cross Mountains. P_1 element; specimen ZPAL cXVI/2503. **H**–**L**. *Alternognathus*? sp. from the *P. jugosus* Zone at Dzikowiec (H, sample Dz-10; I–L, sample Dz-54) in the Sudetes. P_1 elements, specimens ZPAL cXVI/2387, 2990–2992, and 2989. **M**, **N**. *Pinacognathus*? *praesulcatus* (Sandberg, 1972) from the *D. trigonica* Zone at Kowala (sample Ko-166) in the Holy Cross Mountains. P_1 elements, specimens ZPAL cXVI/2389 and 2390.

Material. — 50 specimens.

Diagnosis. — Icrion in P_1 elements gradually tapering dorsally, with narrow tip.

Remarks. — *Alternognathus costatiformis* of Matyja (1993), with its virtually equal height of lateral and medial denticles in the icrion and a distinct separation of icrion from the free blade, is so similar to *Scaphignathus* that it probably belongs in this genus.

Occurrence. — The *C. quadrantinodosa* to *P. trachytera* zones at Łagów and Jabłonna.

Scaphignathus leptus Ziegler *et* Sandberg, 1984
(Figs 110A–F and 137)

Type horizon and locality: Upper trachytera Zone, Hemberg Limestone at Ballberg near Balve (Ziegler and Sandberg 1984).

Material. — 77 specimens.

Diagnosis. — Parallel margins of the icrion and relatively blunt dorsal end in mature P_1 elements.

Remarks. — Because of significant changes in the ontogeny of P_1 elements and population variability the available material of relatively few specimens from many samples is too small to be sure of species distinctions in this genus. The proposed diagnoses remain thus provisional until a more precise picture of their evolution is achieved.

Occurrence. — The *L. styriacus* Zone at Ostrówka and Miedzianka.

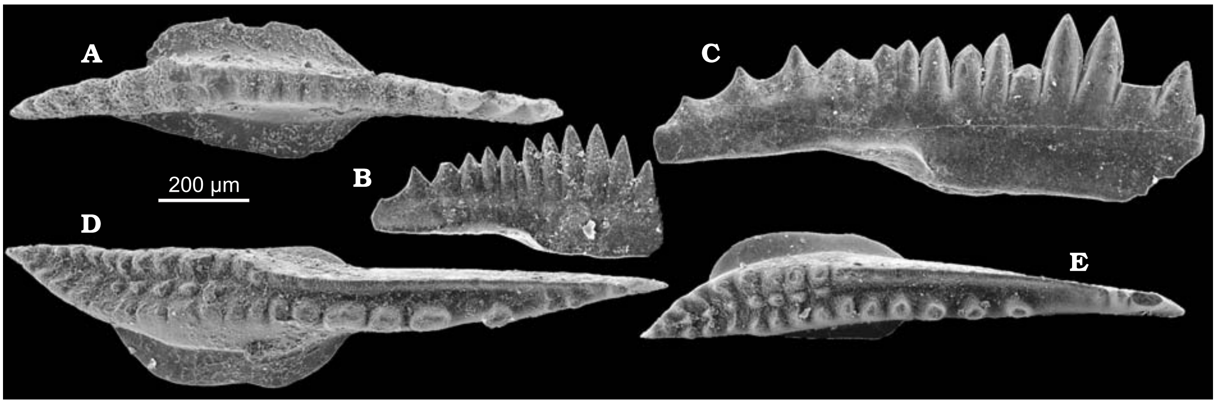

Fig. 111. Early probable cavusgnathid *Pseudopolygnathus jugosus* (Branson *et* Mehl, 1934) from its nominal Zone at Jabłonna (A–C, bed 27) and Ostrówka (D, E, sample Ost-185) in the Holy Cross Mountains. P_1 elements; specimens ZPAL cXVI/2212, 2211, 2210, 2295, and 2296, respectively.

Genus ***Pseudopolygnathus*** Branson *et* Mehl, 1934

Type species: *Pseudopolygnathus prima* Branson *et* Mehl, 1934 from the Tournaisian of Missouri.

Diagnosis. — Icrion in P_1 elements composed of rows of tubercles and frequently a longitudinal ridge, basal cavity wide and shallow.

Remarks. — The Devonian species attributed here were classified in *Bispathodus* Müller, 1962, although its type species *Spathodus spinulicostatus* E. R. Branson, 1934 is of Early Carboniferous age. Its holotype, similar to that of *S. costatus*, is probably the end member of the variability range of the co-occuring type species of *Pseudopolygnathus*, *P. primus*, as suggested by samples from elsewhere (Dzik 1997). Whatever is the real nature of this specimen, these genera are clearly closely related and there is no way to distinguish them in a satisfactory way.

According to Ziegler *et al*. (1974), the icrion developed independently in the branch of *P. jugosus* and *P. ziegleri* from the ancestral situation of *P. stabilis*. I have not been able to confirm or exclude this. However, *P. ostrovkensis*, with its robust and wide icrion, appears earlier at Kowala than *P. jugosus*, much less advanced in this respect. Perhaps *Pseudopolygnathus*, as understood here, is truly polyphyletic and the *P. jugosus* lineage should be classified in *Dasbergina*.

Pseudopolygnathus jugosus (Branson *et* Mehl, 1934)
(Figs 111, 112, and 137)

Type horizon and locality: Famennian at Dixie, Missouri (Ziegler 1977, p. 313).

Material. — 3,111 specimens.

Diagnosis. — Icrion in the dorsal part of mature P_1 element composed of two rows of denticles and additional medial row of minute denticles.

Remarks. — Icrion developed in this species by widening denticle tips in juveniles and shows axial symmetry owing to asymmetric position of the sharp ridge along the ventral portion of the blade. Mirror-image symmetry is still clearly expressed in curvature of the blade.

Occurrence. — The *P. jugosus* and *D. trigonica* zones at Kowala, Jabłonna, Ostrówka, and Dzikowiec.

Pseudopolygnathus ostrovkensis sp. n.
(Figs 113 and 137)

Holotype: Specimen ZPAL cXVI/2298 (Fig. 113F).

Type horizon and locality: Sample Ost-185, late Famennian *P. jugosus* Zone at Ostrówka, Holy Cross Mountains.

Derivation of name: From the name of the type locality.

Material. — 2,927 specimens.

Diagnosis. — Usually wide icrion of P_1 elements; in the dorsal part composed of three rows of robust denticles, the medial row being of the same height as the lateral ones.

Remarks. — P_1 elements of this species from the borehole Kowala have already been illustrated as *Bispathodus ultimus* by Nehring-Lefeld (1990, pl. 2: 13, 14). Probably also specimens identified with the

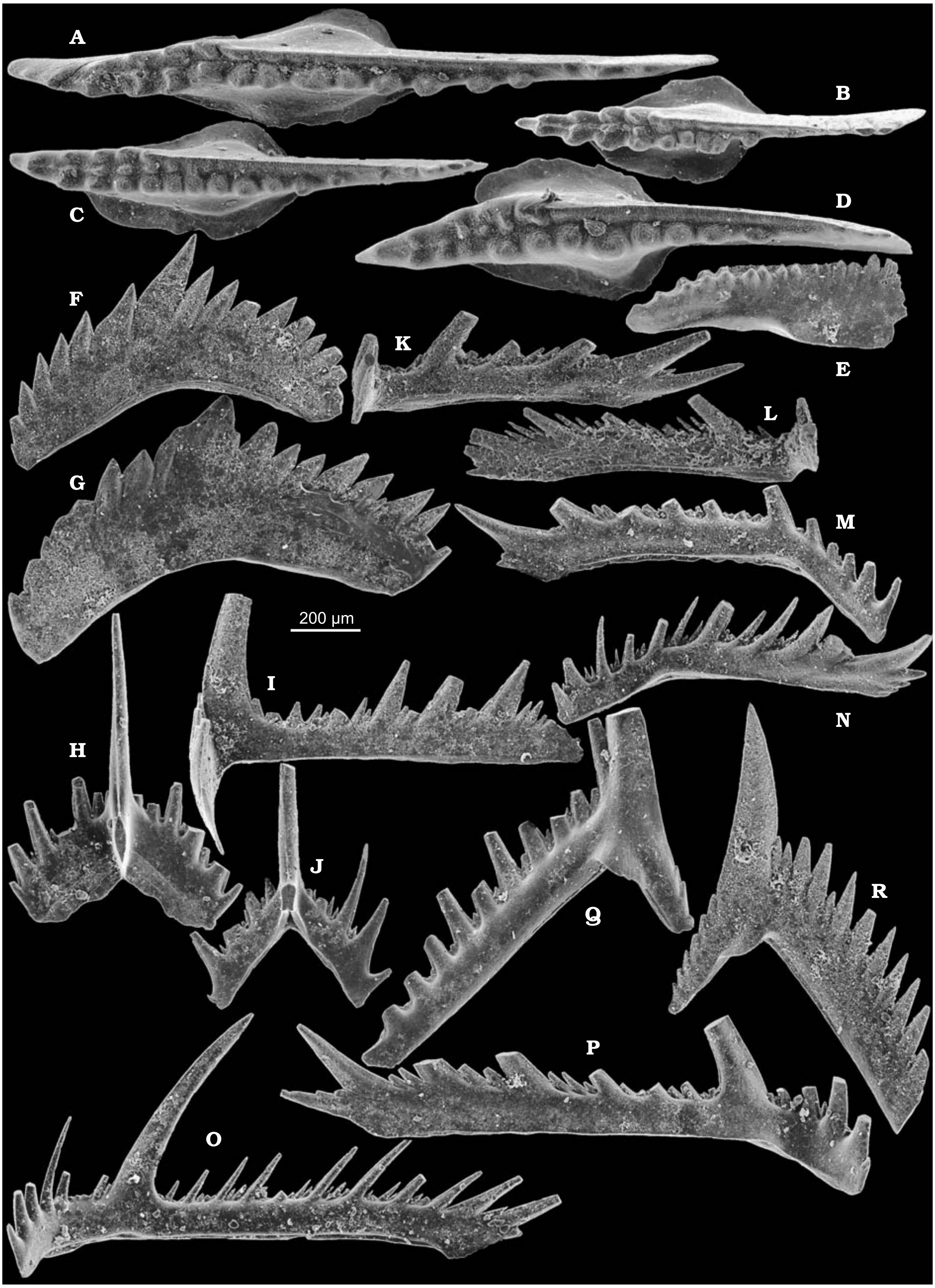

Fig. 112. Advanced probable cavusgnathid *Pseudopolygnathus jugosus* (Branson *et* Mehl, 1934) from its nominal Zone at Jabłonna (sample J-51) in the Holy Cross Mountains. P_1 (A–E), P_2 (F, G), S_0 (H–J), S_1 (K, L), S_2 (M, N), S_{3-4} (O, P), and M (Q, R) elements; specimens ZPAL cXVI/2225, 2226, 2286–2288, 2227, 2289, 2290, 2228, 2229, 2230, 2291, 2231, 2292, 2232, 2293, 2233, and 2294, respectively.

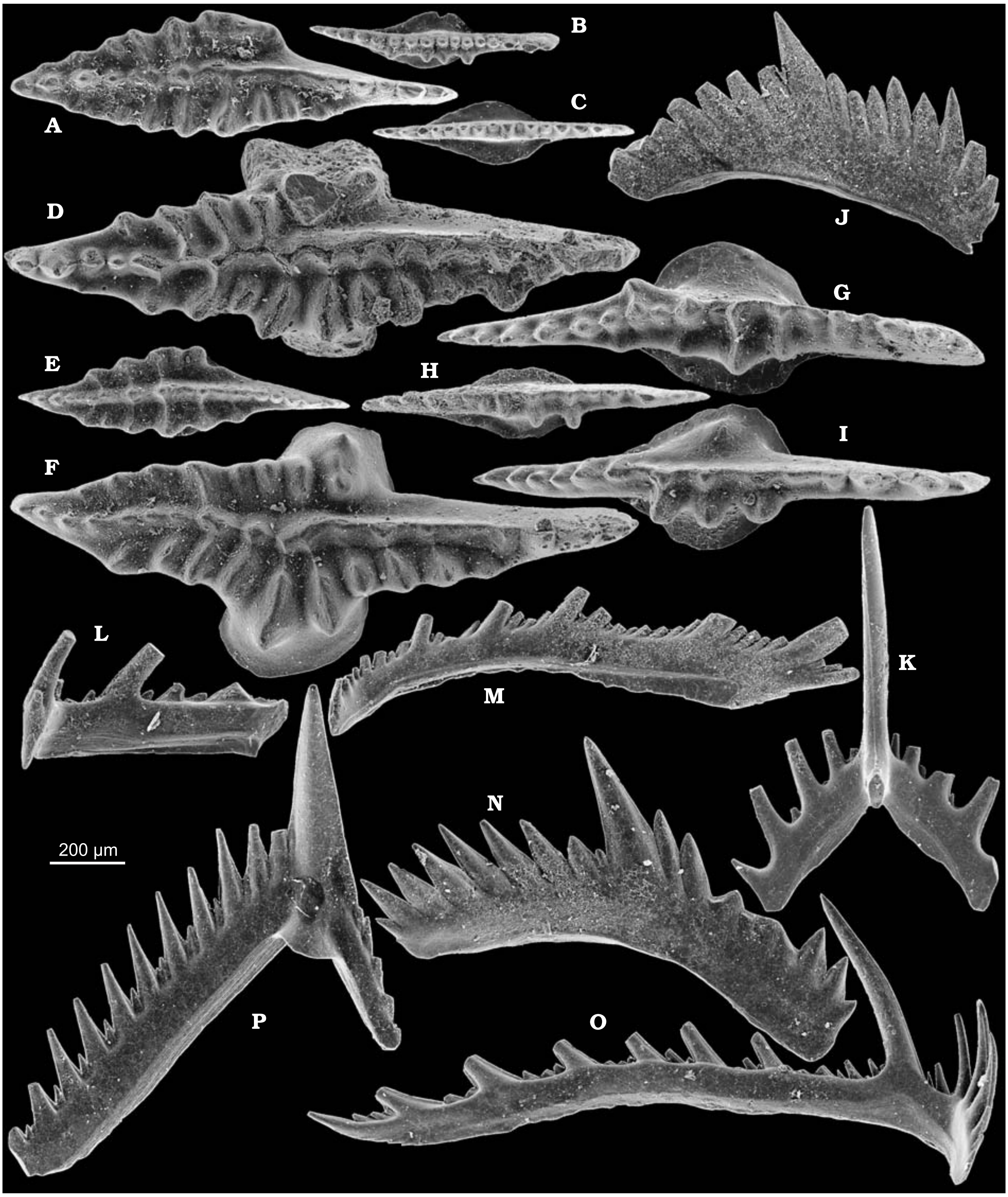

Fig. 113. Probable cavusgnathid *Pseudopolygnathus ostrovkensis* sp. n. from the *P. jugosus* Zone at Ostrówka (sample Ost-185) in the Holy Cross Mountains. P_1 (A–I), P_2 (J, N), S_0 (K), S_1 (L), S_2 (M), $S_{3–4}$ (O), and M (P) elements; specimens ZPAL cXVI/2213, 2214, 2303, 2297, 2301, 2298 (holotype, F), 2299, 2302, 2300, 2215, 2305–2307, 2304, 2308, and 2309, respectively.

Tournaisian *Pseudopolygnathus vogesi* by Dreesen *et al*. (1976, pl. 4: 1–5) from the Famennian of Belgium are conspecific. There is a possibility that this is the beginning of the *P. primus* lineage, as suggested by findings of populations morphologically close and transitional in time (e.g., Bouckaert and Groessens 1976; Sanz-López *et al*. 1999). However, an independent origin of the Carboniferous *Pseudopolygnathus* from a less elaborate latest Famennian *Pseudopolygnathus* seems more likely because of the substantial gap in continuity in the late Famennian and much wider population variability of *P. primus* (covering also morphologies typical for the late Famennian) than is observed in *P. ostrovkensis* sp. n.

Occurrence. — The latest *L. styriacus* to *D. trigonica* zones at Jabłonna, Ostrówka, Kowala, and Dzikowiec.

Pseudopolygnathus aculeatus (Branson *et* Mehl, 1934)
(Figs 114A–D and 137)

Type horizon and locality: Probably the Saverton Shale near Monroe City, Missouri (Ziegler 1975, p. 17).

Material. — 1,014 specimens.

Diagnosis. — Denticles developed only on one side of the sharp ridge formed by the blade; left and right elements only slightly differ in their axial symmetry.

Remarks. — This is probably a successor of *P. jugosus*, but it apparently originated as a result of allopatric speciation and their ranges partially overlap in Polish sections. They probably were adapted to different environment, but the nature of these differences remain to be clarified.

Occurrence. — Late *P. jugosus* to the end of the Famennian in all studied localities.

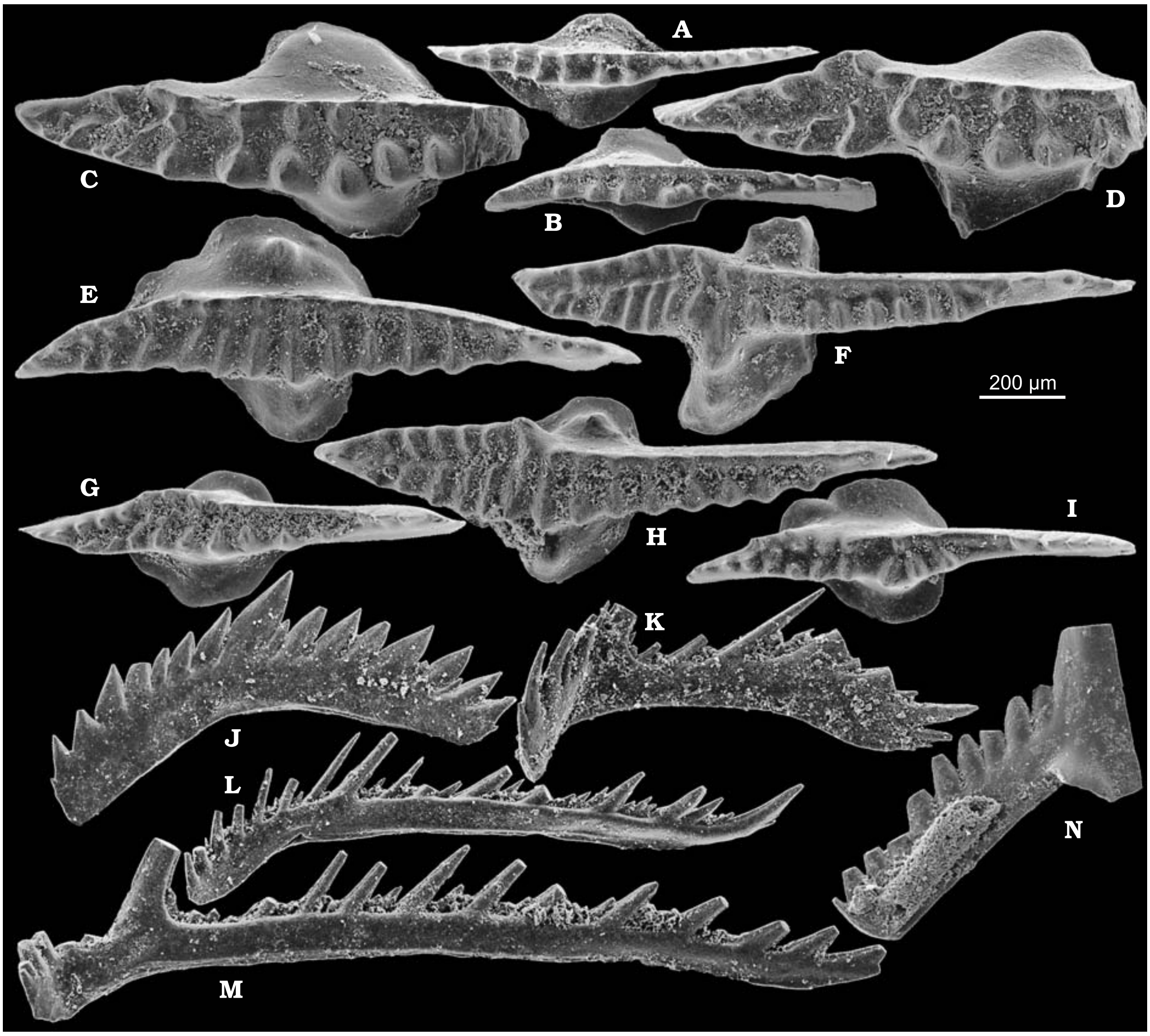

Fig. 114. Probable cavusgnathids *Pseudopolygnathus* in the Holy Cross Mountains. **A**–**D**. *P. aculeatus* (Branson *et* Mehl, 1934) from the *P. jugosus* (A, B, sample Ko-54) and *D. trigonica* (C, D, sample Ko-110) zones at Kowala. P_1 elements; specimens ZPAL cXVI/2332, 2333, 2321, and 2320, respectively. **E**–**N**. *P. ziegleri* (Rhodes, Austin *et* Druce, 1969) from the *D. trigonica* Zone at Ostrówka (sample Ost-3). P_1 (E–I), P_2 (J), S_0 (K), S_2 (L), S_{3-4} (M), and M (N) elements; specimens ZPAL cXVI/2322, 2324, 2325, 2323, and 2326–2331, respectively.

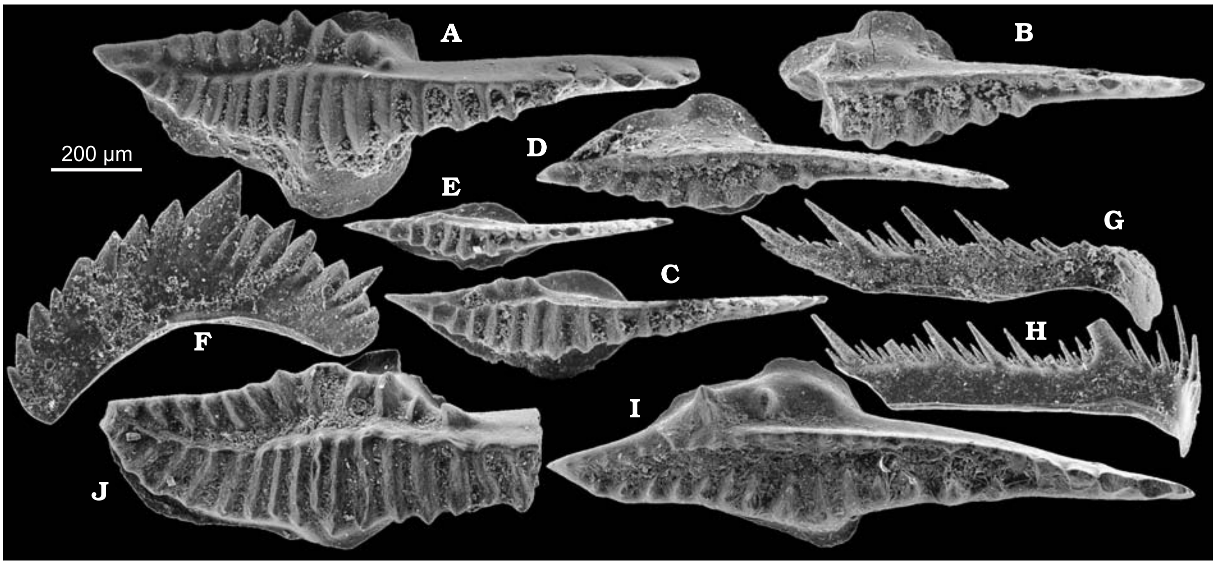

Fig. 115. Probable cavusgnathid *Pseudopolygnathus ultimus* (Bischoff, 1957) from the *P. jugosus* Zone at Dzikowiec (A–H, sample Dz-17) in the Sudetes and the *D. trigonica* (I, J, sample Ko-110) Zone at Kowala in the Holy Cross Mountains. P_1 (A–E, I, J), P_2 (F), S_2 (G), and $S_{3–4}$ (H) elements; specimens ZPAL cXVI/2310–2319, respectively.

Pseudopolygnathus ziegleri (Rhodes, Austin *et* Druce, 1969)
(Figs 114E–N and 137)

Type horizon and locality: Upper costatus Zone in the Hönnetal road cut near Balve, Rhenish Slate Mountains (Ziegler 1975).

Material. — 112 specimens.

Diagnosis. — Icrion in the dorsal part of P_1 elements composed of three rows of denticles; the medial higher than the lateral ones that tend to develop transverse ridges.

Remarks. — Left and right elements show different morphology of the icrion, as already shown by Ziegler and Sandberg (1984) classifying the latter under the name of *Bispathodus ultimus*. In Kowala *P. ziegleri* was replaced by *P. ultimus* between deposition of strata represented by samples Ko-114 and Ko-113, thus after emergence of *D. trigonica*, whereas at Dzikowiec *P. ultimus* appears before *D. trigonica*. Probably this change was controlled ecologically and not directly related to evolution, as suggested by the re-appearance of *P. ziegleri* before the end of the Famennian at Kowala.

Occurrence. — The late *P. jugosus* Zone at Kowala, Ostrówka, and Dzikowiec.

Pseudopolygnathus ultimus (Bischoff, 1957)
(Figs 115 and 137)

Type horizon and locality: The type locality of the *Wocklumeria* beds at Wocklum, Rhenish Slate Mountains (Bischoff 1957; Ziegler 1975).

Material. — 1,333 specimens.

Diagnosis. — The lateral rows of denticles in the dorsal part of the icrion of P_1 elements transformed into wide transverse ridges separated in the middle by a longitudinal escarpment, sometimes forming also a low crest.

Remarks. — Left and right elements differ in width of icrion and prominence of its ribbing. The species seems to be a direct successor of *P. ziegleri* but the transition was probably long-lasting and population variability wide. It is thus hardly of much correlative value in stratigraphy.

Occurrence. — The latest *P. jugosus* and *D. trigonica* zones at Kowala and Dzikowiec.

Family **Elictognathidae** Austin *et* Rhodes, 1981

Diagnosis. — Secondarily lost axial symmetry in P_1 elements.

Remarks. — Classification of *Siphonodella* in this family was proposed by Sweet (1988) based on the assumption that its apparatus P_2 location was occupied by elements earlier classified as *Elictognathus*. This was followed by myself (Dzik 1994), although only one of the *Siphonodella*-like Tournaisian conodonts may possibly fit such an apparatus concept. P_2 elements of *Elictognathus* morphology co-occur with ramiform elements classified in *Dinodus*, the generic name having priority. The Devonian elements with a morphology resembling *Dinodus* can hardly belong to an apparatus related to the *Siphonodella* lineage and probably are rather of prioniodinid affinities (*Guizhoudella*). The derived morphology of apparatus elements of *Siphonodella* probably did not originate before the Tournaisian. Possibly, the earliest elictognathids were quite different and their roots are to be looked for in *Immognathus*. All this introduces much uncertainty to classification of those conodonts and requires clarification.

Genus ***Pinacognathus*** Branson *et* Mehl, 1934

Type species: *Pinacodus profundus* Branson *et* Mehl, 1934 from the Bushberg Sandstone of Missouri.

Diagnosis. — P_1 elements with lanceolate, flat or inverted basal cavity separated by an escarpment from the rest of the platform base; ramiform elements with relatively short processes.

Pinacognathus? *praesulcatus* (Sandberg, 1972)
(Figs 110M, N and 129)

Type horizon and locality: Top of the Sappington Member of Three Forks Formation at Lick Creek Road, Little Belt Mountains, Montana.

Material. — 17 specimens.

Remarks. — Material at my disposal is rather poor and only sample Ko-116 contains enough specimens of various ontogenetic age to see their variability. It appears that juveniles have a platform usually separated from the blade by a deep depression and the element has the greatest width at the dorsal end of the platform. In mature specimens the middle part of the platform is the widest and it is almost flat with the denticles of the blade somewhat elevated. Elements show mirror symmetry that makes unlikely any relationship to *Alternognathus*. Also the flat or somewhat inverted basal cavity makes it different from *Alternognathus*, where the base remains slightly concave and the margin of the basal cone remains sharp. Variability is expressed mostly in more or less robust transverse ribbing of the platform and in the dorsal margin of the platform, in juveniles being thin and wide or rather narrow and robustly tuberculated. The apparatus remains unknown.

Occurrence. — The *D. trigonica* Zone at Kowala and Dzikowiec.

Family **Idiognathodontidae** Harris *et* Hollingsworth, 1933

Diagnosis. — Generalized late Palaeozoic conodonts with wide basal cavity in P_1 elements and tendency to develop a platform at the basal cone or icrion in the dorsal part of the element; in post-Devonian forms the external process of S_{3-4} elements is arched and recurved.

Genus ***Protognathodus*** Ziegler, 1969

Type species: *Gnathodus kockeli* Bischoff, 1957 from the *Gattendorfia* Stufe in the Rhenish Slate Mountains.

Diagnosis. — Widely gaping and rather deep basal cavity reaching the dorsal tip of P_1 element, gently arched profile of the blade.

Protognathodus kockeli (Bischoff, 1957)
(Figs 116M, N and 138)

Type horizon and locality: Lower part of the *Gattendorfia* Limestone at Wocklum in the Rhenish Slate Mountains.

Material. — 42 specimens.

Remarks. — Specimens from the topmost Famennian strata at Kowala are difficult to clean from clayish cover and thus are not suitable for SEM photography. They show tuberculation of the basal cone typical of the early Tournaisian populations of *Protognathodus* (e.g., Dzik 1997).

Occurrence. — Terminal Famennian at Kowala (samples Ko-51 and Ko-24; Dzik 1997) and Dzikowiec (Dz-75).

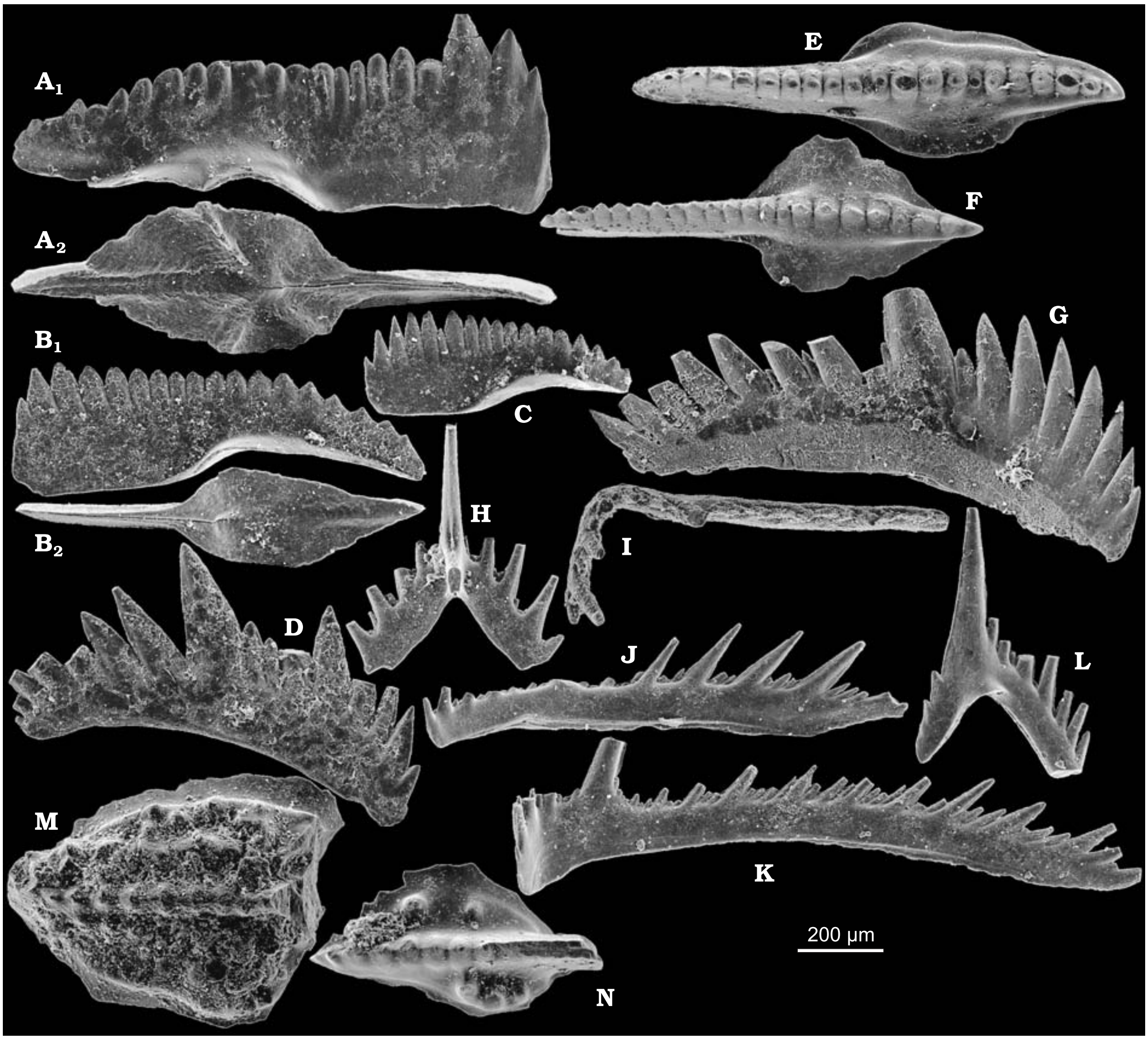

Fig. 116. Early idiognathodontids. **A–L**. *Dasbergina stabilis* (Branson *et* Mehl, 1934) from the *P. jugosus* Zone at Jabłonna (A–D, bed 27) and Ostrówka (E–L, sample Ost-185) in the Holy Cross Mountains. P_1 (A–C, E, F), P_2 (D, G), S_0 (H), S_1 (I), S_2 (J), S_{3-4} (K), and M (L) elements; specimens ZPAL cXVI/2206–2209 and 2261–2268, respectively. **M**, **N**. *Protognathodus kockeli* (Bischoff, 1957) from Dzikowiec (sample Dz-75). P_1 elements, specimens ZPAL cXVI/2965 and 2964.

Genus ***Dasbergina*** Schäfer, 1976

Type species: *Dasbergina ziegleri* Schäfer, 1976 from the bed 93 of a trench at Dasberg, lower costatus Zone.

Diagnosis. — Very shallow conical basal cavity, variously developed platform around the basal cone, apparatus of generalized morphology.

Remark. — Early species of the genus, with weakly developed platform, are transitional to the probably ancestral species of *Pandorinellina*, *P. vulgaris*. The difference between transitional populations is only in the width of the basal cone, in fact, very variable.

Dasbergina stabilis (Branson *et* Mehl, 1934)
(Figs 116 and 138)

Type horizon and locality: Probably the Saverton Shale near Monroe City, Missouri (Ziegler 1975, p. 47).

Material. — 4,491 specimens.

Diagnosis. — P_1 element lacking platform, almost flat cavity of the basal cone with eye-drop outline, continuing to the dorsal tip of the blade.

Remarks. — The apparatus of the species was restored by Over (1992). The basal cavity varies from being virtually flat to distinctly conical. Specimens with very flat base differ from those of *Pandorinellina vulgaris* in their much lower blade and a tendency to develop an incipient platform of low elevation continuing to the tip of the element. From associated juvenile specimens of *Dasbergina micropunctata* such elements differ in having their base (and "platform") gradually narrowing to the tip while in *D. micropuntata* the base has a pear-like outline and terminates significantly in front of the element tip.

The oldest specimens of *D. stabilis* in the densely sampled part of the Kowala section have been found in sample Ko-187. Unfortunately specimens classified in *P. vulgaris* from the sample immediately below are fragmentary, hampering biometrical presentation of the change.

Occurrence. — The *P. trachytera* to *D. trigonica* zones at Jabłonna, Ostrówka, Kowala, and Miedzianka, the Holy Cross Mountains, and Dzikowiec, the Sudetes.

Dasbergina micropunctata (Bischoff *et* Ziegler, 1956)
(Figs 117 and 138)

Type horizon and locality: Dark limestone of toV from the "Rote Scheid" quarry near Marburg (Bischoff and Ziegler 1956).

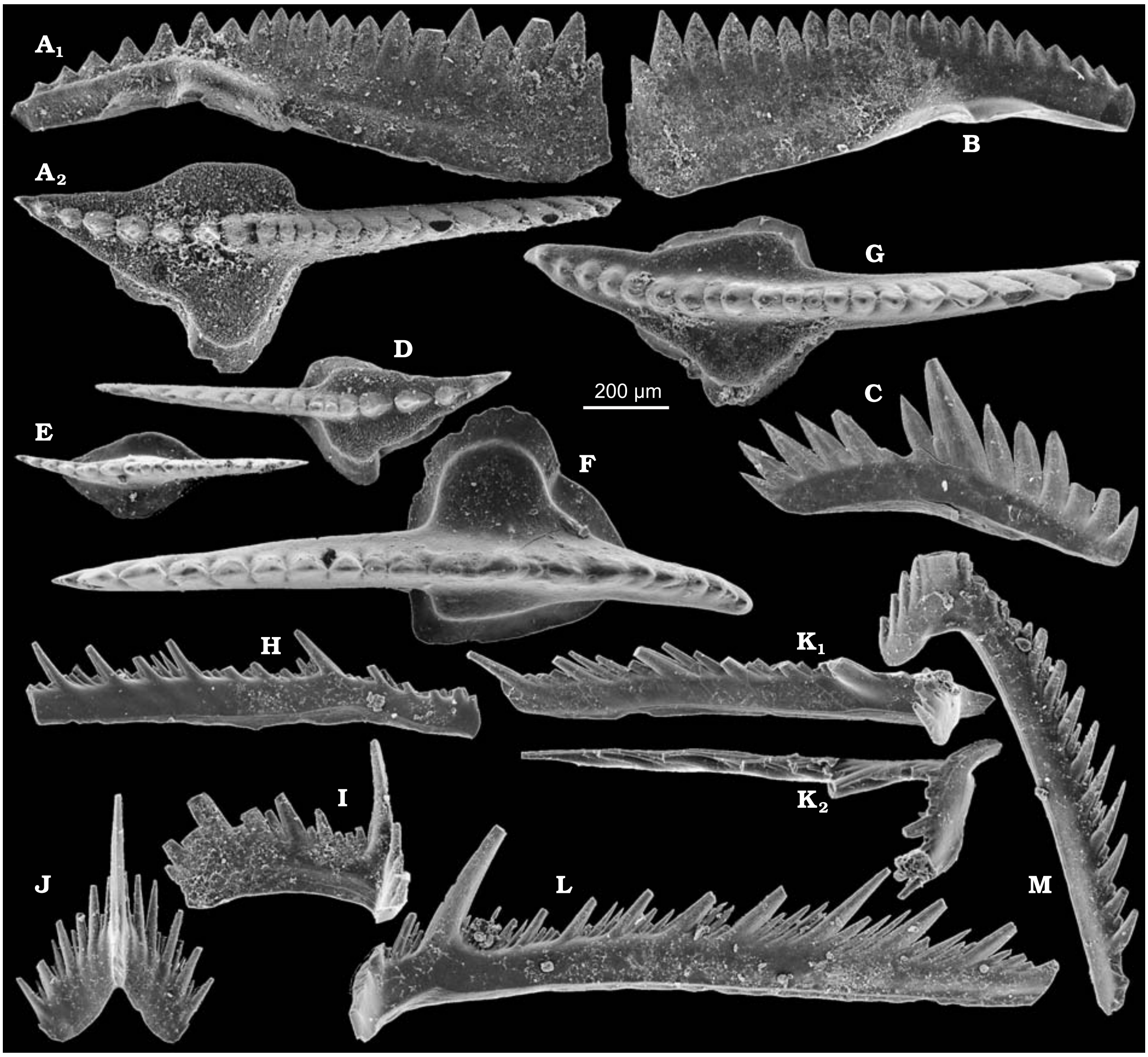

Fig. 117. Idiognathodontid *Dasbergina micropunctata* (Bischoff *et* Ziegler, 1956) from the *P. jugosus* Zone at Jabłonna (A–C, sample J-52) and Ściegnia (D–L ,sample Wzd-13) in the Holy Cross Mountains. P$_1$ (A–F), P$_2$ (G), S$_0$ (I, J), S$_1$ (K), S$_2$ (H), S$_{3–4}$ (L), and M (M) elements; specimens ZPAL cXVI/2235, 2197, 2196, 2234, 2251, 2250, 2252, 2254, 2256, 2255, 2253, and 2257, 2258, respectively.

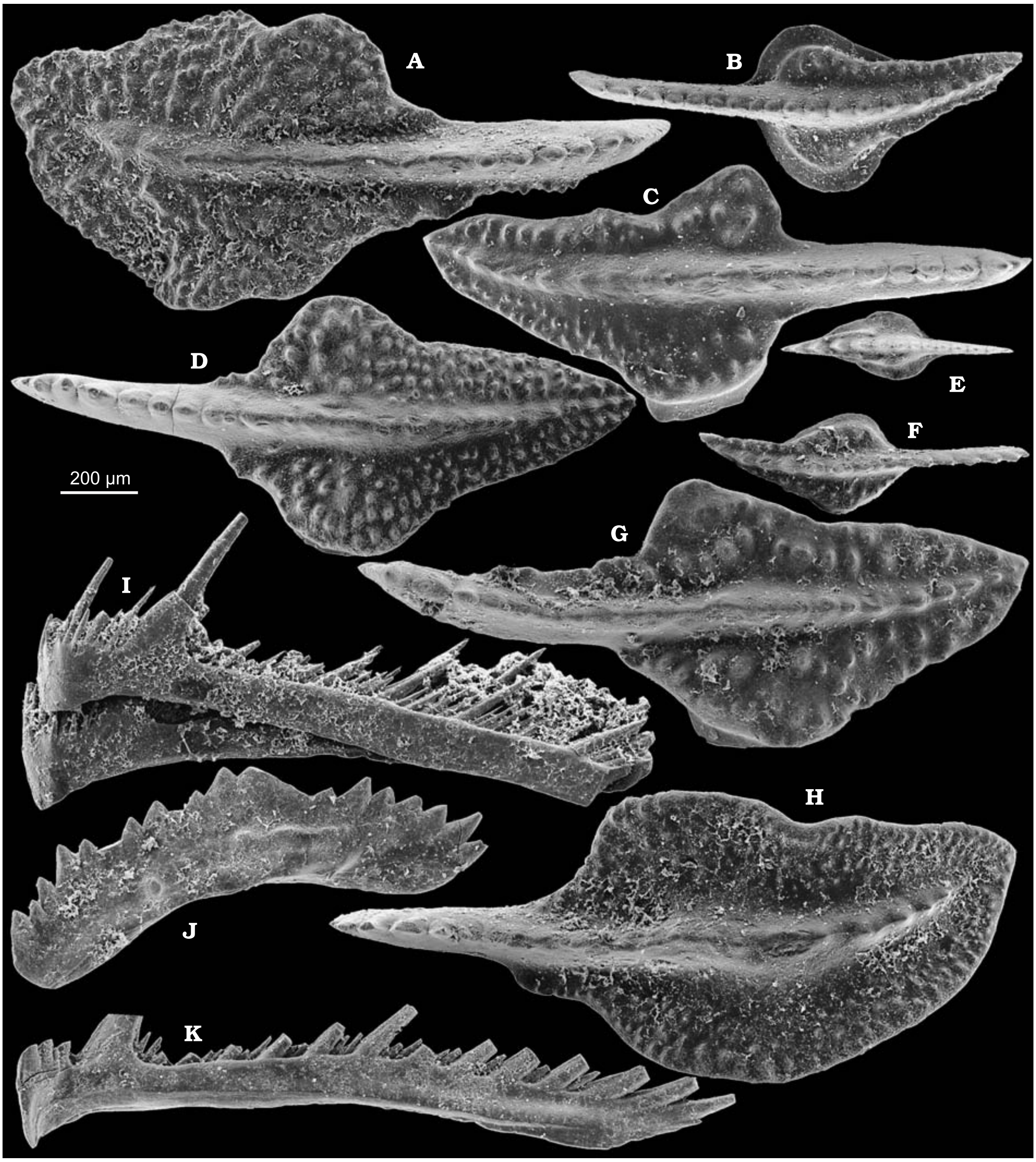

Fig. 118. Idiognathodontid *Dasbergina granulosa* (Ziegler, 1962) from the *L. styriacus* Zone at Ostrówka (A–C, I–K, sample 1a; D–H, sample Ost-12) in the Holy Cross Mountains. P_1 (A–H), P_2 (J), and S_{3-4} (I, cluster of two elements, K) elements; specimens ZPAL cXVI/2271, 2270, 2269, 2275, 2278, 2276, 2277, 2274, 2345, 2272, and 2273, respectively.

Material. — 1,733 specimens.

Diagnosis. — The basal cone of P_1 element with a smooth triangular platform, basal cavity narrows in front of the dorsal tip of the blade.

Remarks. — Some P_1 elements have platform with a completely smooth surface, others show the reticulate pattern of ameloblast imprints. The meaning of this difference is unclear. Triramous S_1 elements may belong to this species.

Occurrence. — The *L. styriacus* to *D. trigonica* zones at Jabłonna, Ostrówka, Kowala, Miedzianka, the Holy Cross Mountains, and Dzikowiec, the Sudetes.

Dasbergina granulosa (Ziegler, 1962)
(Figs 118 and 138)

Type horizon and locality: Bed 0 in the Sessacker II trench, *P. trachytera* Zone.

Material. — 1,732 specimens.

Diagnosis. — The platform of irregularly angular shape ornamented with numerous tubercles, basal cavity forms lobes on both sides of the P_1 element.

Remarks. — This is one of the most robust and largest Famennian conodonts. Mature P_1 elements bear a very wide platform but the conical basal cavity grows to maturity. Some specimens from Kowala and Dzikowiec, with very variable ornamentation and the platform extending far outside the basal cone, but restricted to the center of the element, may be transitional to *Dasbergina* sp. aff. *D. kayseri*.

Occurrence. — The *P. trachytera* to *P. jugosus* zones at Jabłonna, Ostrówka, Kowala, Miedzianka, the Holy Cross Mountains, and Dzikowiec, the Sudetes.

Dasbergina kowalensis sp. n.
(Figs 119A–C and 138)

Holotype: Specimen ZPAL cXVI/2256 (Fig. 119B).

Type horizon and locality: Sample Ko-1, late Famennian early *P. jugosus* Zone at Kowala, Holy Cross Mountains.

Derivation of name: From the latinized name of the type locality.

Material. — 27 specimens.

Diagnosis. — Incipient platform of irregularly angular shape ornamented with a few large tubercles, basal cavity forms wide lobes on both sides of the P_1 element.

Remarks. — This seems to be the oldest member of the *D. trigonica* lineage, perhaps a successor of *D. stabilis*, although the transition has not been demonstrated. The basal cone ornamented with tubercles makes the species similar to *Protognathodus*. This is probably only a convergence; the difference is that the basal cavity is expanded only in proximity to the cusp and strongly narrows dorsally.

Occurrence. — The early *P. jugosus* Zone at Kowala.

Dasbergina marburgensis (Bischoff *et* Ziegler, 1956)
(Figs 119D–I and 138)

Type horizon and locality: Dark limestone of toV unit from the quarry NE Weitershausen in the Rhenish Slate Mountains.

Material. — 190 specimens.

Diagnosis. — Triangular platform of P_1 element ornamented with robust marginal denticles, tending to form irregular transverse rows near the element center; transversely elongated lobes of basal cavity with parallel margins.

Remarks. — Perhaps the most characteristic feature of the species is the basal cavity of the P_1 element. Its narrowly elongated anterior lobe has a rounded tip, whereas the posterior lobe varies from narrowly rounded to angular, with the ventral angle more prominent.

Occurrence. — The late *P. jugosus* Zone at Ostrówka, Kowala, and Dzikowiec.

Dasbergina trigonica (Ziegler, 1962)
(Figs 119J–N and 138)

Type horizon and locality: Sample 3a from the Hönnetalstraße section in the Rhenish Slate Mountains.

Material. — 204 specimens.

Diagnosis. — The basal cavity of P_1 element bifurcates anteriorly.

Remarks. — In successive samples in the upper part of the Dzikowiec section the anterior lobe of the basal cavity of the P_1 element, originally round (Dz-18), gradually becames more angular (Dz-10, Dz-17, Dz-20b) and then its tip narrows and the lobe bifurcates (Dz-19, Dz-47, Dz-4). This marks the transition from *D. marburgensis* to *D. trigonica*. This character shows a significant population variability and juveniles may show angular wide lobes even in samples from high above in the section (e.g., Dz-8).

The species occurs in the borehole Kowala, as shown by Nehring-Lefeld (1990).

Occurrence. — Zone of its own at Kowala and Dzikowiec.

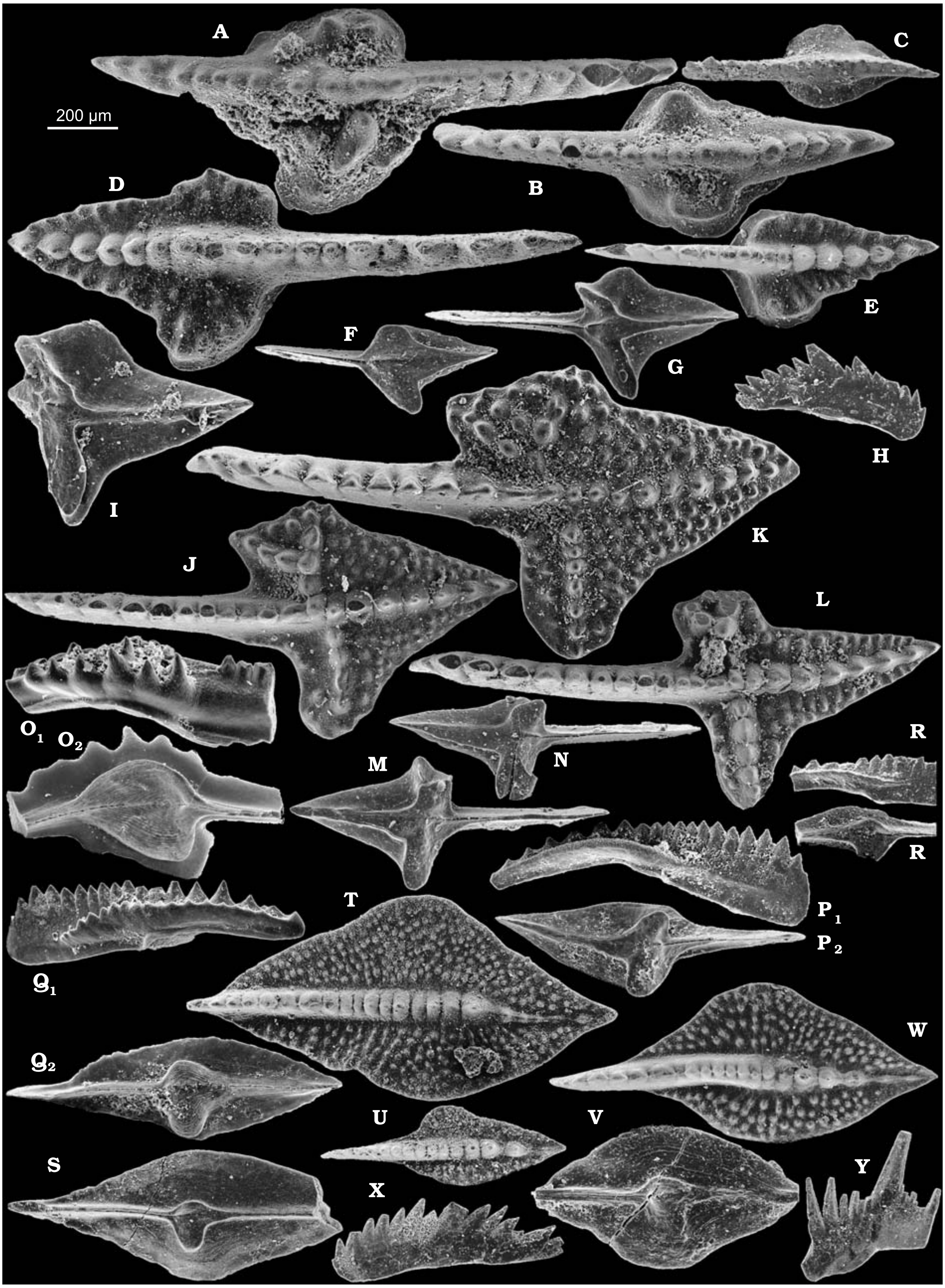

Fig. 119. Idiognathodontids of the *Dasbergina trigonica* and *D. kayseri* lineages. **A**–**C**. *D. kowalensis* sp. n. from the early *P. jugosus* Zone at Kowala (sample Ko-1). P_1 elements; specimens ZPAL cXVI/2245–2247 (holotype, B). **D**–**I**. *Dasbergina marburgensis* (Bischoff and Ziegler, 1956) from the late *P. jugosus* Zone at Ostrówka (D, E, sample Ost-185) and Dzikowiec (F–I, sample Dz-10; late form). P_1 (D–G, I) and P_2 (H) elements; specimens ZPAL cXVI/2280, 2279, 2977–2980, and 2979, →

Dasbergina sp. aff. *D. kayseri* (Bischoff *et* Ziegler, 1956)
(Fig. 119O, P)

Remarks. — At Kowala below the occurrence of *Dasbergina kayseri* an unnamed species occurs with a wide asymmetric basal cavity resembling that of adult *Dasbergina granulosa* and with a higly variable tuberculation of the platform that may be almost smooth in juveniles (e.g., Perri and Spalletta 1991, pl. 9: 5). It even seems that in successive samples the basal cone became smaller and more asymmetric, although too few specimens are known to be sure that this is not a case of very wide population variability. A possibility thus emerges that the latest Famennian *D. keyseri* lineage is an outshoot of *Dasbergina*, homeomorphic with the early Famennian ancyrognathids.

Dasbergina kayseri (Bischoff *et* Ziegler, 1956)
(Figs 119Q–Y and 132)

Type horizon and locality: Dark limestone of toV from the quarry NE Weitershausen near Marburg (Bischoff and Ziegler 1956).

Material. — 80 specimens.

Diagnosis. — Relatively large, asymmetric basal cone (pit); rhomboidal outline of platform in P_1 element reaching almost the ventral end of the blade in mature specimens.

Remarks. — One specimen from Kowala (Fig. 119Q) shows a large basal cavity, transitional in size and shape between that in the preceding species and typical *D. kayseri*. Rare ramiform elements associated with P_1 elements typical of the species are too generalized to prove its generic affiliation, but their morphology does not contradict affinities with advanced *Dasbergina*.

Occurrence. — The *P. jugosus* Zone at Ostrówka and Kowala.

Dasbergina brevipennata (Ziegler, 1962)
(Figs 120A–U and 138)

Type horizon and locality: Sample 1327 from the road section at Hönnetal, late *L. styriacus* Zone.

Material. — 782 specimens.

Diagnosis. — Platform of P_1 element with regularly angular outline and flat surface ornamented with numerous tubercles.

Remarks. — Juvenile P_1 elements of the species show a more lanceolate outline of the platform than preceding species and in this respect they are rather similar to juveniles of *D. ziegleri*.

Occurrence. — The *L. styriacus* Zone at Jabłonna, Kowala, and Ściegnia.

Dasbergina ziegleri Schäfer, 1976
(Figs 120V–Y and 138)

Type horizon and locality: Bed 93 in a trench at Dasberg, lower costatus Zone

Material. — 310 specimens.

Diagnosis. — Wide robust platform extending almost to the whole length of P_1 element, ornamented with robust tubercles and ridges.

Remarks. — *Pseudopolygnathus controversus* Sandberg *et* Ziegler, 1979 is probably conspecific with this species. Notably, the early population of *D. ziegleri* from the *L. styriacus* Zone (Fig. 120V, W), with a rather angular outline of the platform and its fine tuberculation, resembles *D. brevipinnata*. The late population from the *P. jugosus* Zone (Fig. 120X, Y) is similar in those respects rather to *Pseudopolygnathus*

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respectively. **J**–**N**. *Dasbergina trigonica* (Ziegler, 1962) from its nominal zone at Ostrówka (J, K, sample Ost-3) in the Holy Cross Mountains and Dzikowiec (L, sample Dz-7; M, N, sample Dz-74) in the Sudetes. P_1 elements; specimens ZPAL cXVI/2281–2283, 2966, and 2967. **O**, **P**. *Dasbergina* sp. aff. *kayseri* (Bischoff *et* Ziegler, 1956) from the *P. jugosus* Zone at Kowala (sample Ko-192), possible transitional forms from underived *Dasbergina* with wide basal cone to *D. kayseri*. P_1 elements; specimens ZPAL cXVI/2996 and 2997. **Q**. *Dasbergina kayseri* (Bischoff *et* Ziegler, 1956) early form with wide basal cavity from the *P. jugosus* Zone at Kowala (sample Ko-197). P_1 element; specimen ZPAL cXVI/2995. **R**–**Y**. Typical *Dasbergina kayseri* (Bischoff *et* Ziegler, 1956) from *P. jugosus* Zone at Ostrówka (H, K, sample Ost-2; I, J, L, M, sample Ost-185) and Kowala (N, O, sample Ko-198) in the Holy Cross Mountains. P_1 (R–W), P_2 (X), and $S_{3–4}$ (Y) elements; specimens ZPAL cXVI/2998, 2603, 2598, 2599, 2999, and 2600–2602 respectively.

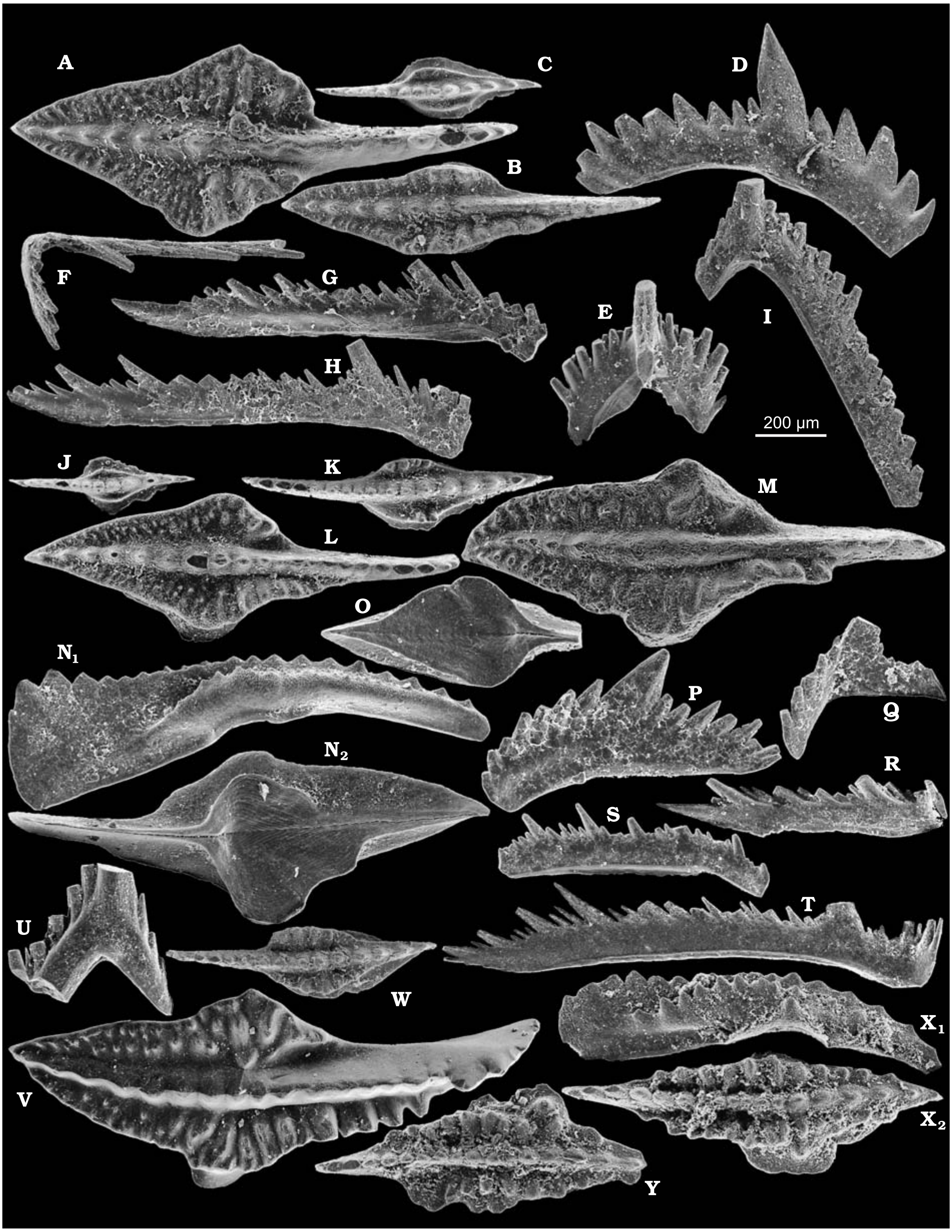


Fig. 120. Idiognathodontids of the *Dasbergina ziegleri* branch from the Holy Cross Mountains. **A**–**U**. *Dasbergina brevipennata* (Ziegler, 1962) from the early *P. jugosus* Zone at Jabłonna (A–I, bed 27) and the late *L. styriacus* Zone at Kowala (J–U, sample Ko-191). P_1 (A–C, J–O), P_2 (D, P), S_0 (E, Q), S_1 (F, R), S_2 (G, S), S_{3-4} (H, T), and M (I, U) elements; specimens ZPAL cXVI/2216–2224, 3000–3011, respectively. **V**–**Y**. *Dasbergina ziegleri* Schäfer, 1976 from the *L. styriacus* Zone at Ostrówka (V, W, sample Ost-7) and the early *P. jugosus* Zone at Kowala (X, Y, sample Ko-1). P_1 elements; specimens ZPAL cXVI/2284, 2285, 2248, 2249.

ostrovkensis. It seems thus that this is an outshoot of the *Dasbergina* lineage homeomorphic with *Pseudopolygnathus* (in fact, both are closely related).

Occurrence. — The *P. jugosus* Zone at Kowala and Ostrówka.

FAUNAL DYNAMICS OF THE FAMENNIAN CONODONTS IN POLAND

While reviewing distribution of particular groups of fossil organisms one has to face the conflict between ecology and phylogeny. Obviously, the supraspecific taxonomic units are by definition based on evolutionary (that is, genetic) relationships among species, which do not need to be related to their environmental preferences. However, many Famennian conodont taxa seem to preserve some ecological coherencey and the review in the introductory chapters of this work presenting conodont ecostratigraphy in the area (Fig. 5, 6) may serve as an useful approximation. To extract the unbiased evidence on the evolution of local environments it would be necessary to address distribution of each species separately. This kind of evidence is offered by quantitative data on their frequency distribution in the part of the work showing the stratigraphic distribution of species (Figs 121–138). Some general comments on the global environmental change as seen from a Polish perspective are presented. This will be followed by a review of the Famennian evolutionary diversification of conodonts, with an attempt to be free as much as possible from its preservational and ecological bias.

SUCCESSION OF THE FAMENNIAN CONODONT FAUNAS

Conodont species with apparatuses containing platform elements represent only a fraction of the complete late Devonian conodont diversity. This is to a great degree obliterated by unbalancing of fossil samples, that is their enrichment in robust platform- or icrion-bearing elements as a result of hydrodynamic sorting and/or fragmentation of fragile ramiform elements of the apparatus. To restore the original numerical contribution of species to the biological productivity of the conodont community this bias should be removed. Let us attempt to do this by replacing counts of platform elements to a selected sample by numbers derived from counts of non-platform elements of the same species. In the standard conodont apparatus with 15 elements, the P_1 elements represent approximately 13% of all elements. To compensate for the possibly greater fragility of ramiform elements in such apparatuses in respect to those without platforms, lets assume that the number of P_1 elements actually found represents 25 % of their original number prior to taphonomic distortion. For rare species known only from platform specimens and for *Icriodus* their number in the count below has been only halved.

If reinterpreted in this way, the terminal Frasnian Kellwasserkalk sample Pł-391 represented by 17,804 specimens (see Dzik 2002) gives a not especially impressive picture of biological diversity of the community (more precisely: its biological production). Only three species significantly contributed to this: the dominant *Polygnathus webbi* (including its variety informally listed as *P.* "*tuberculatus*", do not related to true *P. tuberculatus* Hinde, 1879) with almost 35% of all elements, *Icriodus iowaensis* with about 30% (perhaps more, as the way in which this estimate was done is especially unreliable in this case), and the palmatolepidid *Lagovilepis bogartensis* with 20% contribution. Five species contributed from 1.5 to 3.9% each, so some of them had a chance to be represented in samples of standard size (species of *Ctenopolygnathus*, *Ancyrodella*, *Klapperilepis*, *Ligonodina* and *Dyminodina*). All the remaining seven species of this high-diversity community even after such compensation are represented by less then 1%. They are thus unlikely to be identified in a standard conodont sample taken for stratigraphic purposes (species of *Pelekysgnathus*, *Pluckidina*, *Mehlina*, *Ancyrognathus*, and the palmatolepidids *Manticolepis winchelli*, *M. rhenana* and "*Conditolepis*" *linguiformis*).

All this shows also how unreliable ranges of vertical distribution of taxa may be, even in situations where the fossil record is complete.

Frasnian–Famennian boundary event. — The dramatic change at the Frasnian–Famennian boundary seen from this perspective fades very much (cf. House 2002; Bambach *et al.* 2004; Racki 2005). It is still a significant decrease in diversity, but not unprecedented in the Frasnian record. The three earliest Famennian samples (Pł-20, Pł-16, and Pł-15; Dzik 2002), counted together in the same way to compensate for unbalancing, give a surprisingly similar community structure. Again, only three species dominate: *Icriodus* (different species than in the Frasnian, *I. alternatus*) with its 39% contribution, *Polygnathus* (*P. praecursor*, possibly a successor of the Frasnian *P. webbi*) contribution about 30% and the only palmatolepidid *Klapperilepis ultima* continuing from the Frasnian, of almost 20% share in the community structure. Also other lineages probably continue from the Frasnian, with two of reasonable contribution (*Ctenopolygnathus*, about 10% and *Mehlina* 4%). *Pelekysgnathus*, *Ligonodina*, *Dyminodina* and *Pluckidina* all have below a 1% contribution. It appears thus that except for the termination of *Lagovilepis bogartensis* and replacing one species of *Icriodus* by another, nothing truly unusual happened at this allegedly “one of the greatest extinction events in the World history”, in contrast to the internationally-accepted definition of the F–F mass extinction boundary (see references above). In the Holy Cross Mountains, where the stromatoporoid-coral reef communities of the Frasnian are especially well represented, their growth terminated significantly below this change in conodont communities. There is hardly any reason to believe in a sudden catastrophic event of extraterrestrial cause at the Frasnian–Famennian boundary. No doubt, however, that a profound rebuilding of marine ecosystems and long-distance migrations of pelagic communities took place that time, suggestive of a deep change in the global climate (e.g., Dzik 2002; Joachimski and Buggisch 2002; Joachimski *et al*. 2001, 2004).

Within-Famennian environmental changes. — The earliest Famennian strata in the Płucki section differ from those below in the increased contribution of black shale intercalations. It is thus instructive to compare the first Famennian conodont community with that representing a similar environment of black shale in the mid Famennian. Sample Ko-8a of 1058 specimens from the limestone concretions, collected immediately above the black “paper” shale exposed in the Kowala quarry representing the *Platyclymenia annulata* event, offers such an opportunity (Fig. 4, 6). Counted in the same way it shows an overdomination of the prioniodinid (or the earliest non-platform gondolellid) *Branmehla* (57%), two other species, the palmatolepidid *Tripodellus schleizius* and the cavusgnathid *Alternognathus regularis* contributed 12% and 10%, respectively. All other species (of genera *Icriodus*, *Mitrellataxis*, *Idioprioniodus*, *Vogelgnathus*, *Pandorinellina*, *Mehlina*, *Polynodosus*, *Hemilistrona*, and *Neopolygnathus*) are of insignificant importance in the community. Less then half of them had platform elements in their apparatuses.

Paradoxically, a much more profound rebuilding of the conodont community occurred in time slices not so well noted in connection with purported catastrophic events. The first such fundamental transformation of the conodont communities in the Holy Cross Mountains during the Famennian took place near the end of the *K. triangularis* Zone. Many new lineages immigrated at that time, but most of the preceding diversity survived the change. Obviously, this was connected with a transgressive event immediately after the sea level drop (Johnson *et al*. 1985) that in the Holy Cross region resulted in the submersion of the earlier eroded massive limestone at Kadzielnia, the sedimentary discontinuity surface at Wietrznia, and the redeposition of limestone pebbles at Miedzianka.

Less apparent and generally stepwise changes in composition of the conodont community by immigration of some and disappearance of other lineages took place within the *C. quadrantinodosa* and *C. marginifera* zones. Also these events were related to periodic lowering of sea level, as suggested by the sedimentary discontinuity within this time span in the Łagów section. The change was not connected with competition between members of different lineages but resulted rather from lateral shifts of ecosystems as a result of global environmental changes.

Several events of the sea level rise and increase in biological productivity marked by bituminous shale deposition (see Walliser 1996; House 2002) are well displayed in the Kowala section. These were identified with the *Platyclymenia annulata*, Epinette and Hangenberg events by myself (Dzik 1997). They did not cause any dramatic change in the conodont community. The changes in their relative contribution were not more significant than in the whole upper part of the section, where cyclicity of probably Milanković nature seems to be recorded (Fig. 6). There was a series of two sudden drops in diversity of conodonts near the end of the Famennian. The first one corresponds to the beginning of the *D. trigonica* Zone; from this moment the icrion-bearing *Pseudopolygnathus* dominated the assemblages. The whole pelagic faunal diversity was reduced to a catastrophic level at the time of sedimentation of the Hangenberg black shale (Dzik 1997; see also Brand *et al.* 2004).

In some aspects this situation is similar to that at the Frasnian–Famennian transition. The faunal replacement was even more significant near the end of the Famennian and the new dominant taxa (*Protognathodus kockeli* and *Acutimitoceras*) seem to mark an incursion of cold waters to the area (Dzik 1997). No doubt, however, that elsewhere several Famennian lineages survived and participated in restoring the warm-water

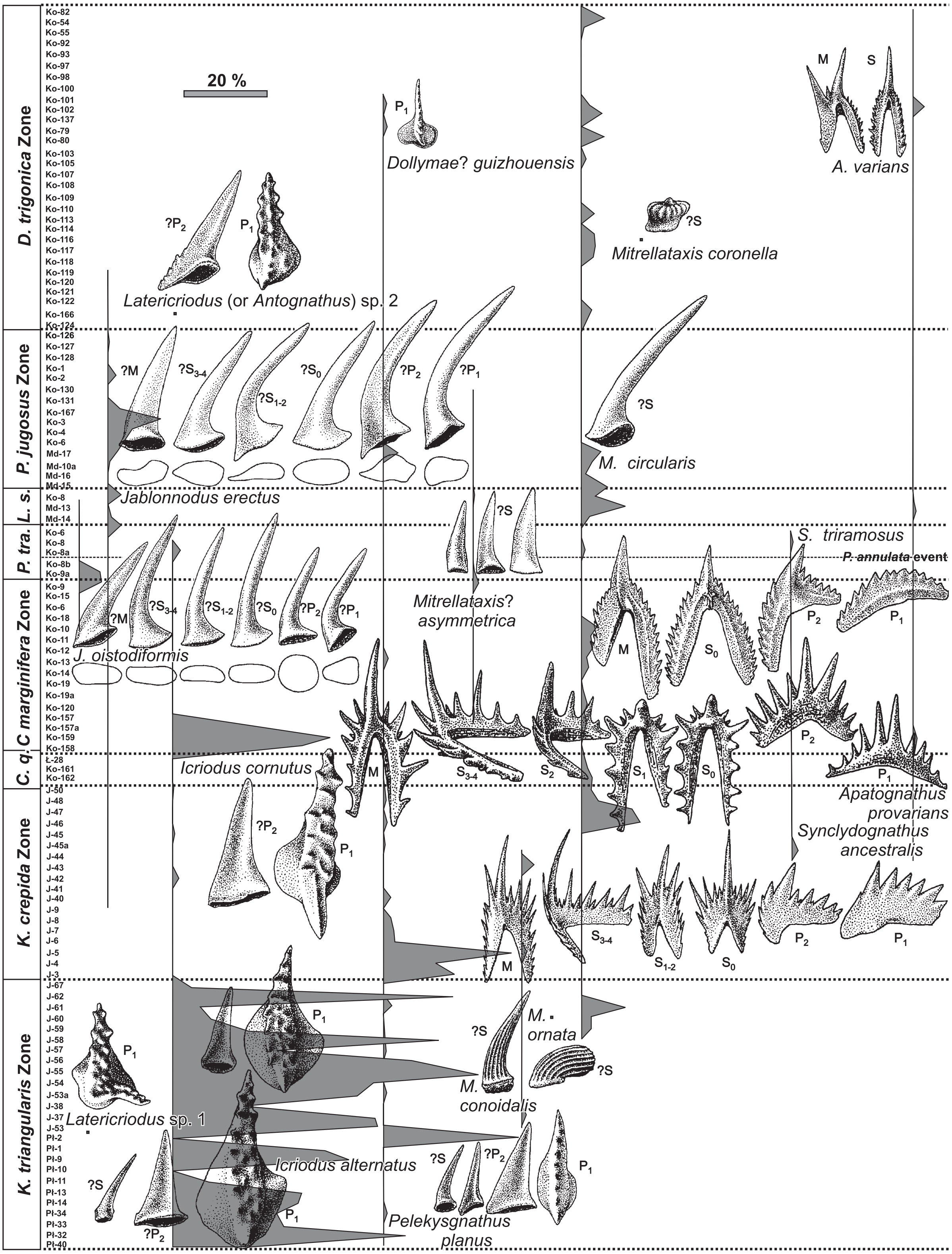


Fig. 121. Stratigraphic distribution of the possible protopanderodontid *Jablonnodus*, icriodontids, and spathognathodontids in the Polish Famennian. Percent contribution to samples in a composite succession assembled with representative sections in the Holy Cross Mountains (sample numbers given in the left column; for species not represented in these sections only vertical line denotes their distribution) and diagrammatic representation of identified apparatus elements is shown. Probable chronospecies of the same lineage are arranged in the same line; bases of lines correspond to immigration events. Note highly irregular frequency distribution of elements in particular lineages, which makes observed extent of ranges very sensitive to differences in sample size and usually not truly meaningful.

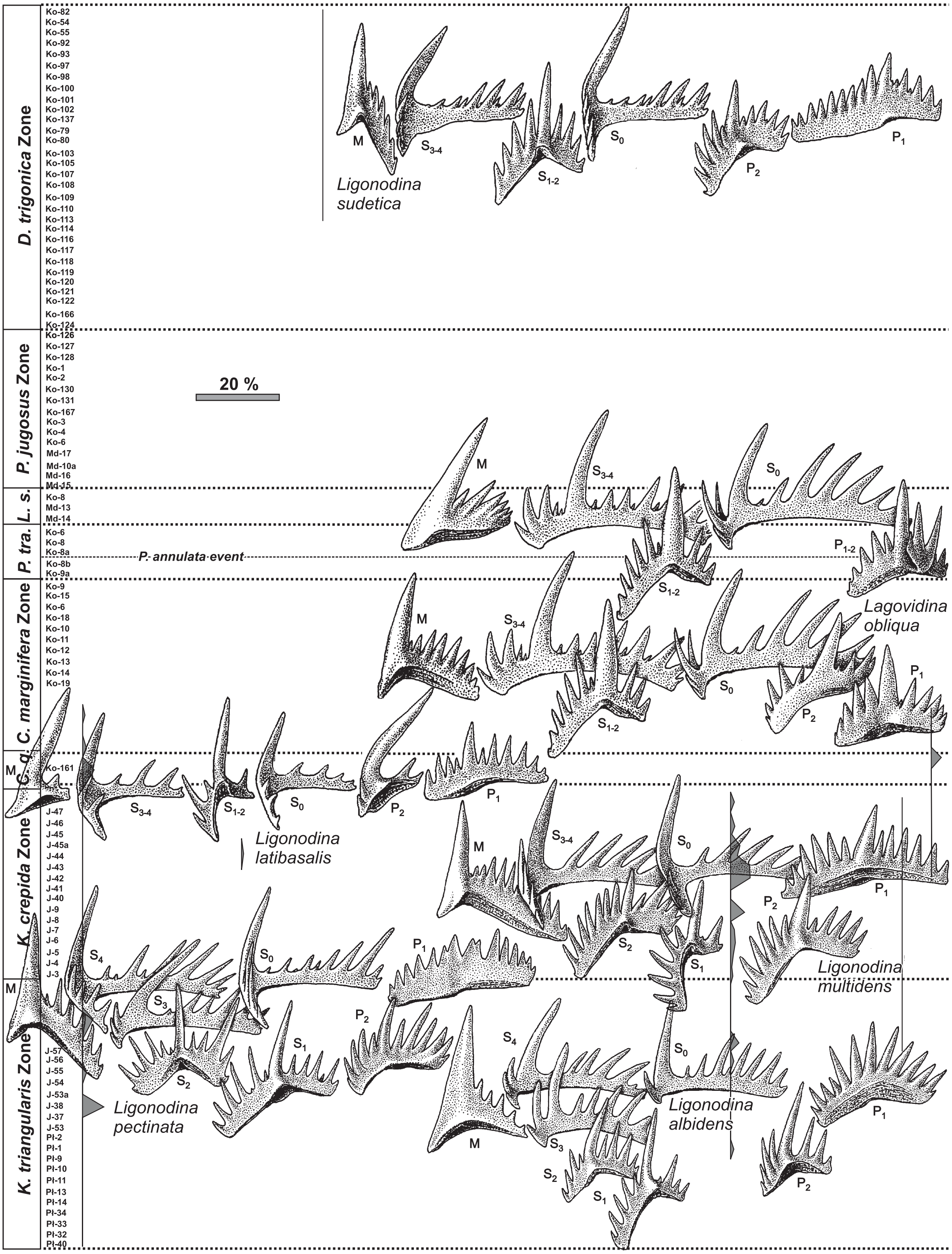


Fig. 122. Stratigraphic distribution of the prioniodinids *Ligonodina* and *Lagovidina* in the Polish Famennian (the same kind of presentation as on Fig. 121).

high-productivity communities of the *Gattendorfia* Limestone (Dzik 1997). Their exact course of evolution remains to be traced.

EVOLUTION OF THE FAMENNIAN CONODONTS

Most of the change in the faunal dynamics of conodonts in the Famennian of Poland appears thus to be caused by migrations, not unlike other examples of the fossil record in tropical environments. Only in a few cases a phyletic evolutionary change is recorded clearly enough to enable quantitative stratophenetic description. It is beyond the scope of the present work to use stratophenetics to show the evolution of the fauna. Its main goal is to present apparatus reconstructions. Their knowledge is still in so early a stage that more basic questions on their relationships haves to be clarified first. However, it has to be pointed out that the available evidence supports a generally gradual pattern of evolution, unless it was truncated by sudden changes in ecological conditions or non-deposition events (Dzik 2005; compare with Donoghue 2001). A brief overview of probable phylogeny of particular Famennian conodont taxa is given below.

Mitrellataxids. — The first coniform *Mitrellataxis* emerges in the Holy Cross Mountains together with *Palmatolepis initialis*. More elaborate *M. ornata* followed soon and this may be an evolutionary succession. It occurred in proximity of the Karczówka mudmound analogous to the Frasnian belodellids. The order in appearance of smooth "simple cones" is from *M. circularis*, through *Jablonnodus erectus* to *J. oistodiformis* (Fig. 121). The end member of the *Jablonnodus* lineage is probably the unnamed late Famennian species with geniculate elements illustrated by Sandberg and Dreesen (1984). If taken literally this would suggest that the morphological distinctions within the apparatus typical of the last species developed gradually. However, no real transition has been demonstrated and this succession may have beeen controlled ecologically. The main lineage of *M. circularis*, although relatively well represented throughout the succession, is too indifferent morphologically to be interpreted in evolutionary terms. Anyway, a secondary homeomorphy with the Ordovician distacodontids remains a valid alternative to inheritance of ancient characters in a lineage of "living fossils".

Icriodontids. — Such "living fossils" are probably the most archaic Famennian icriodontids *Latericriodus*, episodic immigrants from an unknown source area.

The population of the earliest Famennian *Icriodus alternatus* (sample Pł-16) differs morphologically from the latest Frasnian *I. iowaensis* population, and may have roots somewhat deeper in the Frasnian (Dzik 2002). The representation of *Icriodus* throughout the early and mid Famennian is not completely continuous (these shallow-water conodonts were very sensitive to local environmental changes) but it is almost certain that the change from *I. alternatus* to *I. cornutus* was gradual. Also the succession of *Pelekysgnathus*, which replaced *Icriodus* in times of its low frequency and was apparently an open-sea animal, is of that kind. The low number of specimens and their disjunctive occurrence leaves some uncertainty whether *Dollymae*? *guizhouensis* is in the direct ancestor-descendant relationship to older *Pelekysgnathus* or immigrated from another region.

Devonian spathognathodontids. — Biramous symmetrical elements in the apparatus are an ancient feature of the ozarkodinid conodonts. At the beginning of the Silurian in the prioniodinid lineage, and at the beginning of the Devonian in polygnathids, a medial process developed in the S_0 element to be preserved almost without any significant change to the end of the Triassic. Reversal to the biramous condition was recognized only in the Frasnian lineage of the palmatolepidids (Dzik 2002). Therefore it was puzzling that throughout the Carboniferous and Permian the lineage of *Synclydognathus* and *Hindeodus* occurred with an apparatus groundplan closely similar to that of the Silurian spathognathodontid *Ozarkodina*. It was proposed by myself that they represent the same clade (Dzik 1991) and this has found support in the significant reduction of the stratigraphi gap as a result of finding *Synclydognathus* in the early Famennian of the Holy Cross Mountains. This finding disclosed also the affinity of *Apatognathus*, earlier classified among prioniodinids. There is a tendency towards reducing morphologic differences between elements in the apparatus in this lineage. Occurrences of the spathognathodontids remain few and stratigraphically isolated and it is thus difficult to resolve their phylogeny.

Prioniodinids and ancestral gondolellids. — Among the prioniodinids only two lineages seem to display phyletic evolution *in situ*, all others show a disjunctive, ecologically punctuated distribution. The most impressive case of evolutionary transformation is offered by *Lagovidina*. Its origin from earlier *Ligonodina* remains to be demonstrated, but is likely. Like other prioniodinids, these conodonts show a great variability that hampers evolutionary studies with low-number samples, but the latest populations of the lineage show rather stable organization of the apparatus.

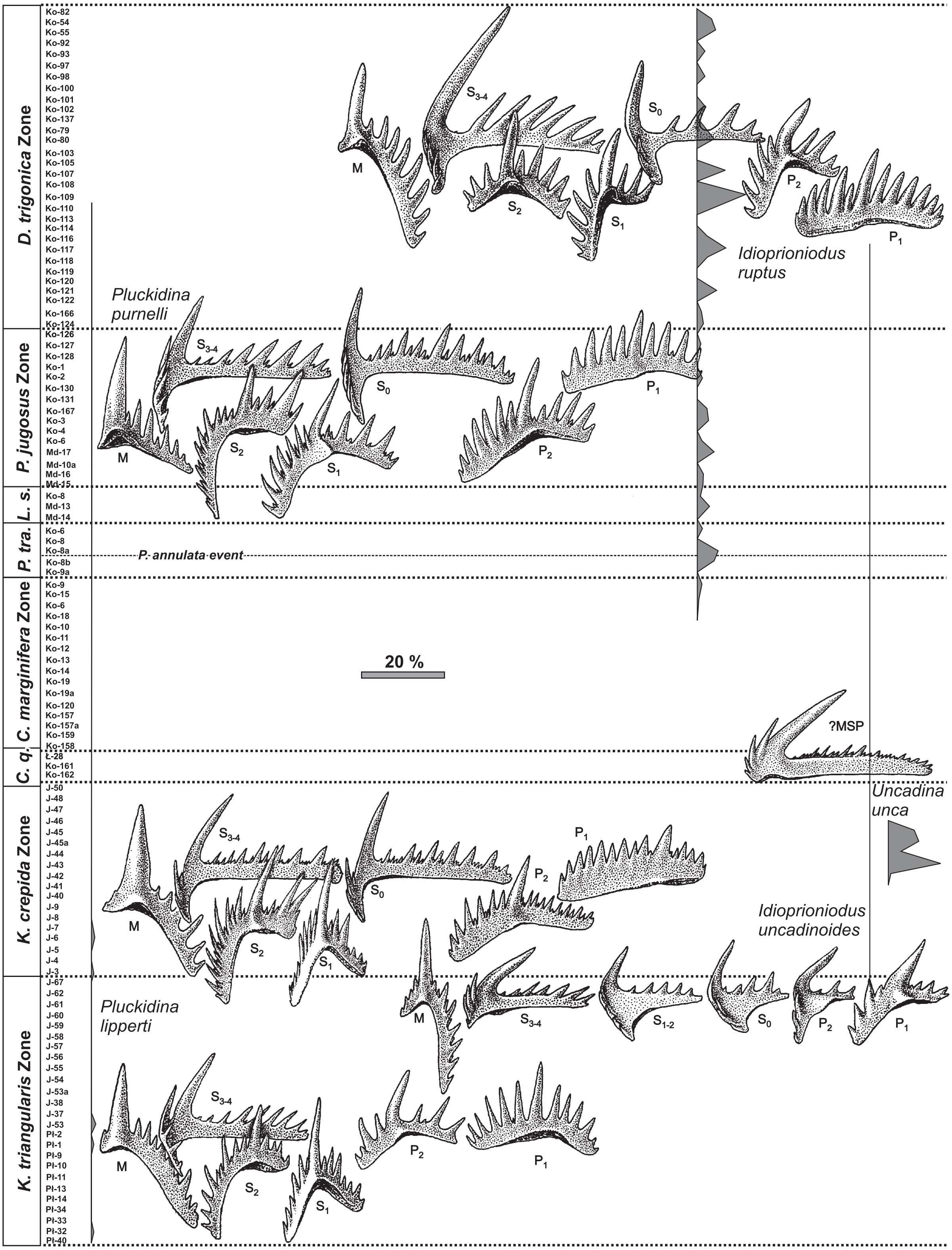


Fig. 123. Stratigraphic distribution of the prioniodinids *Pluckidina*, *Idioprioniodus* and *Uncadina* in the Polish Famennian (same kind of presentation as on Fig. 121).

The Famennian part of the lineage of *Pluckidina* seems to lead towards a gracile appearance of elements with a sharp, delicate denticulation. Unfortunately, only in a few samples are they represented in reasonable number. The late Carboniferous to Triassic branch of the gondolellids (Orchard 2005) for a long time was

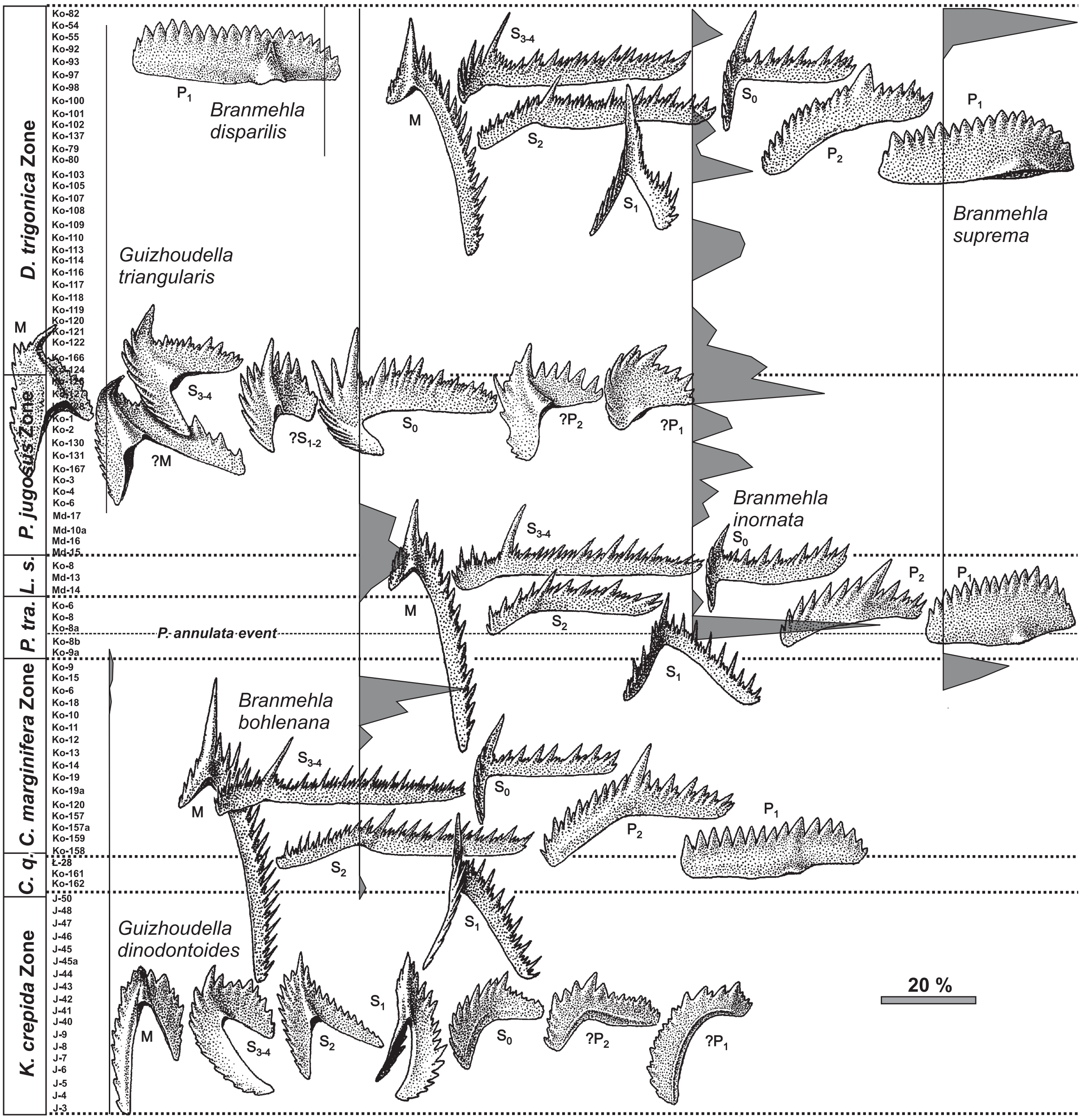


Fig. 124. Stratigraphic distribution of the advanced prioniodinid *Guizhoudella* and earliest gondolellid *Branmehla* in the Polish Famennian (the same kind of presentation as on Fig. 121).

considered to be of cryptic origin. The most characteristic aspect of their apparatus is the unusual shape of the S_1 element ("enantiognathus"), a reduced dorsal process in the P_1 elements, and extremely gracile appearance of other elements. These are features of the latest Devonian members of *Branmehla*. Its origin from *Pluckidina* is likely and it is only a matter of convenience where to place the boundary between the prioniodinids and gondolellids.

The most bizarre lineage of probable prioniodinids is represented by *Uncadina* of unknown origin and geographic source area. Some poorly known species of *Idioprioniodus* show remote similarity but the complete lack of any morphologic differentiation of elements in the apparatus was probably an evolutionary novelty.

Francodinids. — The most unexpected result of this apparatus study is recognition of a whole branch of conodonts with apparatus composition ranging from minute forms of almost Silurian appearance (*Vogelgnathus*, earlier known only from the Carboniferous) to robust apparatuses with elements mimicking the Car-

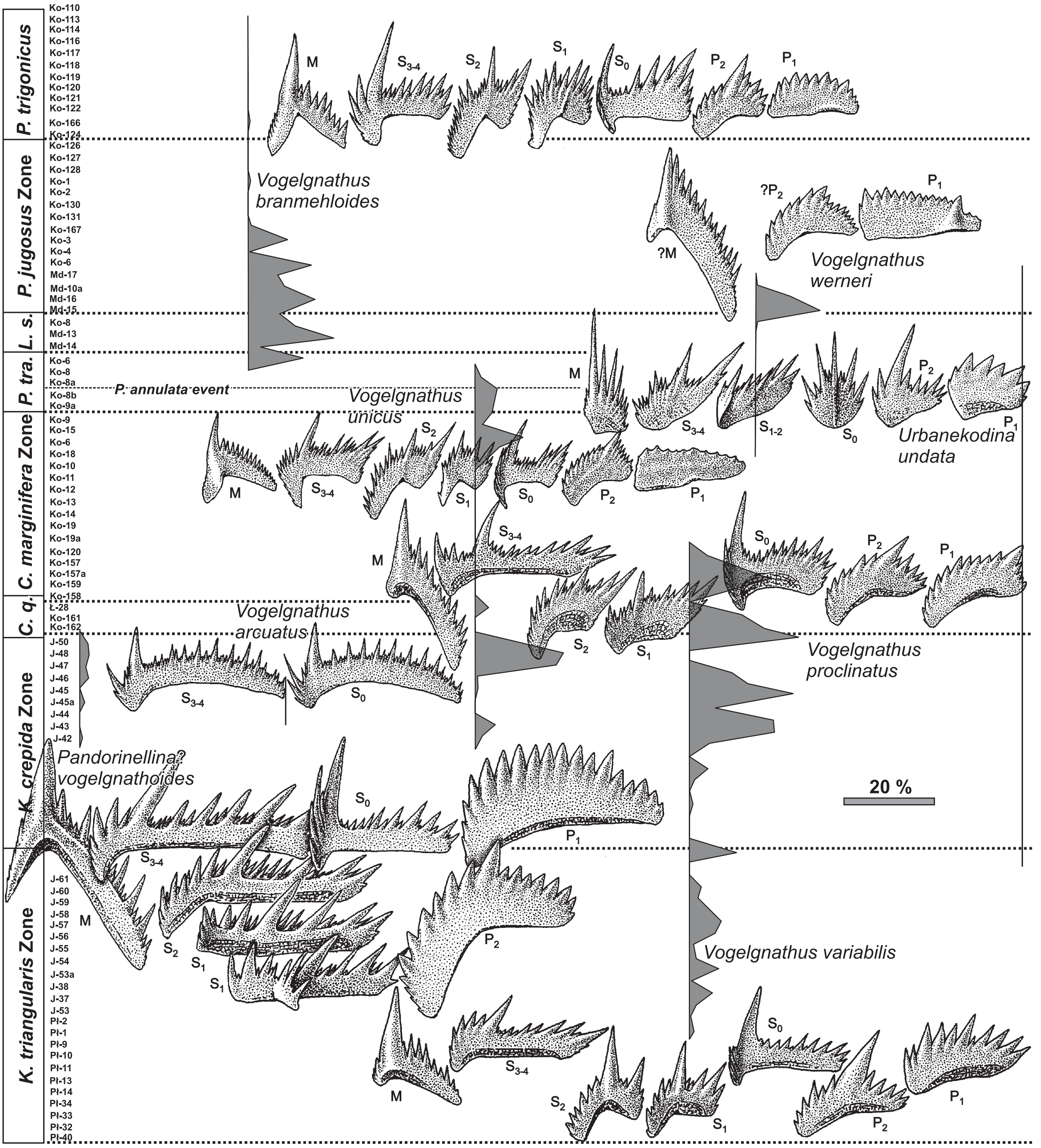


Fig. 125. Stratigraphic distribution of paedomorphic francodinids in the Polish Famennian (the same kind of presentation as on Fig. 121).

boniferous prioniodinid *Kladognathus* (*Planadina*). They share a tendency to paedomorphic shapes and are probably monophyletic, although the earliest stages of their evolution remain unknown. All of several lineages of the family, except for that of *Vogelgnathus variabilis* → *V. proclinatus*, represent brief incursions of exotic, environmentally sensitive forms. Morphologically the most intriguing is the lineage of *Urbanekodina*, long-ranging only at Miedzianka, with extremely small and simplified elements. A fundamental reorganization of the ground plan of the M element, otherwise the most stable in the evolution of conodonts, is offered by the *Francodina* → *Sweetodina* → *Planadina* succession, unfortunately punctuated by migrations and allopatric speciation events.

Mehlinid origin of ornate platforms. — Another unexpected aspect of the evolution of the Famennian conodonts is the probable central role of *Mehlina* in the evolution of platform-bearing polygnathids. A key

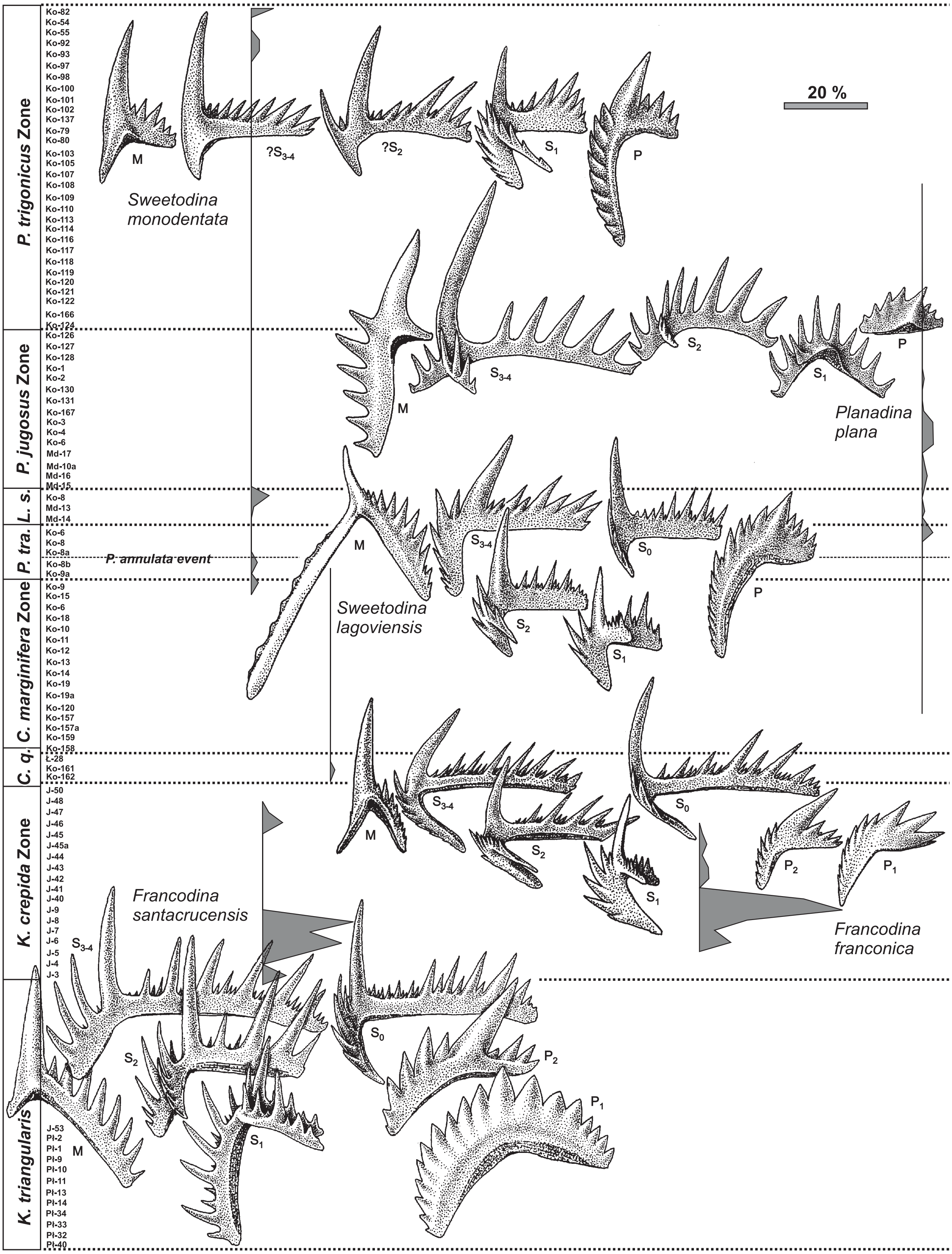


Fig. 126. Stratigraphic distribution of large francodinids in the Polish Famennian (the same kind of presentation as on Fig. 121).

to understanding their relationship was offered by the development of a brush-like peniculus in the early histogeny of the P_2 elements. This character discloses relationships of several lineages of *Polynodosus*, earlier placed in the ancient platform-bearing *Polygnathus* branch. It remains to be resolved how far this

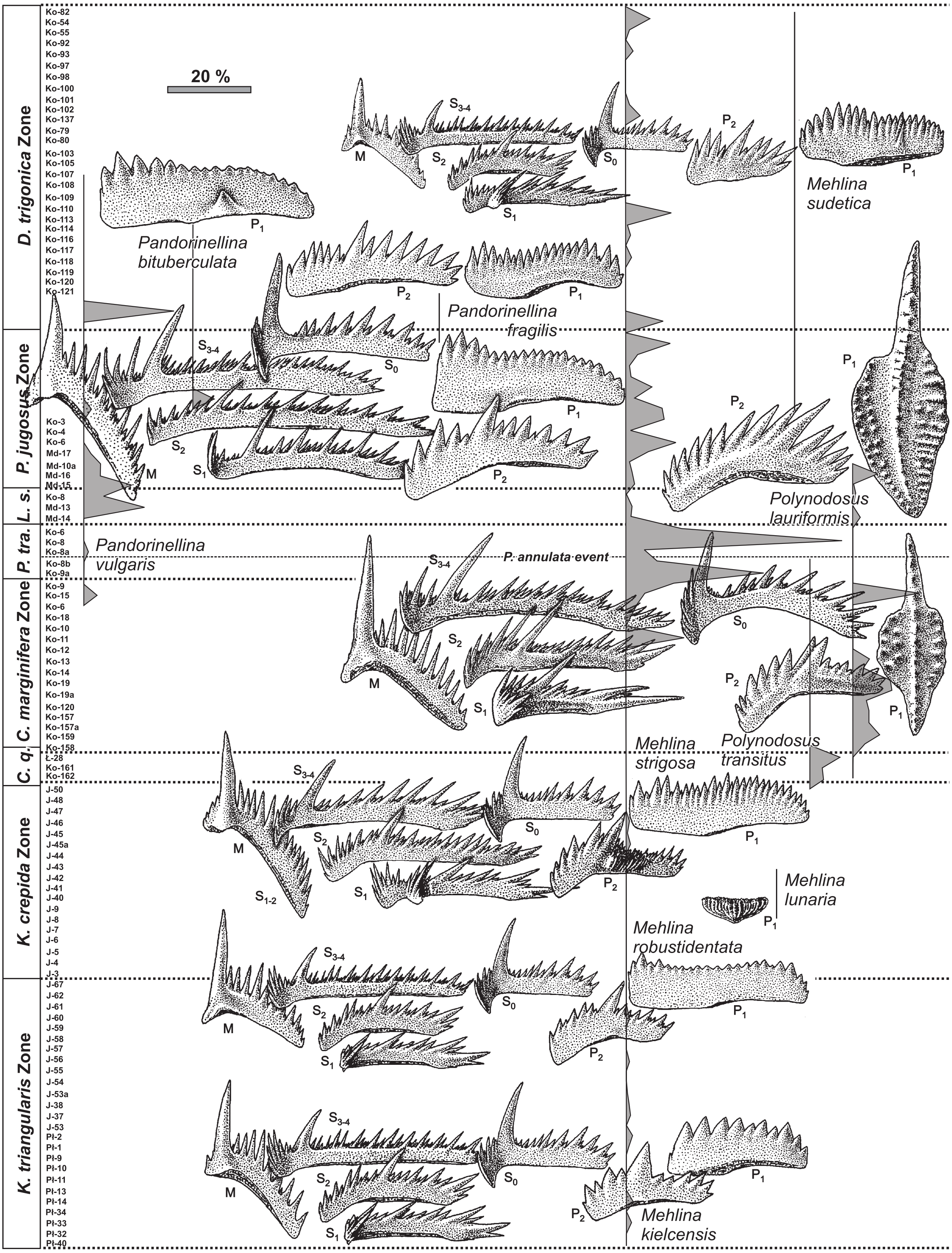


Fig. 127. Stratigraphic distribution of the non-platform polygnathids and the least derived platform-bearing *Polynodosus* species in the Polish Famennian (the same kind of presentation as on Fig. 121).

reached and whether the even more elaborate *Hemilistrona* also belongs there. The end member of this branch is of bizarre morphology with almost completely reduced blades of both types of the P elements (Fig. 128).

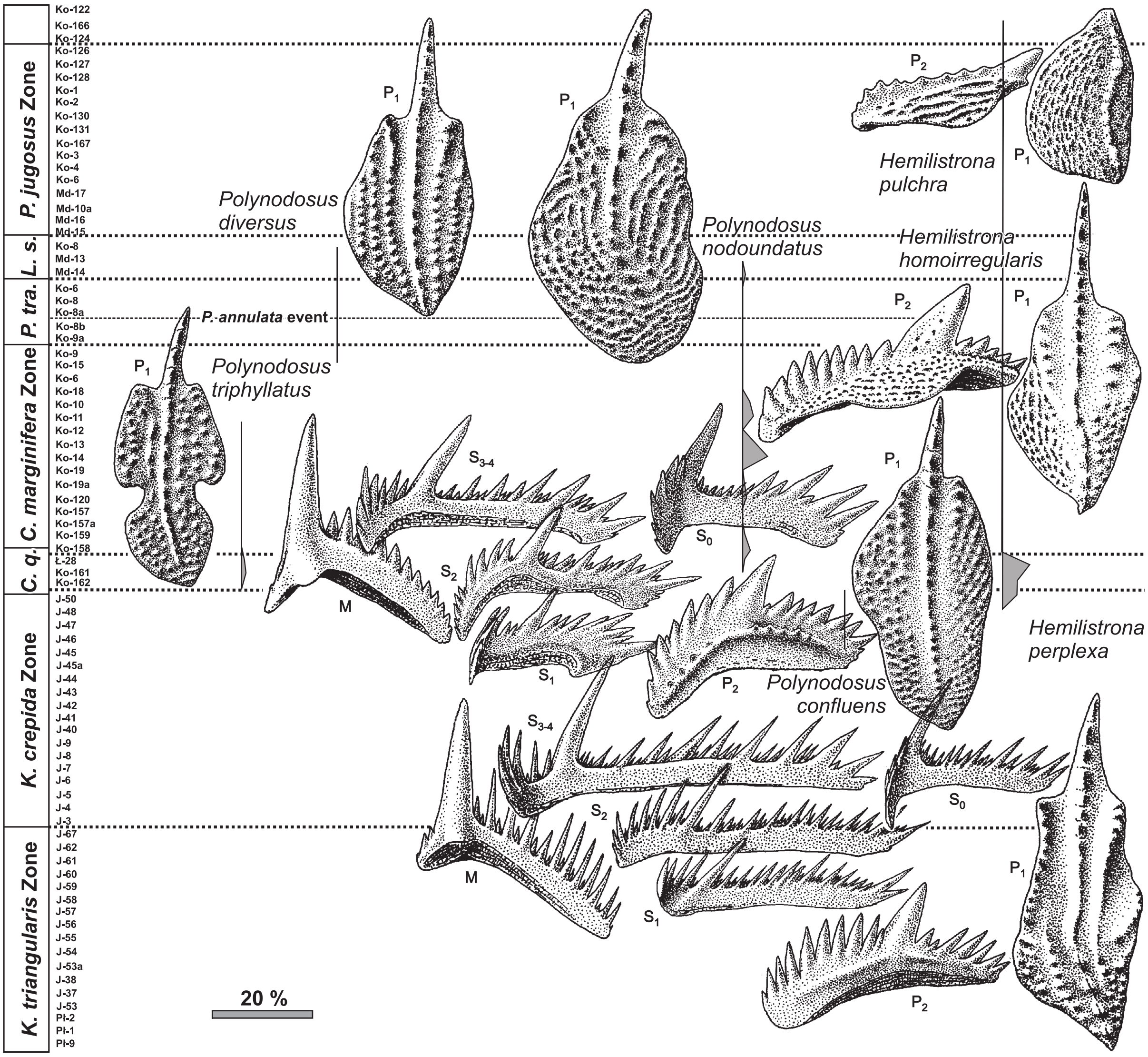


Fig. 128. Stratigraphic distribution of the advanced *Polynodosus* species and *Hemilistrona* in the Polish Famennian (the same kind of presentation as on Fig. 121).

There is a hope that increase in knowledge of the apparatus structure will introduce a long-awaited order in the phylogeny of ornate platform-bearing polygnathids. Studies on the evolution of the *Polygnathus*-group conodonts are difficult because they are highly sensitive environmentally and have punctuated distribution hampering recognition of phyletic evolutionary changes. Moreover, their population variability is high. Unfortunately, apparatuses of the polygnathids are morphologically generalized and usually only the P_2 elements are of significance in diagnosing species. However, a distinct apparatus composition allows separation of the *P. extralobatus*–*P. znepolensis* group and proves that *Polylophodonta* (actually a relative of *Ancyrognathus*) has little to do with the *Polynodosus confluens* → *P. triphyllatus* lineage.

Probable ctenopolygnathid roots of siphonodellids. — There is much uncertainty regarding relationships of the late Famennian and Tournaisian conodonts with a fusiform flat basal cavity in the platform elements. They are believed to be of crucial importance in delimiting, on an evolutionary basis, the Devonian–Carboniferous boundary. Unfortunately, the apparatus reconstructions of various siphonodellids are no more than provisional (Dzik 1997) and even relationships within the clade (classified in the Elictognathidae, based on the assumed controversial apparatus interpretation) are not clear. It may be, however, of importance that the preliminary apparatus reconstructions of the earliest siphonodellids (Dzik 1997)

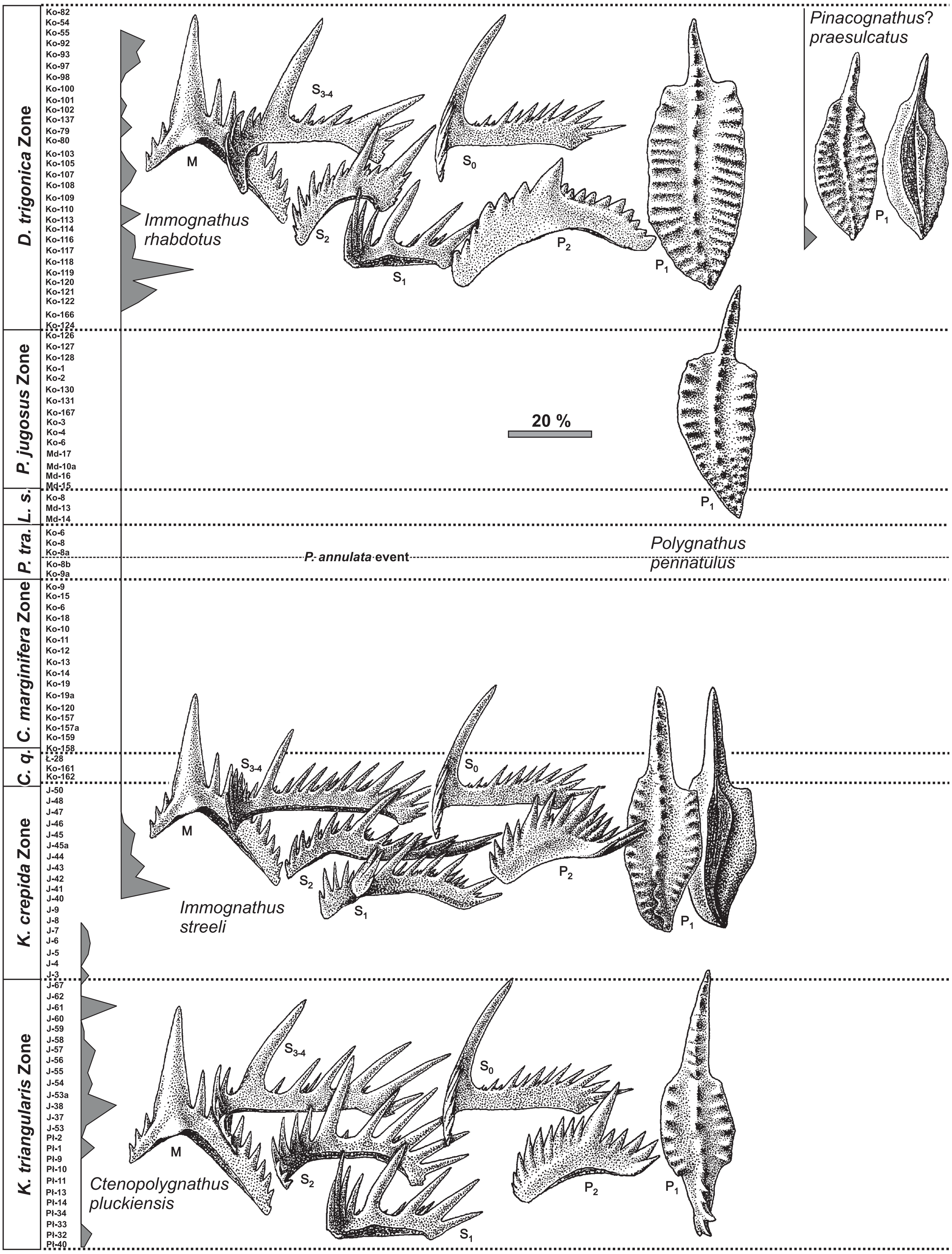


Fig. 129. Stratigraphic distribution of the robust polygnathids *Ctenopolygnathus* and *Immognathus* and possible elictognathid species in the Polish Famennian (the same kind of presentation as on Fig. 121; drawing of *Polygnathus pennatulus* of possible relationship to the *Immognathus* lineage added).

resemble the apparatus of the mid and late Famennian derivative of the robust polygnathid *Ctenopolygnathus*, here named *Immognathus*. In this lineage the peculiar form of *Siphonodella*-like base developed

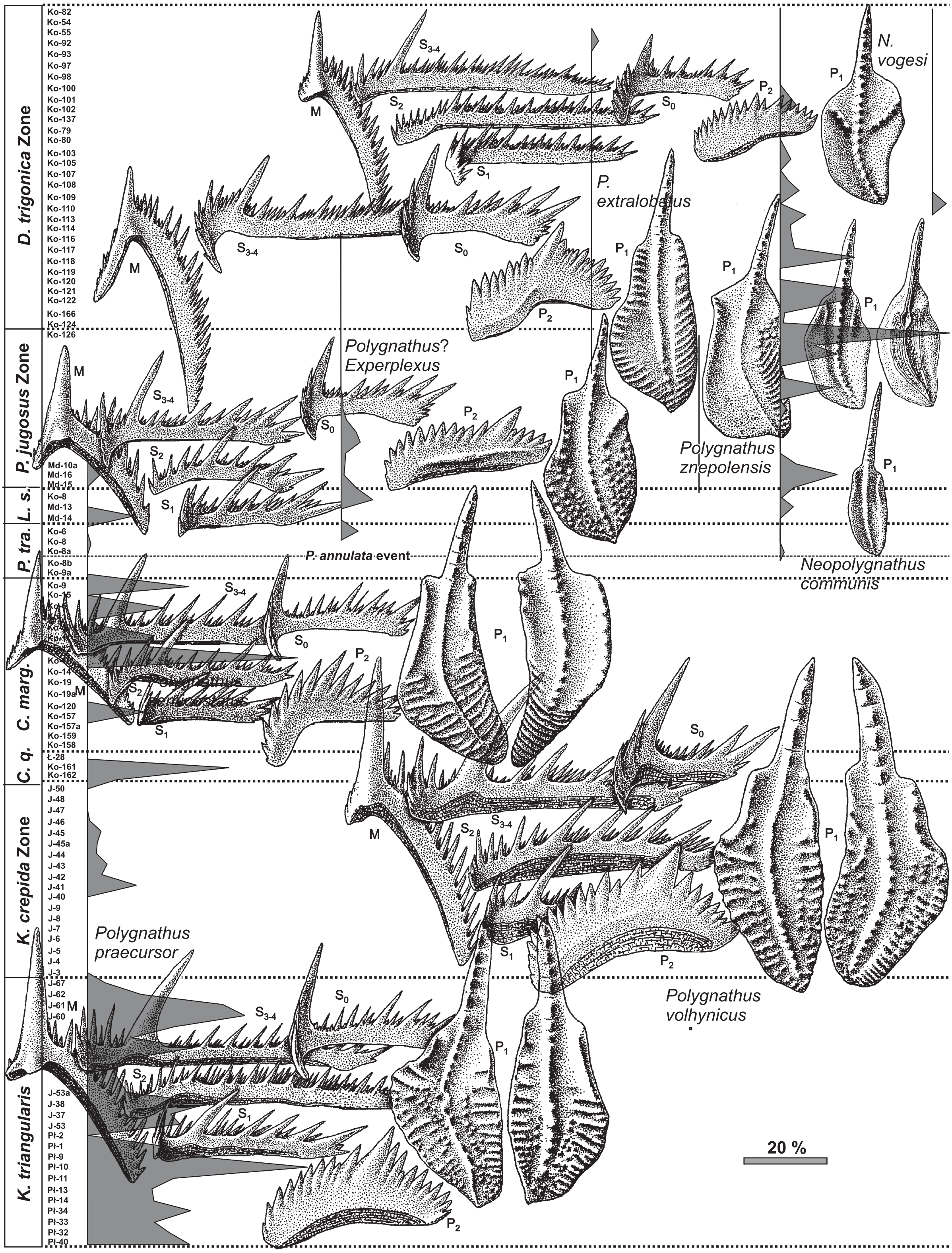


Fig. 130. Stratigraphic distribution of the polygnathids *Polygnathus* and *Neopolygnathus* in the Polish Famennian (the same kind of presentation as on Fig. 121).

independently of the Famennian *Alternognathus*. The latter genus, with its incipient axial symmetry in the P_1 pair, is an unlikely relative of the siphonodellids, being rather ancestral to the Carboniferous cavusgnathids.

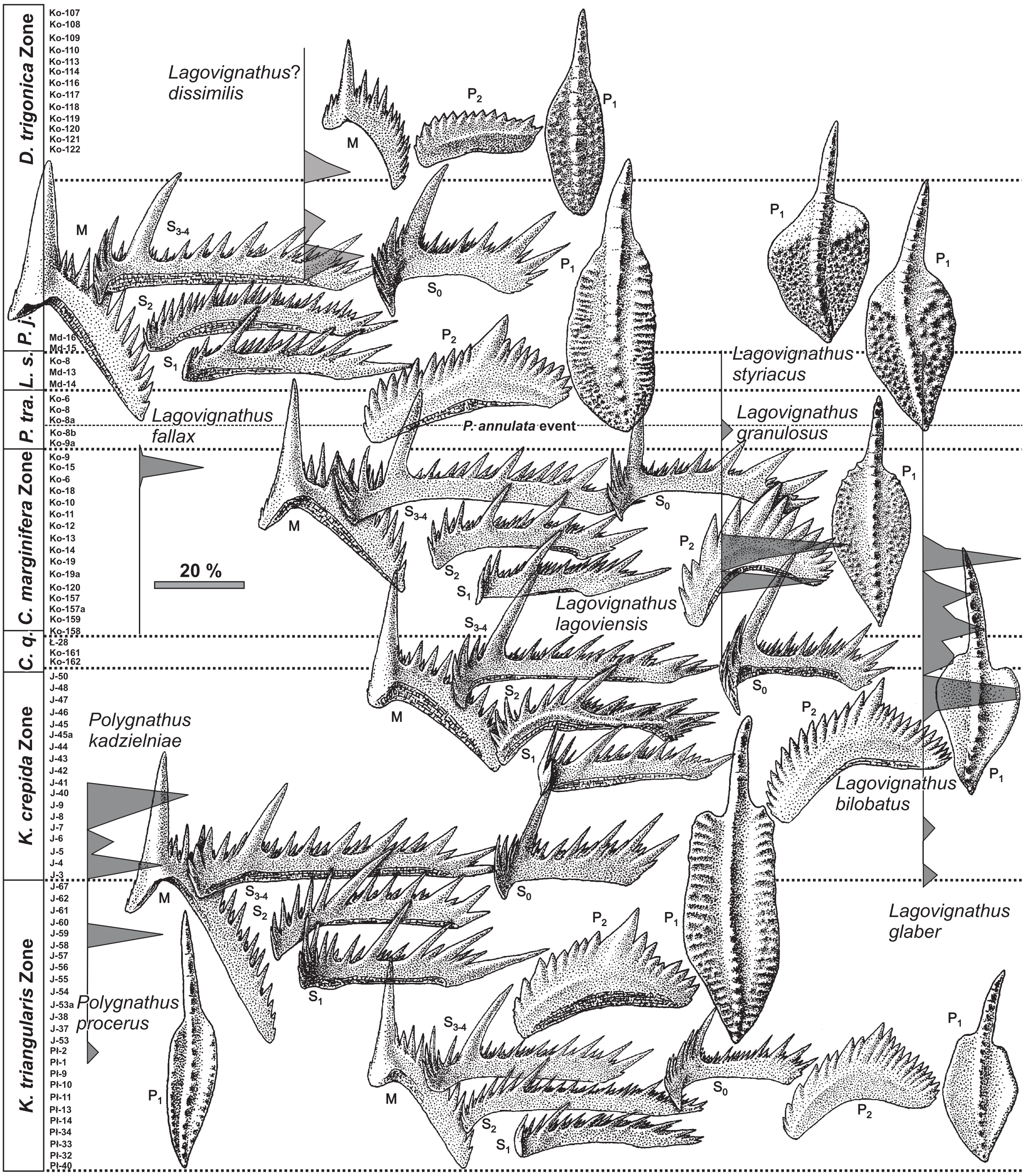


Fig. 131. Stratigraphic distribution of the polygnathid *Lagovignathus* and its possible relatives among *Polygnathus* species in the Polish Famennian (the same kind of presentation as on Fig. 121).

The problem of *Neopolygnathus*. — The common early Carboniferous genus *Neopolygnathus* has Devonian roots. It is difficult, however, to indicate its exact ancestry because its earliest populations show a great population variability and the morphology of its elements is generally degenerative, marked by deep simplification of the unknown original morphology. Their P$_1$ elements are of small size and simple morphology but, paradoxically, a tendency towards simplification and developing a smooth platform (but with imprints of ameloblasts) characterizes one of the most robust polygnathids of the Famennian, *P. semicostatus*. Notably, unusually high population variability is a feature of this species. It seems thus that the characteristic concave base of P$_1$ elements of *Neopolygnathus* is also a degenerative feature, an effect of lowered mineralization of the platform base.

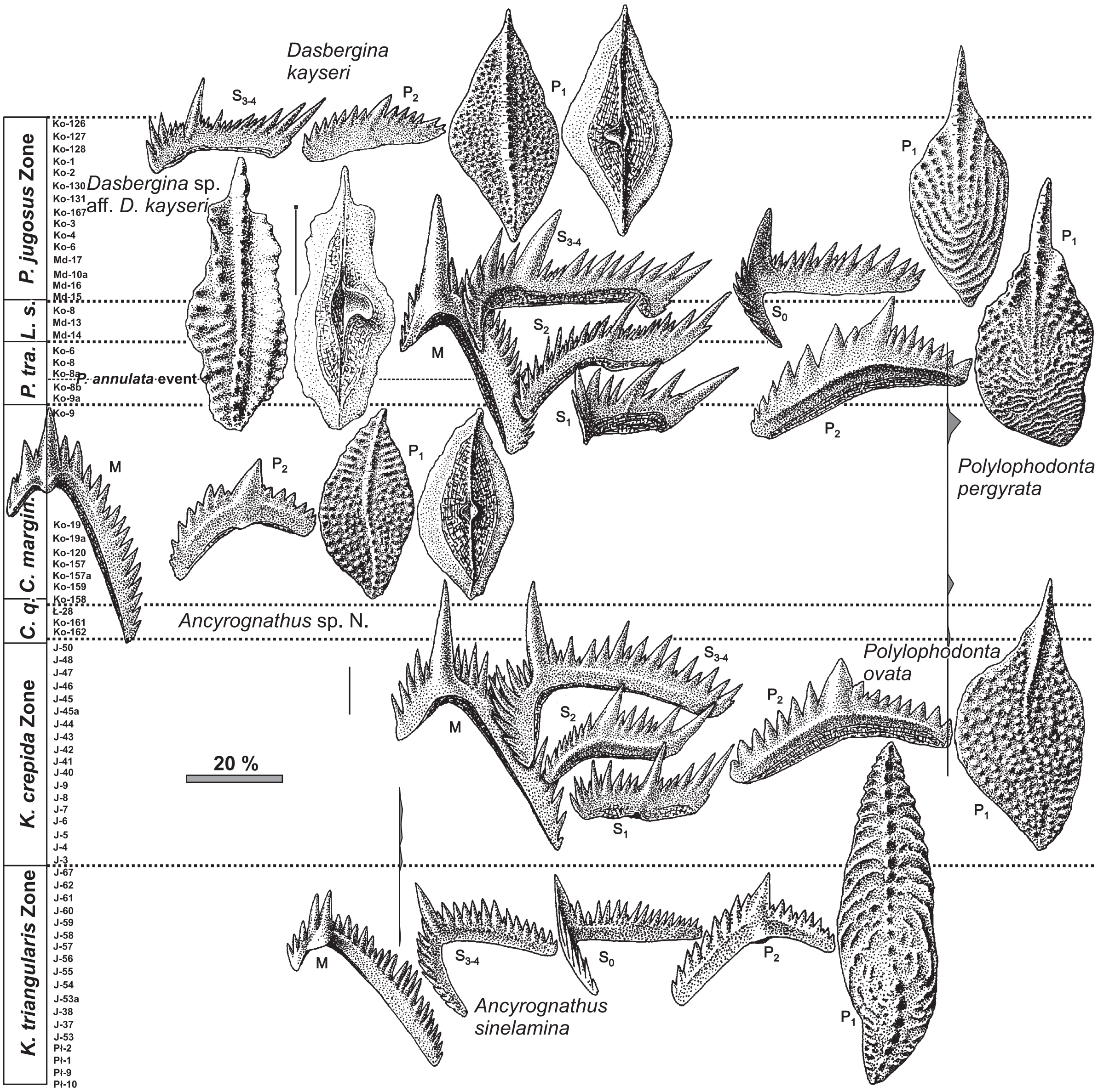


Fig. 132. Stratigraphic distribution of the ancyrognathids and their idiognathodontid homeomorphs in the Polish Famennian (the same kind of presentation as on Fig. 121).

Advanced Carboniferous species of *Neopolygnathus* are almost homeomorphic to another, unrelated polygnathid lineage, here classified in *Lagovignathus*. Several lineages of these conodonts with a thin platform in the P_1 elements occur in the mid Famennian, mostly of ecologically punctuated distribution. Their origin remains unknown but possibly the earliest Famennian *Polygnathus procerus* may connect them with the Frasnian species characterized by an almost symmetrical, thin platform. Only two lineages show a probably phyletic evolution *in situ*. One of them *L. fallax* → *L.*? *dissimilis* is incompletely demonstrated. The other, *L. lagoviensis* → *L. granulosus* → *L. styriacus*, offers a succession of great correlative value.

Palmatolepidids. — Only one local lineage of Famennian palmatolepidids was represented at the beginning of the Famennian. The environmental change that resulted in the disappearance of the typically Frasnian lineages of *Lagovilepis* and *Manticolepis* had no detectable influence on the phyletic evolution of the *Klapperilepis* lineage except for a somewhat delayed increase in its population variability (Dzik 2002). This seems to be a result of a released selection pressure earlier generated by competition of other palmatolepidid species. New lineages emerged sequentially by immigration from their places of origination. The apparent decrease in population variability of *K. ultima* was probably caused by the appearance in the area of species

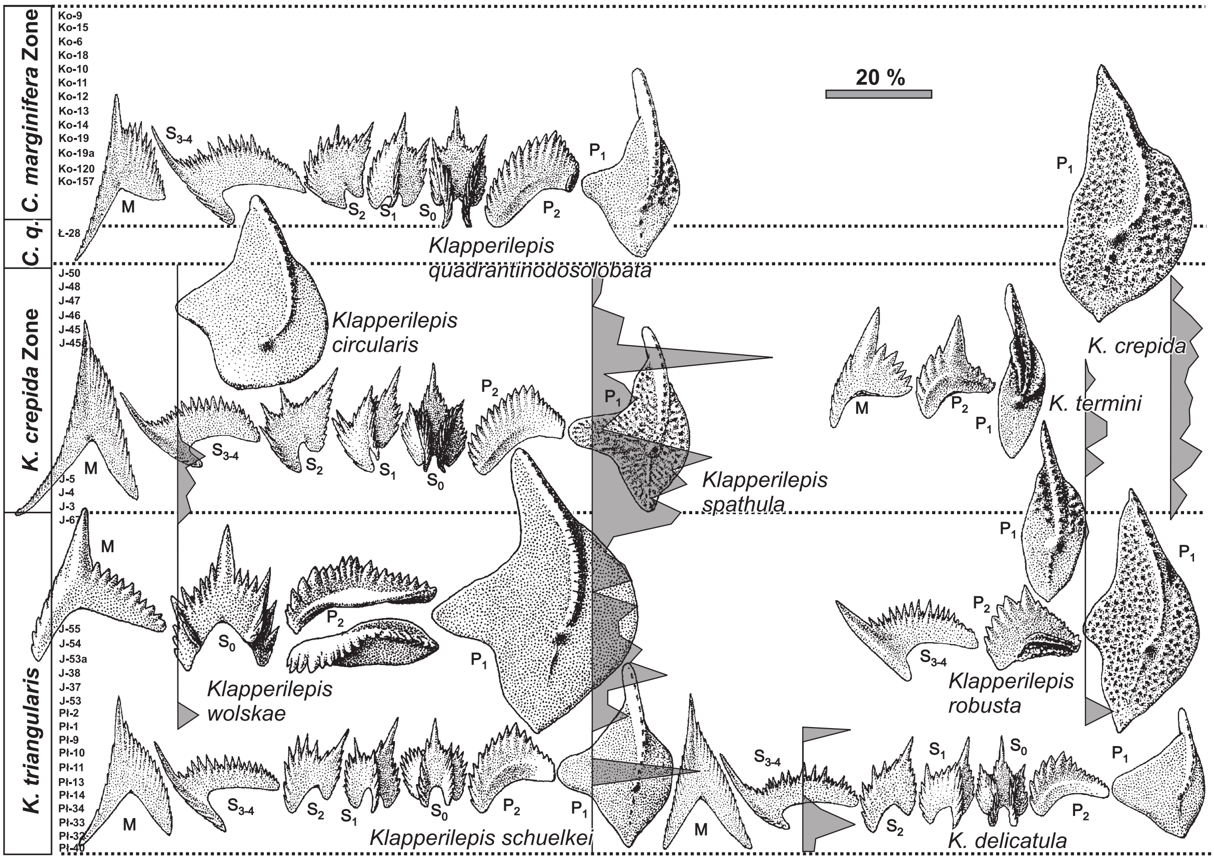


Fig. 133. Stratigraphic distribution of advanced species of the palmatolepidid *Klapperilepis* in the Polish Famennian (the same kind of presentation as on Fig. 121).

that still had similar ecological preferences. Remarkably, the platform elements of the species new in the area only a little increased the total range of shapes earlier represented in the single species, *K. ultima*. However, under the competition from other sympatric species they all had to reduce their variability. Probably the local population was forced to accommodate to the new conditions of partially overlapping ecological niches (the phenomenon of character displacement). The subsequent phylogeny of the Famennian palmatolepidids was reviewed by myself elsewhere (Dzik 2005). The early Famennian is marked by allopatric diversification and the subsequent geographic merging of several lineages of *Klapperilepis*. They preserved an underived apparatus structure but with various morphologies of the P_1 elements.

In the mid Famennian they were replaced by a few lineages of the gradually diversifying branch of *Conditolepis*, with secondarily biramous S_0 elements of the apparatus. The branches of *Palmatolepis* and *Tripodellus* continue throughout the Famennian, usually with not more than two lineages sympatric. Phyletic evolution has been observed in several lineages of the Famennian palmatolepidids. Among those of *Klapperilepis* the most extensive is represented by the lineage *K. schuelkei* → *K. spathula* → *K. quadrantinodosolobata*. The succession *K. wolskae* → *K. circularis* is also rather complete but the observed morphologic change is not profound. A similar extent of transformations characterizes the lineage *K. robusta* → *K. crepida*, the lineage covering early and late, rather different *K. termini*, and the stratigraphically rather punctuated lineage *K. protorhomboidea* → *K. rhomboidea*.

The main lineage of *Tripodellus* offers probably the most extensive morphologic change and complete record (Fig. 134). Apparently gradual and continuous is also the change in the long lineage from *Palmatolepis initialis* up to *P. schindewolfi*. Less continuous but likely to be gradual is the series *P. ampla* → *P. trachytera* → *P. rugosa*. In *Palmatolepis* and *Conditolepis* the processes of the M elements acquired a position closely similar to that in the Frasnian *Manticolepis*. It appears thus that the pelagic palmatolepidids, unlike the generally shallow-water polygnathids, offer a much more complete record of their evolution.

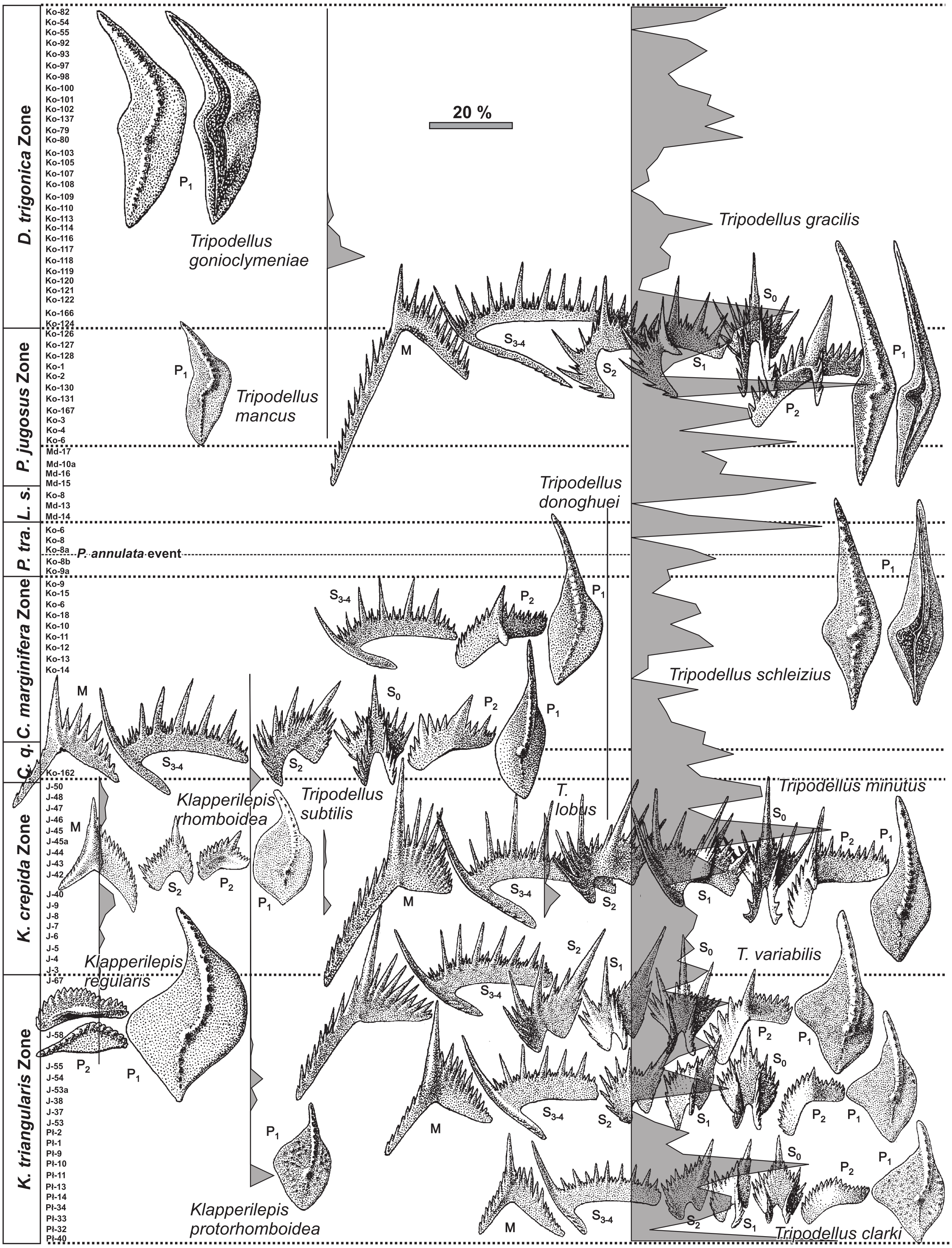


Fig. 134. Stratigraphic distribution of advanced species of the palmatolepidid *Tripodellus* and some *Klapperilepis* species in the Polish Famennian (the same kind of presentation as on Fig. 121).

Origin of axial symmetry of elements. — Left and right elements of many conodonts are not mirror images. This apparently improved their fit in occlusion. In rare cases, however, this tendency went as far as to develop left and right elements of virtually the same shape, seemingly not forming pairs. This is a case of ax-

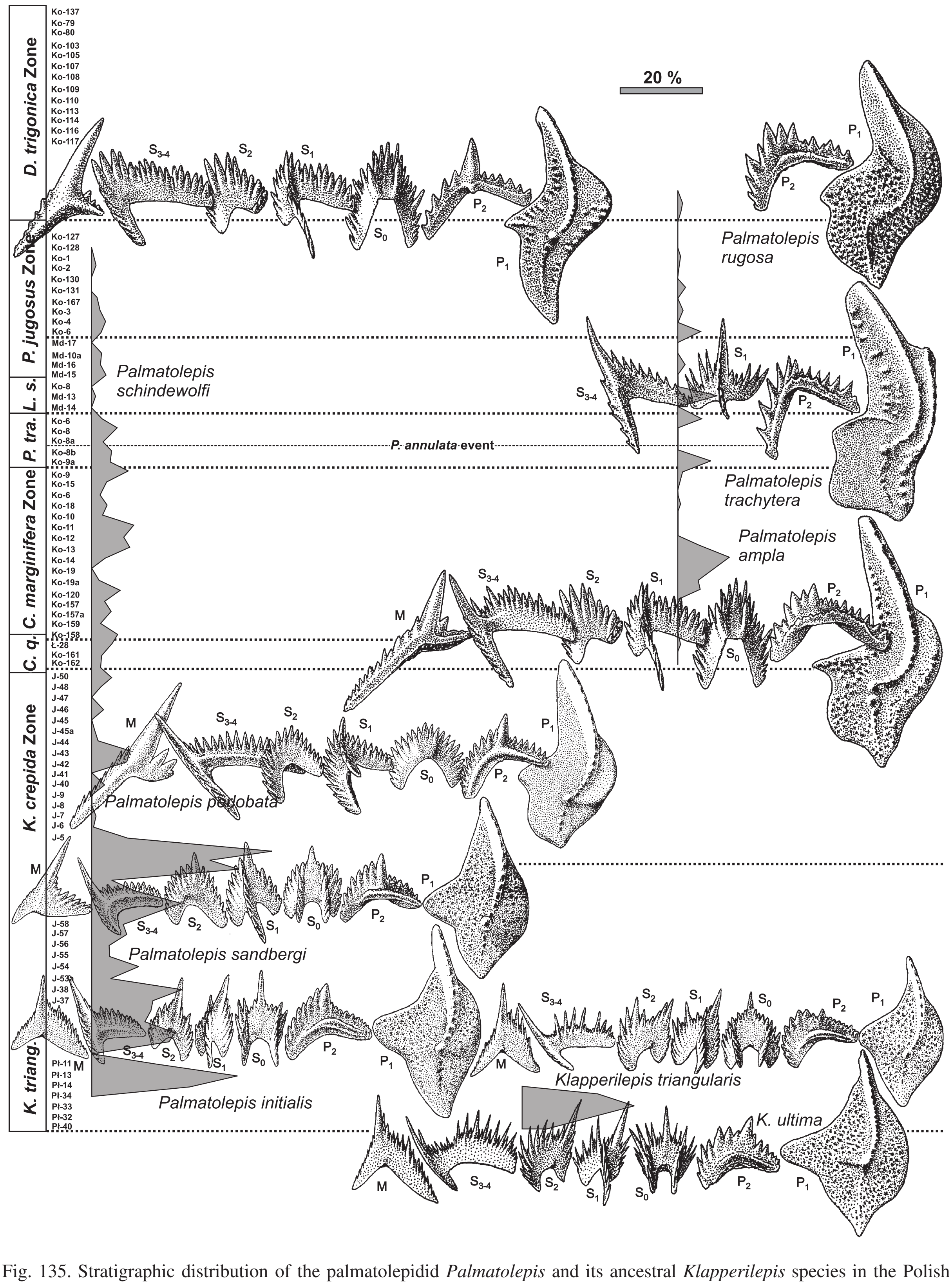


Fig. 135. Stratigraphic distribution of the palmatolepidid *Palmatolepis* and its ancestral *Klapperilepis* species in the Polish Famennian (the same kind of presentation as on Fig. 121).

ial symmetry. Virtually all the conodonts with the P_1 elements of this kind occur in the late Devonian and early Carboniferous. One may thus wonder whether the axial symmetry developed once in the evolution of conodonts or several times independently. The earliest Famennian case of undoubted axial symmetry is rep-

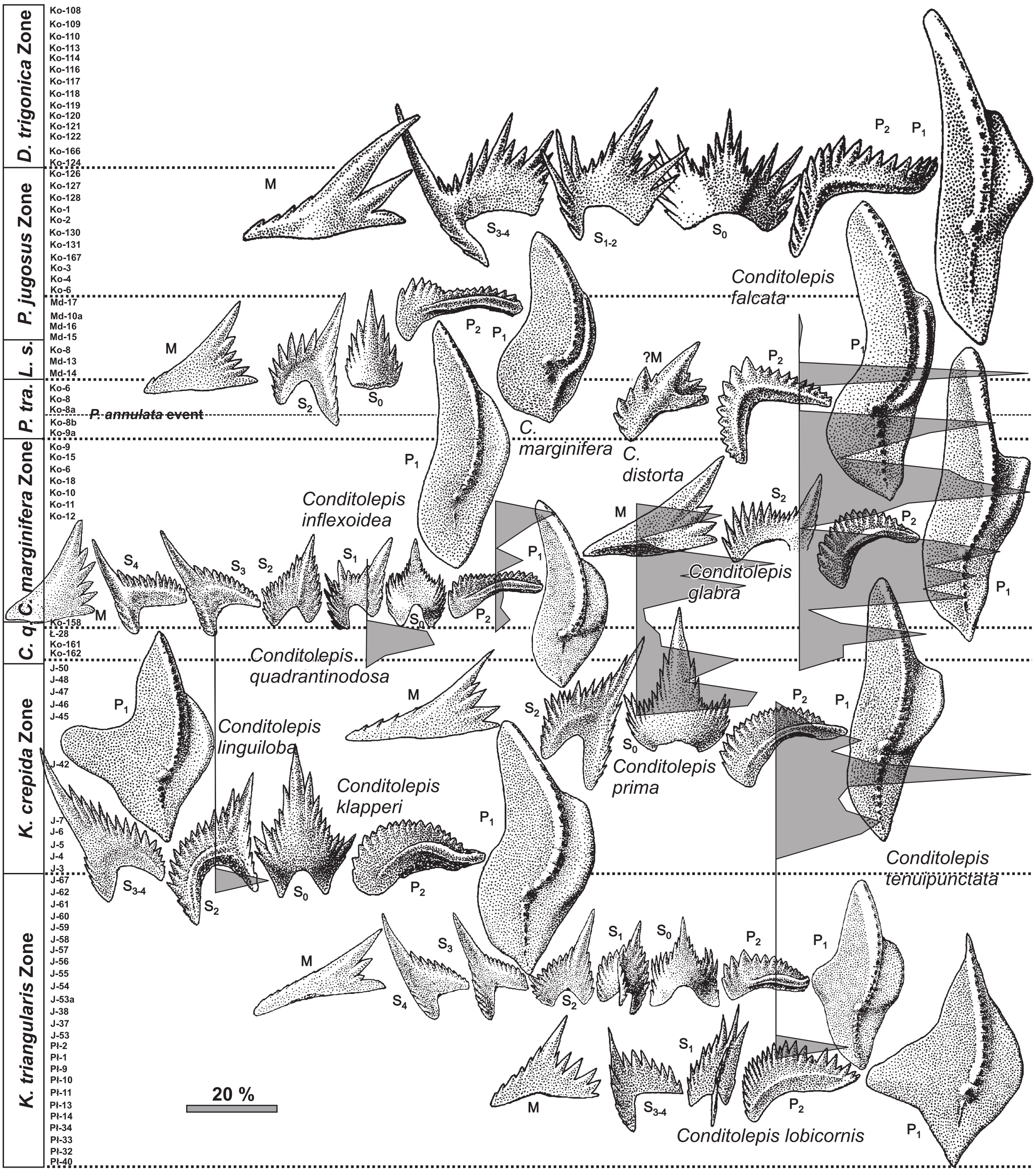


Fig. 136. Stratigraphic distribution of the palmatolepidid *Conditolepis* in the Polish Famennian (the same kind of presentation as on Fig. 121).

resented by the mid Famennian *Scaphignathus*, a branch of the *Alternognathus* lineage with an incipient asymmetry of elements. There is no doubt that *Scaphignathus* gave rise to the Carboniferous branch of *Cavusgnathus* and *Mestognathus*, the model cases of axial symmetry.

There is another group of conodonts with axial symmetry of their P_1 elements. Their basal cavities are basically different from that of *Alternognathus*, resembling rather *Dasbergina* in this respect. However, the exact ancestry of this lineage has not been traced and the situation resembles that among the Carboniferous cavusgnathids. The problem has to be clarified, which may not be so easy, however, because the *Pseudopolygnathus* species are environmentally sensitive and their evolution is poorly recorded. Perhaps the most complete succession is that of the *P. ziegleri* → *P. ultimus* lineage.

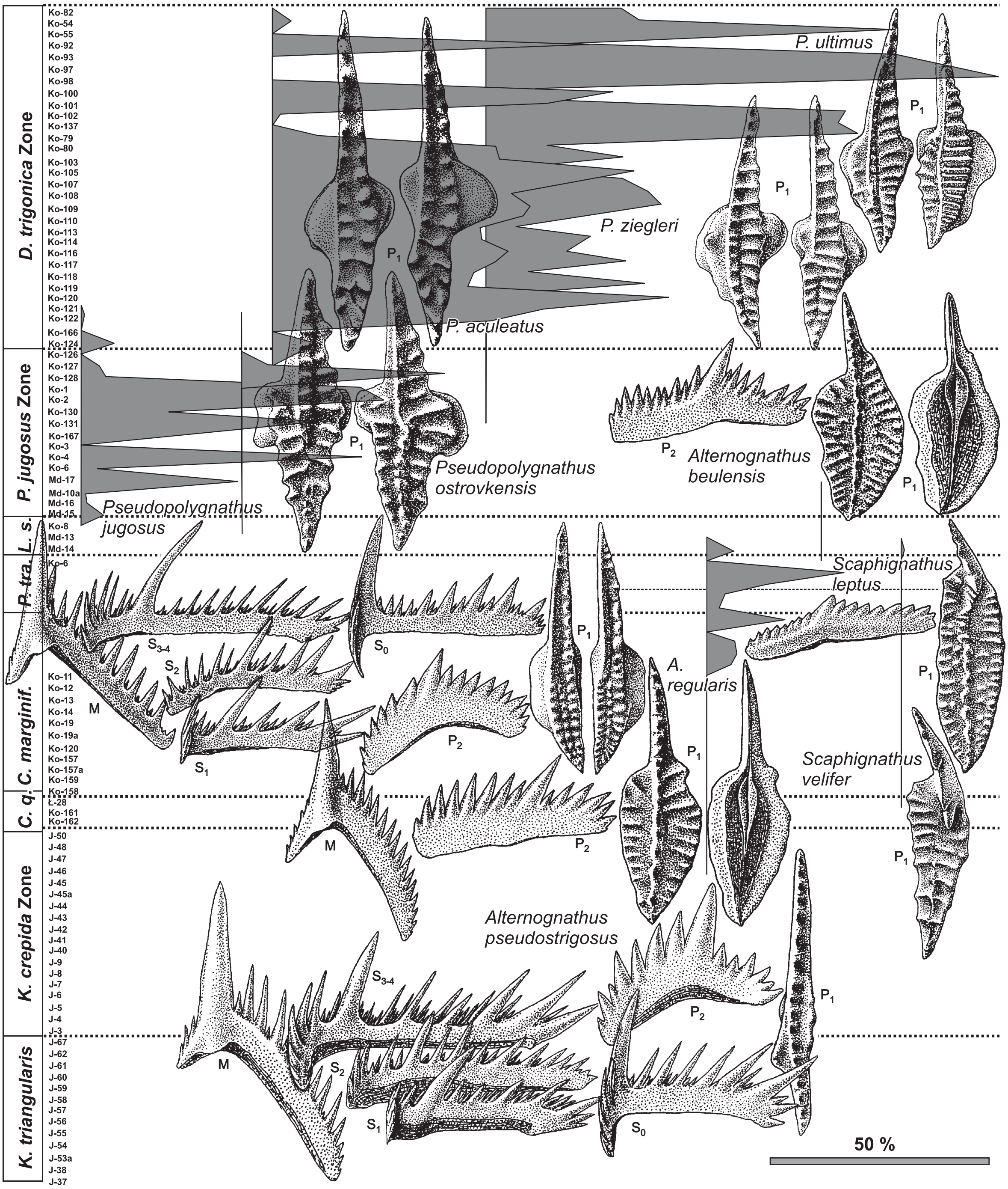


Fig. 137. Stratigraphic distribution of the cavusgnathids in the Polish Famennian (the same kind of presentation as on Fig. 121).

The Devonian roots of the idiognathodontids. — A crucial role in the evolution of the late Paleozoic conodonts was played by a mid Famennian relative of the most generalized polygnathid lineage of that age, *Pandorinellina vulgaris*. This was *Dasbergina stabilis*, the only derived feature of which was the expanded base with a shallow but wide cavity. In several lineages that emerged from *D. stabilis*, the basal cone developed tuberculation or a kind of tuberculated platform. Two relatively fast evolving lineages are of importance in this group. The *D. brevipinnata* → *D. ziegleri* lineage developed an elaborate platform with rows of tubercles. In the *D. kowalensis* → *D. marburgensis* → *D. trigonica* lineage, the originally coarsely tuberculated platform gradually changed into a characteristic ramified structure.

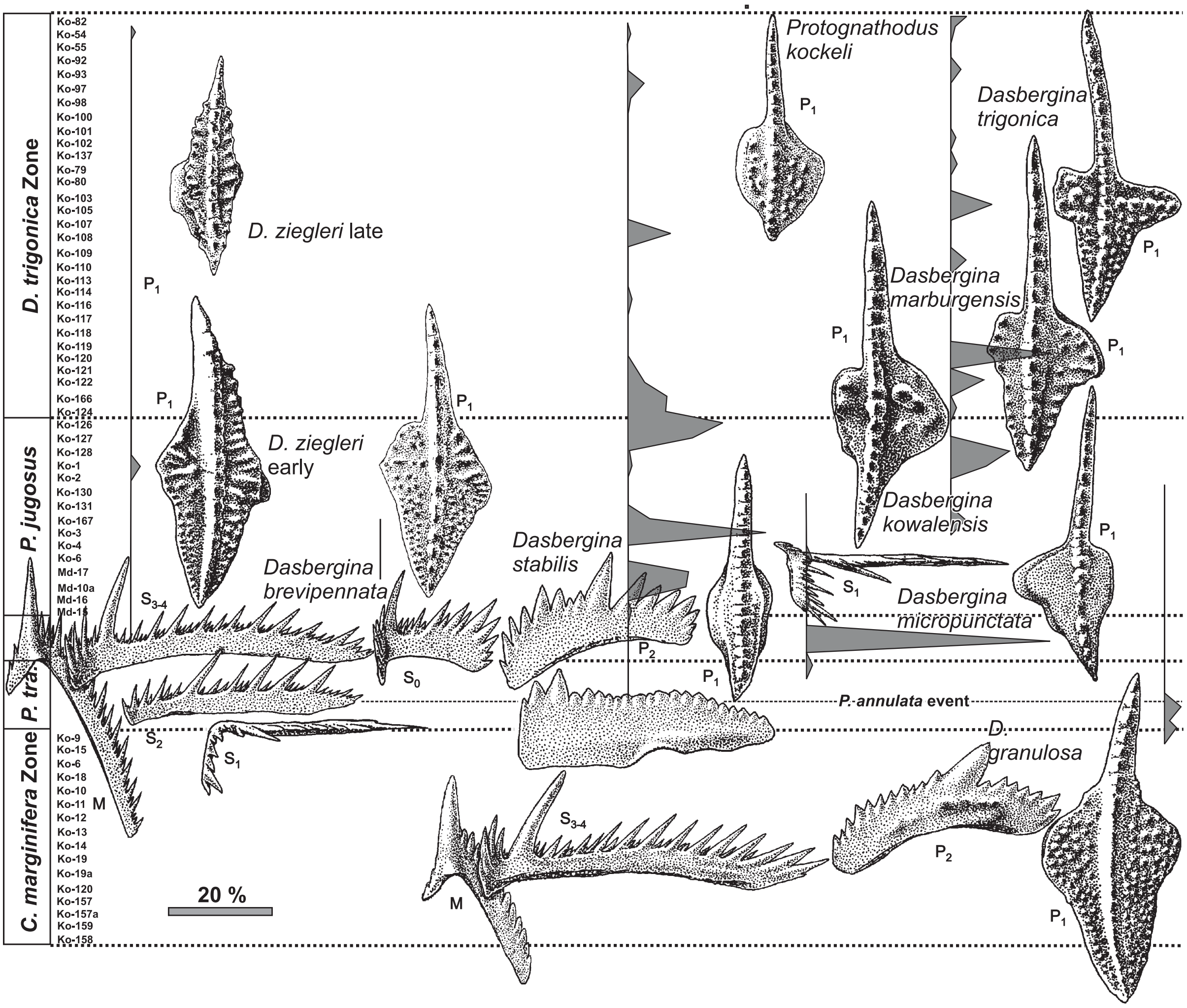


Fig. 138. Stratigraphic distribution of advanced species of the idiognathodontids in the Polish Famennian (the same kind of presentation as on Fig. 121).

Apparently from *Dasbergina* originated also *Protognathodus*, which appeared near the end of the Devonian from an unknown source. Its lineage probably diversified later into the main group of open-sea Carboniferous conodonts, the idiognathodontids. An important change in the ramiform elements of its apparatus took place in the Viséan (Dzik 1997).

Conclusion. — The number of 142 conodont species says more about the nomenclatorial history of their research than about their faunal history. The count of identifiable lineages is somewhat more informative in this respect. Usually they represent brief segments of evolution labelled with a single species name, in some examples being a case of the more extensive record of their evolution, corresponding to a few chronospecies. There are 101 such lineages in the material available to me, 31 of them showing more or less apparent evolutionary change. In the majority of cases the record is not comletely continuous and it is not always clear whether a lineage completely disappeared from the area for some time or is not represented in some samples only because of its locally or periodically small contribution.

The diagrams depicting their time distribution are not calibrated in real time as the length of particular units expresses only completeness of sampled geological sections. Anyway, if so crudely estimated ranges are compared on the basis of their length, it appears that the succession showing more or less certain evolutionary transformations represent almost half (46%) of the summarized observed ranges of conodont lineages in the Holy Cross Mountains and the Sudetes. Their record is not complete and probably not more than half of it is suitable for stratophenetic studies. This is much less than in the temperate climatic zone record represented by the Ordovician succession in the same area (Dzik 1994), but this seems to be a distinction typical of equatorial successions of various ages (Dzik 1983, 1997).

It is a controversial issue how to estimate the complexity of living forms but probably in all aspects that can be considered, the Famennian was the epoch of the greatest anatomical and species diversity of conodonts, comparable with only a few episodes in their earlier history (e.g., Llanvirn to early Caradoc; late Llandovery to early Wenlock), and only one after the Famennian (late Tournaisian). The number of sympatric species (well defined morphological species, not arbitrarily selected morphotypes!) was commonly higher than 25. The Famennian experienced also an invasion of pelagic environments with efficiently swimming large predators. For the first time acanthodians, sharks, and ganoid fishes started to co-occur with conodonts (earlier they inhabited mostly near-shore environments not accessible to conodonts; e.g., Blieck *et al*. 2000). The Famennian marine pelagic fish show some species diversity and significant participation in biological productivity of the pelagic community. Concavicarid and angustidontid crustaceans, with grasping appendages mimicking conodont elements but an order of magnitude larger, were also represented by phosphatized mandibles and carapaces (see below). Both fish and large pelagic crustaceans probably fed also on conodonts (Rolfe and Dzik 2007). Perhaps this was a factor contributing to their late Palaeozoic decline.

AMMONOID CONCHS AND JAWS

The aspects of the ammonoid conch morphology easiest to access are the general geometry and the contact of septa with the conch wall (suture line), well discernible on internal moulds. Growth increments on the conch surface are less commonly preserved because the aragonitic conch wall is rarely transformed into calcite with enough precision. Even less commonly preserved, but of much biological and taxonomic value, are initial whorls of the conch. In the Late Palaeozoic goniatites and Mesozoic ammonites the first whorl of the conch has a smooth surface devoid any marks of growth increments Kulicki *et al*. 2002). This is generally accepted as the evidence of its formation within the egg covers and the ammonitella developmental stage preceding the primary shell constriction is considered embryonic. However, in the orthoceratid nautiloids (Dzik 1981, 1885), bactritids (Doguzhaeva 2002), and earliest ammmonoids (e.g., Klofak *et al*. 1999) the conch development stage corresponding to ammonitella bears distinct growth increments. Apparently juvenile early cephalopods were free living. The transition from free-living larva to development of the larva inside the egg until its metamorphosis was probably gradual and proceeded independently in many lineages, like other molluscs. In some goniatites with a smooth ammonitella conch, adult morphological features develop suddenly, showing that the change was connected with a metamorphosis of anatomy, not just a retardation of growth resulting from hatching. Therefore I prefer to apply the term “larval” to conchs at the pre-metamorphosis stage of the development, equipped with two first septa. In the material from the Holy Cross Mountains a few phosphatized larval conchs have been found, the larval stage is also discernible in pyritic internal moulds found in conodont samples.

Little data are available on the anatomy of the Devonian ammonoids. Rarely discernible muscle scar attachments are known (Richter 2001, 2002; Richter and Fischer 2002). Only in a few cases the conchs can be matched with jaws.

ANAPTYCHI AND APTYCHI

The ammonoid jaws functioned simultaneously also as opercula (Dzik 1981). To be preserved, the mostly organic jaws of the Devonian ammonoids required anoxic conditions of sedimentation, represented by the black shale facies. The only horizon in the Holy Cross Mountains where ammonoid jaws occur in significant number is the calcareous shale at Kowala of earliest Famennian (possibly also latest Frasnian) age.

Unfortunately, no determinable cephalopod conch has been found in association with them, so it can only be speculated, to which ammonoid taxa they belonged. A few single-piece lower jaws (anaptychi) do not differ in outline from those identified in the living chamber of the gephyroceratid *Crickites* by Matern (1931) or closing aperture in *Sphaeromanticoceras* (Clausen 1969). Although the specimens were collected from the scree, it is likely that they come from strata of latest Frasnian age. At Kowala, the cephalopod lower jaws split

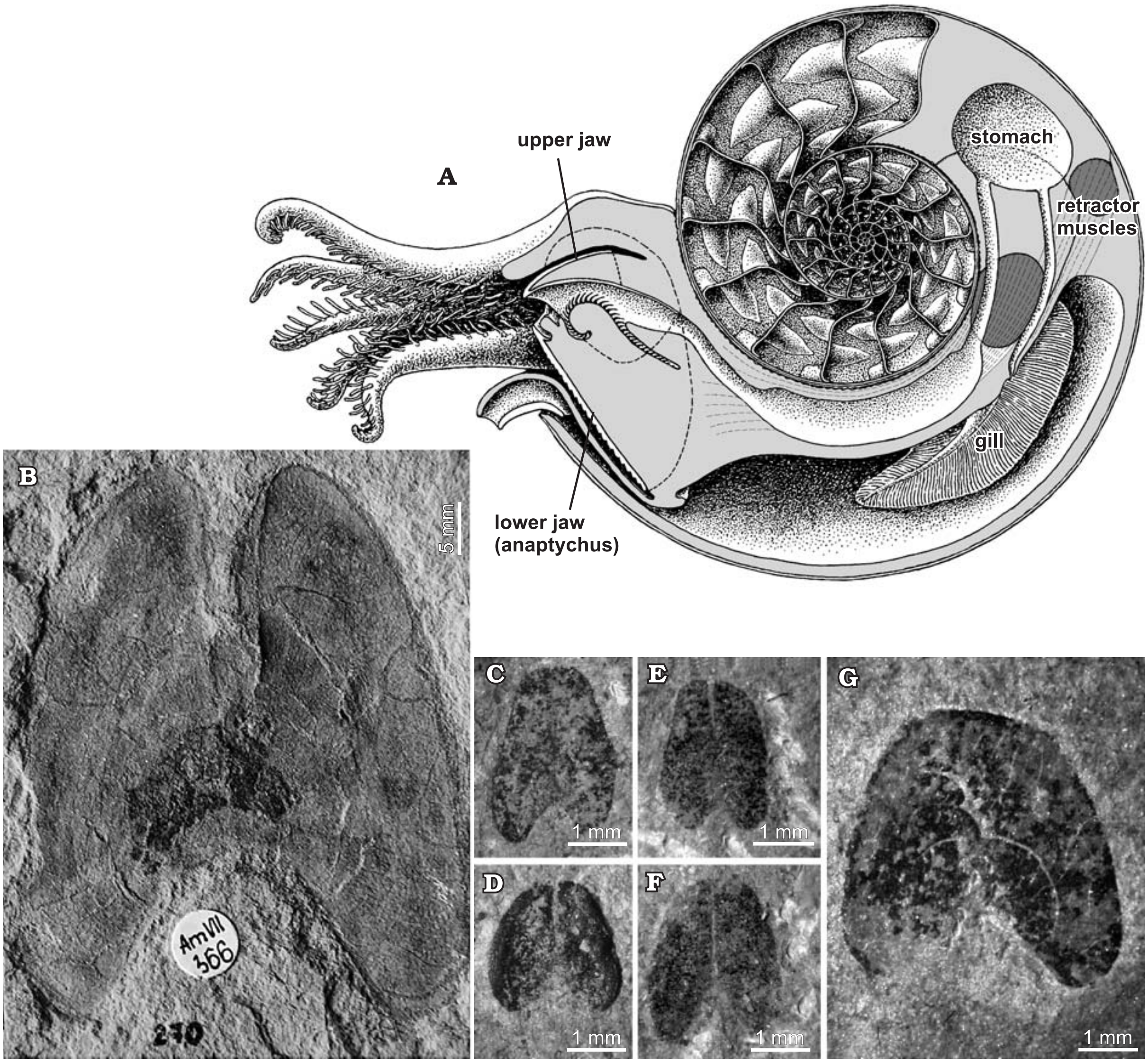


Fig. 139. Probable ammonoid jaws from the Late Devonian at Kowala in the Holy Cross Mountains. **A**. Hypothetical medial section of an advanced tornoceratid showing position of the jaws. **B**. Large aptychus with separated valves from the same stratum, specimen ZPAL AmVII/366. **B**–**F**. Juvenile anaptychi possibly belonging to *Tornoceras*, from the earliest Famennian with the organic chitinous tissue carbonized or pyritized (C), specimens ZPAL AmVII/370, 371, 374, and 373. **G**. Carbonized anaptychus, possibly from the latest Frasnian and belonging to a gephyroceratid, specimen ZPAL AmVII/367.

medially into two valves (aptychi) are much more common. Their occurrence in the Devonian is surprising, as true aptychi are confined to the late Mesozoic, except for those of the Silurian arionoceratid nautiloids. The possibility that the fossils from Kowala represent bactritoid or orthoceratid jaws can be rather excluded because of the size of the largest specimens, many times exceeding that of the late Devonian bactritids (Fig. 139B). Their association with the tornoceratids, the only ammonoids known from strata of this age in Europe, is more plausible. The lower jaw of the early Carboniferous goniatitid *Girtyoceras* (Doguzhaeva *et al*. 1997), as well as its late Carboniferous relative *Eoasianites* (Closs 1967), significantly differ in its shape, being similar rather to the jaws of the nautilids. Whether there were several reversals in the evolution of ammonoid beaks or rather the goniatitids represent a side branch of the main ammonoid lineage, remains to be clarified. The pentagonal shape of the probable anaptychus *Libodiscus* from the early Tournaisian Exshaw Shale of Alberta (Dzik 1997, p. 126) support the idea of continuity between the Frasnian and post-Carboniferous ammonoid jaws with opercular function. Anaptychi of a somewhat similar pentagonal shape have been described from the early *Clymenia* Stufe of the Rhenish Slate Mountains by Korn (2004*b*) and the Cleveland Shale of Ohio (Frye and Feldmann 1991).

The names introduced for ammonoid jaws are valid from the nomenclatorial point of view, and might potentially compete for priority with names based on conchs. This approach has been executed already by Matern (1931), who identified the jaw (anaptychus) *Spathiocaris koeneni* Clarke, 1884 in the living chamber of *Crickites holzapfeli* Wedekind, 1913. The type specimens of both taxa are from the same horizon and region, so their biological identity raises little doubt. This is not so apparent in the case of the type species of *Spathiocaris*, *S. emersonii* Clarke, 1882 from the Frasnian Portage Formation at Naples, Ontario (Clarke 1882). Potentially, *Spathiocaris* may appear to be a senior synonym of, say, *Manticoceras* Hyatt, 1884, but it would not be practical to enforce this nomenclatorial action because of rather indifferent morphology of the Devonian ammonoid mandibles. Fortunately, no such problem is connected with the Famennian ammonoids discussed below.

GROWTH AND FUNCTION OF THE CONCH

It is generally believed that the cephalopod septum geometry is of functional importance, especially when it shows convex areas acting as vaulting in the generally concave septum (when seen from the conch aperture). This is why in the ammonoid and nautiloid taxonomy much value is given to the course of the suture line – a planar representation of the contact between septum and the conch wall. However, the correspondence between the suture line and geometry of the septum is not straightforward and similar sutures may express different patterns of convexities and concavities of the septum. In the simplest situation, the visceral sac of an ammonoid body behaves as a balloon under pressure of internal fluids and its end develops a hemispherical shape in a cylindrical body chamber of the conch (Seilacher 1975). If the cross section of the chamber, determined by the secretive action of the mantle margin at its aperture, is laterally flattened, wide lateral sinuses may develop in the suture line. More complex outlines may produce a quite sophisticated pattern of lobes and saddles without any change in the concavity of the septum (Seilacher 1975; Dzik 1984; Korn 1992, 1999; Dzik and Gaździcki 2002). The situation becomes more complex if the body is locally attached to the shell wall with muscles, which hamper its fast withdrawal. Lobes not related to the conch cross-section may then develop, frequently pointed, and marginal parts of the septum may finally develop vaulting (Seilacher 1975). Yet another mechanism of vaulting and complex septal geometry may be related to non-uniform stiffness of the free surface of the visceral sac. This could have been caused by the translocation of some internal organs towards the venter as a result of increased involuteness of the conch.

The conch involuteness and the whorl expansion rate are independent aspects of the conch geometry. Involute and evolute conchs may have the same whorl expansion rate, and *vice versa*. The whorl expansion rate varied very much among the early ammonoids being clearly connected with their swimming abilities (Klug *et al*. 2004). The Agoniatitina, Gephuroceratina, Prolecanitida and Paraceltitina generally show a high whorl expansion rate and significant control of ontogeny, while Anarcestina, Pharciceratina, Tornoceratina, and Goniatitina show a low expansion rate (Korn and Klug 2001). This is not an evolutionary stable character and within the Tornoceratina there was a change from the tornoceratids with relatively high whorl expansion rate to cheiloceratids with low expansion rate, the character subsequently inherited by the Goniatitina, but changed again during the evolutionary history of the Prolecanitina (Korn 1994).

Wrinkle layer. — The wrinkle layer of the ammonoid shell wall (House 1971) was secreted by the dorsal surface of the animal head while it extended from the living chamber. This is quite clearly shown, among others, by the specimens of *Tornoceras typum* from Jabłonna with preserved intact aperture (Fig. 141A_3). The extent of the wrinkle layer is there clearly delimited. It formed a lobe outside the aperture. The area was in contact with the body only when withdrawn from the conch. The secreting organ was thus rather the animal's head than a specialized part of the mantle. This suggests that the wrinkle layer is homologous to the "black layer" of the nautilids and ceratites, occurring in exactly the same region near the conch aperture (Klug *et al*. 2004).

Korn (2000) compared irregular meandering protrusions on the shell surface of some Famennian ammonoids with the wrinkle layer, using this as the evidence of their conchs being covered with mantle during life. These structures resemble mineralized periostracum protrusions, the feature of conchs of many mollusks, including the Mesozoic ammonites.

Internal thickenings and constrictions of the conch. — Internal thickenings are specific for many Famennian cheiloceratids and a high diagnostic value was attributed to them by Sobolew (1914). It is thus important to understand their origin before their use in taxonomy is supported or abandoned. As shown by some mature specimens of *Cheiloceras subpartitum* from Łagów, which died immediately after developing the last internal thickening of the shell, the thickening was produced at the margin of the aperture or immediately behind it. As a result, in underived cheiloceratids the thickenings tend to follow the growth increments. In *Prionoceras*, there is even a connection between irregularities at the conch surface and the thickening below. In more derived cheiloceratids such a correspondence has disappeared and in their conchs the apertural sinus may co-occur with constrictions forming a prominent ventral saddle (e.g., *Cheiloceras inversum*). Apparently, the place of formation of the thickenings moved behind aperture, although most probably its most distal part was still initiated at, or near, the aperture. This is suggested by the unity of external and internal shell wall features in *Balvia*. The mechanism controlling development of such constrictions remains unknown. It could have been similar to that responsible for the divaricate shell ornamentation in other mollusks, that is the zone of formation of the constriction migrated along the aperture margin with its growth (this does not seem especially likely) or a linear narrow zone of increased secretion of the lamellar aragonite layer of the conch extended across the mantle, initially in connection with its margin.

Terminalized conch growth. — It is generally assumed that a crowding of septa and growth increments near the aperture is sufficient to prove maturity of the ammonoid conch (e.g., Makowski 1991). Actually, these features of the conch are just reflections of delayed growth, which may be accidental, seasonal or connected with spawning, and may thus be misleading. Regrettably, an alternative to this potentially simplistic reasoning is offered in the Famennian only by the conch geometry of the prolobitid goniatites and wocklumeriid clymenias. In both groups the mature body chamber shows a profound change in its cross-section and develops periapertural modifications. Unlike the post-Triassic ammonites, this does not seem to be an expression of sexual dimorphism. The body chamber modification of *Prolobites*, with a constriction near the aperture strengthened with an internal thickening, seems to be a protection agains predators. The mature conch shape of the wocklumeriids probably improved their hydrodynamic properties.

DESCRIPTION AND CLASSIFICATION OF THE AMMONOIDS

In this work a review of the ammonoid faunal dynamics in the Famennian of the Holy Cross Mountains and Sudetes is presented rather than a formal description of the taxa. A reliable taxonomic research, as exemplified by works of Korn (e.g. 1994) and Becker (e.g., 1993b), would require access to the mostly German type and topotype material. In the case of the taxa based on materials from Poland, very few type specimens survived the World War II and these were already reillustrated by earlier authors. The types of Sobolew (1914) and Dybczyński (1913) have not been traced in known museum collections and are probably all lost. Their type strata are no longer accessible (with a few exceptions which were attempted by myself to exploit). In the former Dzieduszycki's Museum collection in Lvov there are many specimens collected by Dybczyński at Sieklucki' brickpit (located in the western part of Kielce, no longer accessible). The pyritized ammonoid specimens occurred there, together with numerous concretions, in the Quaternary sand covering the Famennian shale excavated in the pit (Sobolew 1912a). They were washed out from various stratigraphic units of the Famennian (possibly even Frasnian, if *Beloceras acutodorsatum* Dybczyński, 1913 truly represents the genus) in the Pleistocene and are obviously heterogenous from the stratigraphic point of view. It is potentially possible to select neotypes from this material but these would be of little use, as they in fact lack any stratigraphic information. Fortunately, a closely similar material has been recovered from black shale within the *C. marginifera* Zone at Kowala, which suggests that most (but not all) of the Sieklucki's brickpit material was derived from this horizon.

Most of the evidence presented below is derived from macroscopic internal moulds of the ammonoid conchs with fragments of the original shell preserved. Camera lucida drawings of the suture and growth lines, together with photographs of specimens whitened with ammonia chloride illustrate taxonomic descriptions below. Whenever there is enough evidence, the geometry of the septum is reconstructed in a diagrammatic way.

Taxonomic nomenclature of the Famennian ammonoids. — The type species of the three representative genera of Paleozoic ammonoids, *Cheiloceras*, *Prionoceras*, and *Imitoceras* all have obliquely convex profile of the conch aperture, as well as the same or closely similar shape of the conch and the external part of the suture. They differ in a degree of folding of the dorsal part of the septum and in the distribution or lack of the internal conch thickenings, features do not considered to be diagnostic for high rank ammonoid taxa and distinguishing rather species within particular genera. Yet, these are types of their own superfamilies! This traditional approach is an expression of a general trend in the evolution of taxonomy towards extreme splitting of taxa and rising their ranks. As a result of professional specialization and low number of taxonomists in particular areas of research (in the case of Devonian ammonoids rarely exceeding a few students involved in research at the same time) there is little interest in standardizing taxa. The difference between traditional taxonomy of the Famennian tornoceratine ammonoids (several superfamilies) and that of the coeval palmatolepidid conodonts (single genus), both including a similar numbers of sympatric species, exemplifies this very well.

These differences in classification methodologies would be probably of little importance if not the value that is given to counting taxa in hope to disclose patterns in the evolution of the living world. Moreover, the too deep discrepancy in attitudes makes the Linnean taxonomy methodologically weak and prone to destruction by followers of more radical philosophies of taxonomy. I believe that to make taxonomy truly useful in its main function as a measure of diversity (even if it is unavoidably subjective) some kind of standardization is necessary. This can be achieved by keeping in mind that too many taxa within a taxon of higher rank make classification impractical, difficult to memorize and to use. Approximately similar range of morphologic variability should also be allowed within taxa of the same rank. Obviously, this cannot be done too rigorously. I believe that a controlled subjectivity is still a much better solution than to go into the illusion that taxonomy can be done in a strict and completely objective way (Dzik 2005).

Nomenclatorially invalid “generic” names of Sobolew (1914), cited in the text, are not italicized.

Phylum **MOLLUSCA** Linné, 1758
Class **CEPHALOPODA** Cuvier, 1795
Subclass **AMMONOIDEA** Zittel, 1884
Order **GONIATITIDA** Hyatt, 1884
Suborder **TORNOCERATINA** Wedekind, 1918

Remarks. — The tornoceratine goniatites inherited a low conch expansion rate after their anarcestine ancestors (Korn and Klug 2001). The conchs are generally involute with the area of the septum on both sides of the preceding whorl vaulted in the dorso-ventral plane.

Much value is given to the profile of aperture in the tornoceratine goniatites and an elaborate terminology for various shapes of growth lines and ribs is available. To make the text comprehensible also to non-specialists I avoid such terms and refer only to prominence of ventrolateral protrusions of the aperture (auricles) and depth of the ventral infundibular sinus. Schematic drawings of growth lines offer enough information on their exact course. Also while describing sutures possibly neutral descriptives are used in hope that this will be understandable to followers of various notation systems.

Family **Tornoceratidae** von Arthaber, 1911

Diagnosis. — Conch aperture with auricles and relatively high whorl expansion rate, septum of simple geometry developing only small lateral vaultings (expressed as one set of flank lobes in the suture) with a tendency to simplification in secondarily evolute forms.

Remarks. — The main difficulty with the taxonomy of generalized tornoceratids is the simplicity of their external conch morphology and geometry of the septum. To interpret the latter it seems enough to invoke the “balloon concept” of the cephalopod septum as an interplay of the whorl cross-section and uniformly distributed hydraulic pressure within the animal soft body (Seilacher 1975). Only in more advanced tornoceratids vaulted areas in the septum developed, suggestive of a more complex pattern of muscular attachments of the body to the internal conch wall. The septal and conch morphology of early tornoceratids seems to be sensitive of evolutionary reversals and homeomorphy an thus of low taxonomic value. In fact, the conch shape and the suture line controlled by it seem variable in both the early Frasnian (Bogoslowsky 1971) and latest Frasnian (Dzik 2002) species represented by a large number of specimens.

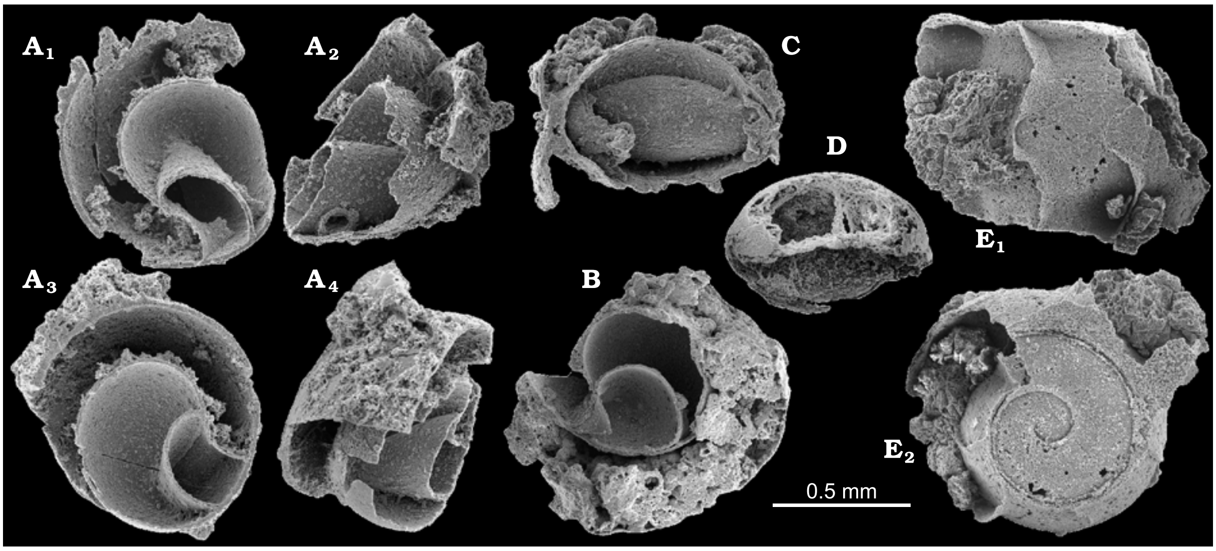


Fig. 140. Silicified juvenile ammonoid conchs from the latest Frasnian at Miedzianka, samples Md-18 (A) and Md-21 (B–E) in the Holy Cross Mountains. **A**. Almost medially split protoconch of a tornoceratid (probably *Linguatornoceras*, the only genus convincingly identified from strata of that age in the area; Dzik 2002) showing swollen first chamber, parts of specimen ZPAL AmVII/1808 in medial and septal views. **B**. Similarly preserved specimen ZPAL AmVII/1810. **C**. First septum of specimen ZPAL AmVII/1811. **D**. Specimen preserved as a partial internal mould of the first chamber, ZPAL AmVII/1812. **E**. Protoconch of a gephyroceratid in lateral view and its ventral surface with remains of septa on the second coil, ZPAL AmVII/1813.

In such a situation the morphology of the first larval septum, deeply concave in at least some tornoceratids (Ruzhentcev 1962; Bogoslovsky 1969) may be of much taxonomic value, because of its uniqueness. The first septum is very different from the succeeding septa and apparently originated under different conditions of secretion. One may speculate that this was a result of secretion of the phragmocone chamber liquid being delayed in respect to secretion of the septal tissue. The volume of the first regular phragmocone chamber was much smaller than that of the protoconch, so subsequent septa originated in a more regular rhythmic pattern. Anyway, this peculiar morphology of the larval (ammonitella) conch may be a useful diagnostic character (synapomorphy) for the least derived trornoceratids.

The problem thus emerges when this concave first septum originated and how long it persisted in the evolution of the tornoceratids. This character was first identified in a typical *Tornoceras* species from the early Frasnian Domanik Formation of Timan (Ruzhentcev 1962; Bogoslovsky 1969). House (1965), while interpreting pyritized protoconchs of the type species of the genus from the Givetian Alden Marcasite horizon within the Ledyard Shale of New York, suggested the presence of an unusually large caecum. It seems possible that this was actually the first septum which developed such a swollen structure. If true, this character might define the origin of the tornoceratid clade more precisely than the conch morphology.

This bizarre first septum morphology is shown by silicified tornoceratid specimens from the topmost Frasnian strata at Miedzianka in the Holy Cross Mountains (Fig. 140) associated with a normally developed (not swollen) siphuncle. Among postlarval tornoceratids of generalized conch morphology only *Linguatornoceras* has been identified in these strata (Dzik 2002). A similar, but not so strongly concave first septum characterizes a tornoceratid from the significantly younger Upper Łagów Beds at Dule (sample Ł-38). Associated protornoceratids show normal development of the first septum. This suggests a gradual disappearance of this character and explains why the clymeniids do not show any signs of its presence, despite their probable tornoceratid ancestry.

Genus ***Tornoceras*** Hyatt, 1884

Type species: *Goniatites uniangularis* Conrad, 1842 from the latest Givetian Leicester Pyrite of New York.

Diagnosis. — Involute discoidal conch with closed umbilicus; the main subventral area of the septum concave, without lateral vaultings; the first septum deeply concave and swollen.

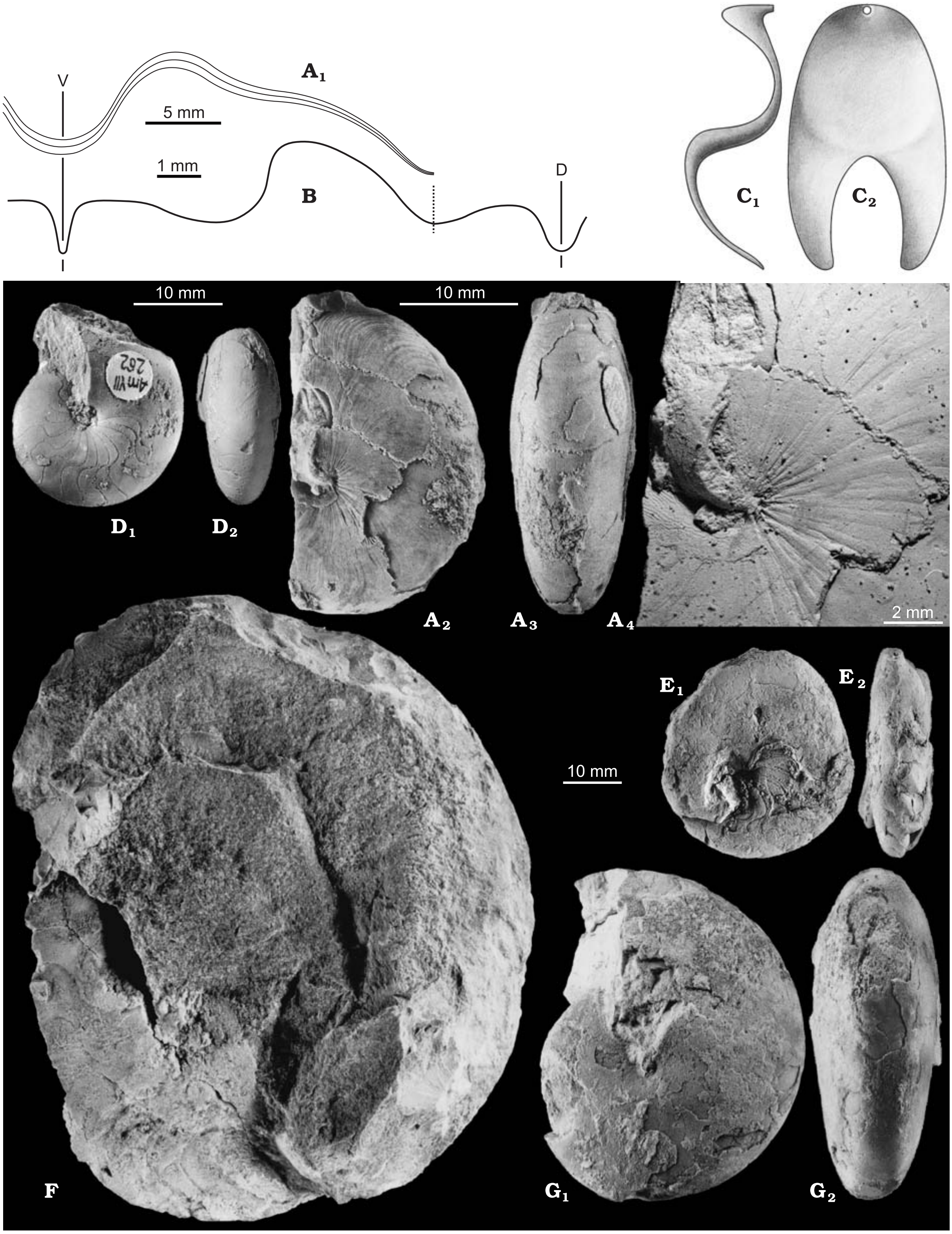


Fig. 141. The most generalized tornoceratid *Tornoceras typum* (Sandberger *et* Sandberger, 1851) from the early Famennian *K. crepida* Zone at Jabłonna (A, B, D, F), Kadzielnia (C, G), and Wietrznia (E) in the Holy Cross Mountains. Growth lines and views of the conch with preserved shell and complete aperture, magnified to show the extend of wrinkle layer (A, bed 7), specimen ZPAL AmVII/299; suture (B) of AmVII/259 (external part; bed 7) and 301 (internal part; bed 6); septal geometry (C) based on specimens AmVII/266 (bed 8) and 301 (bed 6); mature male? conch with exfoliated shell (D, bed 5) ZPAL AmVII/262; internal mould of subadult conch (E, beds with *Concavicaris*) ZPAL AmVII/1692; mature female? conch (F, bed 9) ZPAL AmVII/364; possible macroconch phragmocone(G) with coarsely recrystallized shell ZPAL AmVII/458.

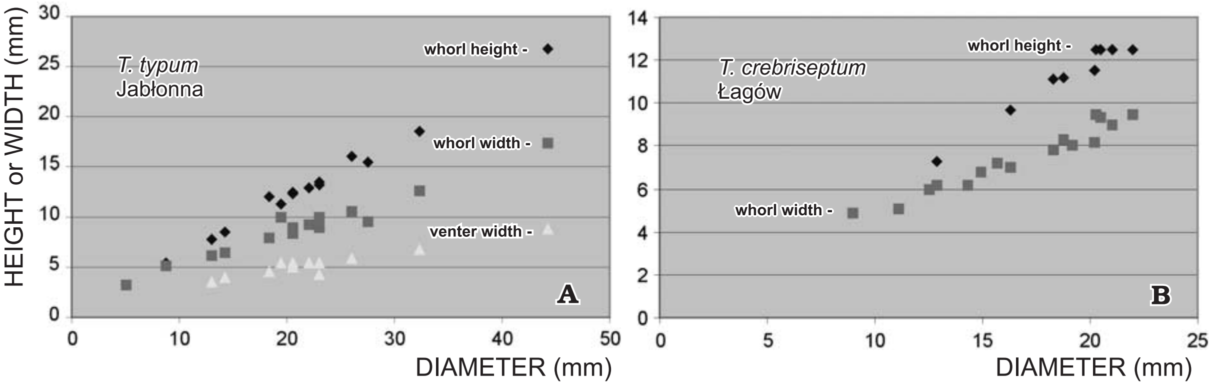


Fig. 142. Variability of conch dimensions of *Tornoceras* **A**. *T. typum* (Sandberger *et* Sandberger, 1851) from the early Famennian *K. crepida* Zone at Jabłonna (beds 5, 6, and 7). **B**. *T. crebriseptum* Raymond, 1909 from the mid Famennian *C. marginifera* Zone at Łagów (samples Ł-5, 28, 29, 30, 31, and 33, probably all from the same bed).

Remarks. — The Frasnian populations of the main lineage of *Tornoceras* differ from those of the Givetian in a less acute outline of the ventral saddles (Bogoslovsky 1971) and from those from the early Famennian in suture lobes restricted to the subventral part of the whorl.

The septum geometry of *Tornoceras* is extremely simple, simpler than one may infer from the relatively complex course of the suture line. There are only concavities in the septum that fits closely the baloon model of Seilacher (1975). The difference between the central concavity located ventrally of the preceding whorl and concavities on its side apparently resulted from different ease of withdrawal of the body while developing a new chamber. This may have been related to the animal's anatomy. One may guess that the internal organs of higher stiffness (liver?) occupied the ventral part of the whorl, resisting the cameral liquid pressure more than the dorsolateral parts.

Tornoceras typum (Sandberger *et* Sandberger, 1851)
(Figs 139B–E?, 141, 142A, and 159)

Type horizon and locality: Probably Frasnian at Seßacker in the Dillenburg region in the Rhenish Slate Mountains (Becker 1993b).

Material. — 23 specimens.

Diagnosis. — Smooth, involute, discoidal conch, deep gently concave flank lobe of the suture line.

Remarks. — This species is usually referred to as *T. simplex* (von Buch, 1832) the original drawing of the type of which shows a specimen with open umbilicus and is a *nomen dubium* (Becker 1993a, p. 182). *T. incrassatus* (Gürich, 1896), based on a specimen from the early Famennian of Karczówka is probably available as a valid name. Although the depository of the original specimen remains unknown, pieces of the rock with ammonoid conchs are preserved in the collection of Dymitr Sobolew in Kharkov, Ukraine.

According to Becker (1993a) this mostly early Famennian species is close to the Frasnian *Linguatornoceras linguum* (Sandberger *et* Sandberger, 1851), the only tornoceratid preceding it stratigraphically in the Holy Cross Mountains (Dzik 2002). Makowski (1991; followed by Becker 1993b) classified the early Frasnian tornoceratids from the Holy Cross Mountains in *T. frechi* (Wedekind, 1918) proposed to be the type species of the new genus *Phoenixites* by Becker (1993b). Unfortunately, similarly as in the case of *T. typum*, the type horizon of *P. frechi* is uncertain. Originally the species was based on an early or mid Frasnian material (Wedekind 1918) and Becker (1993a) proposed the neotype from Seßacker near Oberscheld, probably also of Frasnian age. This would require that these two closely similar tornoceratid lineages co-occurred in both the Frasnian and Famennian, crossing the boundary between these ages. The diagnostic feature of *Phoenixites* is the presence of ventrolateral furrows at the juvenile growth stages. Nothing like that has been recognized in the specimens available to me, their smallest diameter being 5 mm.

There is a significant variation in the conch geometry and suture line within particular samples. In some specimens the flank lobe is strongly concave (as typical for the species), in others shallow, almost approaching the status typical of the mid Famennian *T. crebriseptum*. Juvenile specimens may have rather flat or, instead, globose conchs. Serial ventral thickenings of the aperture, considered by Becker 1993b to define his

Phoenixites sulcatus and *P. varicatus* (Wedekind, 1918), co-occur with those without thickenings (in Jabłonna beds 7 and 24).

The tornoceratids show an apparent bimodality in size frequency distribution interpreted as a case of sexual dimorphism (Makowski 1962, 1963, 1991). Already in the early Frasnian Domanik Formation of the Timan specimens of diameter about 35 mm with densely distributed terminal septa co-occur with conchs of at lest 90 mm diameter (Bogoslowsky 1971). In my material from Jabłonna, a still not mature specimen of 115 mm conch diameter co-occurs with mature specimens of 27 mm size. Makowski (1991) proposed to distinguish a separate chronosubspecies *T. frechi parvum* based on the allegedly small size of macroconchs but the illustrated specimens do not show convincing evidence of growth termination and may be actually juveniles.

In the laminated marls of the earliest Famennian at Kowala, numerous cephalopod jaws occur. Their elongated shape suggests that the conch aperture to which they were fit was rather compressed, with a rounded venter. This would fit the morphology of *Tornoceras*, the only lineage expected to occur in strata of this age. The most unexpected aspect of these jaws is that they show a medial suture; these were actually aptychi (Fig. 139B–E). Minute specimens, probably juvenile, show sometimes an iron mineralization suggestive of substantial original thickness of valves in their marginal parts. Large, probably mature specimen is split along the suture and the ventral tips of valves are rounded also admedially.

Distribution. — Probably the late *K. triangularis* Zone at Karczówka, the early *K. crepida* Zone at Wietrznia, Kadzielnia, Jabłonna (beds 5–7), and Janczyce (Makowski 1991).

Tornoceras subacutum Makowski, 1991
(Figs 143A–H and 159)

Type horizon and locality: Bed 3 of the early Famennian at Janczyce, Holy Cross Mountains.

Material. — 15 specimens.

Diagnosis. — Macroconchs with narrowly trapezoidal cross section of the venter; microconchs with rounded venter (Makowski 1991).

Remarks. — The evolutionary position of the species within the continuous phyletic lineage running from *T. typum* to *T. sublentiforme* was presented by Makowski (1991). Sutures in three specimens (diameters 26 to about 30 mm) show a terminal condensation. The pyritized minute specimen of Gomi-monomeroceras (*Tornoceras*) *kielcense* Sobolew, 1914, from Sieklucki's brickpit may belong to this species although its suture shows a rather unusual symmetrical shape of the flank lobe.

Distribution. — The *K. crepida* Zone at Janczyce (bed 3 of Makowski 1991) and Kadzielnia.

Tornoceras sublentiforme (Sobolew, 1914)
(Figs 143I–N and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — Eight specimens.

Diagnosis. — Acute or very narrowly tabulate venter of adult specimens; generalized tornoceratid suture.

Remarks. — This is the end member of the lineage of *Tornoceras subacutum* as shown by Makowski (1991). Relatively large specimen MD 11090 from Kadzielnia in the collection of the former Dzieduszyckis' Museum in Lvov, about 70 mm in diameter, and mature specimen ZPAL AmVII/991 in my collection, of diameter 57 mm, have an almost acute venter with a very narrow tabulation. The complete lineage seems to be represented at Kadzielnia, but the material comes from loose blocks and the exact stratigraphic position of particular specimens is hard to determine.

Distribution. — The *K. crepida* Zone at Janczyce (beds 4–5 of Makowski 1991), Jabłonna (beds 10, 11, 14), and Kadzielnia; reworked at Sieklucki's brickpit in Kielce.

Tornoceras crebriseptum Raymond, 1909
(Figs 142B, 144A–D and 159)

Type horizon and locality: Mid Famennian (probably *Platyclymenia annulata* Zone) Three Forks Shale north of Three Forks, Montana (D. Korn, personal communication 2005).

Material. — 33 specimens.

Diagnosis. — Relatively shallow flank lobe of the suture.

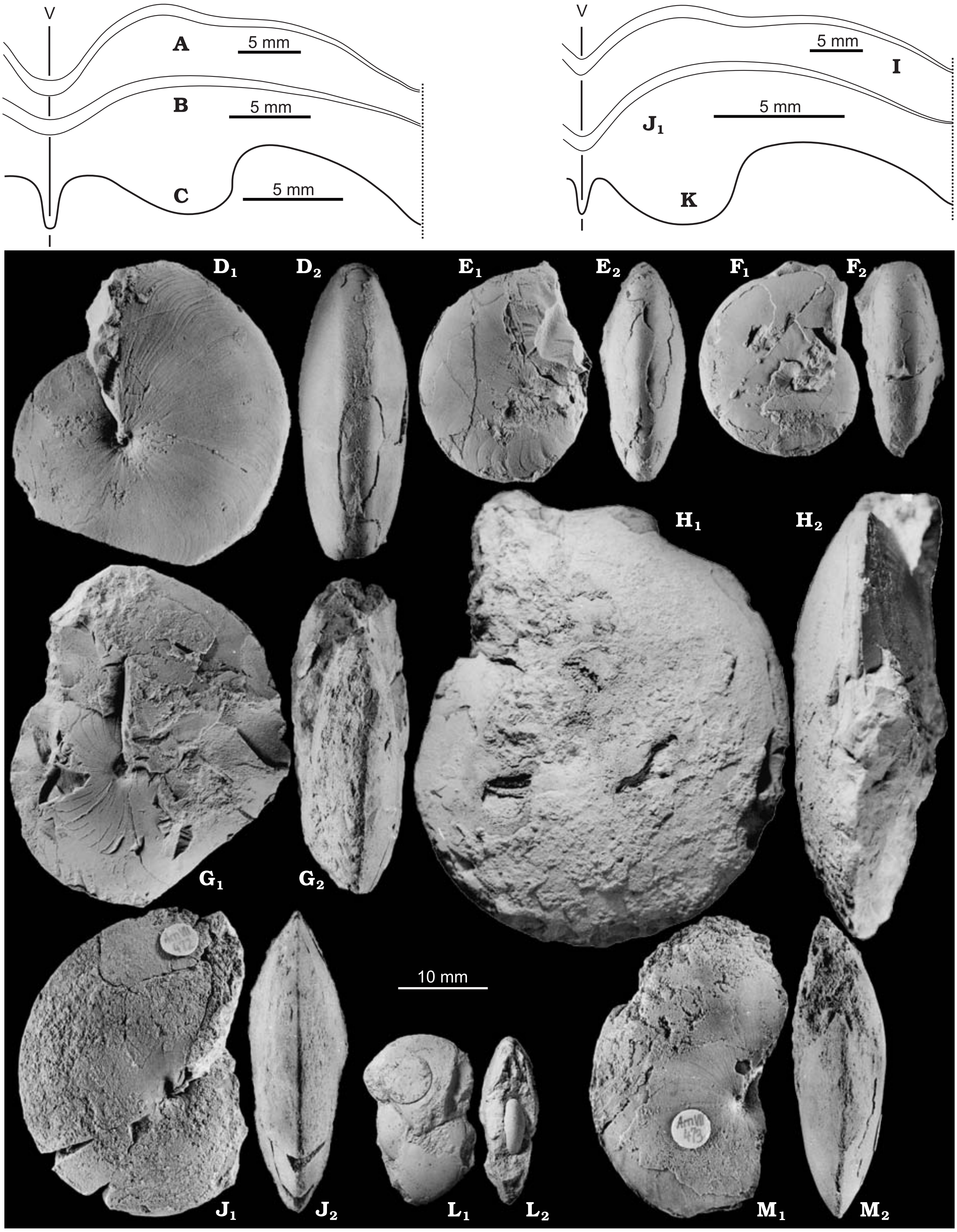


Fig. 143. Tornoceratids with acute conch venter from the early Famennian *K. crepida* Zone of the Holy Cross Mountains. **A**–**H**. *Tornoceras subacutum* Makowski, 1991 from Kadzielnia; growth lines based on unnambered probable macroconch from Makowski's collection (A) and microconch ZPAL AmVII/287 (B), suture line based on specimen ZPAL AmVII/286 (C); probable microconchs ZPAL AmVII/990, 999, and 987 (D–F) and macroconchs ZPAL AmVII/991 (G) and MD 11090 (H). **I**–**N**. *Tornoceras sublentiforme* (Sobolew, 1914) from Janczyce (I, bed 5 of Makowski 1991) and Jabłonna (J–N); growth lines based on unnambered probable macroconch from Makowski's collection (I) and microconch ZPAL AmVII/473 (J, bed 11; also views of the specimen), suture line based on specimen ZPAL AmVII/477 (K, bed 11); juvenile ZPAL AmVII/482 (L, bed 14), and probable microconch ZPAL AmVII/ 472 (M).

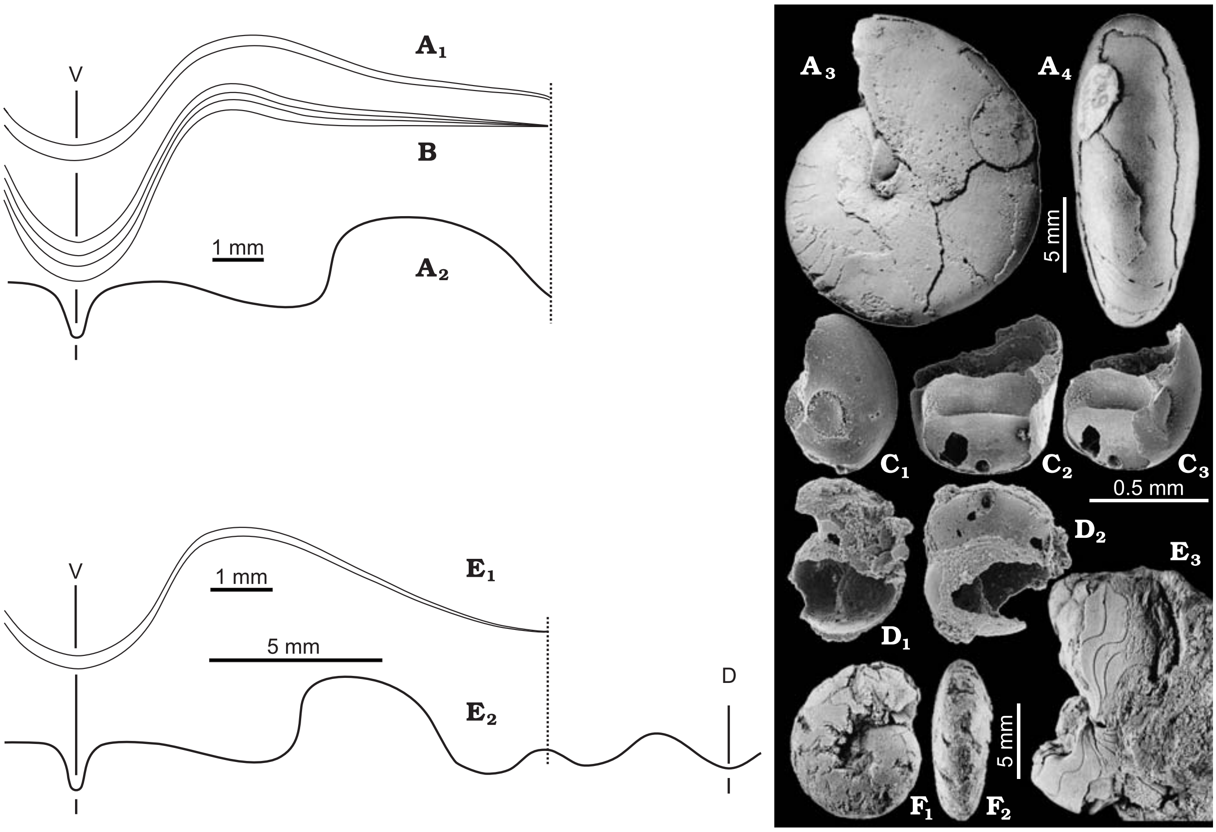


Fig. 144. Late species of *Tornoceras* from the mid Famennian of the Holy Cross Mountains. **A**–**D**. *T. crebriseptum* Raymond, 1909; growth lines traced from imprints on the conch internal mould, suture, and views of specimen ZPAL AmVII/642 from the *C. marginifera* Zone at Łagów-Dule (A, sample Ł-5), growth lines of specimen ZPAL AmVII/646 from the *P. trachytera* Zone at Jabłonna (B, bed 24) with numerous ventral shell thickenings, but do not showing suture, possibly belonging to the same species; and larval (ammonitella) conchs AmVII/1916 and 1614 from the same zone (C, D, sample Ł-38). **E**, **F**. *T. pseudobilobatum* Dybczyński, 1913 from the mid *C. marginifera* Zone at Kowala; growth lines traced from imprints on the conch pyritic internal mould, suture, and views of specimens ZPAL AmVII/1004 (E) and ZPAL AmVII/112 (F).

Remarks. — *Tornoceras applanatus* (Gürich, 1896) based on a specimen from the Upper Łagów beds (Sacculus-Bank) probably refers to the same species. All available specimens are minute in size, up to 22 mm in diameter, three of them with a condensation of sutures suggestive of maturity. Perhaps also Gomire-monomeroceras (*Tornoceras*) *simplicius subacutum* Sobolew, 1914 from the clymeniid limestone at Łagów-Dule belongs to this species, although only the shape of aperture makes it different from associated *Protornoceras simplicius*. In the Czarnocki's collection housed at the State Geological Institute there is a probably adult specimen IG 284 II.290 about 52 mm in diameter, collected from the grey "Laevigites" limestone (*Nodosoclymenia* bed?) at Ostrówka. Its suture is characteristically simple but growth lines are not recognizable.

Another question is whether the North American type population of *T. crebriseptum* is truly conspecific with the Holy Cross Mountains material. Specimens from the Three Forks Shale are pyritic internal moulds with open umbilicus, which may express an increased thickness of the shell forming a kind of umbonal callus (see Fig. 144A). This character was used by Korn and Titus (2006) to substantiate transfer of the species to *Pernoceras* Schindewolf, 1922, the type species of which is *Protornoceras kochi* (Wedekind, 1908. The Montana specimens show a conical depression around umbo, resembling the Polish species of *Protornoceras* from Kowala in this respect but difficult to compare with specimens from Łagów and Jabłonna having the original shell preserved. The species may truly be related to *P. kochi*.

Distribution. — The *C. marginifera* (samples Ł-5, 28, 29, 30, 31, and 33) and possibly the *P. trachytera* zones at Łagów-Dule and Jabłonna (bed 24), perhaps *L. styriacus* Zone at Ostrówka; reworked at Sieklucki's brickpit in Kielce.

Tornoceras pseudobilobatum Dybczyński, 1913
(Figs 144E, F and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — Six specimens.

Diagnosis. — Suture with incipient dorsolateral lobe and relatively straight course of the ventrolateral saddle, otherwise generalized tornoceratid conch.

Remarks. — In the two best preserved relatively large specimens, the siphuncle position is somewhat asymmetric. Juvenile whorls are gently rounded, any relationship to *Falcitornoceras bilobatum* is thus unlikely, contrary to attribution of this species to *F. falcatum* by Becker (1993*b*). This is probably rather an advanced member of the *Tornoceras* branch.

Distribution. — The mid *C. marginifera* Zone at Kowala; reworked at Sieklucki's brickpit in Kielce.

Genus ***Polonoceras*** Dybczyński, 1913

Type species: *Polonoceras planum* Dybczyński from the Famennian of Kielce, Holy Cross Mountains.

Diagnosis. — Acute auricles of the aperture, involute discoidal conch with small umbilicus, flat sides and more or less tabulate venter; weak ventro-lateral vaultings may develop in the septum.

Remarks. — The incipient vaultings of the septum seems to be an expression of locally delayed withdrawal of the visceral sac, attached to the shell with muscles.

Polonoceras sandbergeri (Foord *et* Crick, 1897)
(Figs 145A and 159)

Type horizon and locality: Probably early Famennian at Nehden, Rhenish Slate Mountains (Becker 1993b).

Material. — Two specimens.

Diagnosis. — Auricles of the aperture with relatively blunt, parabolic profile.

Remarks. — The complex nomenclatorial history of the species was clarified by Becker (1993b) who classified it as *Truyolsoceras sandbergeri*. It seems that it represents an early part of the *P. planum* lineage and I find such generic distinction redundant. Perhaps Gomi-monomeroceras (*Tornoceras*) *dorsoplanum avaricatum* Sobolew, 1914 from the Lower Łagów Beds represent this species, although its somewhat wider umbo may suggest affinities to the *Protornoceras* lineage.

Distribution. — The early *K. crepida* Zone (bed 6) at Jabłonna.

Polonoceras bashkiricum Bogoslovsky, 1971
(Figs 145B–D and 159)

Type horizon and locality: Upper part of the *Cheiloceras* Stufe, 200 m from the mouth of the Ishikay River, South Urals (Bogoslovsky 1971).

Material. — Three specimens.

Diagnosis. — Acute tips of auricles of the aperture; distinctly tabulate venter of mature specimens, rounded in juveniles.

Remarks. — The Frasnian-style suture and the subtrapezoidal cross section of the whorl make this specimen similar to the holotype of *Linguatornoceras linguum* (see Becker 1993b, pl. 3: 13, 14). Conchs of the Famennian species attributed to the genus by this author are, however, different from the Łagów specimen in having a very narrow flank lobe of the suture and rounded margins of the umbilicus. In the latter aspect, the specimen discussed resembles the stratigraphically older species attributed here to *Gundolficeras korni* (Becker, 1993) and *Protornoceras simplicius*, being different in the subtrapezoidal whorl section and deep flank lobe of the suture. Specimens from sample Ł-14 tentatively attributed to the latter species may also belong here, as well as the specimen from the Upper Łagów Beds illustrated by Sobolew (1914) as *Tornoceras escoti* Frech, 1902. The species seems both morphologically and stratigraphically transitional between *P. sandbergeri* and *P. planum*.

Distribution. — The late *K. crepida* (bed 15) and probably the *C. marginifera* (bed 17) zones at Jabłonna; the *C. marginifera* Zone at Łagów-Dule; possibly also reworked at Sieklucki's brickpit in Kielce.

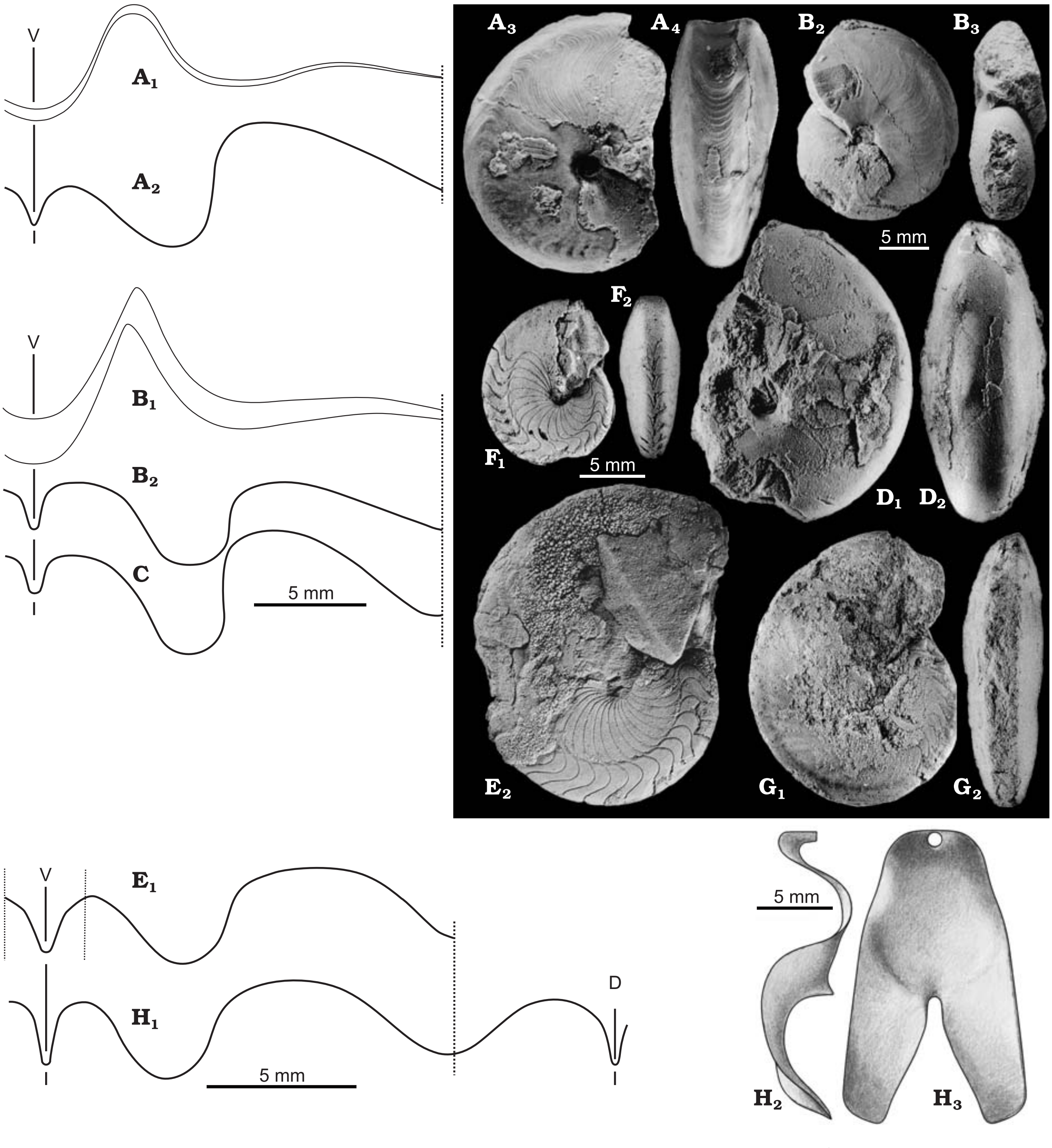


Fig. 145. Underived species of *Polonoceras* from the mid Famennian of the Holy Cross Mountains. **A**. *P. sandbergeri* (Foord *et* Crick, 1897); growth lines, suture, and views of specimen ZPAL AmVII/340 from the *K. crepida* Zone at Jabłonna (bed 6). **B**–**D**. *P. bashkiricum* Bogoslovsky, 1971 from the *C. marginifera* Zone; growth lines and views of specimen ZPAL AmVII/354 from Jabłonna (B, bed 17), suture of ZPAL AmVII/264 (C, bed 15), and views of ZPAL AmVII/1093 from Łagów (D). **E**–**H**. *Polonoceras planum* Dybczyński, 1913 from the mid *C. marginifera* Zone at Kowala; suture and view of specimen ZPAL AmVII/1009 (E), views of ZPAL AmVII/951 and 952 (F, G), suture and septum of ZPAL AmVII/1010 (H).

Polonoceras planum Dybczyński, 1913
(Figs 145E–H and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — 12 specimens.

Diagnosis. — Distinctly tabulate venter even in juvenile specimens, narrow umbilicus.

Remarks. — Tips of auricles are located somewhat dorsally to the tabulate venter, where they sometimes leave a shallow furrow on the phragmocone internal mould. In this respect the species is different from *P. dorsoplanum*, its probable successor.

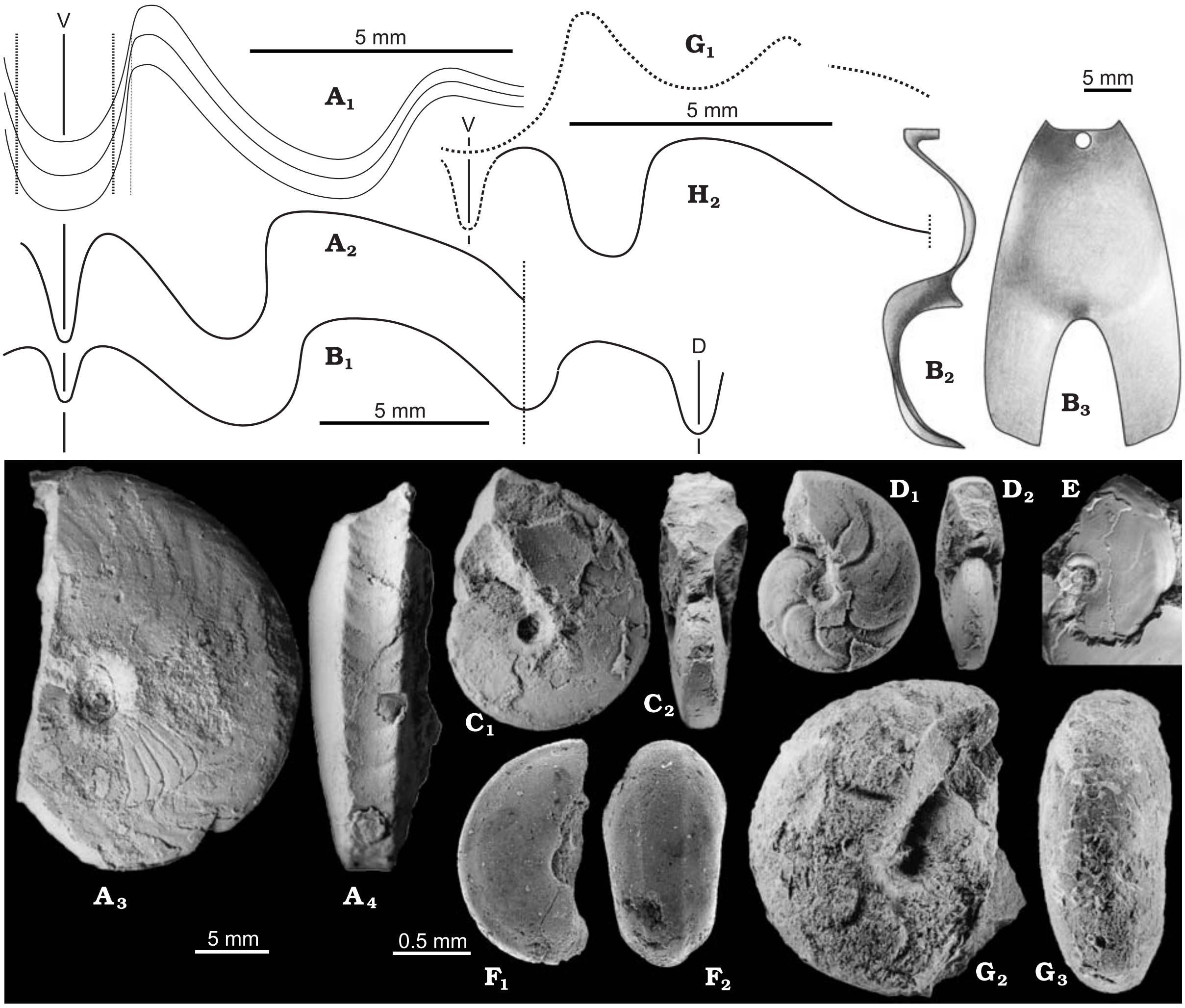


Fig. 146. Advanced species of *Polonoceras* from the Famennian of Poland. **A–E**. *P. dorsoplanum* (Sobolew, 1912) from the *C. marginifera* Zone at Łagów; growth lines, suture, and views of specimen ZPAL AmVII/343 (A), suture and septum of ZPAL AmVII/350 (B), views of specimens ZPAL AmVII/359, 358, and 351, respectively (C–E). **F**. Specifically undeterminable larval (or embryonic) specimen ZPAL AmVII/1837 from the *L styriacus* Zone at Kowala (sample Ko-174) in the Holy Cross Mountains. **G**, **H**. *P. sudeticum* (Renz, 1914) from the *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec in the Sudetes; constriction of the conch and views of ZPAL AmVII/151 (G) and suture of ZPAL AmVII/090 (H).

Distribution. — The mid *C. marginifera* Zone at Kowala; reworked at Sieklucki's brickpit in Kielce.

Polonoceras dorsoplanum (Sobolew, 1912)
(Figs 146A–E and 159)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains (Sobolew 1912b).

Material. — 21 specimens.

Diagnosis. — Deep conical umbilicus with raised margins, acute tips of auricles demarcate the tabulate venter.

Remarks. — Some specimens show periodic constrictions on the conch flanks.

Distribution. — The *C. quadrantinodosa* (samples Ł-28 and 33), *C. marginifera*, and *P. trachytera* zones at Łagów-Dule.

Polonoceras sudeticum (Renz, 1914)
(Figs 146G, H and 159)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

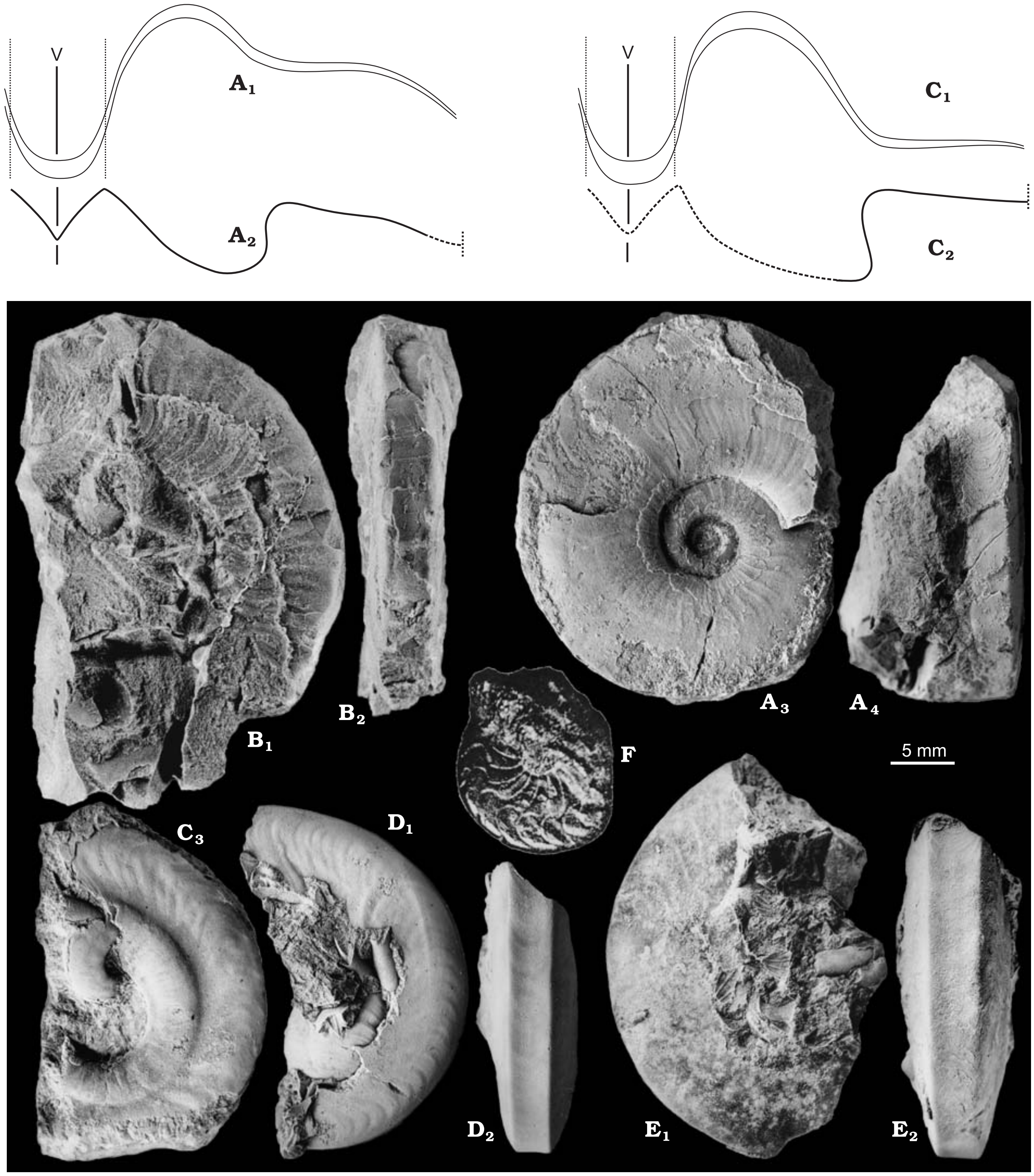


Fig. 147. Species of *Armatites* from the mid Famennian of Poland. **A**, **B**. Early *A. lateroconcavus* (Dybczyński, 1913) from the early *P. trachytera* Zone at Jabłonna (bed 25); growth lines, suture, and views of specimen ZPAL AmVII/341 (A, bed 21), and views of probably mature living chamber ZPAL AmVII/166 (B). **C**–**E**. Late *A. lateroconcavus* (Dybczyński, 1913) from the *L. styriacus* Zone at Jabłonna (A, bed 26) and the late *P. trachytera* Zone at Łagów-Dule (D, E); growth lines, suture, and view (C) of specimen ZPAL AmVII/342, views of fragmentary living chambers ZPAL AmVII/356 and 349 (D, E). **F**. Type specimen of *A. lewinskii* (Dybczyński, 1913) from Quaternary deposits at Sieklucki's brickpit in Kielce (reproduced after Dybczyński 1913, pl. 2: 10).

Material. — Three specimens.

Diagnosis. — Closed umbilicus of conical appearance demarkated by a spiral ridge; roundly tabulate venter; serial constrictions on conch flanks parallel to the aperture, which bears acute auricles; suture with a deep, narrow flank lobe.

Remarks. — Renz (1914) identified his only specimen from Dzikowiec lacking any suture as a new variety of *Oxyclymenia ornata*. The constrictions (not internal thickenings!) in its conch, expressed both on nuclei and the conch surface, are so characteristic that there is little doubt that the newly collected topotype specimens are conspecific. The acute auricles and deep lobe of the suture point to *Polonoceras dorsoplanum* as the ancestor of the species.

Distribution. — The *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec.

Genus ***Armatites*** Becker, 1993

Type species: *Goniatites planidorsatus* Münster, 1839 from the Famennian of Gattendorf in Franconia (Becker 1993b).

Diagnosis. — Conch with tabular or bicarinate venter and flat sides, open umbilicus, generalized tornoceratid suture and aperture with wide, gently rounded auricles.

Remarks. — Among specimens classified in various species of the genus by Becker (1993b) only the lectotype fits the specific morphology of the members of the lineage represented in the Holy Cross Mountains, attributed to *Armatites* here. He later created the new genus *Planitornoceras* for species with a similar apertural profile but a *Protornoceras*-like suture.

Armatites lewinskii (Dybczyński, 1913)
(Figs 147F and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Diagnosis. — Conch with rounded venter and small umbilicus.

Remarks. — The description by Dybczyński (1913) suggests that this may be an early member of the *Armatites* lineage, as indicated by flat flanks and semicircular appearance of flank lobes. Unfortunately, his description and illustrations remain the only source of data on this species. The illustrated specimen is a juvenile and its generalized appearance (especially the rounded venter) may be partly due to the early ontogenetic stage. Both its morphology and probable stratigraphic origin (*C. marginifera* Zone) suggest its ancestral position in respect to other species of *Armatites*.

Distribution. — Reworked at Sieklucki's brickpit in Kielce.

Armatites lateroconcavus (Dybczyński, 1913)
(Figs 147A–E and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — Seven specimens.

Diagnosis. — Flanks of the conch subdivided into two zones by a spiral furrow or escarpment.

Remarks. — Unlike the studied specimens, in the lectotype of *A. planidorsatus* (Becker 1993b, pl. 11: 10) the spiral elevation is restricted to near the umbilicus. All of them show rounded tips of apertural auricles, which makes them different from other specimens attributed to the genus by Becker (1993b). Most of the specimens from Łagów are represented only by ventral parts of the body chamber, only one of them preserved the whole conch flank, with the lateral furrow. This situation seems to be similar to that in the holotype, as described by Dybczyński (1913). The specimen of Petter (1959, pl. 15: 30) from Gourara in Algeria, reillustrated by Becker (1993b) and classified by him in his *A. nudus*, shows a similar aperture to the Polish *A. lateroconcavus*, but narrower umbilicus.

There is an apparent evolutionary change in the lineage. The umbilicus is relatively wide in the geologically oldest specimens from Jabłonna (beds 21–25), with gently rounded margin and flat sides of the conch. In the somewhat younger material from Łagów (sample Ł-14), a shallow furrow in the middle of the flanks developed, achieving the form of a prominent escarpment in the youngest specimen from Jabłonna (bed 26). Closely similar form occurs also in the *Prolobites* horizon in vicinities of the village Spasskij in the South Urals (Perna 1914, pl. 2: 9).

Distribution. — Probably the late *C. marginifera* Zone at Jabłonna (bed 21), the *P. trachytera* Zone at Łagów-Dule (e.g., sample Ł-14) and Jabłonna (beds 23–25); and the *L. styriacus* Zone at Jabłonna (bed 26); reworked at Sieklucki's brickpit in Kielce.

Genus ***Protornoceras*** Dybczyński, 1913

Type species: *Protornoceras polonicum* Dybczyński, 1913 from the Famennian of Kielce.

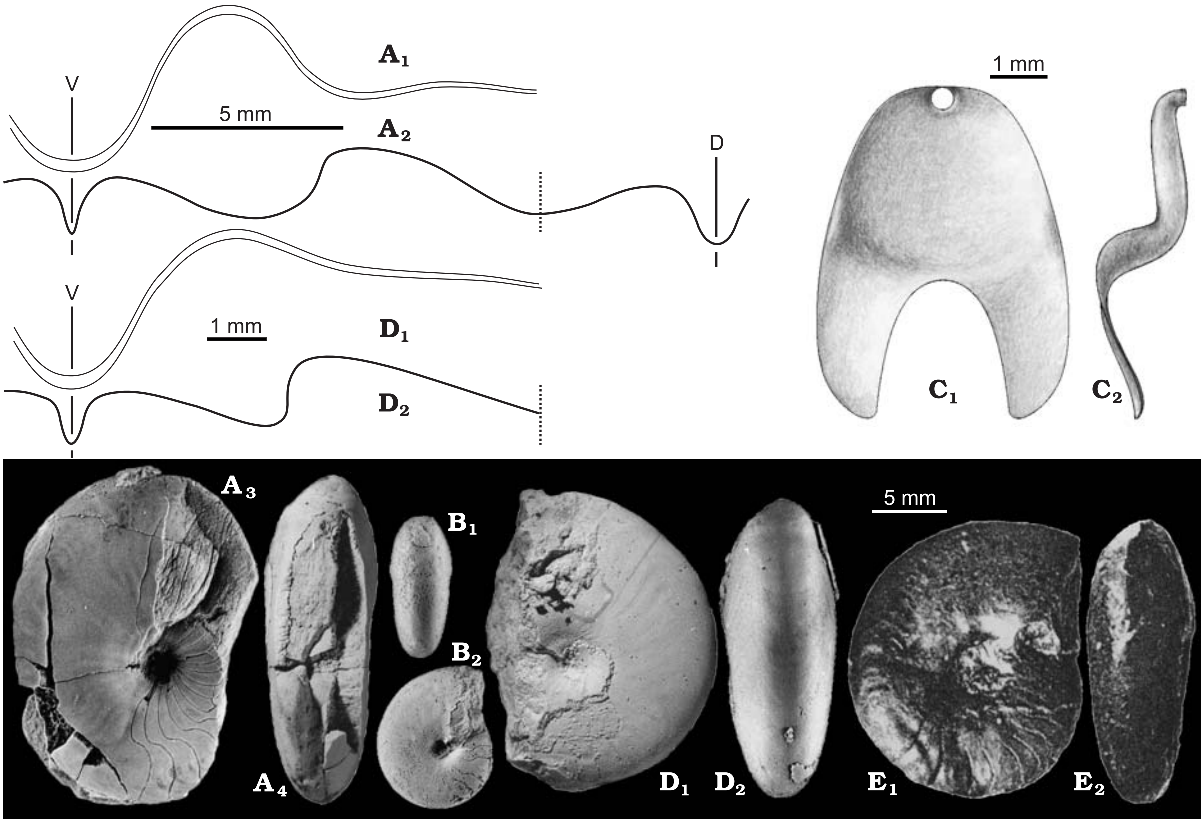


Fig. 148. Species of *Protornoceras* with narrow umbilicus from the Famennian of Poland. **A**–**C**. *P. aphyllitiforme* Dybczyński, 1913 from the mid *C. marginifera* Zone at Kowala; growth lines inferred from wrinkles on the surface of pyritic internal mould, suture, and views of specimen ZPAL AmVII/173 (A), views of specimen ZPAL AmVII/1007 (B), and septum of ZPAL AmVII/956 (C). **D**. *Protornoceras simplicius* (Sobolew, 1914) growth lines, suture, and views of specimen ZPAL AmVII/508 from the *P. trachytera* Zone at Łagów-Dule (sample Ł-9). **E**. *Protornoceras simplificatum* (Sobolew, 1914) from Sieklucki's brickpit in Kielce (reproduced from Sobolew 1914, pl. 9: 27, 28).

Diagnosis. — Simplified suture with a very shallow flank lobe and usually almost straight course of its ventrolateral part; weak ventro-lateral vaultings may develop in the septum; open umbilicus.

Remarks. — This seems to be a separate branch of the tornoceratids evolving towards the clymenoid appearance of the conch and suture. Various forms occur together in the black shale with pyritized ammonoids at Kowala, which suggests their immigration to the Holy Cross Mountains area with the sea transgression of the *C. marginifera* Zone (perhaps at its later stage). Probably the least derived of them is *P. aphyllitiforme*, with almost closed umbo, the most derived is *P. mirabile*. House (1970) proposed the genus *Tornia* for the latter. Perhaps it would be truly reasonable to put the protornoceratids with narrow and wide umbilicus into different genera, but the type species of both *Protornoceras* and *Tornia* are widely umbilicate. Because of the high population variability, their separation seems superfluous. The phylogenetically closest *Kirsoceras* differs in the subventral position of the siphuncle (Bogoslovsky 1971).

Protornoceras aphyllitiforme Dybczyński, 1913
(Figs 148A–C and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — 14 specimens.

Diagnosis. — Narrow umbilicus with the flat adjoining wall of the conch giving it a conical appearance, prominent rounded auricles of the aperture.

Remarks. — The holotype suture is similar to that in juvenile specimens from Kowala. Adult suture (in specimens up to 34 mm in diameter) is more tornoceratid, but it is highly variable. The sample is evidently homogenous, being taken from a single black clay intercalation in the stratigraphically uncondensed, thick rock sequence. An angulation at the dorsal slope of the flank lobe makes some of the Kowala specimens similar to the holotype of *Polonoceras latum* Dybczyński, 1913, which may appear conspecific. Other specimens show a dorsally located indentation in the lobe, having its oblique ventral slope almost straight. This indentation corresponds to a small vaulted area of the septum, a situation closely similar to that in the open-umbilicate *Protornoceras siemiradzkii* Dybczyński, 1913. However, these are distinct species different in the diameter of umbo, the trait less variable than the course of suture in the Kowala material. *Tornoceras obliquum* Perna, 1914 from the *Prolobites* horizon of the Urals shows a similar conch form and suture but unsimilar, pointed auricles of the aperture.

Distribution. — The mid *C. marginifera* Zone at Kowala; reworked at Sieklucki's brickpit in Kielce.

Protornoceras simplicius (Sobolew, 1914)
(Figs 148D and 159)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains.

Material. — 13 specimens.

Diagnosis. — Weakly developed auricles of the aperture; closed conical umbilicus.

Remarks. — Specimens from sample Ł-14, probably representing the type horizon, do not show suture and may be clymenias. In the holotype, the suture is more *Tornoceras*-like than in specimens from the *C. marginifera* Zone (sample Ł-9) but it fits well within the range of variability shown by the stratigraphically somewhat older species from Kowala.

Distribution. — The *C. marginifera* (sample Ł-9) and *P. trachytera* (sample Ł-14) zones at Łagów-Dule, the *L. styriacus* Zone (trench rIVc of Żakowa *et al*. 1986) at Jabłonna.

Protornoceras simplificatum (Sobolew, 1914)
(Figs 148E and 159)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains.

Diagnosis. — Evolute conch with umbo about one fifth of its diameter; oval cross section of the whorl; more or less simplified suture.

Remarks. — No specimen of this morphology has been found by myself in the topotype stratum. Possibly some other taxa by Sobolew (1914) based on Sieklucki's brickpit material belong here: Gomi-re-monomeroceras (*Tornoceras*) *flexuosum* and G. (*T.*) *simplicius rotundatum*.

Distribution. — The *P. trachytera* Zone at Łagów-Dule; possibly also reworked at Sieklucki's brickpit in Kielce.

Protornoceras polonicum Dybczyński, 1913
(Figs 149A–G, 150A, and 159)

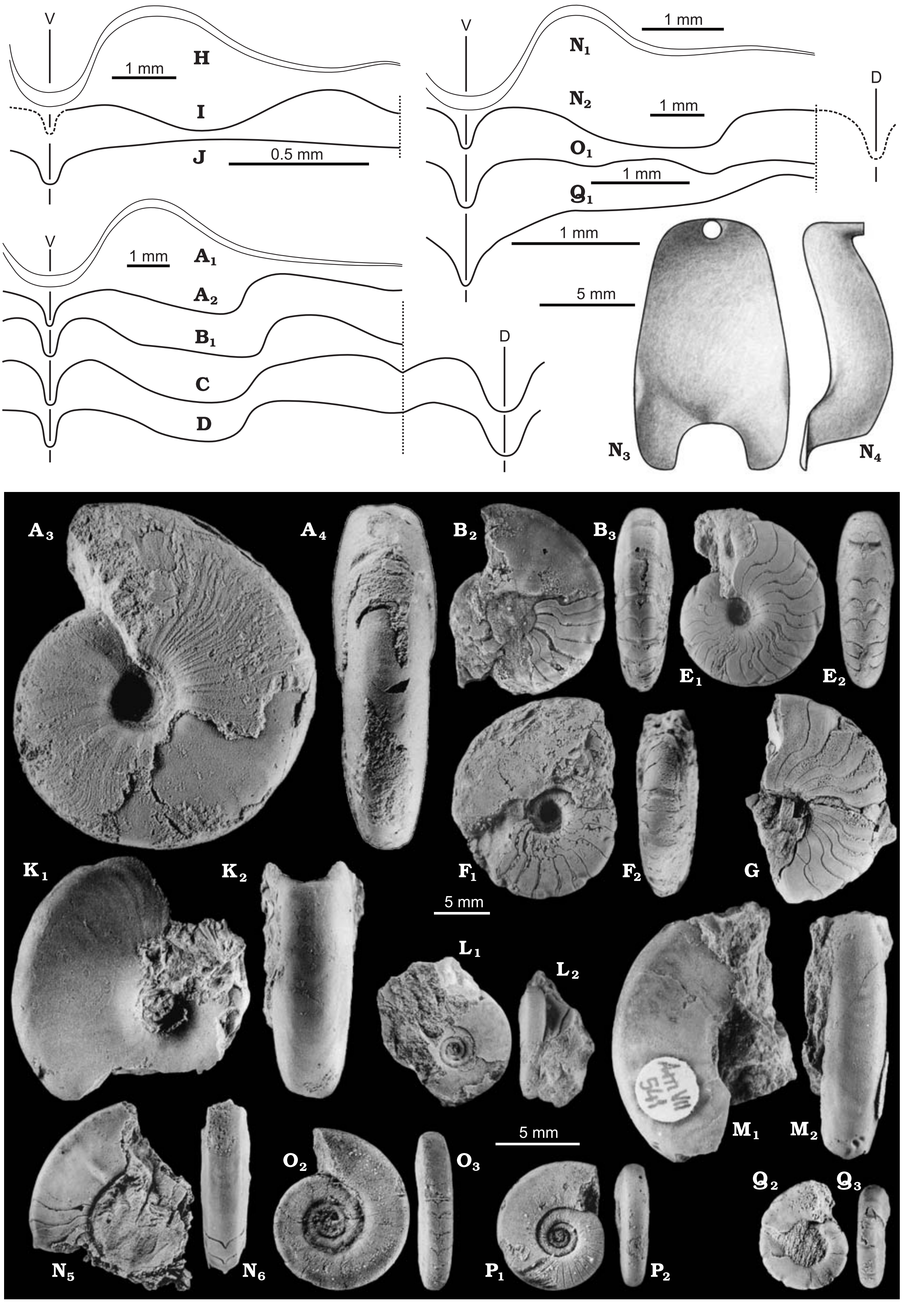
Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — 33 specimens.

Diagnosis. — Open umbilicus of diameter about one tenth of that of mature conch; subtrapezoidal cross section of the whorl; rounded auricles of the aperture.

Remarks. — Similarly to other species of *Protornoceras*, the suture is very variable, especially in respect to concavity of the flank lobe, even within the same specimen. Width of the umbo seems to be of a higher taxonomic value, although it is variable, too (note that all earlier illustrated specimens are pyritic internal moulds). Several species proposed for specimens from Sieklucki's brickpit by Dybczyński (1913), including *P. siemiradzkii*, *P. bilobatiforme*, *P. kielcense*, *P. ornatum*, and *P. zuberi*, and by Sobolew (1914), such as Gomi-re-monomeroceras (*Tornoceras*) *genulobatum planum*, G. (*T.*) *planilobum*, G. (*T.*) *planilobum angulatolobatum*, G. (*T.*) *planilobum avaricatum*, and G. (*T.*) *dorsatum*, may belong here. The holotype of *P. polonicum* is a juvenile specimen with not fully developed suture.

Distribution. — The mid *C. marginifera* Zone at Kowala and Łagów Słupecka 73 (sample ŁSł73-4); reworked at Sieklucki's brickpit in Kielce. Specimens with a similar conch form but the suture not exposed occur in the clymeniid limestone at Łagów-Dule.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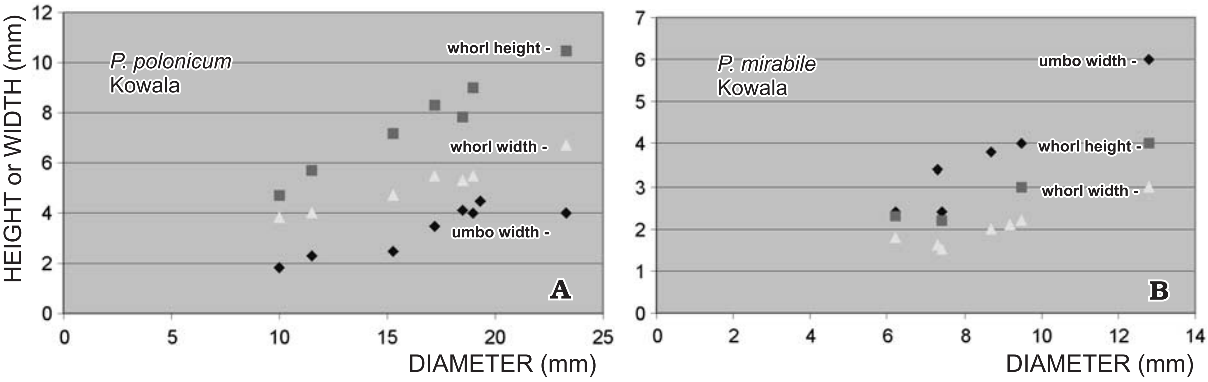

Fig. 150. Variability of conch dimensions (based on measurements of pyritic internal moulds) of *Protornoceras* from the mid *C. marginifera* Zone at Kowala.**A**. *P. polonicum* Dybczyński, 1913. **B**. *P. mirabile* Dybczyński, 1913.

Protornoceras curvidorsatum (Sobolew, 1914)
(Figs 149H-M and 159)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains.

Material. — Ten specimens.

Diagnosis. — Evolute conch with umbo width approaching one third of its diameter; subtrapezoidal cross section of the whorl; more or less simplified suture.

Remarks. — In my material only juvenile specimens exhibit suture, which appears to be extremely simplified. Growth lines are prominent, in one specimen numerous apertural thickenings developed along its venter. From the geologically older *P. mirabile* the species differs in the narrower umbo and higher whorls. Possibly some other taxa based by Sobolew (1914) on the Łagów-Dule clymeniid limestone belong here: Gomi-re-monomeroceras (*Tornoceras*) *planilobum arcuatolobatum*, G. (*T.*) *sinuvaricatum*, and G. (*T.*) *umbilicatoides*.

Distribution. — The *P. trachytera* Zone (sample Ł-14) at Łagów-Dule; possibly also reworked at Sieklucki's brickpit in Kielce.

Protornoceras mirabile Dybczyński, 1913
(Figs 149N–P, 150B, and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — Nine specimens.

Diagnosis. — Evolute conch with the umbo width approaching half of its diameter; subtrapezoidal cross section of the whorl; more or less simplified suture.

Remarks. — This is the type species of *Tornia* House, 1970. The holotype shows a moderately evolute conch, almost straight course of the suture and marks of prominent rounded auricles. In my material the shape of aperture is difficult to trace. However, similarly to other species of the genus, *P. mirabile* population from Kowala shows a tremendous variability in the suture and also, although not so wide, in umbilical width. The whorl cross section shows a remarkable variability ranging from almost tabulate venter and flat flanks to a quite weak angulation. This makes likely conspecificity of some other taxa by Sobolew (1914) based on

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← Fig. 149. Species of *Protornoceras* with wide umbilicus from the Famennian of the Holy Cross Mountains. **A–G**. *P. polonicum* Dybczyński, 1913 from the *C. marginifera* Zone at Łagów locality Słupecka 73 (A, sample ŁSł73-4; with preserved shell wall) and Kowala (B–G; pyritic internal moulds); growth lines, suture, and views of specimen ZPAL AmVII/971 (A), suture and views of ZPAL AmVII/081 (B), sutures of specimens ZPAL AmVII/158 and 909 (C, D), and views of ZPAL AmVII/1006, 1001 and 158 (E–G), respectively. **H–M**. *P. curvidorsatum* (Sobolew, 1914) from the *P. trachytera* Zone at Łagów-Dule (H–J, L, M, sample Ł-14; K, loose specimen), growth lines of specimen ZPAL AmVII/565 lacking suture and of questionable affinity (H), sutures of ZPAL AmVII/705 and 543 (I, J), views of specimens ZPAL AmVII/ 558 and 541 (L, M, sample Ł-14). **N–P**. *P. mirabile* Dybczyński, 1913 from the mid *C. marginifera* Zone at Kowala; growth lines inferred from wrinkles on the surface of pyritic internal mould, suture, and views of specimen ZPAL AmVII/146 (N), suture and views of specimen ZPAL AmVII/114 (O), views of specimen ZPAL AmVII/114 (P), and suture and views of juvenile specimen ZPAL AmVII/120 (O).

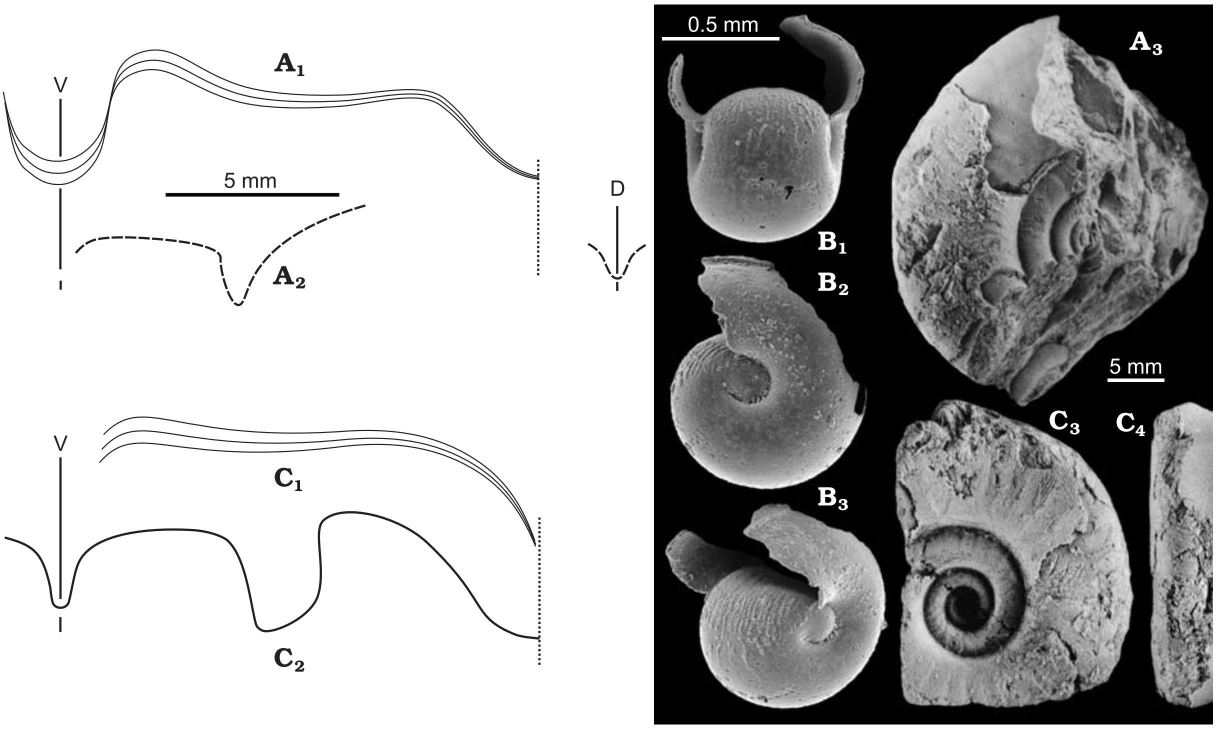


Fig. 151. Species of *Pseudoclymenia* from the Famennian of the Holy Cross Mountains. **A**, **B**. *Pseudoclymenia dillensis* (Drevermann, 1901) from the *C. marginifera* Zone at Łagów-Dule (sample Ł-38); growth lines, suture, and views (A) of specimen ZPAL AmVII/1801 and larval (or embryonic) conch ZPAL AmVII/1818. Note the disposition of wrinkle layer near the aperture and the sudden change in apertural morphology (emergence of auricles) indicating a metamorphosis from the larval conch to teleoconch. The lack of growth increments on the larval conch suggests that the larval development took place completely within the egg covers and that the metamorphosis may have been simultaneous with hatching. **C**. *Pseudoclymenia fundifera* (Perna, 1914) from the *P. trachytera* Zone at Ostrówka, growth lines, suture, and views of specimen IG 284.II.56.

Sieklucki's brickpit material: Gomi-re-protomeroceras *alobatum*, Gomi-re-monomeroceras *umbilicatum*, G. *umbilicatoides*, G. (*Tornoceras*) *simplificatum rotundatum*, and G. (*T.*) *s. subacutum*.

Distribution. — The mid *C. marginifera* Zone at Kowala; reworked at Sieklucki's brickpit in Kielce.

Genus ***Pseudoclymenia*** Frech, 1897

Type species: *Clymenia pseudogoniatites* Sandberger, 1856 from the Famennian of the Rhenisch Slate Mountains.

Diagnosis. — *Aturia*-like flank lobe and incipient dorsolateral lobe of the suture, evolute conch.

Pseudoclymenia dillensis (Drevermann, 1901)
(Figs 151A, B and 159)

Type horizon and locality: Block of clymeniid limestone from a volcanic breccia at Langenaubach near Haiger, Rhenish Slate Mountains.

Material. — One specimen.

Diagnosis. — Somewhat tabulate venter of evolute conch with umbo reaching more than one third of the conch diameter.

Remarks. — The suture in the only available specimen is incomplete, but pointed tip of the flank lobe indicates that this is a species of *Pseudoclymenia*. Its flattened venter suggests species identity with the material of Bogoslovsky (1971; but not Petersen 1975). The originals of Drevermann (1901, pl. 14: 4a, b) are internal moulds and the venter of the specimen illustrated by him is rounded. The relatively narrow umbo (11.5 mm at the conch diameter 30 mm) fits the specimen from Łagów. Larval (or embryonic) and early postlarval phosphatized conchs from the same sample (Ł-38) may also represent this species. Gomi-monomeroceras (*Tornoceras*) *evolutum* of Sobolew (1914) from Sieklucki's brickpit may also represent this or a less derived species of the genus, assuming that the minute original is a juvenile with the suture somewhat worn out.

Distribution. — The *C. marginifera* Zone (sample Ł-38) at Łagów-Dule; possibly also reworked at Sieklucki's brickpit in Kielce.

Pseudoclymenia fundifera (Perna, 1914)
(Figs 151C and 159)

Type horizon and locality: *Prolobites* horizon, Ural River shore 6 km north of the village Kirsy, southern Urals.

Material. — One specimen.

Diagnosis. — Convex ventrolateral lobe of the suture; indistinct auricles of the aperture; oval whorl cross section.

Distribution. — The *P. trachytera* Zone at Ostrówka.

Genus ***Ostrovkites*** gen. n.

Type species: *Ostrovkites numismalis* sp. n.

Derivation of name: From Ostrówka hill, the type locality of the type species.

Diagnosis. — Suture with pointed flank lobe and small secondary ventral lobes; discoidal conch with a tendency to develop longitudinal (spiral) striation.

Remarks. — Suture of the type species is similar to that of the praeglyphioceratid *Lagowites nivae* (Sobolew, 1914) but the auricles of the conch aperture are a tornoceratid feature. The stratigraphic position suggests that the subventral lobation of the suture originated independently of that in advanced *Maeneceras* species.

Ostrovkites numismalis sp. n.
(Figs 152 and 159)

Holotype: Specimen IG 284.II.33 (Fig. 152C).

Type horizon and locality: Black clymeniid limestone of the *P. trachytera* Zone at Ostrówka, Holy Cross Mountains.

Derivation of name: From Latin *numisma* – coin, referring to small size and flat shape of the conch.

Material. — Eight specimens.

Diagnosis. — Minute conch with serial internal thickenings following the aperture on its whole extend, suture with an additional narrow ventral lobe developed on the slope of ventrolateral saddle.

Remarks. — There is a possibility that Sobolew's (1914) Oma-monomeroceras (*Cheiloceras*) *sinuvaricatum* from the Lower Łagów Beds represents the same lineage. The course of internal thickenings in the single known specimen (Sobolew 1914: pl. 7: 10) is similar to that in specimens from Ostrówka, although they

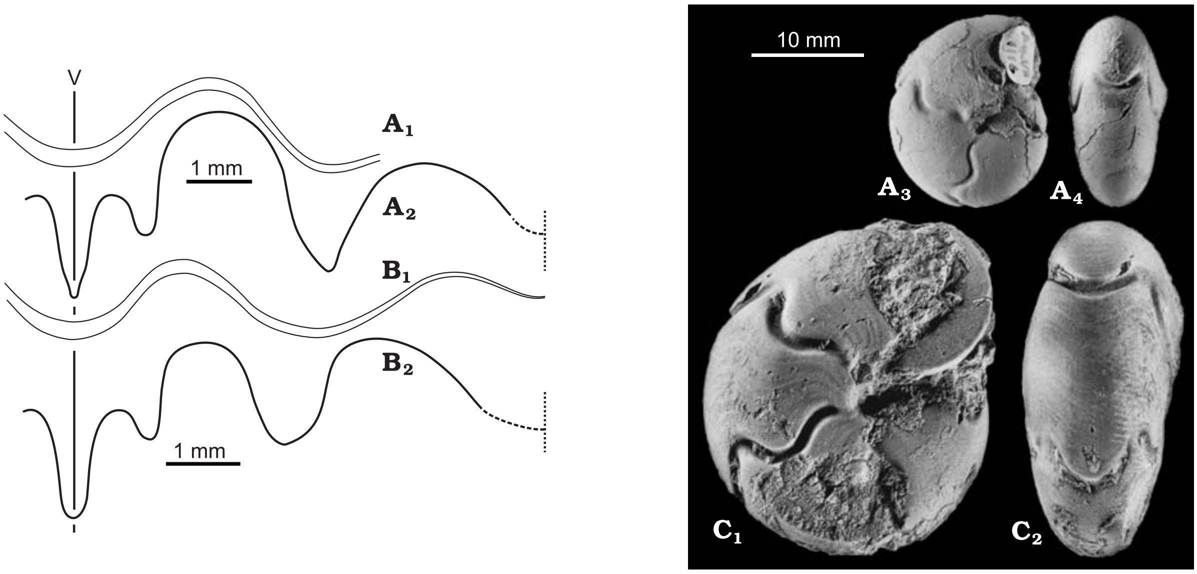


Fig. 152. *Lagowites*-like tornoceratid *Ostrovkites numismalis* sp. n. from the *P. trachytera* Zone at Ostrówka, Holy Cross Mountains; growth lines, suture, and views of specimen ZPAL AmVII/1116 (A, sample Ost-16), growth lines and suture of specimen ZPAL AmVII/016 (A, sample Ost-10), views of the holotype IG 284.II.33 (C).

are less sinuous. Unfortunately, the suture was poorly preserved in the Sobolew's specimen, which is probably lost.

Distribution. — The *P. trachytera* Zone at Ostrówka (samples Ost-10 and Ost-16).

Family **Posttornoceratidae** Bogoslovsky, 1962

Diagnosis. — Suture line with secondary umbonal lobe and a tendency to develop additional ventrolateral lobes (VLU_1:ID → V L^1LU_1UID); conch aperture with auricles; relatively high whorl expansion rate.

Remarks. — Early ontogenetic stages of *Discoclymenia* identified by Becker (1995, fig. 8c, d) show that the dorsolateral lobe in advanced forms is homologous to that in *Gundolficeras*, thus U_1 in Ruzhentcev's notation.

Genus ***Gundolficeras*** Schindewolf, 1936

Type species: *Lobotornoceras bicaniculatum* Petter, 1959 from the Famennian of Algeria.

Diagnosis. — Generalized tornoceratid conch with ventrolateral furrows at early developmental stages; suture with a deep, symmetrical flank lobe and a tendency to developed dorsolateral lobe.

Remarks. — House and Price (1985) questioned relationships between the Famennian tornoceratids with complex suture traditionally classified in *Lobotornoceras* Schindewolf, 1936 and the type species of the genus, *Goniatites ausavensis* Steininger, 1856 from the mid Frasnian Büdesheim Shale of the Eifel Mountains (House 1978). Following this suggestion, Becker (1993*b*) transferred the Famennian species with ventrolateral furrows at early ontogenetic stages to *Falcitornoceras*. They differ rather substantially from the type species of that genus in having rounded auricles and lacking the characteristic juvenile ornamentation. Later (Becker 1995) introduced the genus *Gundolficeras* for some members of this branch. It seems to be the first link in the tornoceratid lineage leading to more and more complex suture, terminating in the acutely discoidal *Discoclymenia*.

Gundolficeras korni (Becker, 1993)
(Figs 153A and 159)

Type horizon and locality: Early Famennian Nehden Shale at Nehden-Schurbusch, Rhenish Slate Mountains.

Material. — Five specimens.

Diagnosis. — Closed umbilicus with the flat adjoining wall of the conch giving it a conical appearance, rounded flank lobe of the suture of otherwise generalized tornoceratid type.

Remarks. — The suture, well visible in two juvenile specimens, fits well that of the type specimen. In the smallest one, indistinct ventrolateral furrows are represented. An adult incomplete specimen with body chamber, of estimated diameter about 55 mm, shows indistinct growth lines with typically tornoceratid rather rounded prominent auricles of the aperture. The conch geometry makes this species similar to *Protornoceras simplicius*, which has a rather simplified and variable suture. Becker (1993b) included it into *Falcitornoceras* although its juvenile conch ornamentation remains unknown. Because of the shape of umbilicus and a rather advanced tornoceratid suture I suggest that this is not *Falcitornoceras*, but is rather related to the *Polonoceras* branch at the stage preceding development of acute auricles.

Distribution. — Probably the *K. crepida* Zone at Jabłonna (wells w150a, b, c dug by Żakowa *et al.* 1984).

Gundolficeras bilobatum (Wedekind, 1908)
(Figs 153B–D and 159)

Type horizon and locality: Early Famennian at Enkeberg, Rhenish Slate Mountains.

Material. — Eight specimens.

Diagnosis. — Narrow ventrolateral saddle, shallow dorsolateral lobe, and very deep and narrow dorsal lobe of the suture; closed umbilicus.

Remarks. — Becker (1993b) included this species into *Falcitornoceras*, referring to furrows on pyritic internal moulds, although its juvenile conch ornamentation remains unknown. Such furrows, preserved also on a juvenile conch from Łagów, are typical of several earliest Famennian tornoceratids and may just be a primitive (plesiomorphic) feature. *Gundolficeras rotersi* Korn, 2002 from the *Platyclymenia annulata* Event

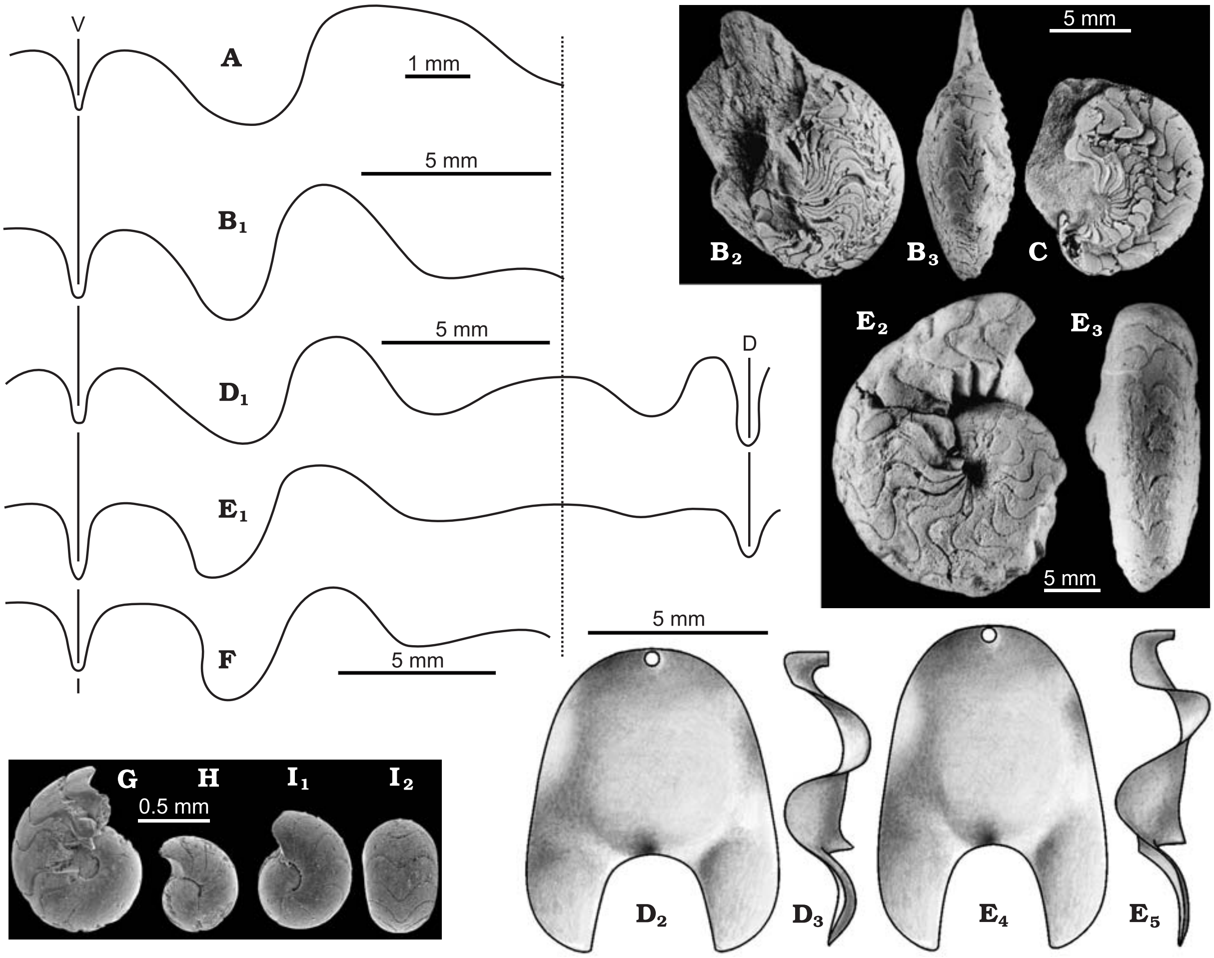


Fig. 153. *Lobotornoceras*-like tornoceratid *Gundolficeras* from the Holy Cross Mountains. **A**. *Gundolficeras korni* (Becker, 1993) from the early Famennian at Jabłonna (probably the *K. crepida* Zone); suture of specimen ZPAL AmVII/659 from well w150c dug by Żakowa *et al*. (1984). **B–D**. *Gundolficeras bilobatum* (Wedekind, 1908) from the mid *C. marginifera* Zone at Kowala (B, C) and probable *C. quadrantinodosa* Zone at Łagów-Dule (D); suture and views of specimen ZPAL AmVII/169 (B), view of specimen ZPAL AmVII/078 (C), suture and septum of specimen ZPAL AmVII/1864 (D, sample Ł-30). **E–I**. *Gundolficeras* sp. n. aff. *G. delepinei* Petter, 1959 from the late Famennian at Kowala (probably the *P. jugosus* Zone), suture and views of specimen IG 284.II.860 (E), suture of unnambered specimen from the same collection (F) and larval (or embryonic) conchs ZPAL AmVII/1833, 1834 (G, H, sample Ko-187, the *P. jugosus* Zone), and 1836 (I, sample Ko-174, the *L. styriacus* Zone) possibly representing the same lineage.

stratum at Kattensiepen in the Rhenish Slate Mountains does not differ from the Holy Cross Mountains material in conch form an suture. Growth lines are not preserved in my material and this precludes reliable comparison.

Distribution. — The mid *C. marginifera* Zone at Kowala; probably the *C. quadrantinodosa* Zone (samples Ł-29, 30, and 34) at Łagów-Dule; reworked at Sieklucki's brickpit in Kielce (Sobolew 1914).

Gundolficeras sp. n. aff. *G. delepinei* Petter, 1959
(Figs 153E–I and 159)

Material. — Two specimens.

Remarks. — Two specimen from the Czarnocki's collection are similar to *Gundolficeras* from the much older strata at the same locality but differ in having a rather wide ventrolateral saddle and shallow dorsal lobe. The first feature is even more apparent in *G. delepinei* from the late Famennian of Algeria (Petter 1959), which may represent the end member of the same lineage (see Becker 1995).

Distribution. — Probably the *P. jugosus* (or the late *L. styriacus*) Zone at Kowala.

Genus **Posttornoceras** Wedekind, 1910

Type species: *Posttornoceras balvei* Wedekind, 1910 from the mid Famennian *Platyclymenia annulata* Zone of the Rhenisch Slate Mountains.

Diagnosis. — Suture with pointed flank lobe and angular or pointed dorsolateral lobe.

Remarks. — Becker (1993b) proposed *Exotornoceras* for the most primitive members of the lineage with a relatively shallow dorsolateral lobe. The difference seems too minor and continuity too apparent to make this taxonomical subdivision practical. Becker (2002) suggested that this lineage was rooted in *Gundolficeras*, which is supported by the data from the Holy Cross Mountains.

The suture of *Posttornoceras* is similar to that of *Sporadoceras*, but these end-members of unrelated lineages differ rather significantly in the geometry of the septum (Becker 1993b; Korn 1999). In *Posttornoceras* the parts of the whorl in contact with the preceding whorl are much less extensive, the dorsolateral saddle is much shorter and of a somewhat angular appearance. This is obviously a reflection of the difference in the whorl expansion rate between the tornoceratids and cheiloceratids.

Posttornoceras superstes (Wedekind, 1908)
(Figs 154A and 159)

Type horizon and locality: Early Famennian at Nehden-Schurbusch, Rhenish Slate Mountains (Becker 1993b).

Diagnosis. — Suture with pointed tip of the flank lobe and roundedly angulate dorsolateral lobe.

Remarks. — *Gephyroceras niedzwiedzkii* of Dybczyński (1913) from Sieklucki's brickpit was represented by a specimen (probably lost) significantly larger than those described by Becker (1993b). The difference in proportions of suture seem to result from this ontogenetic difference, that is mostly from increase of the whorl compression with growth.

Distribution. — Reworked at Sieklucki's brickpit in Kielce.

Posttornoceras balvei Wedekind, 1910? (or *Sporadoceras* sp.)
(Figs 154B, C and 159)

Type horizon and locality: Mid Famennian at Beul near Balve, Rhenish Slate Mountains.

Material. — Three specimens.

Diagnosis. — Suture with tips of all lobes pointed and a narrow ventrolateral saddle.

Remarks. — Serial internal thickenings of the conch developed probably parallel to the aperture, with typically tornoceratid auricles. Despite the inferred form of aperture, the specimens studied may actualy belong to *Sporadoceras*, although restriction of shell thickenings to the venter make it different from species of that genus. Original specimens of both *P. balvei* (Wedekind 1918, pl. 17: 5) and the probably related *P. sodalis* Becker, 1995 (Bogoslovsky 1971, pl. 4: 8) show a high whorl expansion rate, much higher than in the Łagów specimens. This may be related to their early ontogenetic age but is not completely consistent with this identification.

Distribution. — Probably the *C. marginifera* and *P. trachytera* zones at Łagów-Dule.

Posttornoceras fallax Korn *in* Korn *et* Ziegler, 2002
(Figs 154D–F and 159)

Type horizon and locality: Enkeberg, Rhenish Slate Mountains (Becker 1995).

Material. — Ten specimens.

Diagnosis. — Suture with wide, convex ventrolateral saddle.

Distribution. — Probably the *P. jugosus* and *D. trigonica* zones at Kowala; reworked at Sieklucki's brickpit in Kielce.

Posttornoceras (or *Xenosporadoceras*) *posthumum* (Wedekind, 1918)
(Figs 155A–E, 157, and 159)

Type horizon and locality: Lower *Clymenia* Stufe at Hoevel near Balve in the Rhenish Slate Mountains.

Material. — Ten specimens.

Diagnosis. — Suture with wide, convex ventrolateral saddle and acute lateral saddle.

Remarks. — The original drawing of the suture by Wedekind (1918, fig. 47k) does not show the characteristic, advanced appearance of the lateral saddle, but its tracing on the holotype photograph (Wedekind

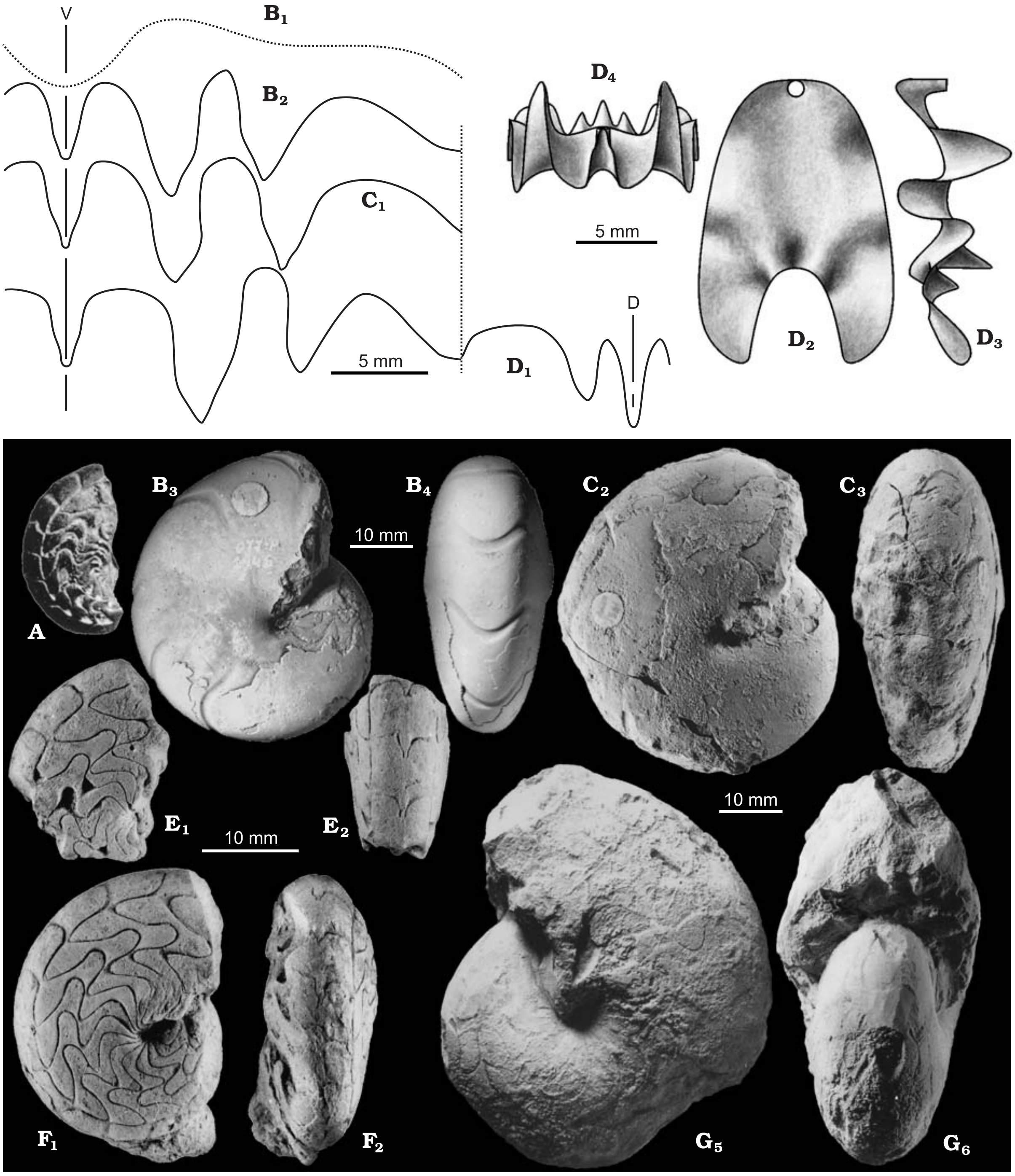


Fig. 154. Advanced tornoceratid *Posttornoceras* from the Holy Cross Mountains and Sudetes. **A**. *Posttornoceras superstes* (Wedekind, 1908) from Sieklucki's brickpit at Kielce (reproduced from Dybczyński 1913, pl. 2: 14; holotype of his *Gephyroceras niedzwiedzkii*, probably lost). **B**, **C**. *Posttornoceras balvei* Wedekind, 1910? (or *Sporadoceras* sp.) from Łagów; internal constriction (probably following the aperture) similar to those of *Sporadoceras* (see Fig. 175) but restricted to the venter, suture and views of specimen ZPAL AmVII/661 (B; black limestone suggestive of the *P. trachytera* Zone); suture and views of specimen ZPAL AmVII/1561 (C; rock matrix suggests the *C. marginifera* Zone). **D**–**F**. *Posttornoceras fallax* Korn, 2002 from the *D. trigonica* Zone at Kowala; suture and septum of unnumbered specimen from Czarnocki's collection (D; dorsal part of suture based on specimen IG 284.II.881); views of specimens IG 284.II.861 (E) and ZPAL AmVII/953. **G**. Probable *Posttornoceras* from the *P. jugosus* Zone at Dzikowiec, the Sudetes; specimen Uwr 2342 (original of *Sporadoceras muensteri* of Tietze 1870 and Frech 1902, pl. 4: 13); diagnostic growth lines not preserved.

1918, pl. 18: 13) rather closely approaches the Kowala specimens. Becker (1997) proposed a neotype for this species and illustrated its suture as well as the specimen (Becker 2002, pl. 2: 11, 12). The conch ornamenta-

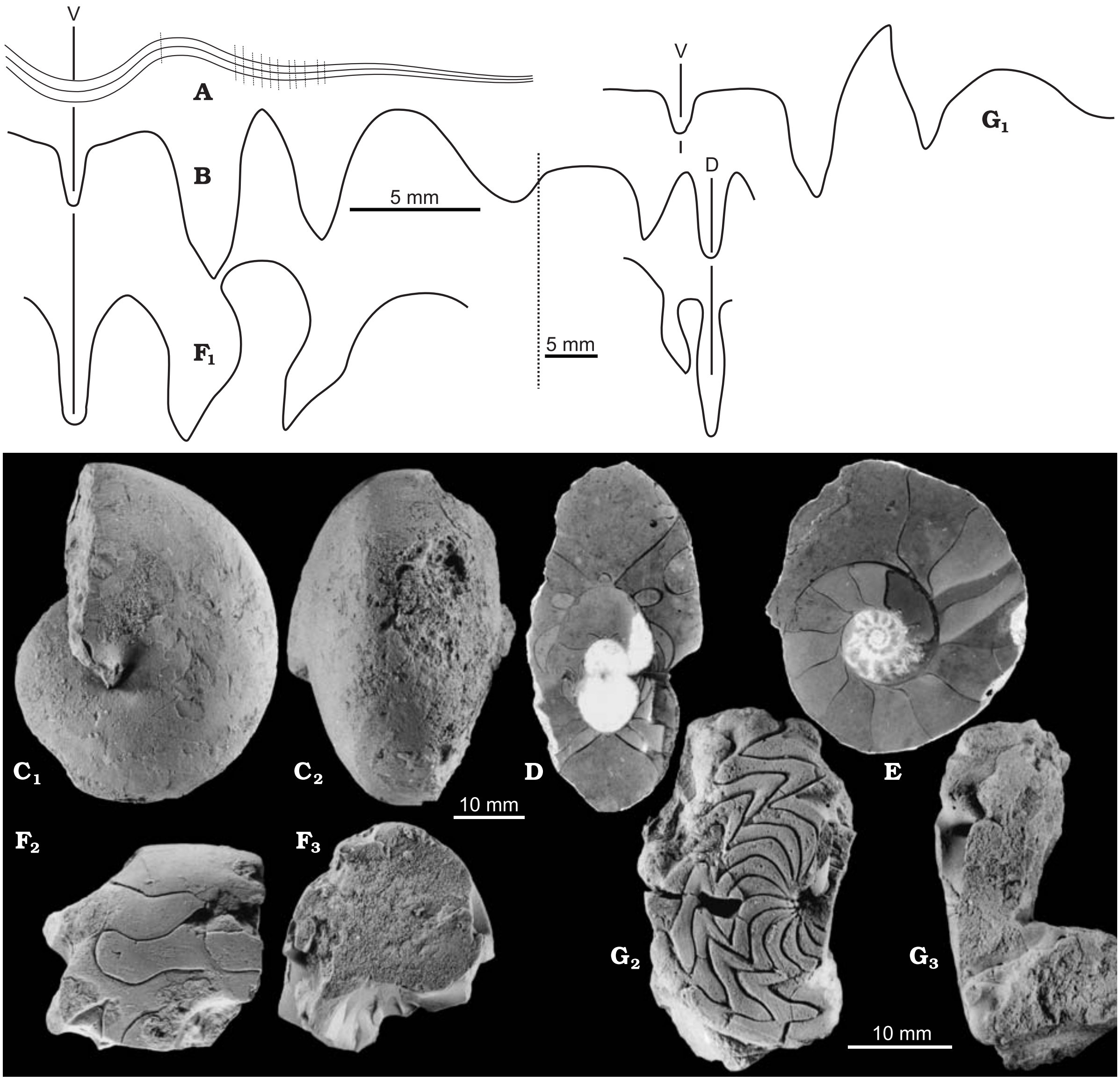


Fig. 155. Various species of *Posttornoceras* from Kowala in the Holy Cross Mountains. **A–E**. *Posttornoceras* (or *Xenosporadoceras*) *posthumum* (Wedekind, 1918) from the *D. trigonica* Zone; growth lines and longitudinal striation of specimen IG 284.II.926; suture of specimens IG 284.II.950 (external) and IG 284.II.953 (internal part; B); views of specimen IG 284.II.926 (C); polished transverse section of specimen IG 284.II.933 (D); medial section of IG 284.II.931 (E). **F**. *Posttornoceras*? *cornwallensis* (Selwood, 1960) probably from the *D. trigonica* Zone; suture and views of fragmentary specimen IG 284.II.880. **G**. *Posttornoceras* aff. *contiguum* (Münster, 1832) from the *P. jugosus* Zone; suture and views of specimen ZPAL AmVII/946.

tion, visible in specimen IG 284.II.926 shows small auricles and probably shallow ventral sinus associated with longitudinal striae, features typical of *Xenosporadoceras ademmeri* Korn, 2002 from the *P. annulata* fauna at Kattensiepen (Korn 2002, fig. 17). The main difference is in a more flattened conch and less derived suture in the mid Famennian species. Whether this is the same lineage characterized by longitudinally striated conchs or rather a case of convergence has to be settled out.

Distribution. — The *D. trigonica* Zone at Kowala.

Posttornoceras? *cornwallensis* (Selwood, 1960)
(Figs 155F and 159)

Type horizon and locality: *Wocklumeria* Zone Stourscombe Beds at Stourscombe, Cornwall.

Material. — One specimen.

Diagnosis. — Pointed ventrolateral saddle of the suture.

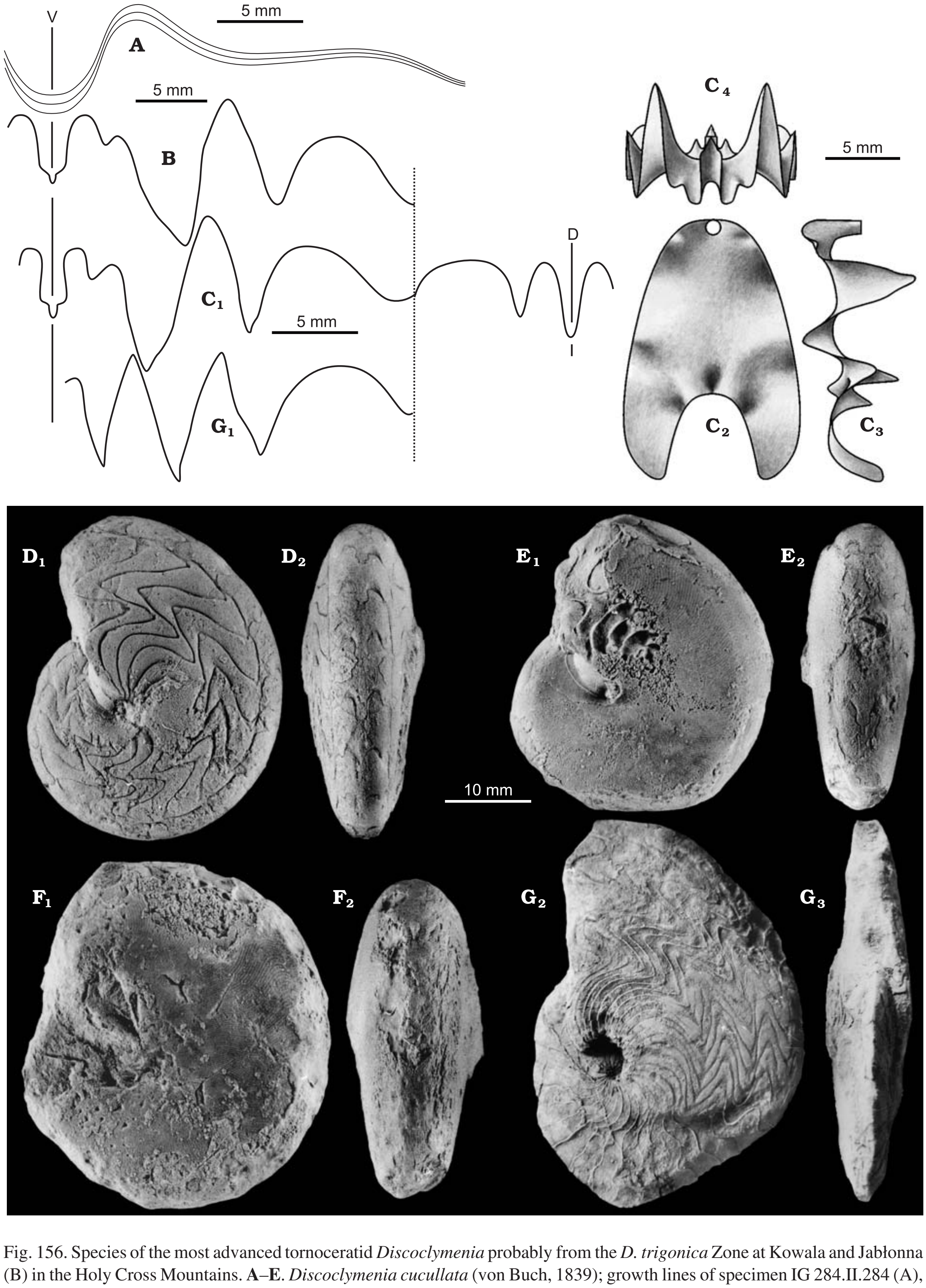


Fig. 156. Species of the most advanced tornoceratid *Discoclymenia* probably from the *D. trigonica* Zone at Kowala and Jabłonna (B) in the Holy Cross Mountains. **A**–**E**. *Discoclymenia cucullata* (von Buch, 1839); growth lines of specimen IG 284.II.284 (A), suture of specimens ZPAL AmVII/597 (B; bed 30 at Jabłonna), suture and septum of specimen UTü Ce 1012/39 (C), and views of specimens IG 284.II.855, 857, and 858 (D–F). **G**. *Discoclymenia zigzag* (Becker, 2002); suture and views of MB.C. 3433 (illustrated earlier by Schindewolf 1944, 1959 and Becker 2002).

Remarks. — This fragment of a large phragmocone shows very characteristic suture matching rather well that of the holotype and the specimen from the *Kamptoclymenia endogona* Subzone at Oberrödinghausen. If the specimen with growth lines was correctly identified by Selwood (1960), this is *Posttornoceras* and not a species of *Sporadoceras* (on this basis Becker 2002 proposed the separate genus *Selwoodites* for the Cornwall species). *Discoclymenia* differs in having one more lobe in its suture.

Distribution. — Probably the *D. trigonica* Zone at Kowala.

Posttornoceras aff. *contiguum* (Münster, 1832)
(Figs 155G and 159)

Material. — One specimen.

Remarks. — This incomplete specimen shows pointed lobes and saddles like *Discoclymenia*. However, the ventrolateral saddle, although incompletely preserved, seems to be subquadrate and undivided. This is a situation transitional between *P. contiguum*, as interpreted by Korn and Ziegler (2002), and *D. cucullata*. Becker (1993b) proposed the neotype for *Goniatites contiguus* Münster, 1832, claiming that this is a species of *Sporadoceras*, not *Posttornoceras*. Although the neotype does not show generically diagnostic growth lines, he later changed his mind and transferred the species back to *Posttornoceras* (Becker 1995; the action extensively discussed in Becker 2002) as was earlier done by Sobolew (1912) and Bogoslovsky (1971). For the sake of taxonomic stability it is probably reasonable to stop these shifts and assume that the second interpretation is correct.

Distribution. — The *P. jugosus* (possibly the late *L. styriacus*) Zone at Kowala.

Genus ***Discoclymenia*** Hyatt, 1884

Type species: *Goniatites Haueri* Münster, 1840 from the late Famennian of Franconia.

Diagnosis. — Suture with minute ventrolateral lobe and pointed tips of dorsolateral lobe and lateral saddle.

Remarks. — *Alpinites* Bogoslovsky, 1971, with *Wedekindoceras kayseri* Schindewolf, 1923 as the type species, and *Discoclymenia* represent (together with *Gundolficeras*, *Exotornoceras*, and *Posttornoceras*) successive grades in the probably monospecific lineage. Until more coeval (thus biological) species are recognized a moderately conservative approach to its taxonomy is thus proposed.

Discoclymenia cucullata (von Buch, 1839)
(Figs 156A–F, 157, and 159)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

Material. — 33 specimens.

Diagnosis. — Suture with small lobe at the tip of narrow ventrolateral saddle.

Remarks. — Some of the specimen from the red limestone at Kowala bear well preserved growth lines, regularly distributed over the conch surface and showing somewhat poined auricles.

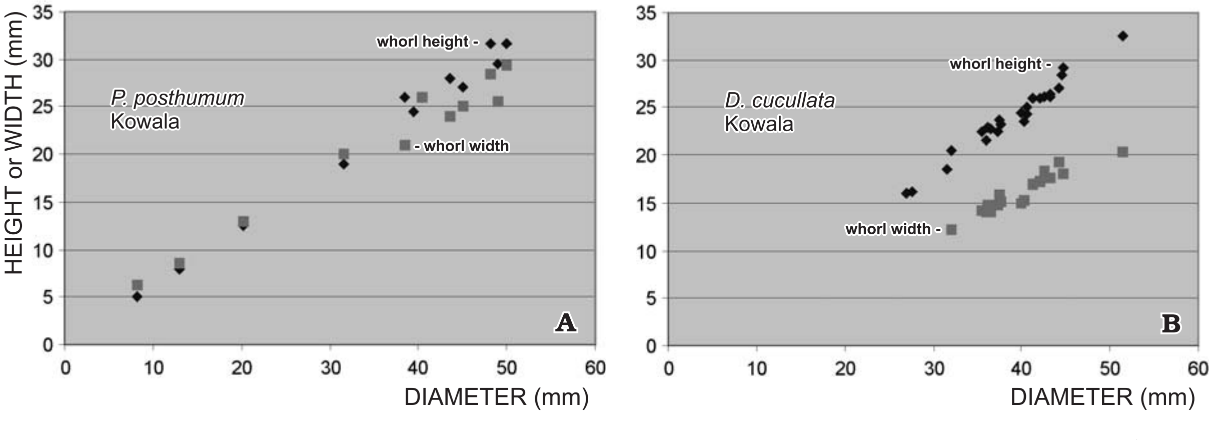


Fig. 157. Variability of conch dimensions of the most advanced tornoceratids from the *D. trigonica* Zone at Kowala. **A**. *Posttornoceras* (or *Xenosporadoceras*) *posthumum* (Wedekind, 1918). **B**. *Discoclymenia cucullata* (von Buch, 1839).

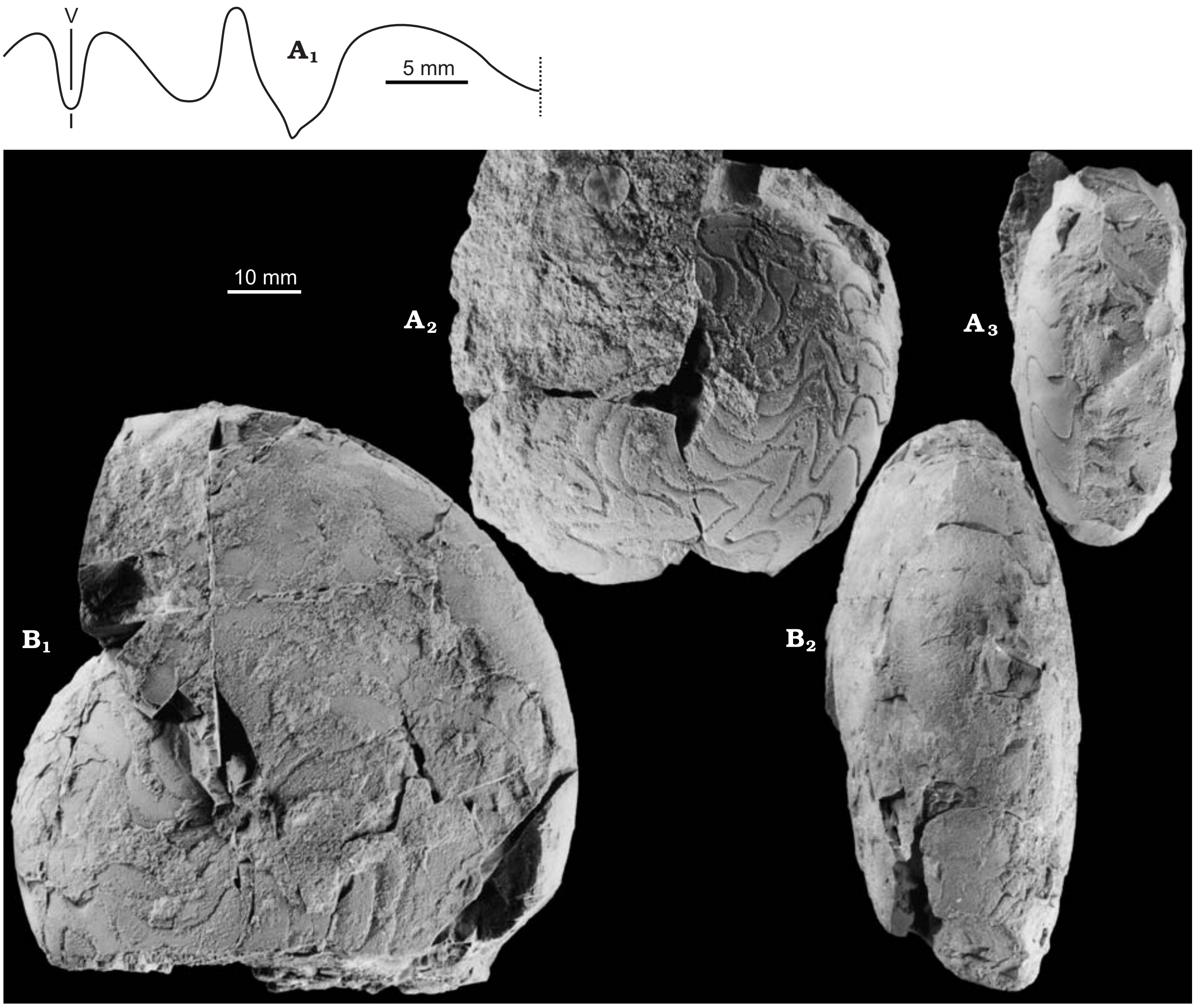


Fig. 158. Probable advanced tornoceratid (or early sporadoceratid) *Maeneceras lagoviense* Gürich, 1896 from the *C. quadrantinodosa* Zone at Łagów (locality Słupecka 73, sample ŁSŁ73-3) in the Holy Cross Mountains; suture and views of specimens ZPAL AmVII/1021 (A) and views of ZPAL AmVII/1022 (B).

Distribution. — The latest *P. jugosus* and *D. trigonica* zones at Kowala, Jabłonna (bed 30), Gałęzice (between Stokówka and Besówka hill), and at Dzikowiec (von Buch, 1839).

Discoclymenia zigzag (Becker, 2002)
(Figs 156G and 159)

Type horizon and locality: *Clymenia* Stufe age Fezzou Shale at Tourart, Morocco.

Material. — One specimen.

Diagnosis. — Thin discoidal conch with acute venter; pointed tips of all lobes and saddles of the suture, the middle flank lobe being the deepest.

Remarks. — The only specimen from Kowala has been already illustrated by Schindewolf (1944, 1959; as *Discoclymenia kayseri*) and Becker (2002). Stratigraphic distribution of other members of the group (classified by him in *Alpinites*) suggest that this was a lineage evolving towards more and more oxyconic conch.

Distribution. — Probably the *D. trigonica* Zone at Kowala.

Genus ?***Maeneceras*** Hyatt, 1884

Type species: *Goniatites acutolateralis* Sandberger et Sandberger, 1851 from the late Famennian of Franconia.

Diagnosis. — Suture with a single set of pointed flank lobes and shallow and wide ventrolateral lobe.

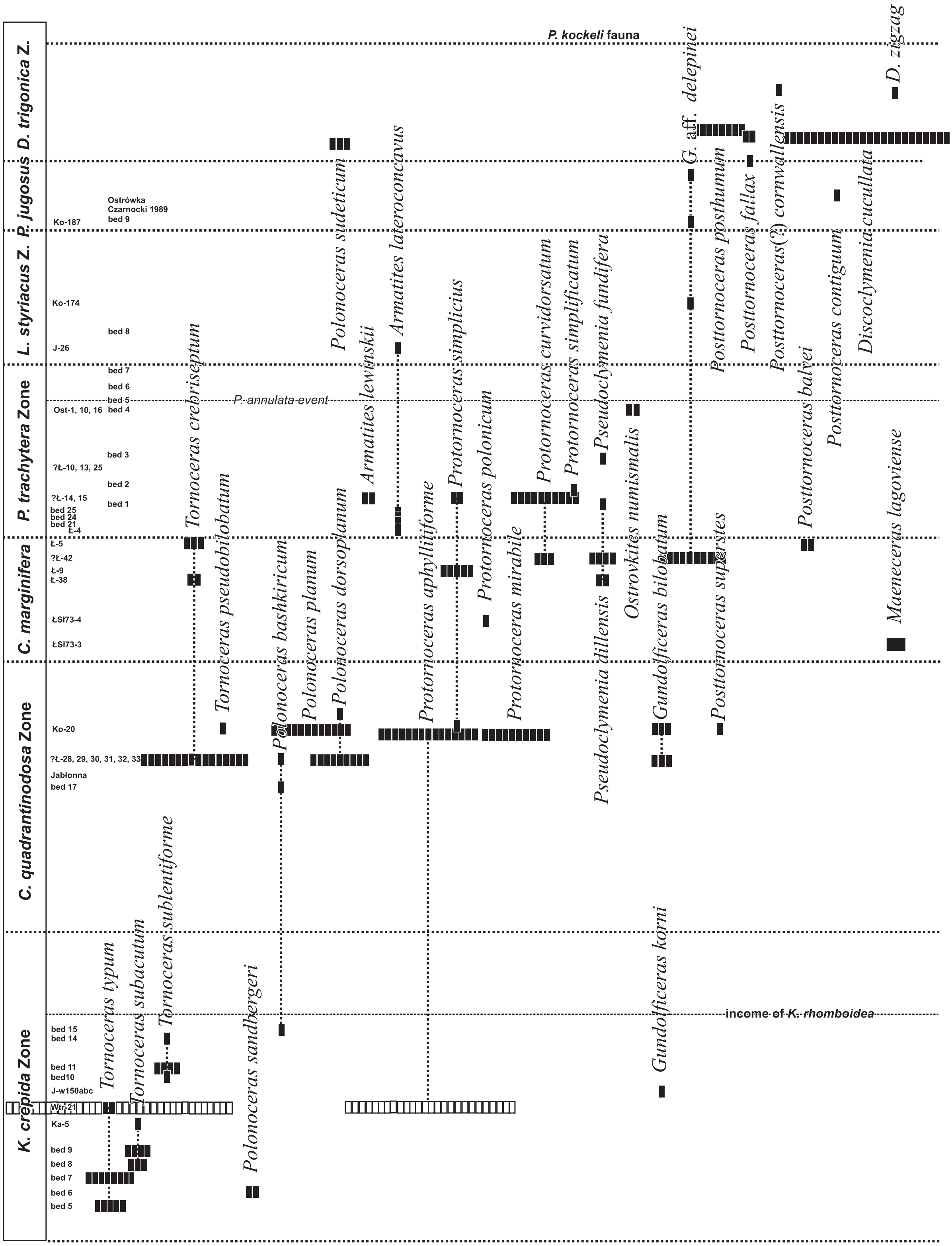


Fig. 159. Stratigraphic distribution of species of Tornoceratidae in the Polish Famennian. Black boxes denote specimens identified in particular sample; blank boxes refer to uncertain identification. Position of samples not included in Figs. 2 and 3 on the geochronological scale is hypothetical.

Remarks. — Complication of septal geometry proceeding from near the venter differs this lineage from the posttornoceratids and makes it similar rather to the sporadoceratids. However, the prominent ventrolateral auricles make *Maeneceras* unsimilar to the cheiloceratid clade and suggest that it is rather a homeomorph of

Felisporadoceras. To prove this a connecting link with either of the lineages has to be looked for. Acutely discoidal *Araneites falcatus* Bogoslovsky, 1971 is probably the end member of this lineage.

Maeneceras lagoviense Gürich, 1896
(Figs 158 and 159)

Type horizon and locality: Early Famennian Upper Łagów Beds at Łagów Dule, Holy Cross Mountains.

Material. — Three specimens.

Diagnosis. — Large conch, suture with asymmetric ventrolateral lobe of parabolic contour.

Remarks. — The holotype (Gürich 1896, pl. 13, 2a–c) is a fragmentary juvenile specimen from the "Sacculus Bank" at Łagów-Dule, with the suture closely similar to that in newly collected larger specimens. Some uncertainty remains, because in slightly younger strata at Łagów-Dule *Felisporadoceras subvaricatum* (Sobolew, 1914) occurs with closely similar suture. The main difference between advanced tornoceratids and cheiloceratids with complex suture is their conch expansion rate, which is expressed in much more extensive dorsolateral saddle in *Felisporadoceras*. The drawings in Gürich (1896) show this saddle to be relatively small, which suggests that this is truly *Maeneceras*.

Maeneceras acutolaterale (Sandberger *et* Sandberger, 1851) may be a closely related member of the same lineage, more advanced in having acute tips of the ventrolateral saddles. Mature conch of the holotype, illustrated by Becker (1993b, fig. 96) is about 160 mm in diameter. Specimens from Łagów are all juveniles but still they are among the largest goniatites from the Famennian of the Holy Cross Mountains. Growth lines are not recognizable on the conch surface but there are serial internal thickenings visible on the venter. They probably parallel aperture, showing a deep ventral sinus and apparently ventrolateral auricles. Similar is the course of internal thickenings in *M. pompeckji* (Wedekind, 1918) as illustrated by Bogoslovsky (1971, pl. 13: 5).

Distribution. — The *C. marginifera* Zone at Łagów Słupecka 73 locality (sample ŁSł73-3) and probably Łagów-Dule; reworked at Sieklucki's brickpit in Kielce.

Family **Cheiloceratidae** Frech, 1897

Diagnosis. — Conch aperture with obliquely convex profile, lacking auricles; relatively low whorl expansion rate; simple septum with weakly developed lateral vaultings.

Genus ***Nehdenites*** Korn *in* Korn *et* Ziegler, 2002

Type species: *Goniatites circumflexus* Sandberger, 1851 from the early Famennian of Nehden in the Rhenish Slate Mountains.

Diagnosis. — Simple, *Tornoceras*-like suture with rounded flank lobe and gently rounded dorsal lobe; conch involute throughout ontogeny.

Remarks. — Because of reasons presented in Korn and Ziegler (2002, p. 462) this generic name is preferred in respect to *Compactoceras* Becker, 2002.

Nehdenites verneuili (Münster, 1839)
(Figs 160A and 181)

Type horizon and locality: Unspecified horizon at Gattendorf in Franconia (Becker 1993b).

Material. — Eight specimens.

Diagnosis. — Internal thickening of the conch parallel to aperture, well developed only ventrally; discoidal, relatively flat conch with gently rounded venter; suture almost straight ventrally.

Remarks. — Sobolew's (1914) Oma-monomeroceras (*Cheiloceras*) *discoidale* (labeled *discoideum* on plate 1), O. (*Ch.*) *depressum*, and O. (*Ch.*) *lenticulare*, from the Lower Łagów Beds probably also belong here, but pyritic specimens from Sieklucki's brickpit attributed to the same species by Sobolew (1914) may rather represent a species of *Tornoceras*.

Distribution. — The *K. crepida* Zone at Kadzielnia, probably also at Łagów-Dule.

Nehdenites circumflexus (Sandberger *et* Sandberger, 1851)
(Figs 160B and 181)

Type horizon and locality: Early Famennian of Nehden, Rhenish Slate Mountains (Becker 1993b).

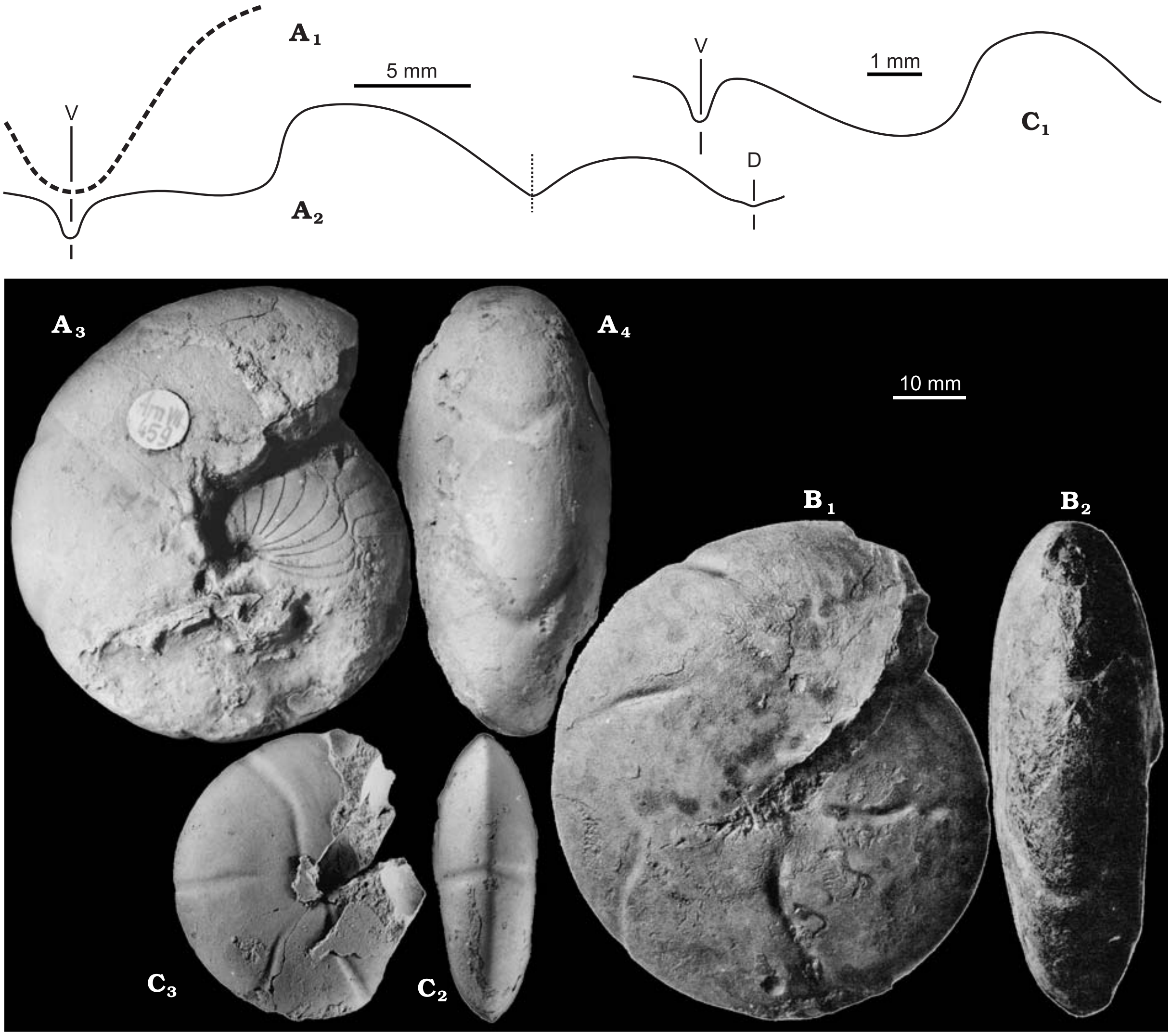


Fig. 160. Species of the ancestral cheiloceratid *Nehdenites* from the early Famennian of the Holy Cross Mountains. **A**. *N. verneuili* (Münster, 1839) from the *K. crepida* Zone at Kadzielnia; internal thickening, suture, and views of specimen ZPAL AmVII/459. **B**. *N. circumflexus* (Sandberger *et* Sandberger, 1851), from the Lower Łagów Beds (probably the late *K. crepida* Zone) at Łagów-Dule; views of the holotype of *Cheiloceras tenue* reproduced from Sobolew (1914, pl. 7: 8 and 8: 1). **C**. *N. praelentiformis* (Sobolew, 1914) from the *C. quadrantinodosa* Zone probably at Łagów-Dule (sample Mak-4); suture and views of specimen ZPAL AmVII/1861.

Diagnosis. — Internal thickenings of the conch parallel to aperture, may extend to flanks; flat conch with parabolic venter; relatively deep, rounded flank lobe of the suture.

Remarks. — Sobolew's (1914) Oma-monomeroceras (*Cheiloceras*) *praepolonicum*, and O. (*Ch.*) *tenue* from the Lower Łagów Beds probably also belong here. Unfortunately, the original specimens of Sobolew (1914) are probably lost and no more material has been collected from the type locality or coeval strata in the Holy Cross Mountains.

Distribution. — The latest *K. crepida* or *C. quadrantinodosa* Zone at Łagów-Dule.

Nehdenites praelentiformis (Sobolew, 1914)
(Figs 160C and 181)

Type horizon and locality: Early Famennian Lower Łagów Beds at Łagów Dule, Holy Cross Mountains.

Material. — One specimen.

Diagnosis. — Flat conch with acute venter; relatively deep, rounded flank lobe of the suture.

Remarks. — Becker (1993b) confirmed validity of the species and illustrated its specimen from the Rhenish Slate Mountains. The only specimen available to me lacks suture and its provenance is not clear (it comes from material discarded by Henryk Makowski, probably from Łagów, sample Mak-4).

Distribution. — The *C. quadrantinodosa* Zone at Łagów-Dule.

Genus ***Cheiloceras*** Frech, 1897

Type species: *Goniatites subpartitus* Münster, 1839 from the early Famennian of Franconia.

Diagnosis. — Suture running transversely in ventral part of the whorl with pointed narrow flank lobe of various depth; transverse internal thickenings of the conch do not following the course of aperture; conch involute except for the earliest few whorls in advanced species.

Remarks. — The concept of the genus has been extensively discused by Becker (1993) who applied much importance to evolute early whorls of the type species and exclude completely involute early species from the genus.

Cheiloceras pompeckji (Wedekind, 1908)
(Figs 161A–E and 181)

Type horizon and locality: Early Famennian of Nehden, Rhenish Slate Mountains (Becker 1993b).

Material. — 23 specimens.

Diagnosis. — Transverse internal thickenings of the conch virtually parallel to aperture, may be somewhat more acute ventrally, suture with a minute blunt indentation in the flank lobe with almost straight ventral slope.

Remarks. — The specimens from Kadzielnia are similar to those of *Nehdenites verneuili* from the same locality (but probably not the same stratum) having a somewhat more globose appearance and indented flank lobe of the suture. The lectotype of the species (Becker 1993b, pl. 20: 1, 2) is of a more discoidal appearance. The topotype specimen considered by Becker (1993b, pl. 20: 5, 6) to be within the range of variability fits the morphology of juvenile specimens from Jabłonna better than the lectotype. Oma-monomeroceras (*Nehdenites*) *verneuili*, O. (*Ch.*) *avaricatum*, and O. (*Ch.*) *avaricatum* from the Lower Łagów Beds of Sobolew (1914) may also belong to this species.

Distribution. — The *K. crepida* Zone at Kadzielnia and Jabłonna (wells W150b, c dug by Żakowa *et al*. 1984), possibly also Łagów-Dule.

Cheiloceras amblylobum (Sandberger *et* Sandberger, 1851)
(Figs 161F, G and 181)

Type horizon and locality: Early Famennian of Nehden, Rhenish Slate Mountains (Becker 1993b).

Material. — 11 specimens.

Diagnosis. — Radially running internal thickenings of the conch; *Tornoceras*-like suture; relatively globose conch.

Remarks. — Sobolew's (1914) Oma-monomeroceras (*Cheiloceras*) *globulare* from the Lower Łagów Beds may belong here.

Distribution. — The *K. crepida* Zone at Jabłonna (bed 5).

Cheiloceras inversum (Sobolew, 1912)
(Figs 161H–P and 181)

Type horizon and locality: Early Famennian Upper Łagów Beds at Łagów Dule, Holy Cross Mountains (Sobolew 1912b).

Material. — 34 specimens.

Diagnosis. — Internal thickenings of the conch tending to develop ventral saddle; suture with variously developed blunt indentation in the flank lobe; relatively globose conch.

Remarks. — Sobolew (1914) considered the presence and course of internal thickenings to be of much taxonomic importance. His view has not been generally accepted and the distribution of thickenings is known to be variable even within a single specimen. It is difficult to estimate the range of variability of the species because the material in my disposal may be heterogenous as it was collected mostly from loose blocks. In the collection of Otto Schindewolf housed at the Museum für Naturkunde in Berlin there is a sample probably coming from the same bed (his "Schicht 4" definitely do not corresponding to bed 4 of Sobolew

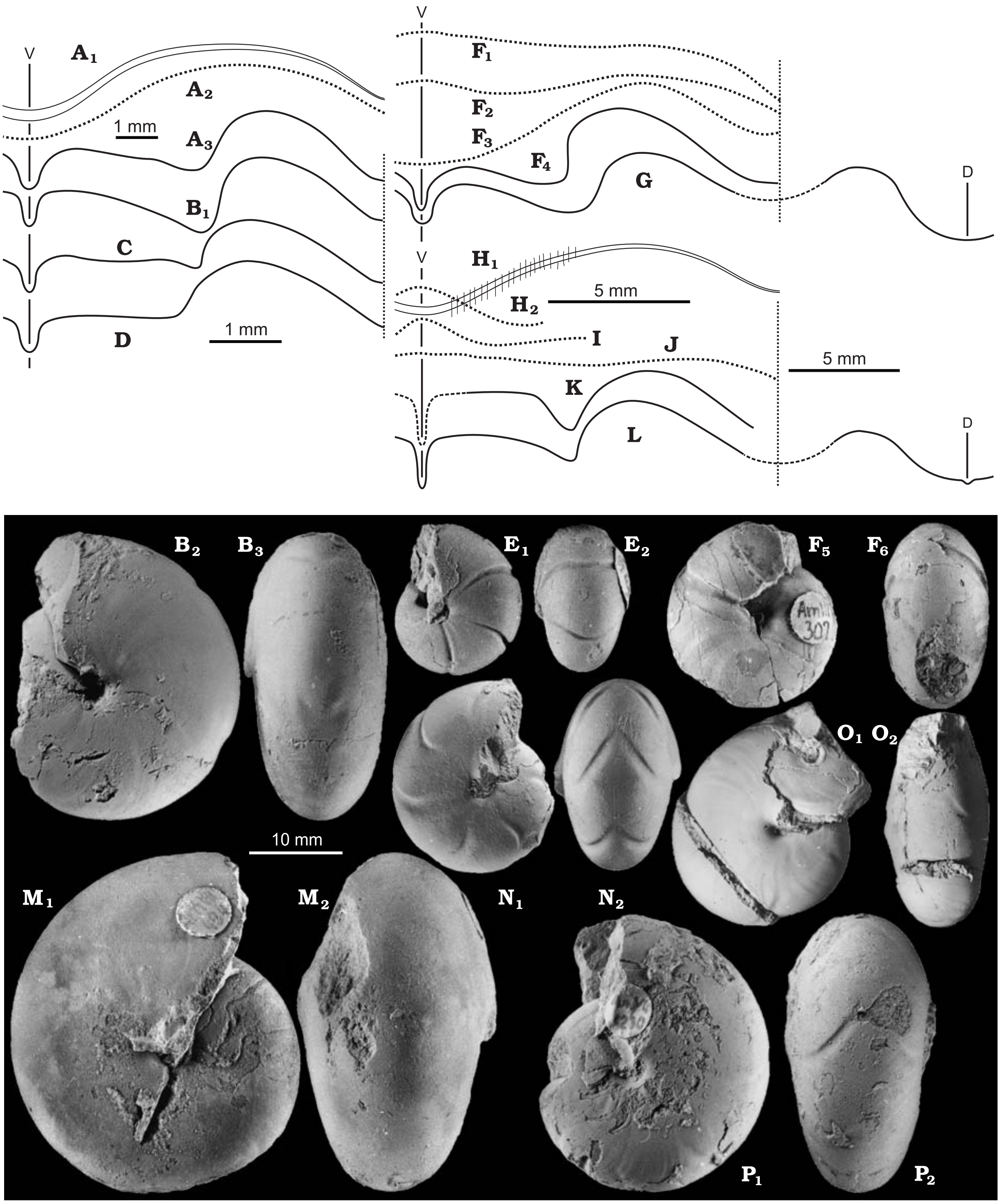


Fig. 161. Species of *Cheiloceras* with globose conch from the early Famennian of the Holy Cross Mountains. **A**–**E**. *Ch. pompeckji* (Wedekind, 1908) from the *K. crepida* Zone at Jabłonna (A, C–E; well w150c of Żakowa *et al*. 1984) and Kadzielnia (B); growth lines, internal thickening, suture and views of specimen ZPAL AmVII/319 (A); suture and views of specimen ZPAL AmVII/363 (B); and sutures of specimens ZPAL AmVII/326 and 315 (D, E). **F**, **G**. *Ch. amblylobum* (Sandberger *et* Sandberger, 1851) from the *K. crepida* Zone at Jabłonna; internal constrictions, suture and views of specimen ZPAL AmVII/307 (F, bed 5); suture of specimen ZPAL AmVII/312 (G, bed 8). **H**–**P**. *Ch. inversum* (Sobolew, 1912), from the *C. marginifera* Zone at Łagów-Dule; growth lines and internal thickening of specimen ZPAL AmVII/514 (H); thickenings of specimens IG.J.87b and ZPAL AmVII/306 (I, J); sutures of specimens ZPAL AmVII/362 and 509 (K, L, latter from sample Ł-5) and views of specimens ZPAL AmVII/494, 1235, and 351 (see also Fig. 146E for associated *Polonoceras dorsoplanum*), and 1230 (M–P).

1912b). There are 37 discoidal specimens probably representing *Ch. lagoviense* among them, 39 specimens with the ventral sinus of the internal thickening resembling what is here classified in *Ch. pompeckji*, 3 specimens with asymmetric course of thickenings, 17 with transverse thickenings, 19 specimens with a ventral saddle of the thickenings, and 29 specimens without thickenings. This is not consistent, however, with results of my collecting. In particular blocks specimens with clearly demarkated ventral saddle dominate, which seems to support taxonomic value of this character.

Distribution. — The *C. quadrantinodosa* and *C. marginifera* zones at Łagów-Dule (samples Ł-5, 28, and 29, Mak-4).

Cheiloceras subpartitum (Münster, 1839) *sensu* Becker, 1993
(Figs 162A, 181)

Type horizon and locality: Bed 4 at Gattendorf in Franconia (Becker 1993b).

Material. — One specimen.

Diagnosis. — Discoidal, relatively thick conch with transverse thickenings well developed also on flanks.

Remarks. — The neotype of the species selected by Becker (1993b) shows proportions of the conch and suture similar to the specimen from Jabłonna, without any pointing of the flank lobe. Perhaps Sobolew's (1914) Oma-monomeroceras (*Cheiloceras*) *disco-transversale* from the Upper Łagów Beds represents the same lineage. O. (*Ch.*) *tenue* from the clymeniid limestone at Łagów Dule may be a surprisingly late member of the lineage.

Distribution. —The *K. crepida* Zone at Jabłonna (bed 8).

Cheiloceras angustivaricatum (Sobolew, 1914)
(Figs 162B, C and 181)

Type horizon and locality: Early Famennian Lower Łagów Beds at Łagów Dule, Holy Cross Mountains.

Material. — Two specimens.

Diagnosis. — Minute conch with flat flanks and radially running sinuous internal thickenings; suture with angular flank lobe.

Remarks. — Sobolew's (1914) Oma-monomeroceras (*Cheiloceras*) *subpartitum* Münst. *angustivaricatum* from the Lower Łagów Beds and O. (*Ch.*) *s. lativaricatum*, from both the Lower (the holotype) and Upper Łagów Beds apparently represent morphotypes of the same species. Becker's (1993b) denomination of the neotype of *Ch. subpartitum* changed its traditional meaning and one of the names used by Sobolew (1914) offers a replacement. Perhaps also his Oma-monomeroceras (*Aganides*) *atavum* from Sieklucki's brickpit belongs here or to *Ch. discoidale*.

Distribution. — The *K. crepida* Zone at Jabłonna (bed 10), Kadzielnia (sample Ka-5), and Łagów-Dule (Sobolew 1914).

Cheiloceras discoidale (Sobolew, 1914)
(Figs 162D–M, 164, and 181)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — 220 specimens.

Diagnosis. — Suture with acutely pointed shallow flank lobe; minute conch with flat flanks and radially running sinuous internal thickenings.

Remarks. — There is a variation in development of the flank lobe, ranging from an angulation similar to that in *Ch. angustivaricatum* to a quite apparent, narrow, acutely pointed lobe. This may be an expression of the evolutionary change towards a more elaborate suture. Even more variable is the course of internal thickenings.

Distribution. — The *C. quadrantinodosa* and *C. marginifera* zones at Łagów-Dule (samples Ł-5, 11, 28, and 29), reworked at Sieklucki's brickpit in Kielce.

Cheiloceras cf. *praecursor* (Frech, 1902)
(Figs 163A and 181)

Type horizon and locality: Early Famennian at Bleiwäsche in the Rhenisch Slate Mountains (Becker 1993b).

Material. — Six specimens.

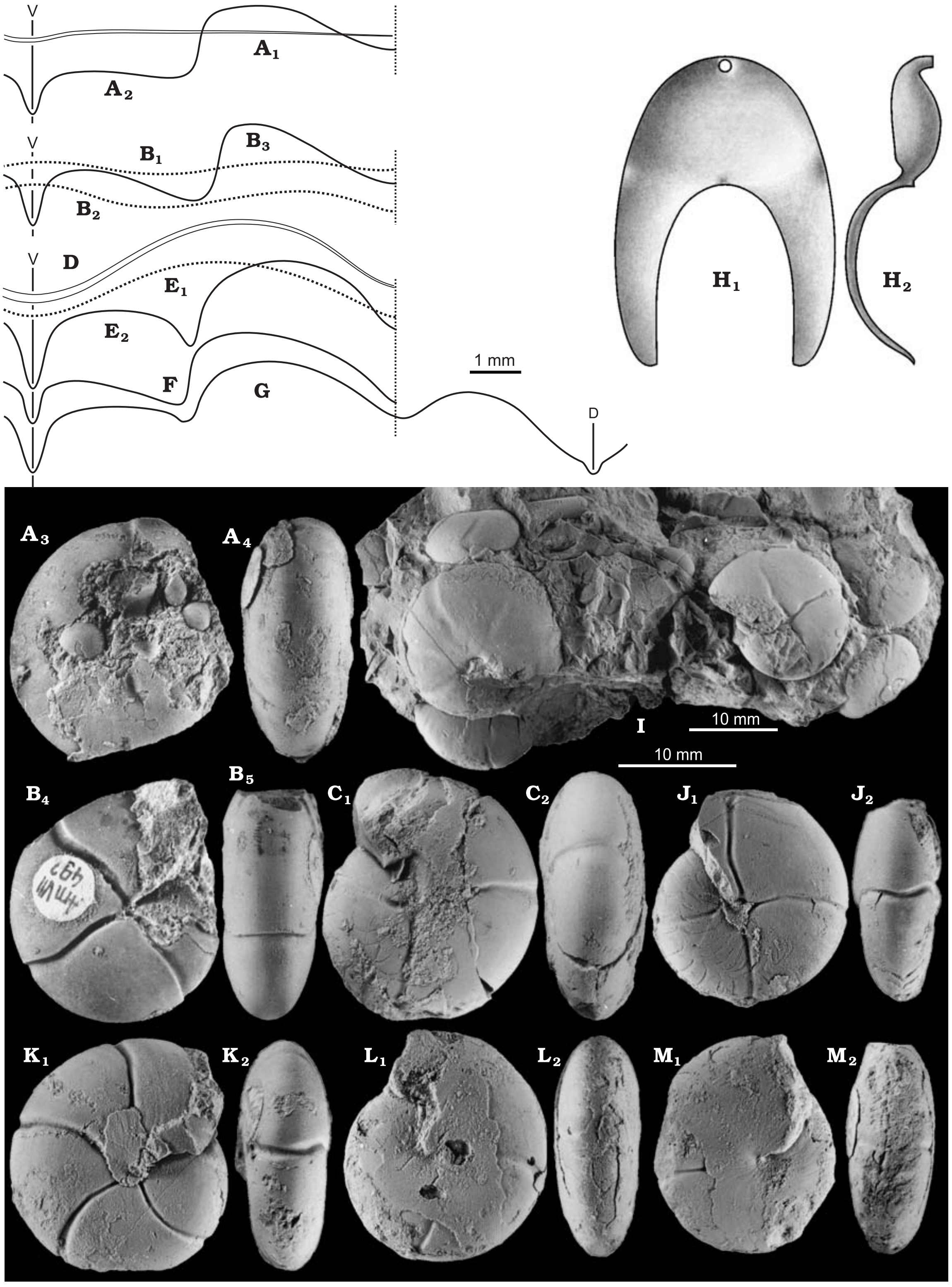


Fig. 162. Typical species of the *Cheiloceras* lineage from the Holy Cross Mountains. **A**. *Ch. subpartitum* (Münster, 1839) *sensu* Becker, 1993 from the *K. crepida* Zone at Jabłonna (bed 8); growth lines, suture and views of specimen ZPAL AmVII/310. **B**, **C**. *Ch. angustivaricatum* (Sobolew, 1914) from the *K. crepida* Zone at Jabłonna (B, bed 10) and Kadzielnia (C, sample Ka-5); internal thickenings and views of specimen ZPAL AmVII/310. **D**–**M**. *Ch. discoidale* (Sobolew, 1914) from Łagów-Dule, growth lines of specimen ZPAL AmVII/515 (D, sample Ł-5, the *C. marginifera* Zone), internal thickening and suture of specimen ZPAL AmVII/516 (E, sample Ł-11); sutures of specimens ZPAL AmVII/1336 and 1335 (F, G, sample Ł-29, the *C. quadrantinodosa* Zone); septum of specimen ZPAL AmVII/1334 (H, sample Ł-29); slab ZPAL AmVII/1228 with mass occurrence of the species (I); views of specimens ZPAL AmVII/1218, 1245, 1261, and 1331 (J–M, sample Ł-29).

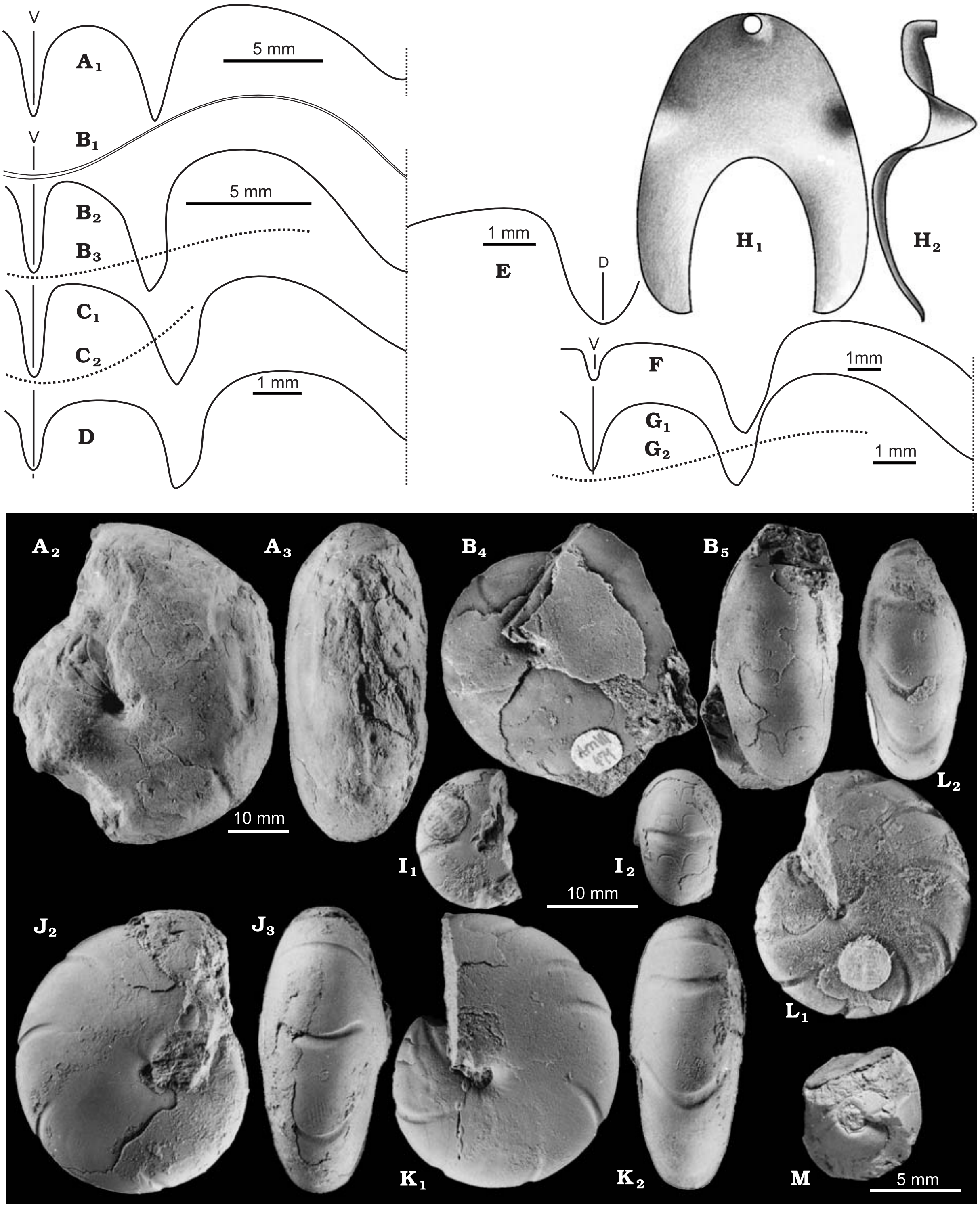


Fig. 163. Species of *Cheiloceras* with compressed conch and acute lobe of suture from the Famennian of the Holy Cross Mountains. **A**. *Ch. praecursor* (Frech, 1902) from the late *K. crepida* or early *C. quadrantinodosa* Zone at Kadzielnia; suture and views of specimen IG 175.II.7 collected by H. Makowski in 1949. **B**–**L**. *Ch. lagoviense* (Gürich, 1901) from the *C. quadrantinodosa* Zone at Łagów-Dule and Jabłonna (E); growth lines, suture, internal thickening, and views of specimen ZPAL AmVII/471 (B, sample Ł-12); sutures and internal thickenings of specimens ZPAL AmVII/475, 1445, 650, 1122 and 478 (C, sample Ł-21; D, sample Ł-33; E, well w150a at Jabłonna; F, sample Ł-34; G, loose from Łagów-Dule); septum reconstruction based on specimen ZPAL AmVII/657 (H); views of specimens ZPAL AmVII/478, 1449, 1122, and 469 (I, sample Ł-12; J, sample Ł-33; K, sample Ł-34; L, loose from Łagów-Dule). **M**. Juvenile cheiloceratid, possibly *Ch. praecursor*, from the *C. quadrantinodosa* Zone at Jabłonna (borehole IG-1 depth 67.6–68.00 m); specimen ZPAL AmVII/336.

Diagnosis. — Suture with acutely pointed, deep flank lobe and rounded ventrolateral saddle; medium-size thick discoidal conch with rare internal thickenings following the course of aperture.

Remarks. — From the geologically younger *Ch. lagoviense* the species differs in a more robust conch appearance and the shape of ventrolateral saddle of the suture. The two juvenile specimens illustrated by Becker (1993b) differ in prominence of the ventrolateral saddle. The suture of the neotype proposed by him is close to that shown by the specimen from Kadzielnia.

From the earliest species of *Dimeroceras* the species differs in the narrow juvenile umbilicus of about 1 mm width and the weak periumbonal lobe.

Distribution. — Late *K. crepida* or *C. quadrantinodosa* Zone at Kadzielnia as suggested by the marly matrix.

Cheiloceras lagoviense (Gürich, 1901)
(Figs 163B–L, 164, and 181)

Type horizon and locality: Early Famennian Upper Łagów Beds at Łagów Dule, Holy Cross Mountains.

Material. — 37 specimens.

Diagnosis. — Suture with acutely pointed, relatively deep flank lobe and trapezoidal ventrolateral saddle; medium-size discoidal conch with numerous internal thickenings following the course of aperture.

Remarks. — Among Gürich's (1901, pl. 14: 4a–c) specimens only the lectotype represents this species. The paratype (Gürich 1901, pl. 14: 5a, b) with radially arranged internal thickenings best visible on flanks and a more globose conch represents another cheiloceratid, possibly *Ch. amblylobum*. Sobolew's (1914) *Ch. sublagoviense* and *Ch. longilobum*, probably from the same stratum, may be conspecific. The latter species probably corresponds to more globose variants deviating from the main trajectory of the *Ch. lagoviense* ontogeny (Fig. 164B). This deviation is strong enough to suspect that a separate species is represented in the sample. Unquestionably homogenous natural assemblage is necessary to prove this.

Distribution. — *C. quadrantinodosa* and *C. marginifera* zones at Łagów-Dule (samples Ł-5, 12, 21, 28, 29, 30, 31, 33, 34, and Mak-3), possibly also at Jabłonna (well w150a of Żakowa *et al*. 1986).

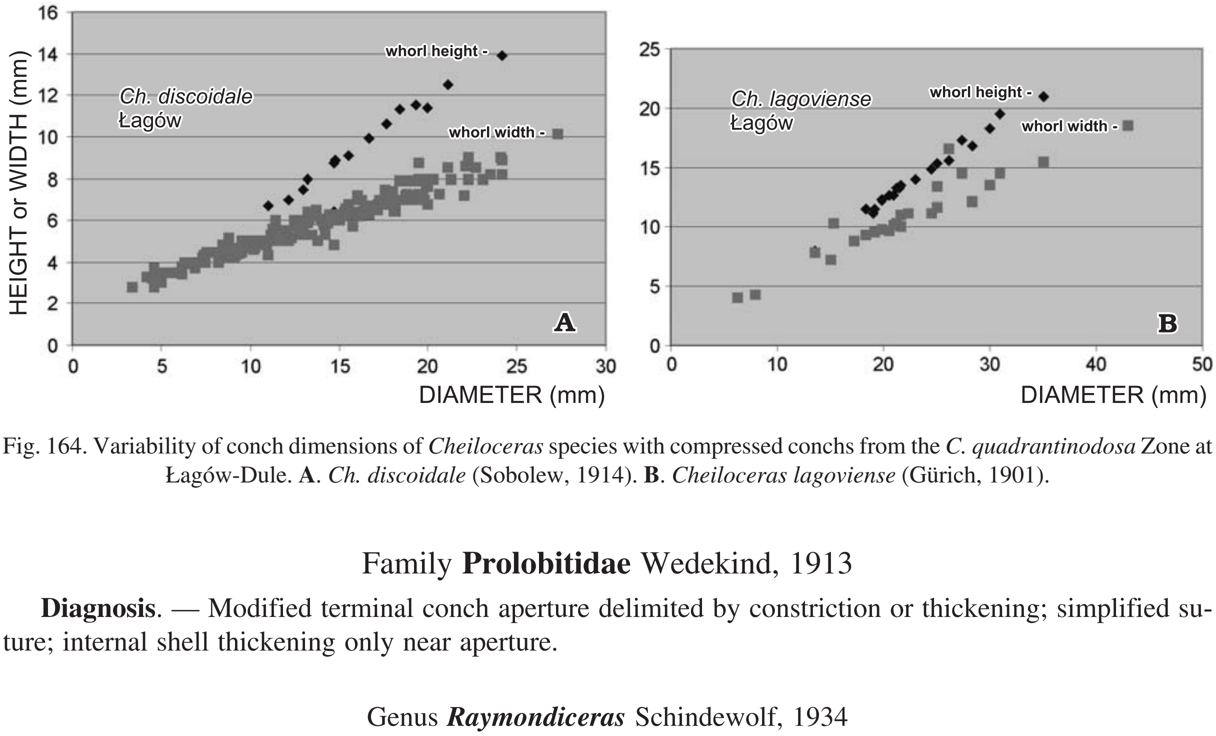


Fig. 164. Variability of conch dimensions of *Cheiloceras* species with compressed conchs from the *C. quadrantinodosa* Zone at Łagów-Dule. **A**. *Ch. discoidale* (Sobolew, 1914). **B**. *Cheiloceras lagoviense* (Gürich, 1901).

Family **Prolobitidae** Wedekind, 1913

Diagnosis. — Modified terminal conch aperture delimited by constriction or thickening; simplified suture; internal shell thickening only near aperture.

Genus ***Raymondiceras*** Schindewolf, 1934

Type species: *Prolobites simplex* Raymond, 1909 from the Three Forks Shale at Three Forks, Montana.

Diagnosis. — Regularly spiral conch with narrow or closed umbilicus.

Remarks. — Korn (2002) introduced genus *Roinghites* for prolobitids with simple suture, but its distinction in respect to *Raymondiceras* has to be confirmed by findings of mature specimens of the latter.

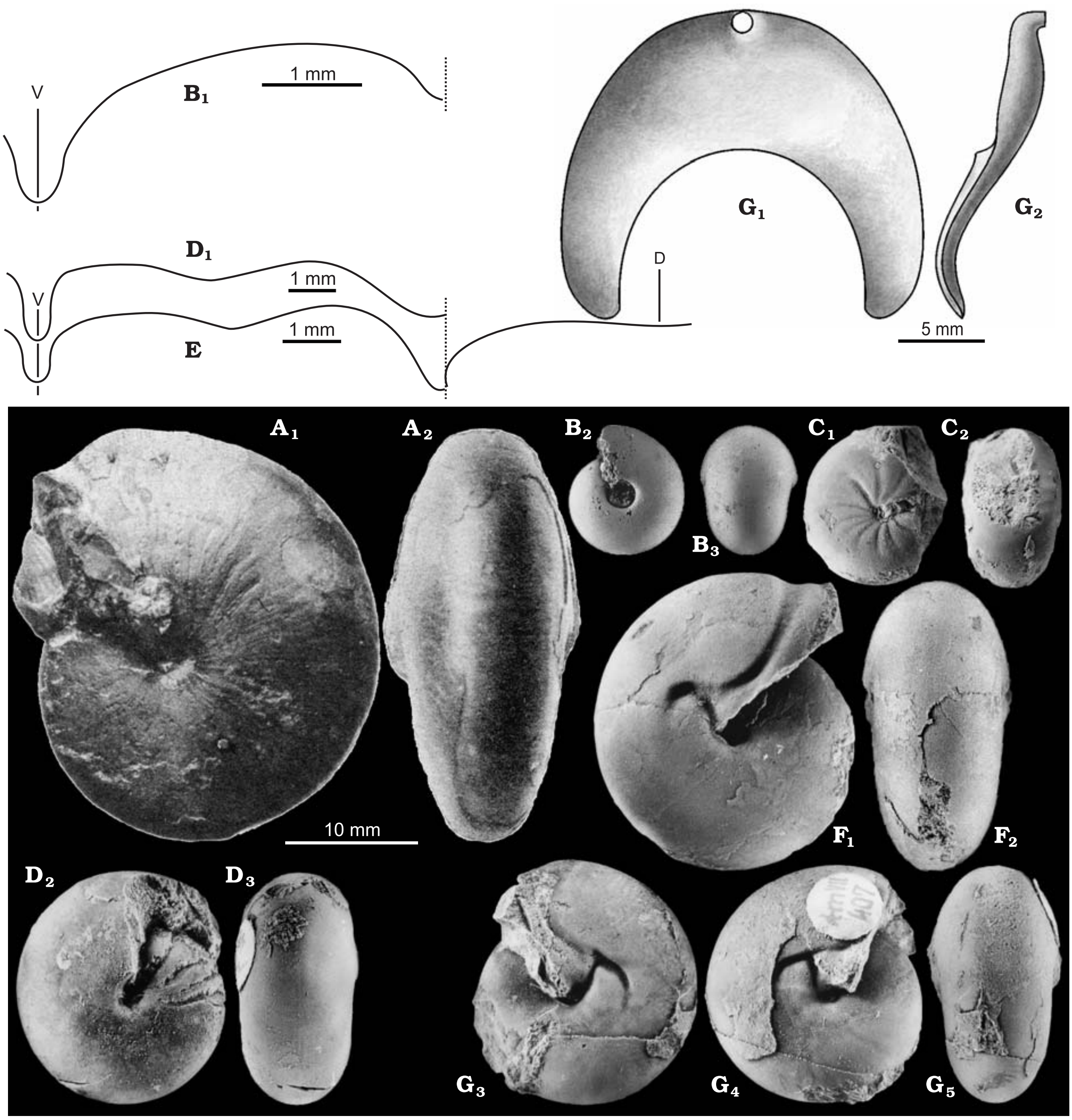


Fig. 165. Species of the prolobitid *Raymondiceras* from the Famennian of the Holy Cross Mountains. **A**. *R.*? *praelagoviense* (Sobolew, 1914) probably from the *C. quadrantinodosa* Zone at Łagów-Dule (reproduced from Sobolew 1914, pl.1: 3). **B**. *R. umbilicatum* (Sobolew, 1914) from the mid *C. marginifera* Zone at Kowala; suture and views of specimen ZPAL AmVII/1005. **C**. Possible *Raymondiceras* from Jabłonna (trench 123a of Żakowa *et al.* 1986); views of specimen ZPAL AmVII/613. **D**–**G**. *R. korni* sp. n. from the *P. trachytera* Zone at Łagów (D, G) and Ostrówka (E, F); suture and views of specimen ZPAL AmVII/407 (D); suture of views of specimen ZPAL AmVII/1070 (E, sample Ost-14); views of specimen IG 175.II.85 collected by J. Czarnocki (F); restored septum and views of the holotype ZPAL AmVII/407 (G).

Raymondiceras? *praelagowiense* (Sobolew, 1914)
(Figs 165A and 181)

Type horizon and locality: Early Famennian Lower Łagów Beds at Łagów Dule, Holy Cross Mountains.

Diagnosis. — Discoidal conchs with almost straight transverse profile of aperture and simplified suture with weak flank lobe.

Remarks. — Seven pyritized specimens from Sieklucki's brickpit of probably this species are represented in the collection of Dybczyński at Lvov (MD 13044). This confirms validity of the species, although photograph of the type specimen remains the only source of information on the conch morphology.

Distribution. — Probably the *C. quadrantinodosa* Zone at Łagów-Dule; reworked at Sieklucki's brickpit in Kielce.

Raymondiceras umbilicatum (Sobolew, 1914)

(Figs 165B and 181)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — One specimen.

Diagnosis. — Extremely simplified suture and open umbilicus.

Remarks. — The figures provided by Sobolew (1914) to his Oma-re-protomeroceras *umbilicatum* are not especially informative. However, the wide, V-shaped ventral lobe seems to identify this species rather convincingly. Moreover, most of the material represented in Sieklucki's brickpit seems to come from strata of the same age as the horizon with pyritized ammonoids at Kowala. The specimen is actually indistinguishable from corresponding ontogenetic stages of *Prolobites delphinus* but cannot be attributed there because of its significantly older geological age. Becker *et al*. (2002) placed this species with reservation in their *Afrolobites*.

Distribution. — The mid *C. marginifera* Zone at Kowala.

Raymondiceras korni sp. n.

(Figs 165D–G and 181)

Holotype: Specimen IG 284.II.85 (Fig. 165G).

Type horizon and locality: Black clymenoid limestone at Łagów, Holy Cross Mountains.

Material. — 33 specimens.

Diagnosis. —Discoidal conchs of simple geometry with £-shaped internal thickening near aperture; suture with shallow flank lobe; umbilicus closed at juvenile stages.

Remarks. — *Roinghites bottkei* Korn, 2002 from the *Platyclymenia annulata* black shale at Kattensiepen is a closely related species different in a somewhat larger mature size, more discoidal conch, and less prominent internal shell thickenings (Korn 2002).

The single specimen from Jabłonna attributed here does not show suture and bears numerous serial conch constrictions or thickenings on flanks. Its taxonomic identification is highly tentative.

Distribution. — The *P. trachytera* Zone at Ostrówka (samples Ost-14 and 15), Besówka, and Łagów-Dule (sample Mak-2), possibly also Jabłonna (trench 123a of Żakowa *et al*. 1986; Fig. 165C).

Genus ***Prolobites*** Karpinsky, 1886

Type species: *Goniatites bifer* var. *delphinus* Sandberger *et* Sandberger, 1850 from the Rhenish Slate Mountains.

Diagnosis. — Mature living chamber with hood-like apertural part delimited by whorl constriction and internal shell thickening.

Remarks. — A troublesome aspect of the taxonomy within this genus is the tremendous difference in size of mature specimens co-occurring in the same bed. It remains unclear whether these are different species, different sexual morphs within the same species, or just a very wide population variability. It is noteworthy that in the most prolific *Prolobites* sample known in literature, from the locality Kara Dzhar in the southern Urals (Bogoslovsky 1969, p. 52) more than 600 specimens of *P. delphinus* are associated with 350 specimens of minute *P. nanus*. This suggests the sexual dimorphism but in the very rich sample from Kattensiepen in the Rhenish Slate Mountains minute prolobitids are apparently missing (Korn 2000). Rare associated specimens classified in four other species differ from each other in more or less ovoid shape of the last chamber and extension to maturity of the juvenile characters, that is open umbo and simplified suture. These may represent end-members of the populations variability of *P. delphinus*. The material available to me is too small to decide on this.

Prolobites delphinus (Sandberger *et* Sandberger, 1850)

(Figs 166A–D and 181)

Type horizon and locality: the Rhenish Slate Mountains.

Material. — 15 specimens.

Diagnosis. — Mature specimens reaching about 30 mm in diameter; suture with rounded deep lobe; evolute juvenile conch.

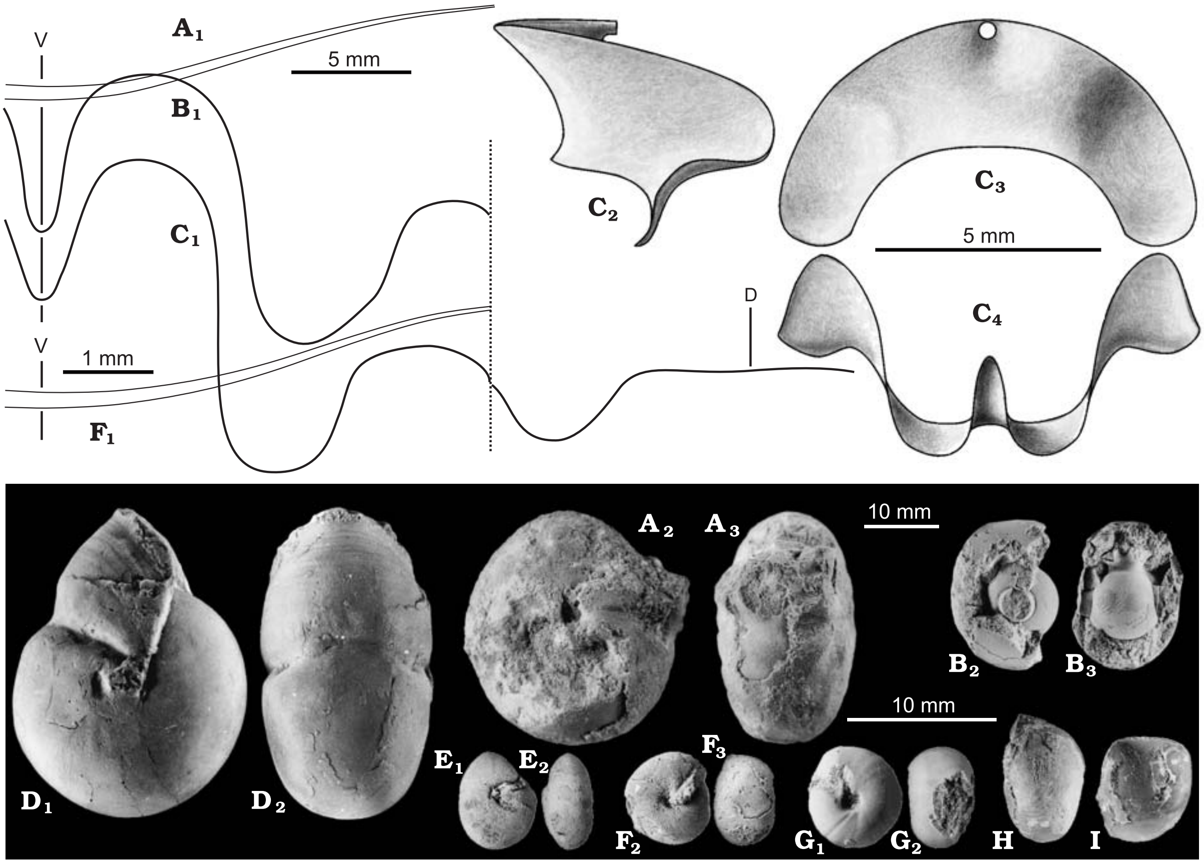


Fig. 166. Species of *Prolobites* from the Famennian of the Holy Cross Mountains. **A–D**. *Prolobites delphinus* (Sandberger *et* Sandberger, 1850) from the *P. trachytera* Zone at Ostrówka; growth lines and views of specimen ZPAL AmVII/200 with grey-green marly limestone matrix (A); suture and views of incomplete specimen IG 175.II.41 (B); suture and restored septum of specimen IG 175.II.49 (C); views of complete specimen IG 175.II.40 colected by J. Czarnocki (D). **E–I**. Possible *Prolobites nanus* (Perna, 1914) and related forms from Jabłonna; views of mature ovoid specimen ZPAL AmVII/623 (E, trench rIVc and f of Żakowa *et al*. 1986); growth lines and views of specimen ZPAL AmVII/621 (F, same trench); views of specimen ZPAL AmVII/620 (G, trench rIVf); fragmentary specimens ZPAL AmVII/145 and 121 (H, I; bed 24).

Remarks. — Suture has been traced only in two specimens and they differ significantly in shape of the flank lobe, subcircular in one, and parabolic in the other. I am thus skeptical regarding taxonomic value of this character in distinguishing species of the genus. In fact, data presented by Bogoslovsky (1969) show that virtually all characters of the species are extremely variable, with possible exception of the apertural modifications (see Korn *et al*. 1984; Korn 2002). The specimen with well preserved shell (Fig. 166A) shows coarse growth lines characteristic of the species but most specimens from the Państwowy Instytut Geologiczny in Warsaw collection are devoid of the external shell layer.

Distribution. — The *P. trachytera* Zone at Ostrówka (beds 2 and 3 of Czarnocki 1989). Specimens from Czarnocki's collection are preserved in black limestone, similar to that with *R. korni* sp. n. (well represented also in my material). The only specimen collected by myself at the locality from the scree is preserved, however, in a greyish-green marly limestone. This suggests that *R. korni* (occurring alone at Łagów) and *P. delphinus* did not come from the same bed.

Prolobites nanus (Perna, 1914)
(Figs 166E–I and 181)

Type horizon and locality: Locality 839 near Kirsy, the southern Urals.

Material. — Five specimens.

Remarks. — A few extremely small mature prolobitid conchs have been recovered from a not precisely defined horizons at Jabłonna. They are of size from 8 to 11 mm and may, with some difficulty, be fit in the range of variability of *P. nanus* (Perna, 1914) (ranging from 7 to 16 mm; Bogoslovsky 1969, p. 186).

Distribution. — The *P. trachytera* (bed 24) and *L. styriacus* (trenches rIVc and f of Żakowa *et al*. 1986) zones at Jabłonna.

Family **Dimeroceratidae** Hyatt, 1884

Diagnosis. — Suture with umbonal lobe and trifid dorsal lobe; evolute juvenile conch; conch aperture with oblique convex profile; relatively low whorl expansion rate.

Genus ***Dimeroceras*** Hyatt, 1884

Type species: *Goniatites mamillifer* Sandberger *et* Sandberger, 1850 from Enkeberg in the Rhenish Slate Mountains (Becker 1993b).

Diagnosis. — Suture with incipient dorsolateral lobe; mature conch discoidal.

Dimeroceras kontkiewiczi Dybczyński, 1913

(Figs 167 and 181)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — Five specimens.

Diagnosis. — Juvenile conch discoidal with open umbo about 3 mm wide; at the venter internal thickenings parallel to the aperture.

Remarks. — An angulation of the dorsolateral saddle marks an incipient dorsolateral lobe of the same kind as in *D. globosoides*. The difference between these species consists in a less globose conch shape and internal thickenings parallel to aperture in the Jabłonna population, which seems also to be stratigraphically older that that at Łagów.

Early stages of the ontogeny and the conch form indistinguishable from typical species of *Cheiloceras* make this species a good connecting link between families, as already pointed out by Becker (1993b), who included it in his genus *Praemeroceras*.

The holotype of the species is a juvenile 17 mm in diameter with well exposed suture (Dybczyński 1913, pl. 2: 16), rather poorly preserved but the conch globosity and narrow umbo at such ontogentic stage fits that of the Jabłonna specimens, making it unlike more advanced species of *Dimeroceras*. In Otto Schindewolf 's sample "Schicht 4", mentioned above in connection with *Cheiloceras inversum*, there are specimens with a depressed area surrounding the closed umbo and probably representing a button-like internal thickening. Such specimens were classified by Sobolev (1914) in his *C. depressum*.

Distribution. — Probably early part of the *C. marginifera* Zone at Jabłonna (well w86b of Żakowa *et al*. 1986); reworked at Sieklucki's brickpit in Kielce.

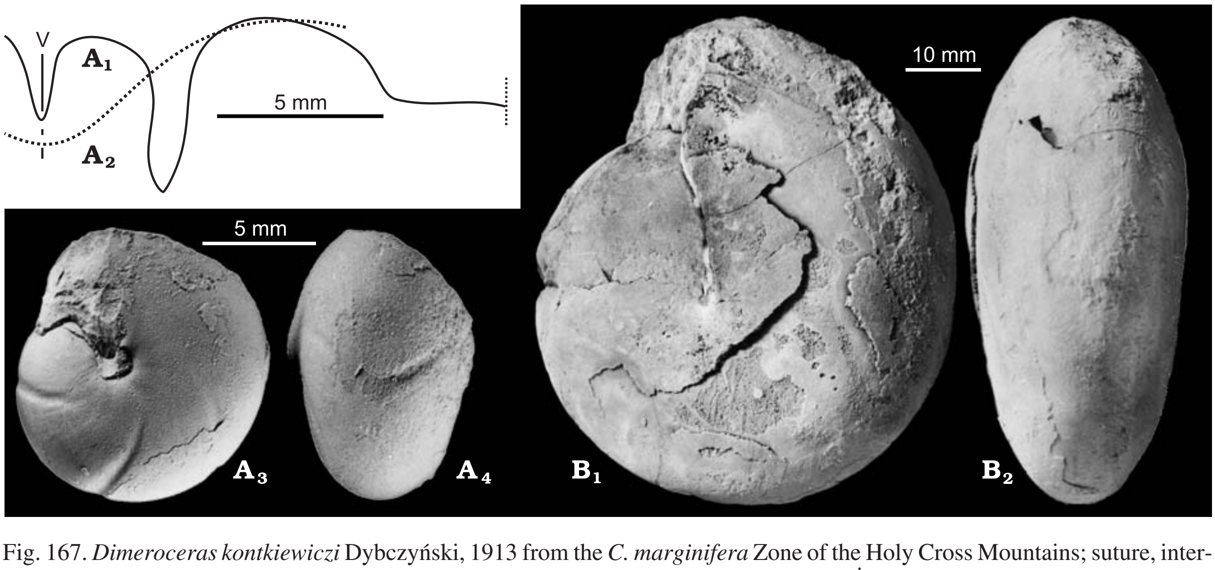


Fig. 167. *Dimeroceras kontkiewiczi* Dybczyński, 1913 from the *C. marginifera* Zone of the Holy Cross Mountains; suture, internal thickening and views of specimen ZPAL AmVII/728 from Jabłonna (A, well w86b of Żakowa *et al*. 1986); complete mature specimen MfN, unnambered, from coeval strata at Łagów-Dule (B; O. Schindewolf collection, his "Schicht 4") possibly belonging to this species (suture not exposed).

Dimeroceras globosoides (Sobolew, 1914)
(Figs 168 and 181)

Type horizon and locality: Early Famennian Upper Łagów Beds at Łagów Dule, the Holy Cross Mountains.

Material. — 18 specimens.

Diagnosis. — Suture with incipient umbonal lobe; juvenile conch globose with umbo about 3 mm wide; internal shell thickenings, if present, of radial course.

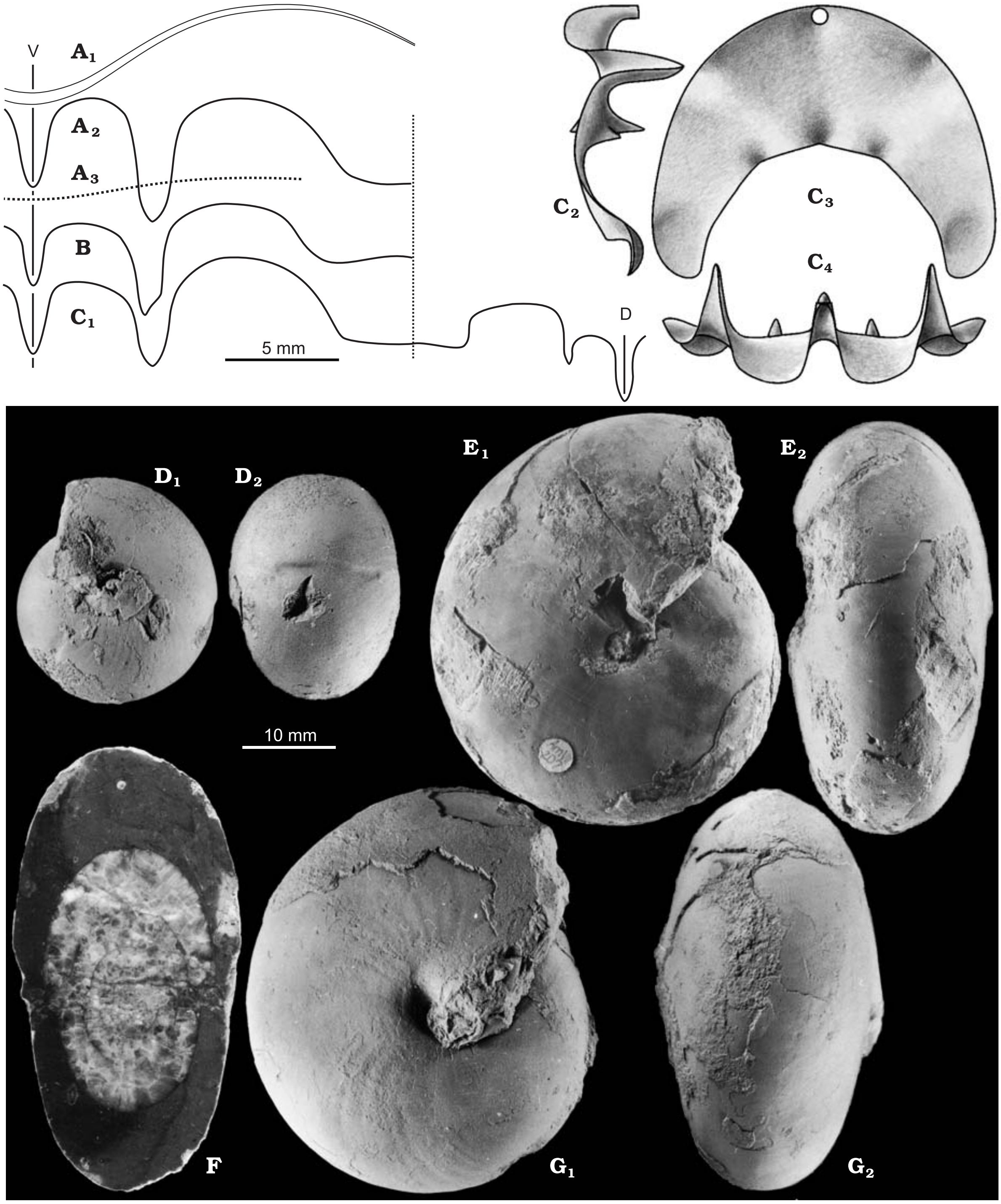


Fig. 168. *Dimeroceras globosoides* (Sobolew, 1914) from the late *C. marginifera* Zone at Łagów in the Holy Cross Mountains; growth lines, suture, and internal thickening of specimen ZPAL, unnambered (A, sample Ł-33); suture of specimen ZPAL AmVII/071 (B); suture and restored septum of specimen ZPAL AmVII/216 (C); views of specimens ZPAL AmVII/1441, 207, 1437, and 205 (D–G, D and G from sample Ł-33).

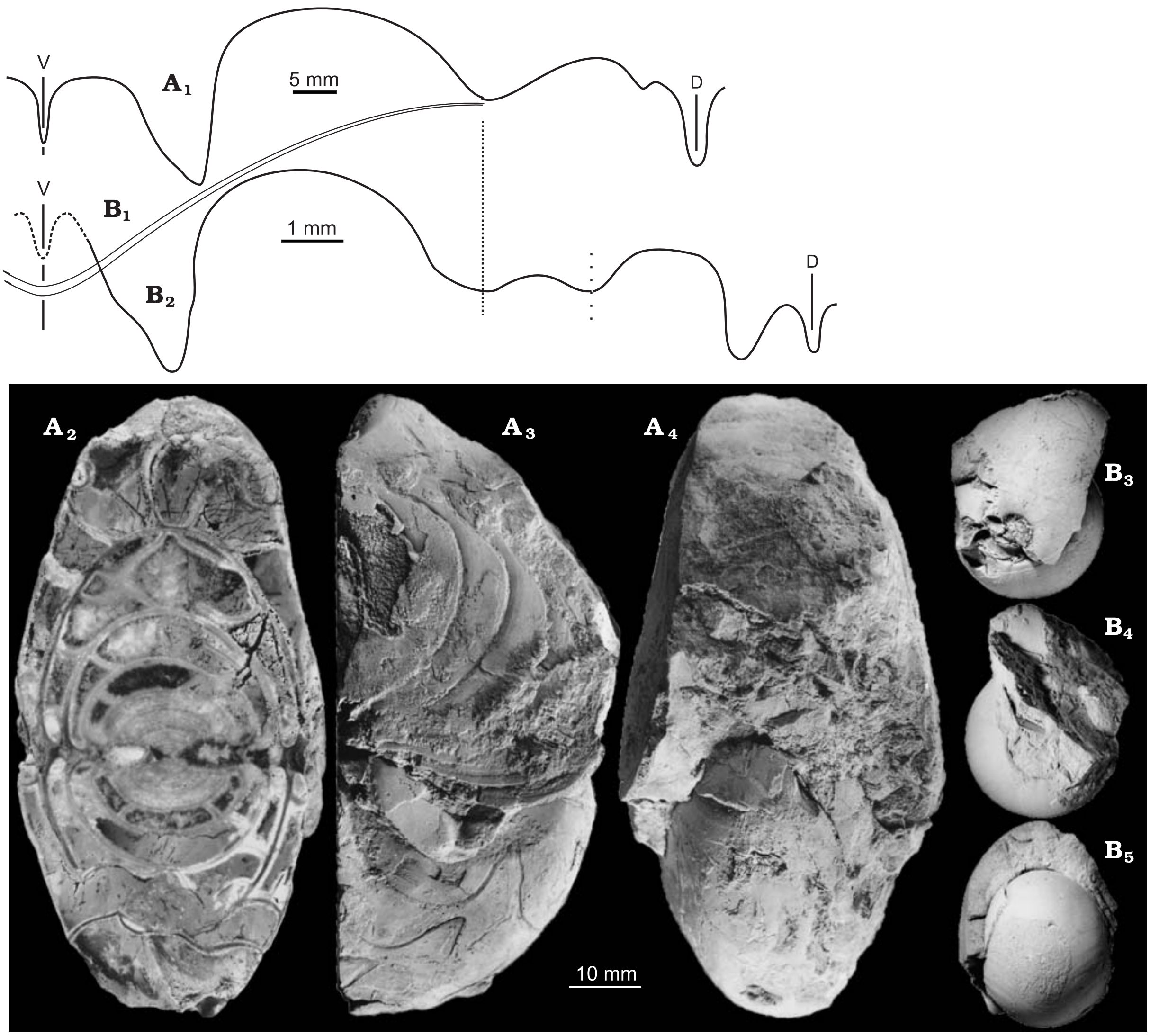


Fig. 169. Species of *Dimeroceras* with wide juvenile umbilicus from the Famennian of the Holy Cross Mountains. **A**. *D*. cf. *petterae* Petersen, 1975, probably from the *C. quadrantinodosa* Zone at Kadzielnia; suture, and views of specimen ZPAL AmVII/1856. **B**. *Dimeroceras umbilicatum* Sobolew, 1914, probably from the *P. trachytera* Zone at Łagów-Dule; growth lines, suture and views of specimen ZPAL AmVII/451.

Remarks. — This is a relatively long-ranging lineage, in the *P. trachytera* Zone represented by Sobolew's (1914) Oma-monomeroceras (*Cheiloceras*) *globosum* and possibly O. (*Ch.*) *praeglobosum*. The problematic O. (*Ch.*) *umbiliferum* has a better developed umbonal lobe and more evolute juvenile conch. An unnambered Otto Schindewolf 's mature specimen from his "Schicht 2", do not exposing suture but possibly belonging to this species, shows gradually opening umbilicus in the last half-whorl, reaching 85 mm in diameter.

Distribution. — The late *C. marginifera* to *P. trachytera* zones at Łagów-Dule (samples Ł-5 and 33).

Dimeroceras cf. *petterae* Petersen, 1975
(Figs 169A and 181)

Type horizon and locality: Middle Virgin Hills Formation, Canning Basin of western Australia.

Material. — One specimen.

Diagnosis. — Suture with very weak umbonal lobe; large discoidal mature conch with globose juvenile stage.

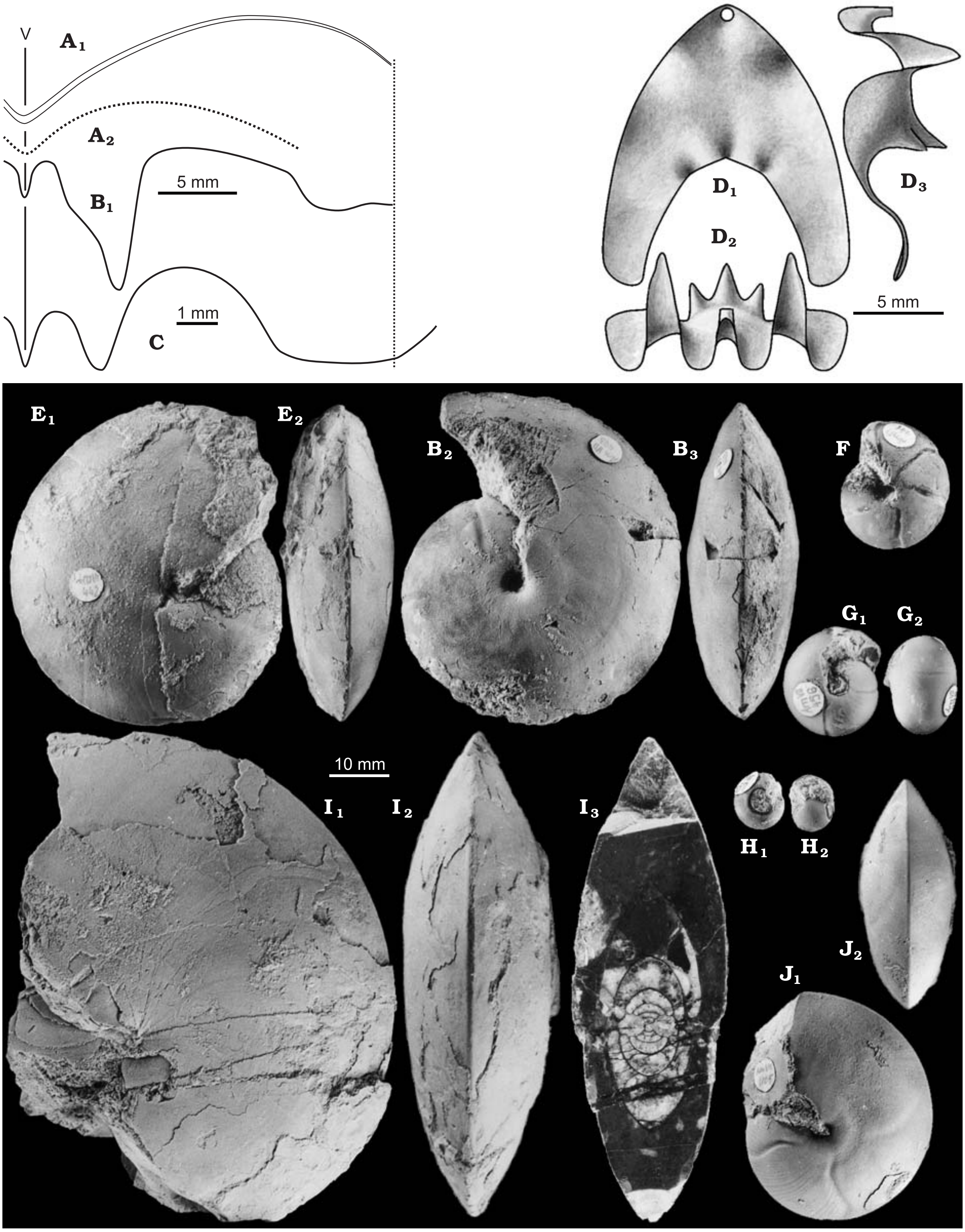


Fig. 170. *Dimeroceras polonicum* (Gürich, 1896) from the late *C. marginifera* Zone at Łagów-Dule in the Holy Cross Mountains; growth lines and internal thickening of specimen ZPAL AmVII/453 (A); suture and views of specimen ZPAL AmVII/443 (B); suture of specimen ZPAL AmVII/440 (C); restoration of septum based on specimen ZPAL AmVII/1101 (D); views of specimens ZPAL AmVII/442, 441, 456, 444, 1076, and 1105 (E–J).

Remarks. — The only specimen was found in the scree from a Famennian marl at the Kadzielnia quarry in Kielce. Specimen of *Conditolepis falcata* extracted from a piece of the specimen is the only basis for its precise dating. The most unusual aspect of the species is very wide whorl cross section at early ontogenetic stages, exceeding that of *D. petterae* but closely approaching that of the specimen attributed to *D*. cf. *D. bredelarense* from the same stratum (Petersen 1975, text-fig. 12). The species was identified also at Enkeberg by Becker (1993b).

Distribution. — The *C. quadrantinodosa* or younger Zone at Kadzielnia.

Dimeroceras umbilicatum Sobolew, 1914

(Figs 169B and 181)

Type horizon and locality: Black clymeniid limestone at Łagów Dule, the Holy Cross Mountains.

Material. — One specimen.

Diagnosis. — Juvenile umbo reaching about 8 mm diameter; suture with shallow and relatively wide umbonal lobe.

Remarks. — An angular aperture suggests acutely discoidal mature conch shape although only juveniles are known.

Distribution. — Łagów-Dule; black limestone matrix suggests the *P. trachytera* Zone.

Dimeroceras polonicum (Gürich, 1896)

(Figs 170 and 181)

Type horizon and locality: Early Famennian Upper Łagów Beds at Łagów Dule, the Holy Cross Mountains.

Material. — 41 specimens.

Diagnosis. — Acute venter of mature conch.

Remarks. — *D. polonicum* differs from other species of *Dimeroceras* in its acute venter. It is a matter of convenience whether an oxyconic conch form is anough to separate a species at generic level or not. *Paratornoceras* Hyatt, 1900 with *Goniatites lentiformis* Sandberger, 1857 from Enkeberg in the Rhenish Slate Mountains as its type species, is available for this purpose. The suture of the latter species, illustrated by Ebbinghausen *et al*. (2002, text-fig. 13: 3), is closely similar to that of the Łagów specimens. Its conch, described by Becker (1993b) as *Paratornoceras acutum* (Münster, 1840) (considered *nomen dubium* by Ebbinghausen *et al*. 2002), is much more compressed and thus derived.

Gürich (1901) referred to this species as *Brancoceras lentiforme*. *Tornoceras acutiforme* Gürich, 1896 is probably based on a juvenile specimen of the same species from the same stratum.

Distribution. — The *C. marginifera* Zone at Łagów-Dule (samples Ł-5, 21, 30, 32, 34, and Mak-3, all probably from the same single fossiliferous limestone lens).

Family **Praeglyphioceratidae** Ruzhentcev, 1957

Diagnosis. — Suture with trifid ventral lobe; conch aperture with obliquely convex profile; relatively low whorl expansion rate.

Genus ***Lagowites*** Bogoslovsky, 1957

Type species: α-Oma-dimeroceras (*Praeglyphioceras*) *niwae* Sobolew, 1914 from Łagów in the Holy Cross Mountains.

Diagnosis. — Suture with shallow additional ventral lobes.

Lagowites niwae (Sobolew, 1914)

(Figs 171A–E and 181)

Type horizon and locality: Black clymeniid limestone at Łagów Dule, the Holy Cross Mountains.

Material. — 12 specimens.

Diagnosis. — Globose conch with radially running internal constrictions and almost transverse aperture; weak spiral striation.

Remarks. — α-Oma-dimeroceras (*Praeglyphioceras*) *lagowiense* Sobolew, 1914 from the same bed seems to be conspecific.

Distribution. — The *C. marginifera* (sample Ł-38) and *P. trachytera* (samples Ł-8, 9, and 14) zones at Łagów-Dule and Jabłonna (beds 22 and 24).

Genus ***Erfoudites*** Korn, 1999

Type species: *Erfoudites zizensis* Korn, 1999 from the *Platyclymenia annulata* Zone in the Tafilalt, Morocco.

Diagnosis. — Conch aperture transverse or with very weak ventrolateral auricles, with longitudinal (spiral) striation; suture with additional ventral lobes in the middle of ventrolateral saddle.

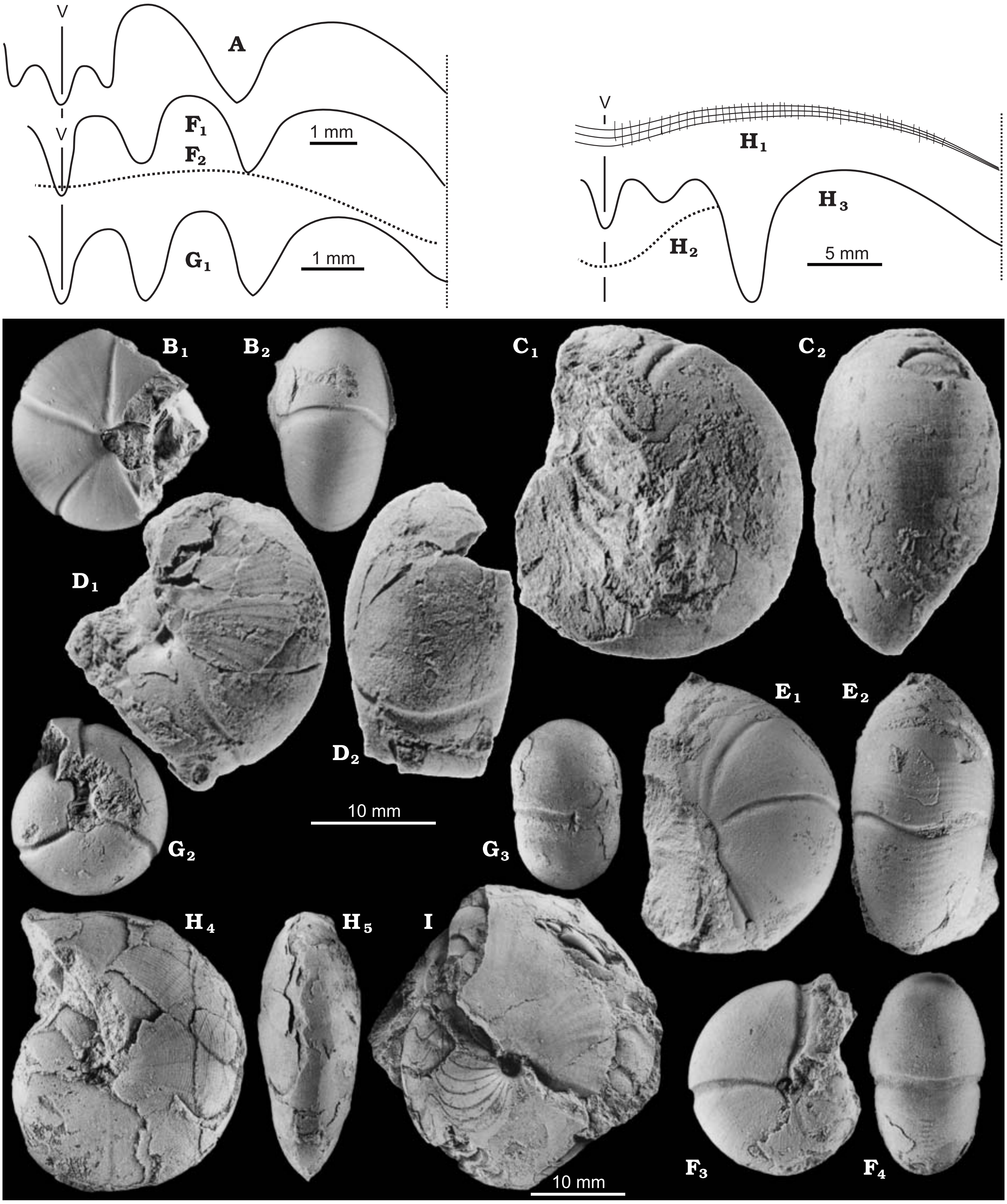


Fig. 171. Praeglyphioceratids from the Holy Cross Mountains. **A**–**E**. *Lagowites niwae* (Sobolew, 1914); suture and views of specimens ZPAL AmVII/867 and 719 from the *P. trachytera* Zone at Jabłonna (A, bed 24; E, bed 22), views of specimens ZPAL AmVII/306, 1809, and 1804 from the *C. marginifera* Zone at Łagów-Dule (B–D; C, D from sample Ł-38). **F**–**I**. *Erfoudites ungeri* (Münster, 1840) probably from the *P. trachytera* Zone at Besówka (collected by J. Czarnocki); growth lines, internal thickening and views of juvenile specimen IG 284.II205b (F); suture and views of specimen IG 284.II205c (G); growth lines, internal thickening, suture and views of specimen IG 284.II205a (H); view of specimen IG 284.II205d (I).

Remarks. — Korn (2002) introduced the subfamily Xenosporadoceratidae to include longitudinally striated sporadoceratids with transeverse apperture bearing incipient auricles. This implies that the auriculate (biconvex) aperture is of secondary origin. Quite well also the complex suture may be a homeomorphy in respect to the sporadoceratids and these may have been praeglyphioceratids with a discoidal, auriculate tornoceratid conch morphology.

Erfoudites ungeri (Münster, 1840)
(Figs 171F–I and 181)

Type horizon and locality: Schübelhammer near Heinersreuth in Frankenwald?

Material. — Five specimens.

Diagnosis. — Discoidal minute conch with almost transverse aperture and dense longitudinal (spiral) striation; suture with additional ventral lobe in the middle of ventrolateral saddle.

Remarks. — The ventral part of the phragmocone in the only available specimen from Jabłonna is crushed, but it is not likely that additional ventral lobes were originally represented.

Praeglyphioceras moravicus of Rzehak (1910) found in a loose block of bituminous limestone (possibly Hády Limestone) at Líšeň in Moravia seems to be conspecific with the Holy Cross Mountains material. Becker *et al.* (2004) synonymized it with *E. ungeri*. *Xenosporadoceras ademmeri* Korn, 2002 has a closely similar suture, spiral striation and conch proportions. It differs only in having small auricles of the aperture. It cannot be excluded that this is a case of evolutionary reversal and that these are close relatives.

Distribution. — Probably the *P. trachytera* Zone at Besówka near Gałęzice (lower *P. annulata* beds according to Czarnocki's label) and the *L. styriacus* Zone at Jabłonna (trench rIVc of Żakowa *et al.* 1986).

Family **Sporadoceratidae** Miller *et* Furnish, 1957

Diagnosis. — Suture with additional ventral lobes developing in the middle of ventrolateral saddle; convex profile of the conch aperture; relatively low whorl expansion rate.

Genus ***Felisporadoceras*** Korn, 2002

Type species: *Prionocears felix* Korn, 1992 from *Platyclymenia annulata* Zone at Kattensiepen in the Rhenish Slate Mountains.

Diagnosis. — Suture with additional ventral lobes shallower than the flank lobes.

Felisporadoceras kowalense sp. n.
(Figs 172 and 181)

Holotype: ZPAL AmVII/815 (Fig. 172C)

Type horizon and locality: Black shale of the mid *C. marginifera* Zone at Kowala, Holy Cross Mountains.

Material. — Five specimens.

Diagnosis. — Suture with shallow additional ventral lobe asymmetrically subdividing the ventral saddle and located closer to ventral than to flank lobe.

Remarks. — Gürich (1901, p. 351, pl. 14: 6) illustrated, as *Sporadoceras subbilobatum* (Münster, 1839), the suture of a specimen from the Sacculus Bank at Łagów-Dule, that is from the Upper Łagów Beds, which fits that of the Kowala specimens. *Goniatites subbilobatus* Münster, 1839 is now interpreted as a species of *Acutimitoceras* (Korn 1984) so this name cannot be used in the meaning given to it by Gürich (1901). From some reason Sobolew (1914), while referring to the same specimen, suggested that it may come from the clymeniid limestone. This seems to be contradicted by the new Kowala findings. Specimen ZPAL AmVII/562 from Łagów shows growth lines of *Sporadoceras* and suture closely similar to that of the holotype. Judging from its rock matrix it is from the latest *C. marginifera* Zone.

Sporadoceras rotundum Wedekind, 1908 is similar but the drawing of the suture in the type specimen (Wedekind 1908, pl. 39: 210) shows a symmetrical appearance of the additional ventral lobe.

Distribution. — The mid *C. marginifera* Zone at Kowala and Łagów-Dule (Gürich 1901).

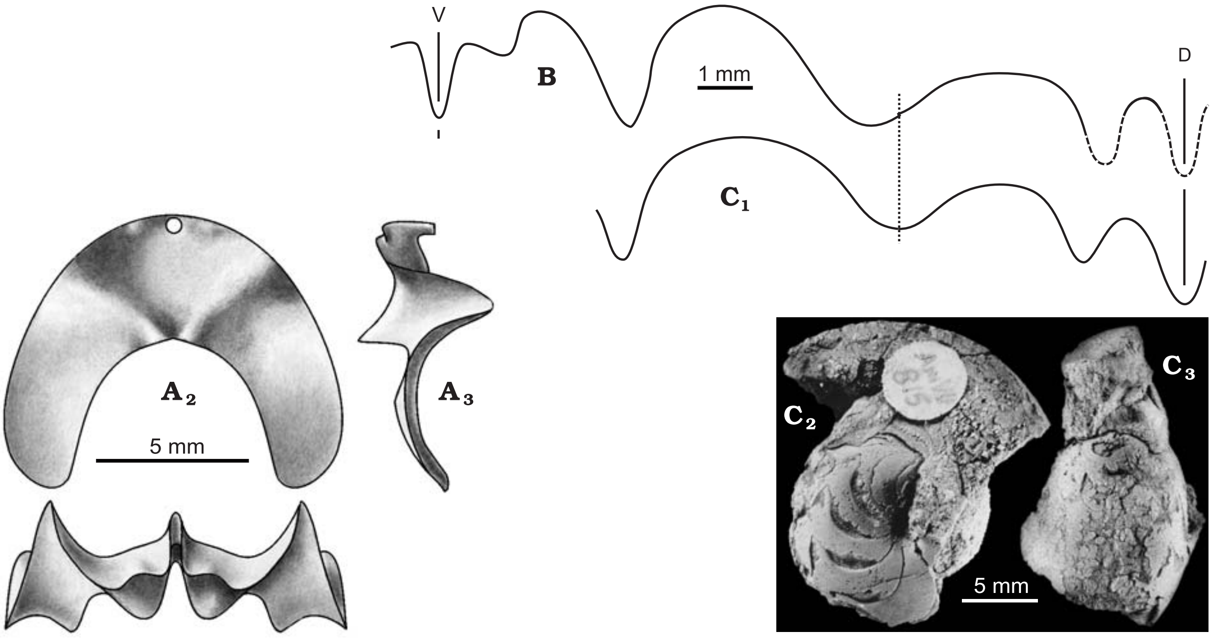


Fig. 172. The least derived sporadoceratid, *Felisporadoceras kowalense* sp. n. from the mid *C. marginifera* Zone at Kowala in the Holy Cross Mountains; restoration of septum based on specimen ZPAL AmVII/1019 (A); suture of ZPAL AmVII/177 (B); suture and views of the holotype ZPAL AmVII/815 (C).

Felisporadoceras subvaricatum (Sobolew, 1914)
(Figs 173A, B and 181)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains.

Material. — Eight specimens.

Diagnosis. — Suture with shallow additional ventral lobes asymmetrically subdividing the ventral saddle and located closer to ventral than to flank lobe.

Remarks. — Bockwinkel *et al*. (2002, p. 291) noticed that Sobolew (1914) used the name of his α-Oma-dimeroceras (*Sporadoceras*) *subvaricatum* to two different species and choose the lectotype that allegedly is a *Maeneceras*. Oma-dimeroceras (*Sporadoceras*) *polonicum* of Sobolew (1914) from Sieklucki's brickpit probably belongs to this species.

Distribution. — The *C. marginifera* (sample Ł-9) and *P. trachytera* (sample Ł-14) zones at Łagów-Dule, reworked at Sieklucki's brickpit in Kielce.

Felisporadoceras kielcense (Sobolew, 1914)
(Figs 173C–F and 181)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — Eight specimens.

Diagnosis. — Suture with deep additional ventral lobes asymmetrically subdividing the ventral saddle and located closer to ventral than to flank lobe.

Remarks. — Bogoslovsky (1971) attributed specimens of this morphology to *Sporadoceras biferum* (Phillips, 1841). Wedekind (1908) illustration of the suture of the species interpreted by him as *S. biferum* shows a symmetrical appearance of the additional ventral lobe.

Admittedly, the similarity between sutures of *Maeneceras lagoviense* and *F. kielcense* is striking. It is possible that these are actually members of the same lineage and the difference in the profile of aperture is of secondary importance in disclosing phylogenetic affinities.

Distribution. — The mid *C. marginifera* Zone at Kowala, reworked at Sieklucki's brickpit in Kielce.

Genus ***Sporadoceras*** Hyatt, 1884

Type species: *Ammonites Münsteri* von Buch, 1832 probably from the Rhenish Slate Mountains (Becker 1993b).

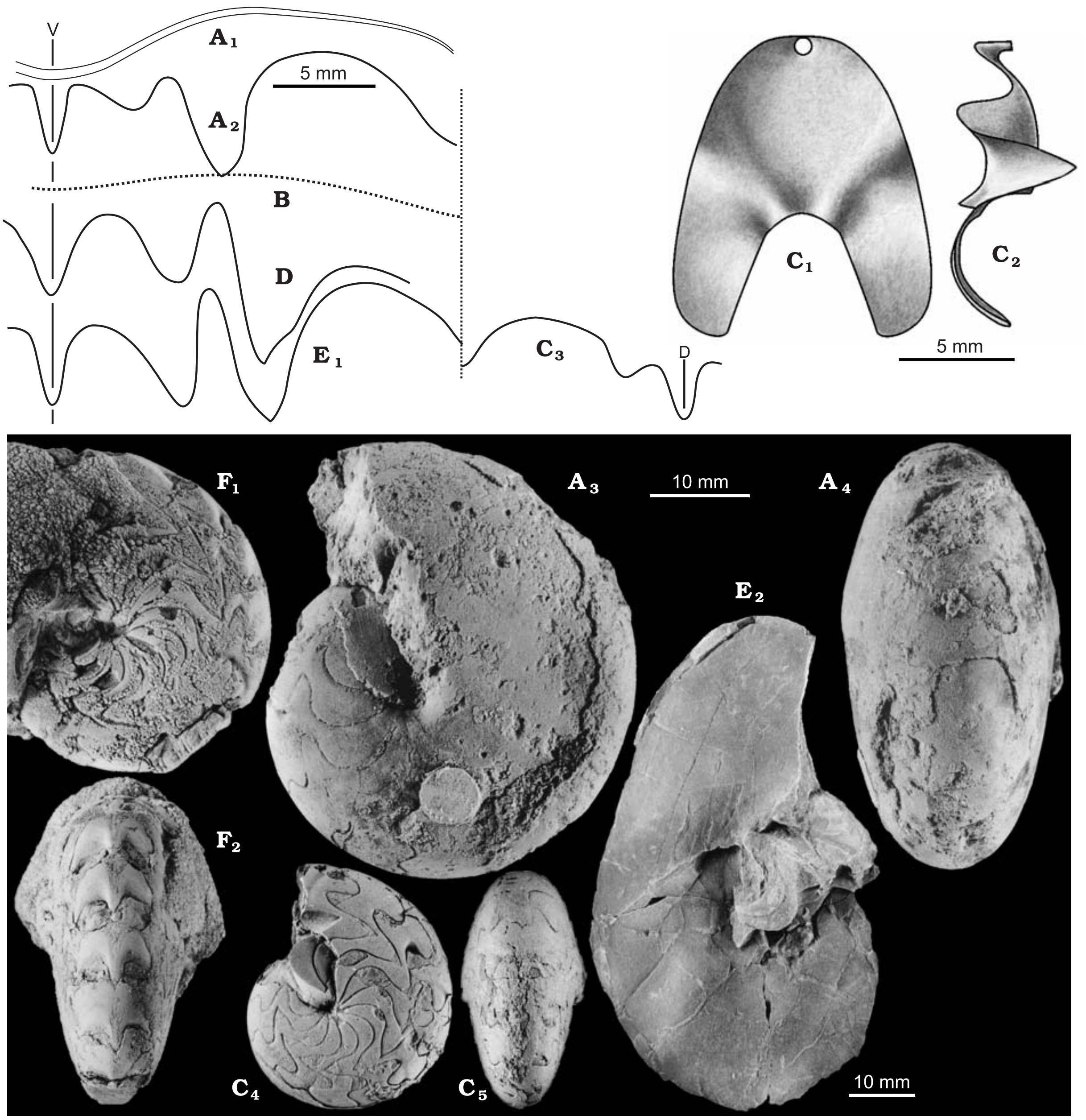


Fig. 173. Species of *Felisporadoceras* from the Holy Cross Mountains. **A**, **B**. *F. subvaricatum* (Sobolew, 1914) from the *C. marginifera* Zone at Łagów-Dule; growth lines, suture and views of specimen ZPAL AmVII/562 (A); internal thickening of specimen ZPAL AmVII/211 (B, sample Ł-9). **C**–**F**. *F. kielcense* (Sobolew, 1914) from the mid *C. marginifera* Zone at Kowala; restoration of septum, suture and views of specimen ZPAL AmVII/1003 (C); suture of specimen ZPAL AmVII182 (D); suture and view of specimen ZPAL AmVII/6 (E); views of specimen ZPAL AmVII/1842 (F).

Diagnosis. — Suture with acutely pointed additional ventral lobe of dept similar to that of the flank lobe.

Sporadoceras lagowiense (Sobolew, 1914)

(Figs 174 and 181)

Type horizon and locality: Black clymeniid limestone at Łagów Dule, Holy Cross Mountains.

Material. — Nine specimens.

Diagnosis. — Suture with the additional ventral lobe of the same depth as the flank lobe and with narrow ventral saddles; conch discoidal; internal thickenings usually weakly developed, a few per whorl.

Distribution. — The mid *C. marginifera* Zone at Kowala, late *C. marginifera* Zone at Łagów-Dule, reworked at Sieklucki's brickpit in Kielce.

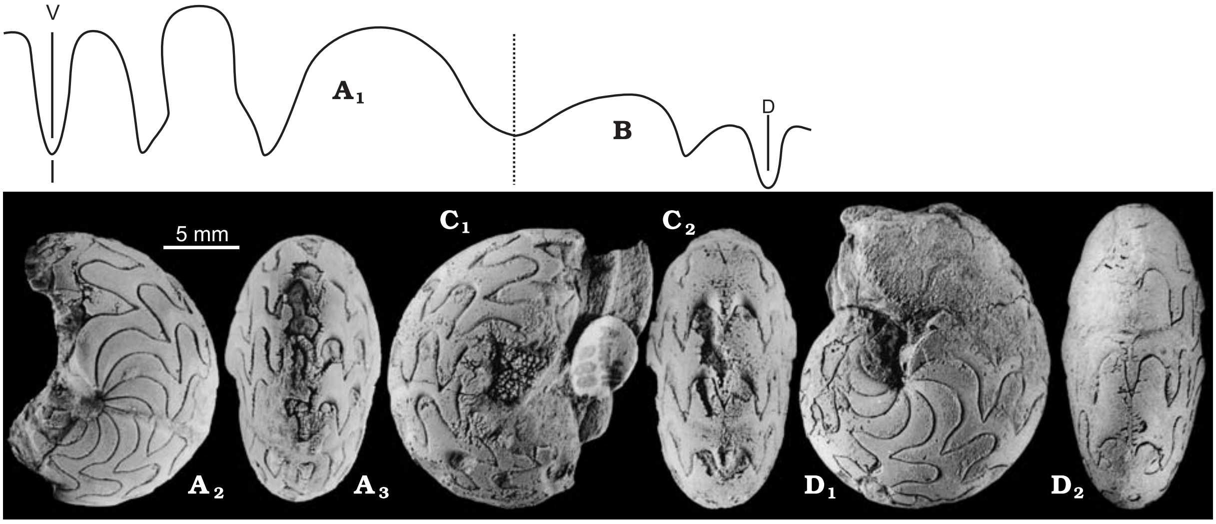


Fig. 174. Discoidal *Sporadoceras lagowiense* (Sobolew, 1914) from the mid *C. marginifera* Zone at Kowala in the Holy Cross Mountains; external suture and views of specimens ZPAL AmVII/82 (A); internal suture of specimen ZPAL AmVII/872 (B); views of specimens ZPAL AmVII/888 and 1002 (C, D).

Sporadoceras varicatum Wedekind, 1908.
(Figs 175 and 181)

Type horizon and locality: Bed 12 with *Prolobites delphinus* and *Clymenia involuta* at Enkeberg, Rhenish Slate Mountains.

Material. — 49 specimens.

Diagnosis. — Internal thickenings usually well developed on conch flanks, about six per whorl; conch discoidal in shape; suture with additional ventral lobe deeper than flank lobe and with wide ventral saddles.

Remarks. — From the type species of the genus this one differs in regularly distributed internal constrictions of the shell. In the Ostrówka sample, large specimens show ventral sinus of the internal conch thickening deeper than it is in juveniles. This suggests that small specimens from other localities represent the same species. The difference between *S. varicatum* and *S. lagoviense* is thus mostly in the morphology of suture. Growth lines are visible only in juvenile specimen ZPAL AmVII/672 from Łagów, of questionable affiliation.

Distribution. — The *P. trachytera* Zone at Łagów-Dule (sample Ł-10 and 13), Jabłonna (beds 23 and 24; trench rIVf), and Ostrówka (samples Ost-10, 11, 14, 15); the *L. styriacus* Zone at Kowala.

Sporadoceras nux (Sobolew, 1914)
(Figs 176A and 181)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — Four specimens.

Diagnosis. — Globose conch; suture with narrow additional ventral and flank lobes of subequal depth.

Distribution. — The mid *C. marginifera* Zone at Kowala and the *P. trachytera* Zone at Jabłonna (bed 24); reworked at Sieklucki's brickpit in Kielce.

Sporadoceras terminus sp. n.
(Figs 176B–G and 181)

Holotype: Specimen ZPAL AmVII/3 (Fig. 176G)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

Derivation of name: Referring to its terminal position in the *Sporadoceras* lineage.

Material. — Ten specimens.

Diagnosis. — Suture with bulbous lobes and saddles, additional ventral and flank lobes of subequal depth; rather globose conch.

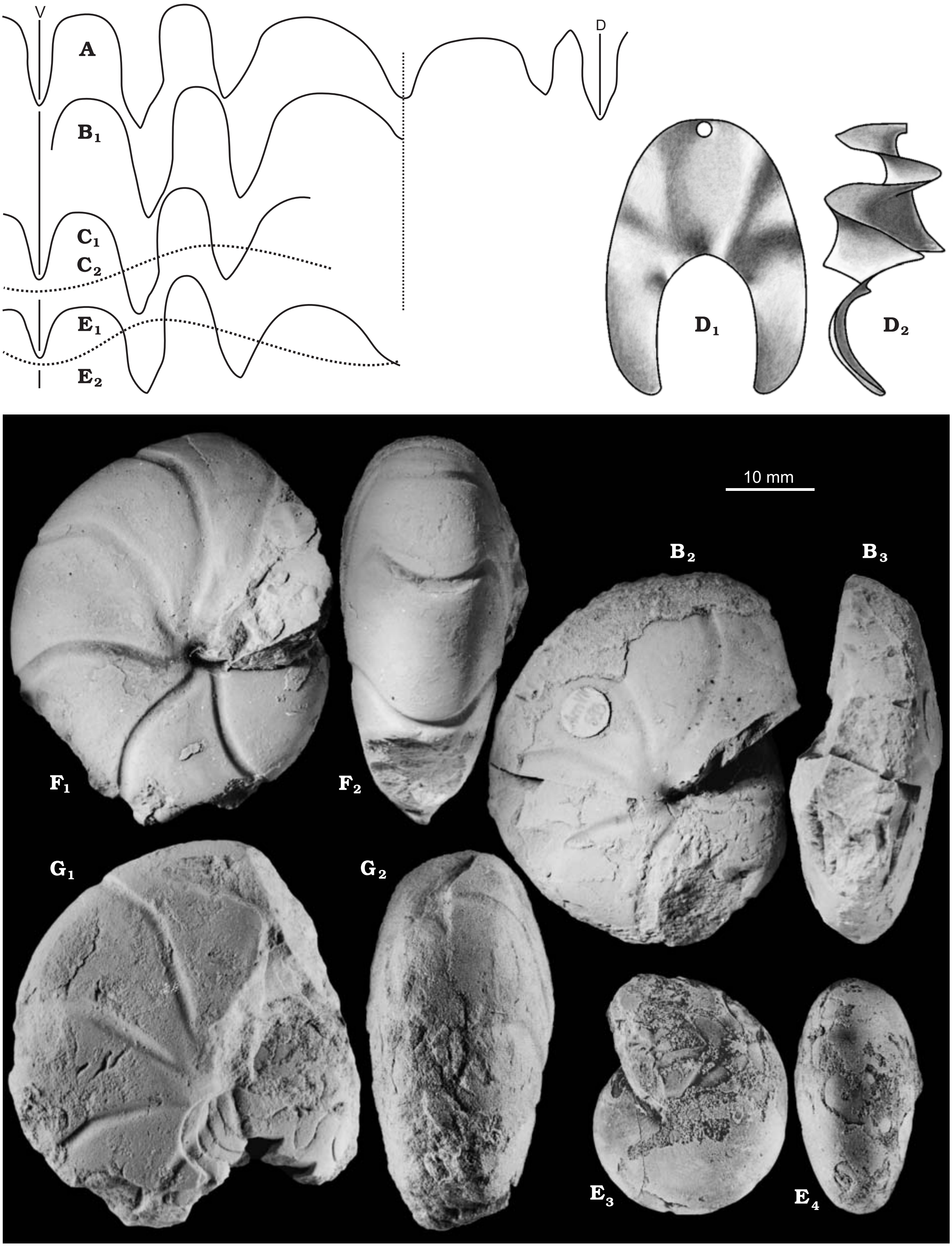


Fig. 175. Discoidal *Sporadoceras varicatum* Wedekind, 1908 from the *P. trachytera* Zone at Ostrówka (A, D, F), Jabłonna (B), Łagów-Dule (C, E), and the *L. styriacus* Zone at Kowala (G) in the Holy Cross Mountains; suture of specimen ZPAL AmVII/1063 (A, sample Ost-14); suture and internal thickening of specimen ZPAL AmVII/596 (C); restoration of septum (D) based on specimens ZPAL AmVII/1084 (sample Ost-15) and 602 (bed 24 at Jabłonna); suture, internal thickening and views of specimen ZPAL AmVII/667 (E); views of specimens ZPAL AmVII/92 and 1621 (F).

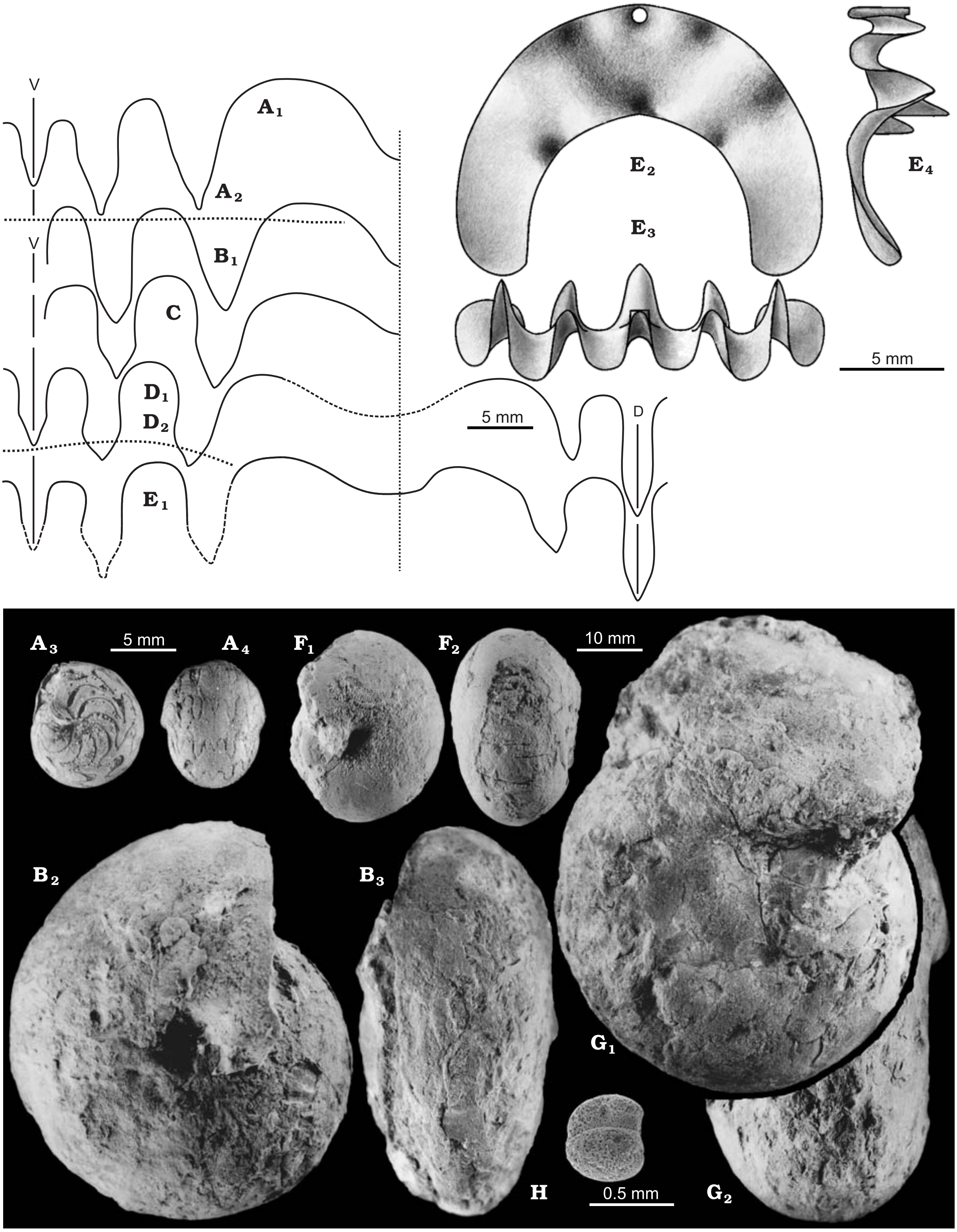


Fig. 176. Globose species of *Sporadoceras* from the Holy Cross Mountains and protoconch of a non-prionoceratid goniatite from *D. trigonica* Zone at Dzikowiec in the Sudetes. **A**. *S. nux* (Sobolew, 1914) from the mid *C. marginifera* Zone at Kowala, suture, internal thickening, and views of specimen ZPAL AmVII/813. **B**–**G**. *S. terminus* sp. n. from the *P. jugosus* Zone at Dzikowiec (B, C, G) and Kowala (D–F); sutures of specimen ZPAL AmVII/4 and 242 (B, C); suture and internal thickening of specimen IG 284.II.892 (D); suture and restoration of septum of specimen IG 284.II.956 (E, also ZPAL AmVII/1862); views of specimens IG 284.II.956 (F) and holotype ZPAL AmVII/3 (G). **H**. Possible sporadoceratid, specimen ZPAL AmVII/1825 (sample Dz-7).

Remarks. — *Sporadoceras orbiculare* (Münster, 1832) as interpreted by Korn (1999; Korn and Klug 2002) may represent a connecting link between *S. nux* and *S. terminus* sp. n., being intermedioate in its geological age and in the inferred conch globosity at comparable stages of the ontogeny.

Distribution. — The *P. jugosus* (possibly also *D. trigonica*) Zone at Kowala and Dzikowiec.

Family **Prionoceratidae** Hyatt, 1884

Diagnosis. — Large protoconch 0.7 to 1.0 mm in width; suture with pointed lateral and trifid dorsal lobes; conch aperture with oblique convex profile; relatively low whorl expansion rate.

Remarks. — *Cheiloceras polonicum* Sobolew, 1912 from the black clymeniid limestone at Łagów-Dule (Sobolew 1914b; *P. trachytera* Zone; see Fig. 180C) shows rare internal thickenings and the external part of its suture of *Prionoceras* morphology. It is stratigraphically transitional between the lowest occurrence of the true *Prionoceras* and the typical cheiloceratids. Unfortunately, the internal part of its suture remains unknown and no other specimen has been collected.

The characteristic barrel-shaped protoconch of unusually large size emerged together with first conchs of the *Prionoceras* morphology at Jabłonna (Fig 178K-I) to continue into the Carboniferous (Dzik 1997). Probably this is the most characteristic evolutionary novelty (synapomorphy) do define the family, although its knowledge if far from being satisfactory.

Genus ***Prionoceras*** Hyatt, 1884

Type species: *Goniatites divisus* Münster, 1832 from Schübelhammer in Franconia.

Diagnosis. — Minute more or less globose conch with closed umbilicus at all stages; internal shell thickenings correspond to external constrictions, expressed mostly on the conch flanks and are regularly distributed, usually three per whorl.

Remarks. — Korn (1988, 1994) proposed to separate advanced members of the *Prionoceras* branch into his genus *Mimimitoceras*, basing distinctions on slight differences in the shape of aperture and the course of constrictions. Perhaps subgeneric rank would be more appropriate for this taxon.

Prionoceras frechi (Wedekind, 1913)
(Figs 177A–C and 181)

Type horizon and locality: *Platyclymenia annulata* Zone at Beul near Balve in the Rhenish Slate Mountains.

Material. — One specimen.

Diagnosis. — Compressed mature conch with diameter exceeding the whorl thickness more than two times; oblique profile of the conch aperture with a rather deep ventral sinus.

Distribution. — Early *L. styriacus* Zone (bed 26) at Jabłonna. The specimen from Dzikowiec, MB.C. 4657, may also belong to this species, which would require its ranging to much younger strata (at least *P. jugosus* Zone).

Prionoceras divisum (Münster, 1832)
(Figs 177D–H and 181)

Type horizon and locality: Probably *Platyclymenia annulata* Zone at Schübelhammer in Franconia (Korn 1994, 2002).

Material. — 21 specimens.

Diagnosis. — Globose mature conch with diameter exceeding whorl thickness about 1.5 times.

Remarks. — The specimens from Jabłonna are crushed, but some of them show the original conch globosity and irregularities on the conch surface corresponding to the thickening underneath.

Distribution. — *L. styriacus* Zone (trench rIVc of Żakowa *et al.* 1984) at Jabłonna.

Prionoceras lineare (Münster, 1832)?
(Figs 177I–O and 181)

Type horizon and locality: Probably *Clymenia* Stufe at Schübelhammer in Franconia (Korn 1994).

Material. — 36 specimens.

Remarks. — Actually, the only basis for identification of this species is its geological age (see Korn 1994) as the distinctions in the conch shape and course of internal thickenings are hardly significant. Speci-

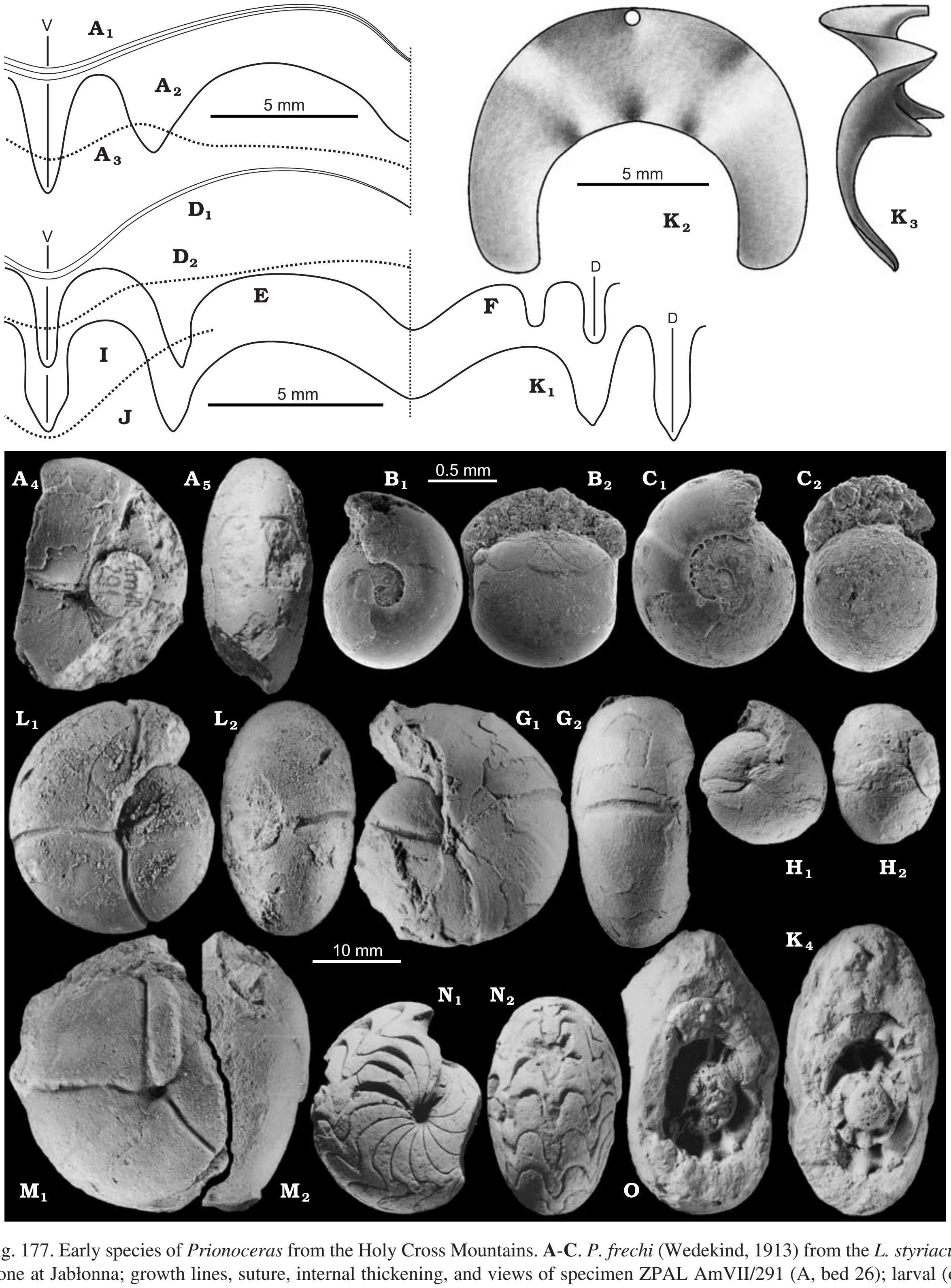


Fig. 177. Early species of *Prionoceras* from the Holy Cross Mountains. **A**-**C**. *P. frechi* (Wedekind, 1913) from the *L. styriacus* Zone at Jabłonna; growth lines, suture, internal thickening, and views of specimen ZPAL AmVII/291 (A, bed 26); larval (or embryonic) conchs ZPAL AmVII/1827 (B, bed 24) and 1838 (C, sample J-35). **D**–**H**. *Prionoceras divisum* (Münster, 1832) from the *L. styriacus* Zone (trench rIVc of Żakowa *et al*. 1984)) at Jabłonna; suture and internal thickening of specimen ZPAL AmVII/722 (D); external and internal parts of suture of specimens ZPAL AmVII/727 and 736 (E, F); views of specimens ZPAL AmVII/726 and 742 (G, H). **I**–**O**. *P. lineare* (Münster, 1832)? from the early *P. jugosus* Zone at Kowala; external suture of specimen ZPAL AmVII/1057 (I); internal thickening of specimen ZPAL AmVII/1623 (J, with unusually deep ventral sinus); internal suture, restoration of septum, and view of specimen ZPAL AmVII/102 (K); views of specimens ZPAL AmVII/1039, 939, Uwr 2183 (collected by M. Schwarzbach), and ZPAL AmVII/101 (L–O).

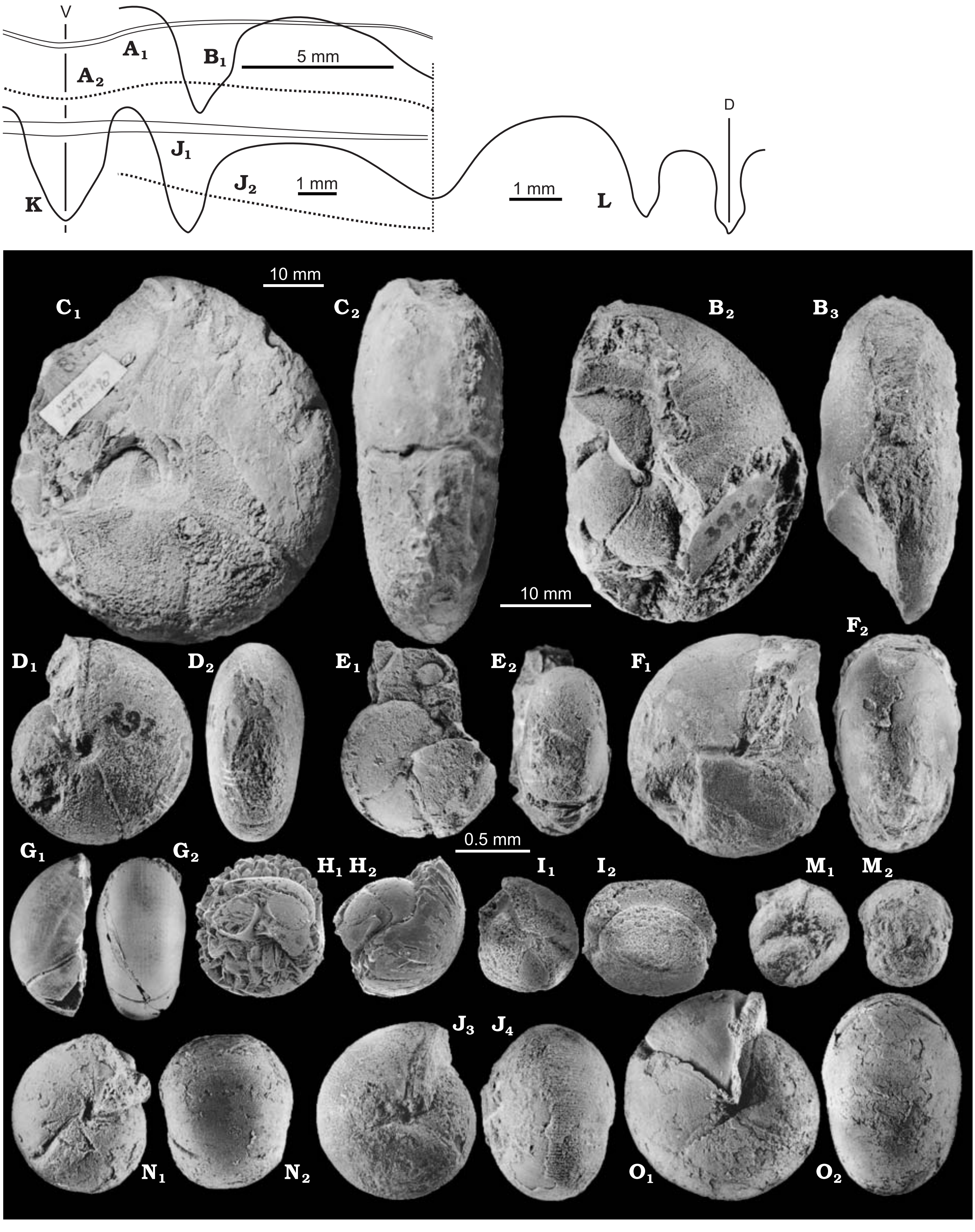


Fig. 178. Late species of *Prionoceras* from the *P. jugosus* Zone of the Sudetes and the Holy Cross Mountains. **A**–**G**. *P. fuerstenbergi* (Korn, 1992) from Dzikowiec; growth lines and conch constriction of specimen ZPAL AmVII/153 (A, also 149), suture and views of specimen ZPAL AmVII/162 (B, inside a clymeniid), probably mature specimen MB.C. 4672 (C), views of specimens ZPAL AmVII/154, 1030, 149, and 937 (D–G; the latter from sample Dz-180 associated with *Parawocklumeria*). **H**, **I**. Larval (or embryonic) conchs probably representing the same species; specimens ZPAL AmVII/1835 and 1823 from Kowala (I, sample Ko-187) and Dzikowiec (J, sample Dz-4). **J**–**O**. *P. lentum* (Korn, 1992) from Dzikowiec (J–M), Ostrówka (N), and exposure between Besówka and Stokówka near Gałęzice (O), growth lines, conch constriction, and views of specimen ZPAL AmVII/153 (J), external and internal parts of suture of specimens ZPAL AmVII/32 and 39 (K, L), and views of specimens ZPAL AmVII/446, IG 284.II.762, and 333 (M–O).

mens from Kowala do not not have the original shell preserved, so features of shell ornamentation cannot be taken into accout.

Distribution. — The *P. jugosus* Zone at Kowala.

Prionoceras fuerstenbergi (Korn, 1992)
(Figs 178A–G and 181)

Type horizon and locality: *Parawocklumeria paradoxa* Zone (bed 28 in trench 1) at Müssenberg, Rhenish Slate Mountains.

Material. — 30 specimens.

Diagnosis. — Globose mature conch with diameter exceeding whorl thickness about 1.3 times, transverse conch aperture.

Distribution. — The *P. jugosus* and *D. trigonica* zones at Dzikowiec, Jabłonna (bed 30), and Kowala.

Prionoceras lentum (Korn, 1992)
(Figs 178J–O and 181)

Type horizon and locality: Late *Parawocklumeria paradoxa* Zone (bed 1 in the street section) at Ober-Rödinghausen, Rhenish Slate Mountains.

Material. — 23 specimens.

Diagnosis. — Compressed mature conch with diameter exceeding whorl thickness almost 2 times, transverse conch aperture with small ventral sinus.

Distribution. — The *P. jugosus* and *D. trigonica* zones at Dzikowiec and Kowala.

Genus ***Balvia*** Lange, 1929

Type species: *Gattendorfia globularis* Schmidt, 1924 from the *Wocklumeria* Stufe at Ober-Rödinghausen, Rhenish Slate Mountains.

Diagnosis. — Minute conch with internal shell thickenings and corresponding external constrictions forming anteriorly oriented saddle; umbilicus open at early growth stages.

Balvia prima sp. n.
(Figs 179A and 181)

Holotype: ZPAL AmVII/26 (Fig. 179A).

Type horizon and locality: *Lagovignathus styriacus* Zone at Ostrówka (sample Ost-7) in the Holy Cross Mountains.

Material. — Two specimens.

Diagnosis. — Relatively large mature conch with very narrow ventral protrusion of the shell thickening.

Remarks. — Probably also specimen IG 284.II.343 of diameter about 27 mm, collected by Czarnocki in a grey limestone (labelled as *Gonioclymenia* beds) belongs to the species. This is a good connecting link between the *Prionoceras* and *Balvia* lineages.

Distribution. — The *L. styriacus* Zone at Ostrówka (sample Ost-7).

Balvia minutula Korn, 1992?
(Figs 179B–G and 181)

Type horizon and locality: Early *Parawocklumeria paradoxa* Zone at at Dasberg (bed 1 in southern trench), Rhenish Slate Mountains.

Material. — 15 specimens.

Diagnosis. — Mature conch with shell thickening showing a narrow ventral saddle.

Remarks. — The only specimen from Ostrówka is more globose at corresponding ontogenetic stage than those from Dzikowiec.

Distribution. — The *P. jugosus* Zone at Dzikowiec (samples Dz-2a, 4a, and 7) and Ostrówka (red *Gonioclymenia* limestone).

Balvia biformis (Schindewolf, 1937)
(Figs 179H and 181)

Type horizon and locality: *Wocklumeria* Stufe at Ober-Rödinghausen, Rhenish Slate Mountains.

Material. — One specimen.

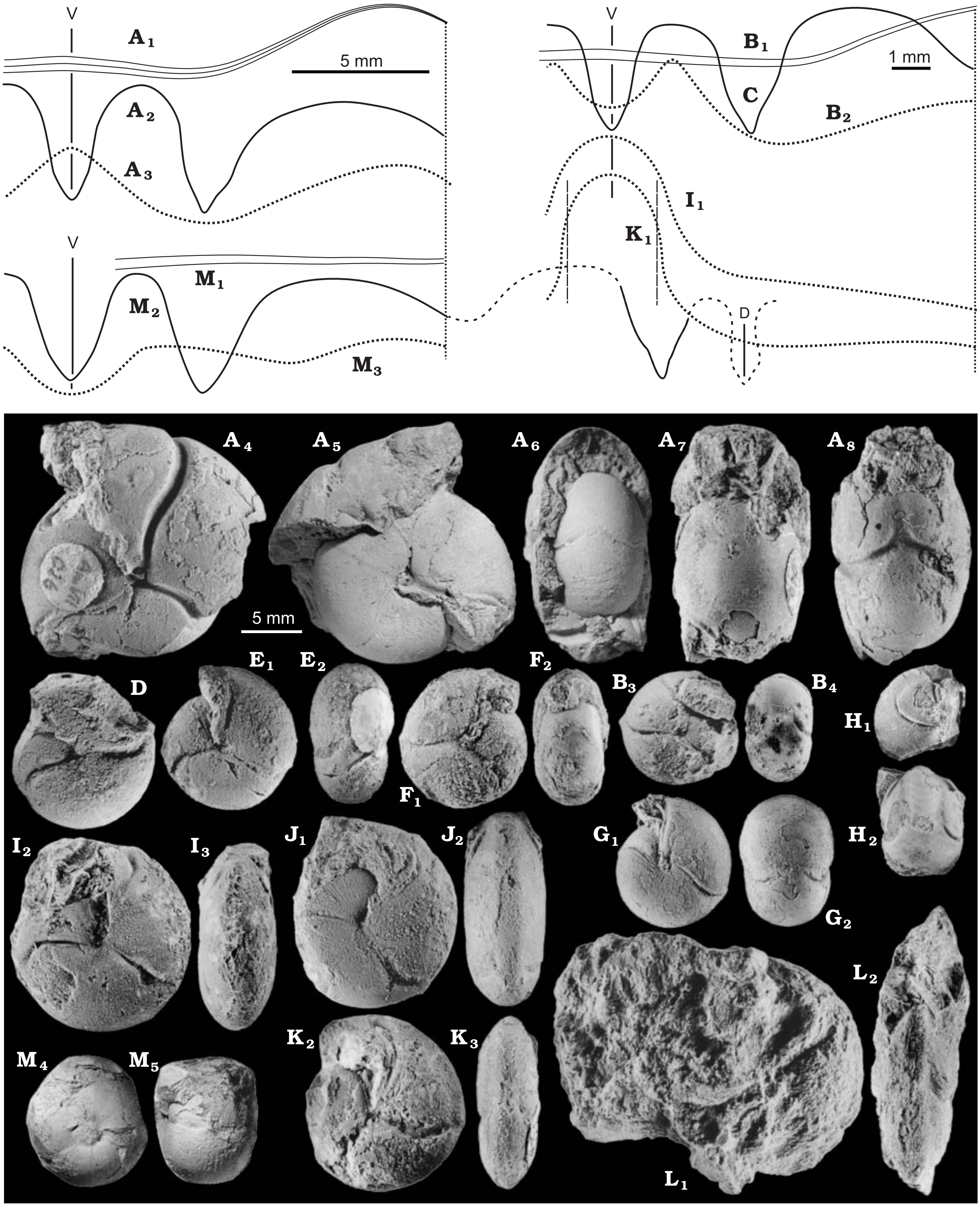


Fig. 179. Species of the derived prionoceratid *Balvia* from the *L. styriacus* Zone at Ostrówka in the Holy Cross Mountains (A), the *P. jugosus* Zone at exposure between Besówka and Stokówka near Gałęzice (G) and probably the *D. trigonica* Zone at Dzikowiec in the Sudetes (B–F, I–M). **A**. *B. prima* sp. n.; growth lines, suture, conch constriction, and views of the holotype ZPAL AmVII/26 (sample Ost-7). **B**–**G**. *B. minutula* Korn, 1992? growth lines, conch constriction, and views of specimen ZPAL AmVII/31 (B); suture of specimen ZPAL AmVII/1048 (C); views of specimen ZPAL AmVII/1041, 801, 113, and IG 284.II.334 (D–G). **H**. *B. biformis* (Schindewolf, 1937); views of specimen ZPAL AmVII/941 (sample Dz-180; associated with *Parawocklumeria paradoxa*). **I**, **J**. *B. falx* Korn, 1992; conch constriction and views of specimens ZPAL AmVII/172 and 1028. **K**, **L**. *B. lens* Korn, 1992; conch constriction and views of specimens ZPAL AmVII/235 and 227. **M**. *Balvia globularis* (Schmidt, 1924); growth lines, suture, conch constriction, and views of specimen ZPAL AmVII/252.

Diagnosis. — Mature conch with ventral saddle of the shell thickening delimited by longitudinal furrows.

Remarks. — In *Balvia nucleus* the area delimited by longitudinal furrows is much wider (see Korn 1994).

Distribution. — The *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec (sample Dz-180).

Balvia falx Korn, 1992
(Figs 179I, J and 181)

Type horizon and locality: Early *Parawocklumeria paradoxa* Zone (bed 12 in the street section) at Ober-Rödinghausen, Rhenish Slate Mountains.

Material. — Ten specimens.

Diagnosis. — Discoidal mature conch with parabolic profile of the venter.

Distribution. — The *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec (samples Dz-4a and 7).

Balvia lens Korn, 1992
(Figs 179K, L and 181)

Type horizon and locality: Late *Gonioclymenia subarmata* Zone at Effenberg (bed T), Rhenish Slate Mountains.

Material. — Three specimens.

Diagnosis. — Discoidal mature conch with the ventral area bordered by longitudinal depressions.

Remarks. —All the specimens come from a single block collected near the southern end of the quarry; they are thus apparently of different geological age (younger?) than specimens of *B. falx* found at the northern end of the quarry.

Distribution. — The *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec.

Balvia globularis (Schmidt, 1924)
(Figs 179M and 181)

Type horizon and locality: *Wocklumeria* Stufe at Ober-Rödinghausen, Rhenish Slate Mountains.

Material. — One specimen.

Diagnosis. — Globose mature conch with umbilicus open at ealy stages.

Distribution. — The *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec in the Sudetes.

Genus ***Acutimitoceras*** Librovich, 1957

Type species: *Imitoceras acutum* Schindewolf, 1923 from the *Gattendorfia* Stufe at Gattendorf in Franconia.

Diagnosis. — Discoidal conch without thickenings or constrictions and more or less acute venter.

Acutimitoceras guerichi (Frech, 1902)
(Figs 180A and 181)

Type horizon and locality: *Wocklumeria* Stufe at Ober-Rödinghausen, Rhenish Slate Mountains.

Material. — Two specimens.

Diagnosis. — Large mature conch with parabolic venter in cross section.

Remarks. — The holotype does not show any traces of growth increments and only its large size makes it different from other Dzikowiec prionoceratids. The discoidal conch shape suggests that this is a member of the lineage leading to acute Tournaisian species, as alredy pointed out by Korn (1994).

Distribution. — The *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec.

Acutimitoceras prorsum (Schmidt, 1925)
(Figs 180B and 181)

Type horizon and locality: Stockum Limestone near Stockum, Rhenish Slate Mountains (Korn 1994).

Material. — Numerous crushed and fragmentary specimens covering slabs of tuffite.

Diagnosis. — Conch aperture with radially running lateral margins and gentle ventral sinus; rounded conch venter with no signs of angulation.

Remarks. — The species does not fit the diagnostic character of the genus in respect to the conch form but the shape of aperture resembles that in the type species and this supports its ancestral position within the lineage. Apparently on this basis Korn (1981, 1994) classified it in *Acutimitoceras*. All specimens from

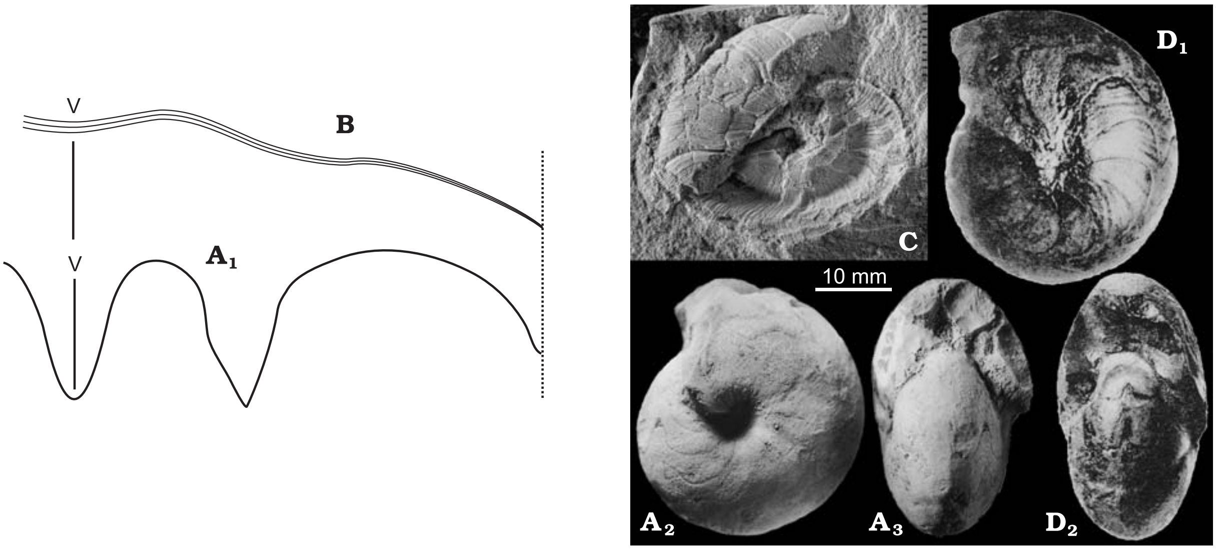


Fig. 180. Famennian prionoceratids. **A**. *Acutimitoceras guerichi* (Frech, 1902) probably from the *D. trigonica* Zone at Dzikowiec in the Sudetes; suture and views of of the holotype Uwr 23337. **B**. *Acutimitoceras prorsum* (Schmidt, 1925) from the *Protognathodus kockeli* horizon at Kowala in the Holy Cross Mountains; growth lines and crushed conch ZPAL AmVII/1855 in tuffite (sample Ko-52, see Dzik 1997). **C**. "*Cheiloceras*" *polonicum* Sobolew, 1914 from the *P. trachytera* Zone at Łagów-Dule, possibly the ancestral *Prionoceras* (reproduced after Sobolew 1914).

Kowala (illustrated earlier in Dzik 1997, fig. 27) are flattened and fragmentary but some show the original geometry leaving little doubt that this is a generalized prionoceratid with an oval whorl cross section. The distinct growth lines are not so apparent in the German material illustrated by Korn (1981, 1994) but this may be due to exfoliation of the conch surface.

Distribution. — The *P. kockeli* horizon at Kowala.

Order **CLYMENIIDA** Hyatt, 1884

Remarks. — The only character that distinguishes the earliest clymenias from the co-occurring or slightly older protornoceratid goniatites is the dorsal location of their siphuncle. All other conch and septal morphology characters are virtually identical. This was the basis for indication of the tornoceratids as the clymenias' ancestors by House (1970). Exquisitely preserved material of the oldest clymenias from the Urals (Bogoslovsky 1976, 1981) shows that in the larval conch the siphuncle perforated the first septum near the protoconch venter, centrally in the second, and centrodorsally in the third septum. Thus, not before the metamorphosis an early clymenia developed the diagnostic dorsal location of its siphuncle. This looks like a recapitulation of phylogeny in the early ontogeny and points towards *Kirsoceras rotundatum* (Perna, 1914) from the *Cheiloceras* Stufe of the Urals, having the siphuncle significantly departing from the venter in adult specimens, as the probable ancestor of the clymenias.

However, the typical members of the Tornoceratidae and the clymenias differ fundamentally from each other in their larval (ammonitella) conch organization. The difference between the *Tornoceras* and clymeniid suture ontogeny was the main argument against any close relationship between these ammonoids (reviewed by Bogoslovsky 1981). If *K. rotundatum* is truly a connecting link between evolute tornoceratids and the earliest clymenias, then its protoconch morphology has to be also transitional. *Kirsoceras* is known after only four specimens from locality 839 of Perna (1914) near the village Spasskiy, possibly representing the range of variability within the same species (suggested by the labile conch morphology of probably related protornoceratids from the Holy Cross Mountains) and there is little chance for a new material, as it was not available to Bogoslovsky (1981). The crucial evidence has to be thus looked for in the Holy Cross Mountains material of evolute tornoceratids. Such data are available and have been presented above. The advanced tornoceratids do not differ substantially in their larval conch internal structure from the stratigraphically proximal clymenias.

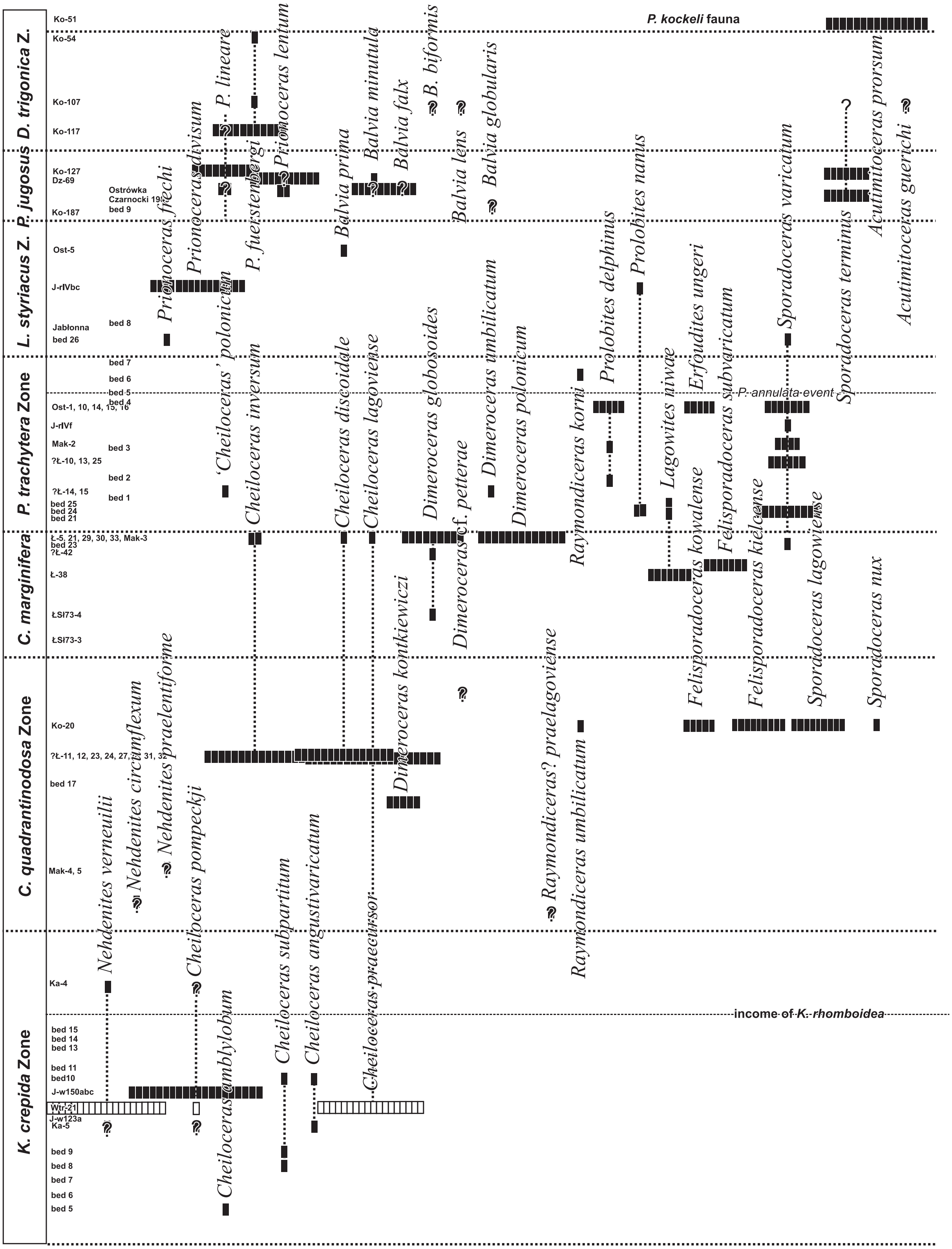


Fig. 181. Stratigraphic distribution of species of Cheiloceratidae, Praeglyphioceratidae, Sporadoceratidae, and Prionoceratidae in the Polish Famennian. Position of samples not included in Figs 2 and 3 on the geochronological scale is hypothetical.

The origin of clymenias from the tornoceratid goniatites implies that the ancestral forms were of a rather complex morphology, with a relatively involute conchs and marginally vaulted septum. This conch morphology continued, with a somewhat more complicated septum, in the most long-ranging lineage of *Cymaclymenia* (Korn 1981, 1991; Korn *et al*. 2004). The vaulting of the septum in the evolute *Clymenia* and *Kosmoclymenia* is apparently rooted in this ancestral status. Also the lineages ending in the highly sophisticated septal morphologies of *Dimeroclymenia* and *Gonioclymenia* are rooted, idependently of each other, in the early vaulted cymaclymeniids. In the lineage of *Cyrtoclymenia*, the ancestral involute conch geometry with open umbilicus was preserved, but with a simplified (balloon-type) septum. A more evolute conch combined with simple septum characterize *Platyclymenia*. In the wocklumeriids, a complication of suture morphology developed *de novo* from a rather simple septal morphology.

The dorsal location of siphuncle makes its length significantly shorter in respect to the phragmocone than in goniatites. Some clymeniids (Biloclymeniidae) show unusually wide siphuncle (Bogoslovsky 1981, p. 17), proposed by Gottobrio and Saunders (2005) to be an adaptation to preserve the area of contact of the siphonal tissue with the cameral liquid similar to that in goniatites. Interestingly, they show also extremely long septal necks (Bogoslovsky 1981, p. 16), a feature undoubtedly limiting fluid and gas exchange between the sipho and phragmocone chambers (like in the Tertiary nautiloid *Aturia* with dorsally located siphuncle, but also in the endoceratid nautiloids, having similarly wide siphuncle).

Family **Cymaclymeniidae** Hyatt, 1884

Diagnosis. — Septum with marginal vaulting in the middle of its height, expressed in suture as a tongue-like pointed flank lobe; moderately evolute conch with rounded trapezoidal whorl cross section.

Remarks. — Bogoslovsky (1979) introduced genera *Ornatoclymenia*, *Kazakhoclymenia*, and *Loganoclymenia* based mostly on differences in their whorl cross section and resulting complications of the ventral part of suture. Their septal topology seems to be identical with *Cymaclymenia*.

Genus ***Genuclymenia*** Wedekind, 1908

Type species: *Clymenia frechi* Wedekind, 1908 from *Prolobites* beds at Enkeberg, Rhenish Slate Mountains.

Diagnosis. — Suture with deep rounded flank lobe and shallow ventrolateral lobe; moderately evolute conch.

Remarks. — The type species of the genus is closely similar to early *Cymaclymenia*, being different only in a shallower flank lobe of its suture. The Polish species show a even more ancestral, tornoceratid-like appearance in having a somewhat narrower umbilicus and more rounded whorl cross section.

Genuclymenia humboldti (Pusch, 1837)
(Figs 182A–F, 186A and 196)

Type horizon and locality: Bituminous calcareous shale exposed at the foot of Kadzielnia hill in Kielce, Holy Cross Mountains.

Material. — 26 specimens.

Diagnosis. — Umbo covering about one third of the conch diameter; slopes of the flank lobe merging approximately at right angle, the ventral one obliquely crossing the conch flanks.

Remarks. — Probably *Ammonites humboldtii* Pusch, 1837, based on a pyritized specimen from bituminous calcareous shale exposed at the foot of Kadzielnia hill in Kielce, is the first reference to this species, but Pusch (1837) was uncertain whether the siphuncle is ventral or dorsal. Roemer (1866, p. 675, pl. 13: 1) illustrated a specimen of probable *Protornoceras* from apparently the same exposure, suggesting that Pusch's *A. humboldti* and *A. buchi* represent variants of the same goniatite species (which seems highly unlikely). Gürich (1896, p. 329) used his collection of specimens, considered by him conspecific and coming probably from the same stratum exposed between Kadzielnia and Psiarnia hills, to prove that this was a clymeniid and transferred the species to *Cyrtoclymenia*. Although the original Pusch's collection has not survived to our days, one of the specimens studied by Gürich (1896) was illustrated by Frech (1902, pl. 4: 5). This emendation of the first reviser should thus be binding, so more that it was accepted by Sobolew (1914, p. 64) who distinguished two varieties within Gomi-monomeroclymenia *humboldti*. The variety G. *h. genulobata*, based on the material from Sieklucki's brickpit, with pointed flank lobe of the suture seems to fit within the range of the species, as suggested by additional material assembled by Czarnocki (1989) and myself. However, Czarnocki (1989, p. 64) preferred to abandon Pusch's species name and to replace it with his *Flexiclymenia*

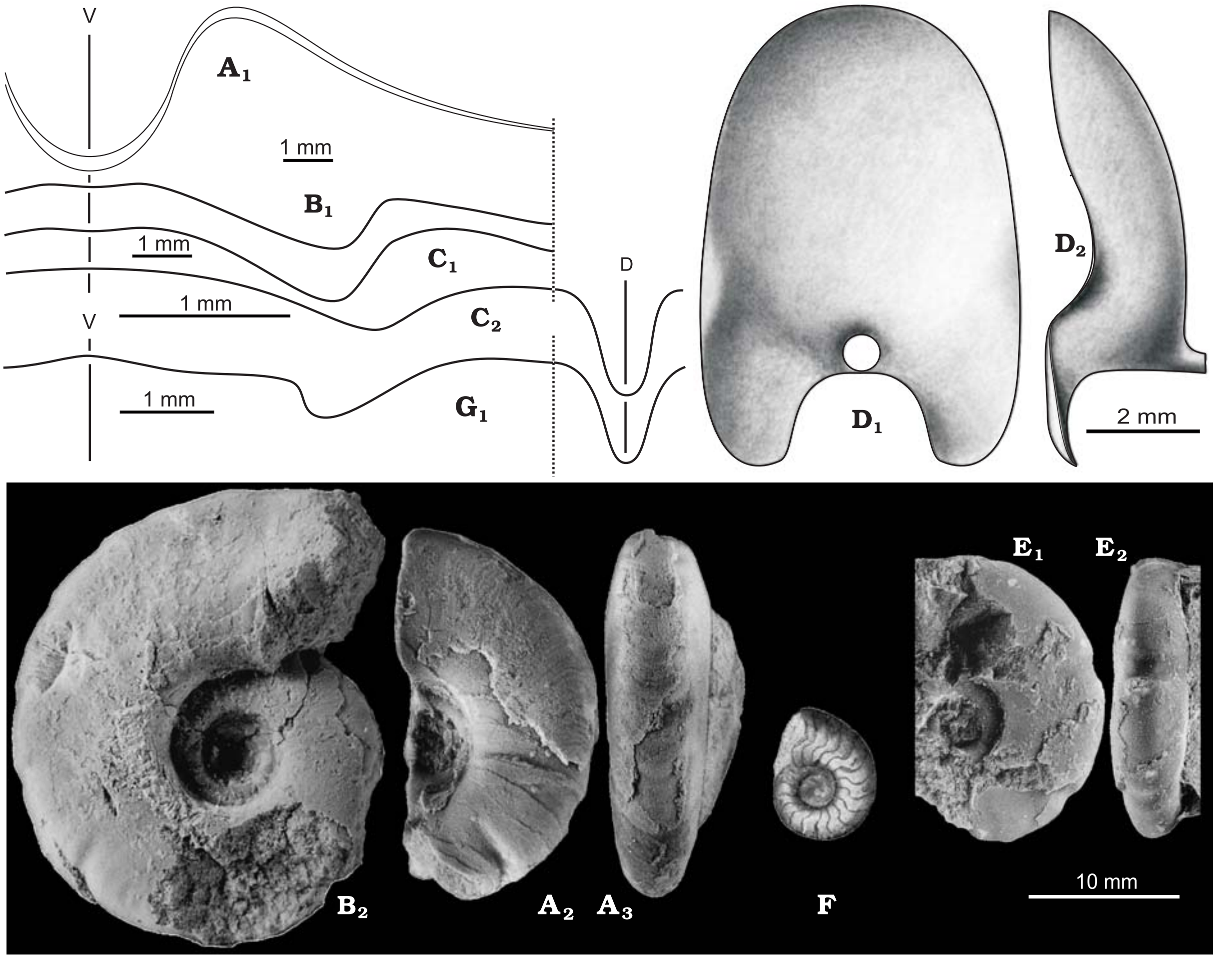


Fig. 182. Early tornoceratid-like clymenia *Genuclymenia humboldti* (Pusch, 1837) from the *P. trachytera* (bed 24) and early *L. styriacus* (beds 25 and 26) zones at Jabłonna (A–E) and Kadzielnia (F) in the Holy Cross Mountains; growth lines and views of specimen ZPAL AmVII/714 (A, bed 24); suture and view of ZPAL AmVII/700 (B, bed 26); two stages in development of suture of ZPAL AmVII/639 (C, bed 26); reconstructed septum of ZPAL AmVII/851 (D, bed 25); views of ZPAL AmVII/168 (E, bed 25); original specimen of Gürich (1896; reproduced from Frech 1902, pl. 5: 5).

puschi. He proposed the holotype collected at Ostrówka from the *Prolobites* Zone strata (thus his beds 1–3) which seems to represent another Sobolew's species, here referred to as *Praeflexiclymenia curvidorsata*. I believe that *Flexiclymenia tempestiva* Czarnocki, 1989, *F. staszici* Czarnocki, 1989 and *F. simosa* Czarnocki, 1989 are conspecific with *G. humboldti*.

Distribution. — The *P. trachytera* (bed 24) to the early *L. styriacus* (beds 25 and 26) zones at Jabłonna; probably the *L. styriacus* Zone at Ostrówka (upper *Platyclymenia* beds of Czarnocki 1989); black shale at Kadzielnia and reworked to Quaternary sediments at Sieklucki's brickpit in Kielce.

Genus ***Cymaclymenia*** Hyatt, 1884

Type species: *Planulites striatus* Münster, 1832 from Schübelhammer near Heinersreuth in Frankenwald (Korn 1981).

Diagnosis. — *Aturia*-like flank lobe with sinous dorsal slope in the middle of conch flanks; relatively involute conch.

Remarks. — The type species of *Genuclymenia*, *G. frechi* from Enkeberg in the Rhenish Slate Mountains is almost exactly transitional in the conch form, its ornamentation, and suture between *G. humboldti* and this species. Its stratigraphic position also fits the chronomorphocline. The early part of the lineage of Cymaclymenia seems thus relatively well documented.

The course and prominence of growth increments and the shape of the flank lobe of the suture are considered to be the most important diagnostic character of species within this genus (e.g., Korn 1981). However

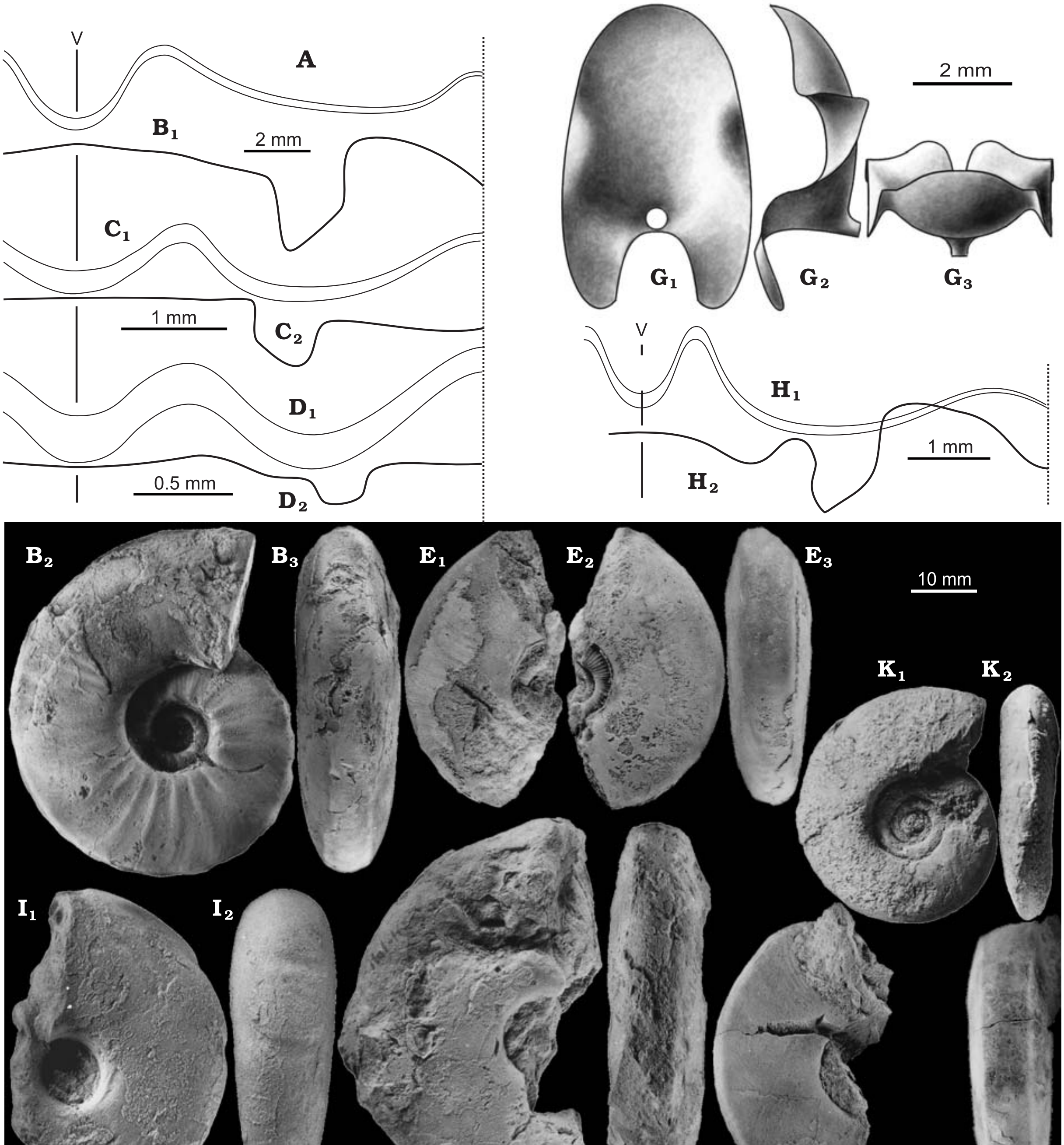


Fig. 183. Early and last *Cymaclymenia*. **A**–**F**. *C. inflata* Czarnocki, 1989 from the *P. trachytera* Zone at Ostrówka (B) and the early *L. styriacus* Zone at Jabłonna (A, C–F; trench rIVc of Żakowa *et al*. 1984) in the Holy Cross Mountains; growth lines of specimen ZPAL AmVII/435 (A); suture and views of the holotype IG 284.II.142 (B; also Czarnocki 1989, pl. 26: 10); two stages in the development of suture and growth lines of ZPAL AmVII/393 and 394 (C, D); views of ZPAL AmVII/698 and 699 (E, F). **G**–**J**. *Cymaclymenia* sp. n. from the early *P. jugosus* Zone at Kowala in the Holy Cross Mountains; restoration of septum based on ZPAL AmVII/948 (G); growth lines and suture of ZPAL AmVII/013 (H), and views of ZPAL AmVII/1099 (I, sample Ko-63) and 1616 (J; 30 cm below the black shale). **K**. *C. evoluta* (Schmidt, 1924)? from Dzikowiec in the Sudetes; specimen MB.C. 4083.2.

both these traits show significant variation even within the same specimen (Fig. 184B). It is difficult to match the Holy Cross Mountains material with the topotype German specimens of earlier introduced species. either they tend to be endemic or this is due to differences between local populations representing the same species. Their actual number may thus appear smaller than now estimated.

Cymaclymenia inflata Czarnocki, 1989
(Figs 183A–F, 186B, and 196)

Type horizon and locality: Grey crinoid limestone, lower part of *Platyclymenia* Stufe at Ostrówka, Holy Cross Mountains.

Material. — Ten specimens.

Diagnosis. — Flank lobe of the suture with a blunt tip.

Remarks. — The ancestral position of this species in respect to more advanced cymaclymeniids was noticed by Czarnocki (1989). Probably his report of *C. striata* in bed 7 in the description of the Ostrówka section refers to this species.

Distribution. — The late *P. trachytera* Zone at Ostrówka (samples Ost-7 and 10) and the *L. styriacus* Zone at Jabłonna (trench rIVc of Żakowa *et al*. 1986).

Cymaclymenia sp. n.
(Figs 183G–J and 196)

Material. — 16 specimens from near the Epinette Event black shale and 45 specimens from around sample Ko-116.

Remarks. — The most specific aspect of the *Cymaclymenia* specimens from the upper part of the *Clymenia* Stufe grey limestone and the basal part of the reddish limestone at Kowala is a rounded conch venter and prominent acute auricles in aperture. A similar growth lines and suture characterize the much younger geologically *C. warsteinensis* Korn, 1979, but its conch is more evolute (Korn 1981). In fact, most specimens are internal moulds offering no data on the course of growth lines and only rarely well preserved suture can be traced. It seems that specimens from the lower part of the range of this form have a little tabulate venter, which is the primitive feature in the lineage

Distribution. — Most specimens from the lower part of the range were collected from the scree and they probably come from the fossiliferous strata with *Clymenia* about 2 m below the black shale horizon, that is the late *L. styriacus* and early *P. jugosus* zones. A few specimens can be rather safely determined as coming from near the black shale; a large sample of rather poorly preserved specimens have been derived from the nodular bed of sample Ko-116.

Cymaclymenia costellata (Münster, 1832)
(Figs 184A–E, 186C, and 196)

Type horizon and locality: Schübelhammer near Heinersreuth in Frankenwald (Korn 1981).

Material. — 23 specimens.

Diagnosis. — Aperture with somewhat angular convexity on flanks and relatively sharply delimited deep ventral sinus; umbo covering one fourth of the conch diameter in adult conchs.

Remarks. — Specimens from the same strata classified by Czarnocki (1989) in *C. compressa* (Münster, 1832) belong here. According to Korn (1981) the type specimen of this species is too poorly preserved to be identifiable. Czarnocki's specimens come from the red marly limestone and have unusully well preserved, as for the locality, shells. No similar material has been encountered later, which may mean that they occurred in a lens of restricted extend. The sample seems thus homogenous and shows the actual range of variability (Fig. 186C). It is expressed not only in the conch proportion, but also in the shape of aperture, believed to be of high diagnostic value. The course of growth lines may dramatically differ even in different parts of the same conch (Fig. 184B).

Distribution. — The *D. trigonica* Zone at Kowala.

Cymaclymenia sp. aff. *C. striata* (Münster, 1832)
(Figs 184F and 196)

Material. — One specimen.

Remarks. — In the presence of pointed auricles and gently concave flanks of the aperture, the specimen from Jabłonna resembles those of *C. striata* (see Korn 1981) but the straight course of suture across the venter makes it different from all other species of the genus. This may be an expression of the population variability but my material does not allow to determine its range in species of the genus.

Distribution. — The *P. jugosus* Zone at Jabłonna.

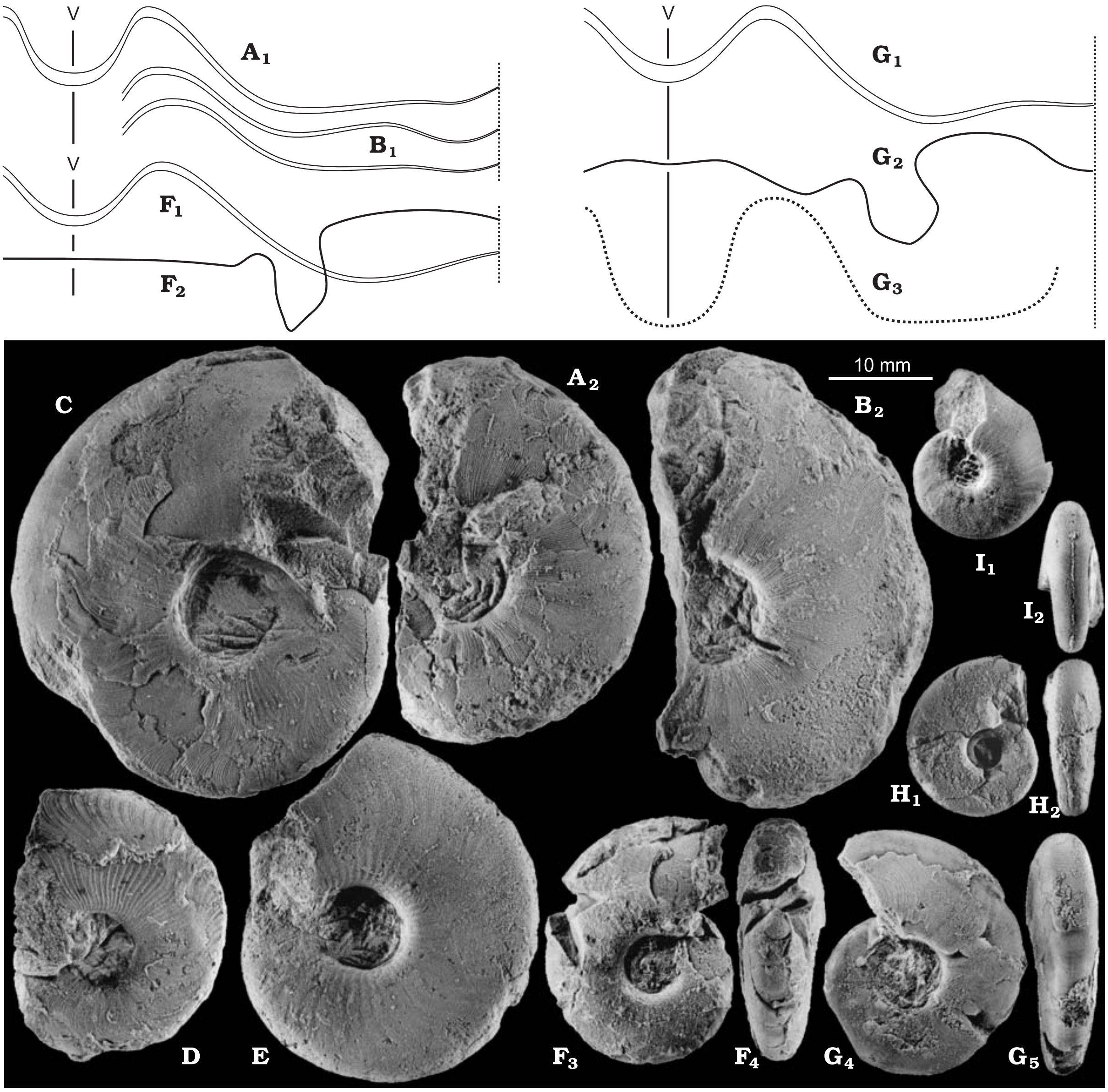


Fig. 184. Advanced *Cymaclymenia*. **A**–**E**. *C. costellata* (Münster, 1832) from the *D. trigonica* Zone at Kowala in the Holy Cross Mountains; growth lines and view of specimen IG 284.II.1070 (A); variability of growth lines and view of IG 284.II.1044 (B); views of IG 284.II.1057, 1070, and 1040 (C–E). **F**. *C.* sp. aff. *C. striata* (Münster, 1832) from the mid *P. jugosus* Zone at Jabłonna in the Holy Cross Mountains; growth lines, suture and views of ZPAL AmVII/382. **G**–**I**. *C.* sp. aff. *C. evoluta* (Schmidt, 1924) from the late *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec in the Sudetes; growth lines, suture, internal shell thickening, and views of ZPAL AmVII/150 (G); views of ZPAL AmVII/1604 and 386 (H, I, the latter of problematic affinity, may represent *C. silesiaca*).

Cymaclymenia sp. aff. *C. evoluta* (Schmidt, 1924
(Figs 184G–I and 196)

Material. — Five specimens.

Remarks. — In a rather acute apertural auricles and evolute compressed conch the species resembles remotely *Postclymenia evoluta* Schmidt, 1924 (see Price and Korn 1989; Korn *et al*. 2004) but its bizarre, almost symmetrical, obliquely oriented flank lobe looks rather like that of *C. fundilobata* Czarnocki, 1989.

Distribution. — Probably the late *P. jugosus* at Dzikowiec.

Cymaclymenia evoluta (Schmidt, 1924)?
(Figs 183K and 196)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

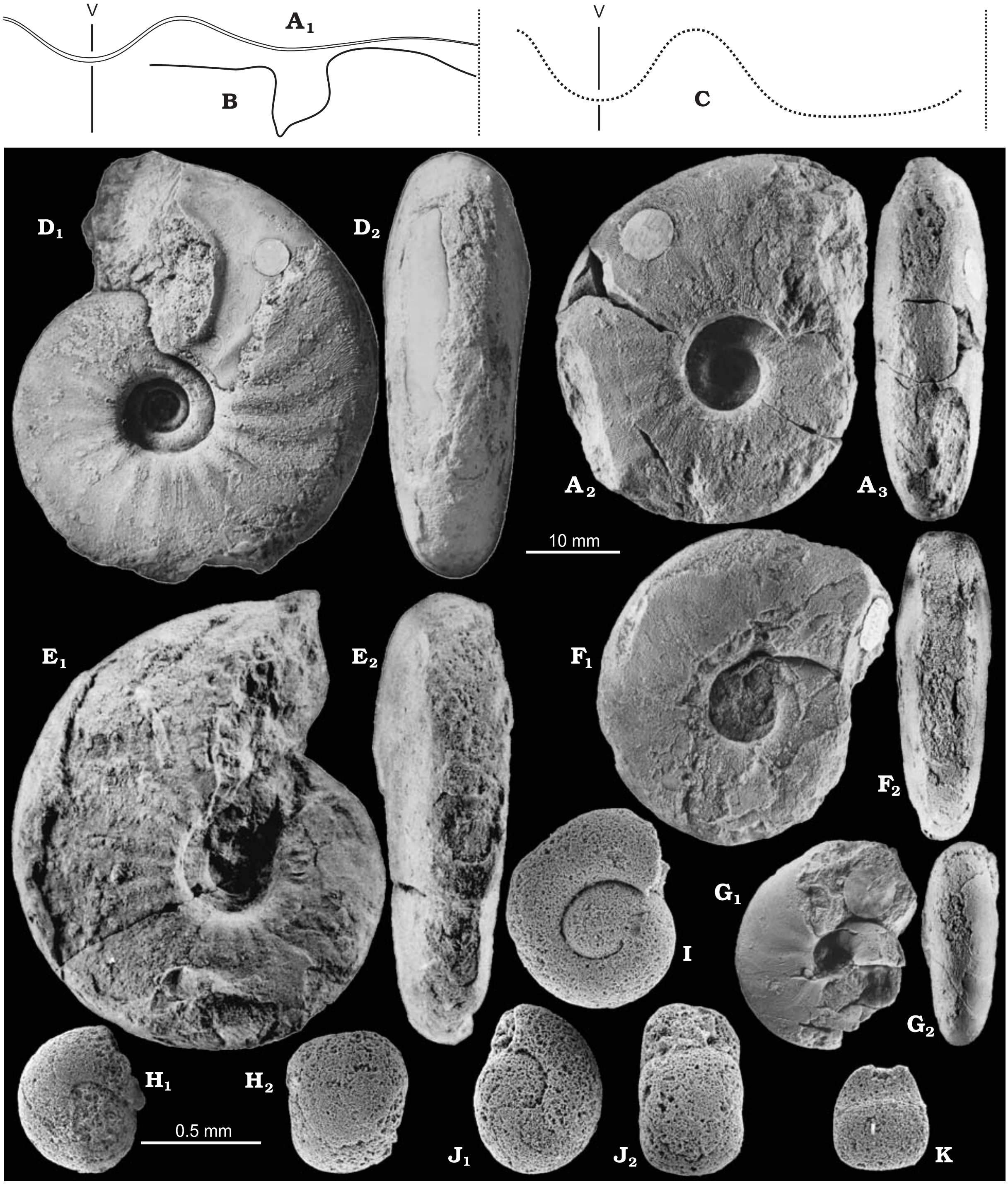


Fig. 185. **A**–**G**. *Cymaclymenia silesiaca* (Renz, 1913) from the late *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec in the Sudetes; growth lines and views of ZPAL AmVII/171 (A); suture of ZPAL AmVII/62 (B); internal shell thickening of ZPAL AmVII/388 (C); views of MB.C. 4167 (D, also Frech 1902, pl. 5: 1), ZPAL AmVII/157, 57, and 1592 (E–G). **H**–**K**. Larval conchs with two septa of generalized clymenias (*Cymaclymenia* and/or *Kosmoclymenia*) from Dzikowiec in the Sudetes; ZPAL AmVII/1822 and 1821 (H, I, sample Dz-4, the late *P. jugosus* Zone; living chamber incomplete in H) and ZPAL AmVII/1826 and 1824 (J, K, sample Dz-7, the *D. trigonica* Zone; only embryonic part preserved in K).

Material. — One specimen.

Diagnosis. — Relatively evolute conch.

Remarks. — The single specimen MB.C. 4083.2 labeled *Cymaclymenia cordata* may belong to this species, as suggested by the evolute conch. It comes from a light yellowish-pink limestone occurring near the top

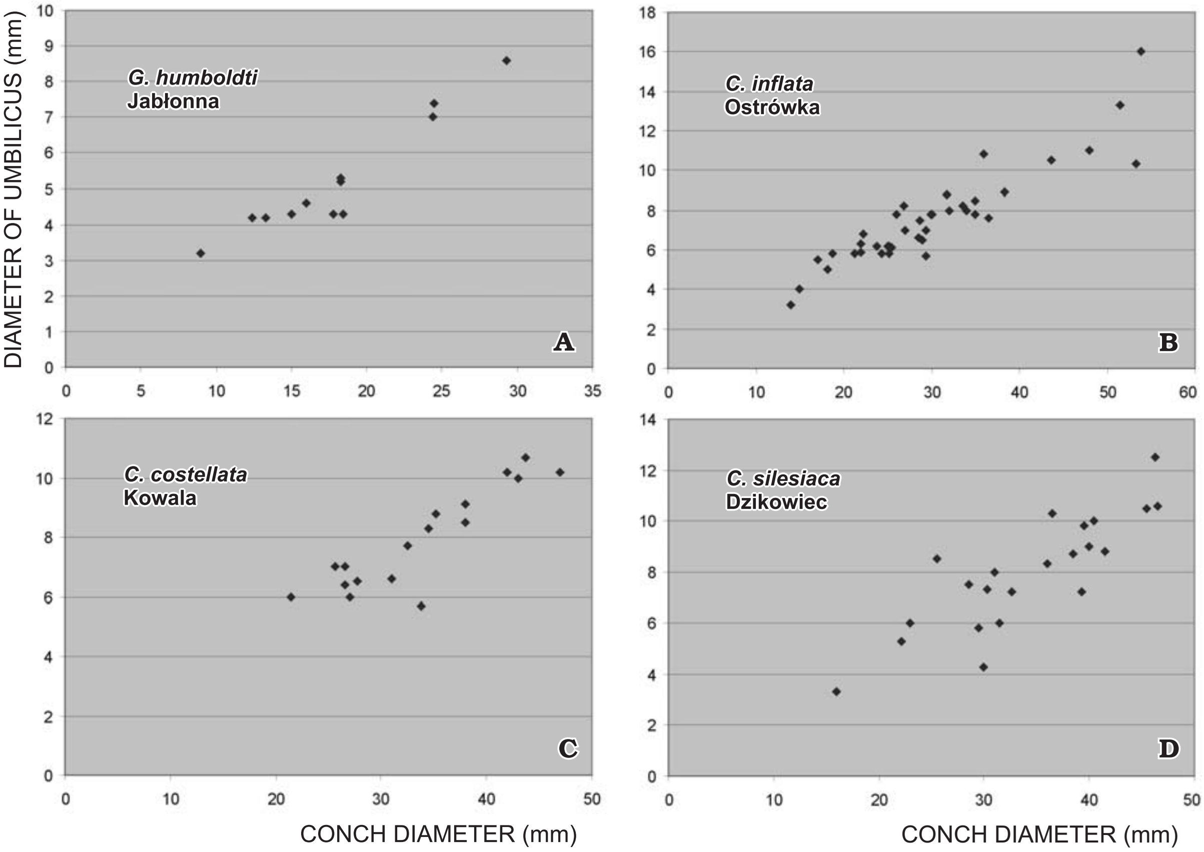


Fig. 186. Variability of umbilical width in species of the Cymaclymeniidae. **A**. *Genuclymenia humboldti* (Pusch, 1837) from the *P. trachytera* to early *L. styriacus* zones at Jabłonna in the Holy Cross Mountains. **B**. *Cymaclymenia inflata* Czarnocki, 1989 from the *P. trachytera* Zone at Ostrówka. **C**. *C. costellata* (Münster, 1832) from the late *P. jugosus* Zone at Kowala. **D**. *Cymaclymenia silesiaca* (Renz, 1913) from the late *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec in the Sudetes.

of the Dzikowiec succession (Korn et al. 2005, fig. 2). Two more specimens derived from a similar rock (MB.C. 4083.1 and 4180) differ in a somewhat narrower umbo. All are compressed and have a rather rounded whorl cross section. Possibly a lineage of *Cymaclymenia* independent of *C. silesiaca* (occuring in dark purple limestone) is represented at Dzikowiec, but stratigraphic evidence is too poor to prove this.

The species was originally classified in the separate genus *Postclymenia*, the view revived by Korn *et al*. (2004).

Distribution. — Probably *D. trigonica* Zone (perhaps the *P. kockeli* fauna) at Dzikowiec.

Cymaclymenia silesiaca (Renz, 1913)

(Figs 185, 186D, and 196)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

Material. — 24 specimens.

Diagnosis. — Aperture with low auricles and shallow ventral sinus; rounded conch venter.

Remarks. — This is a rather generalized conch morphology and the preservation of specimens is not always good enough to allow determination of crucial characters. It is possible that also other species of *Cymaclymenia* are represented in the material from Dzikowiec.

Distribution. — The *P. jugosus* Zone at Dzikowiec.

Family **Clymeniidae** Edwards, 1849

Diagnosis. — Evolute conchs; septum with marginal lateral vaulting expressed in suture as more or less acute lobe with gentle dorsal slope.

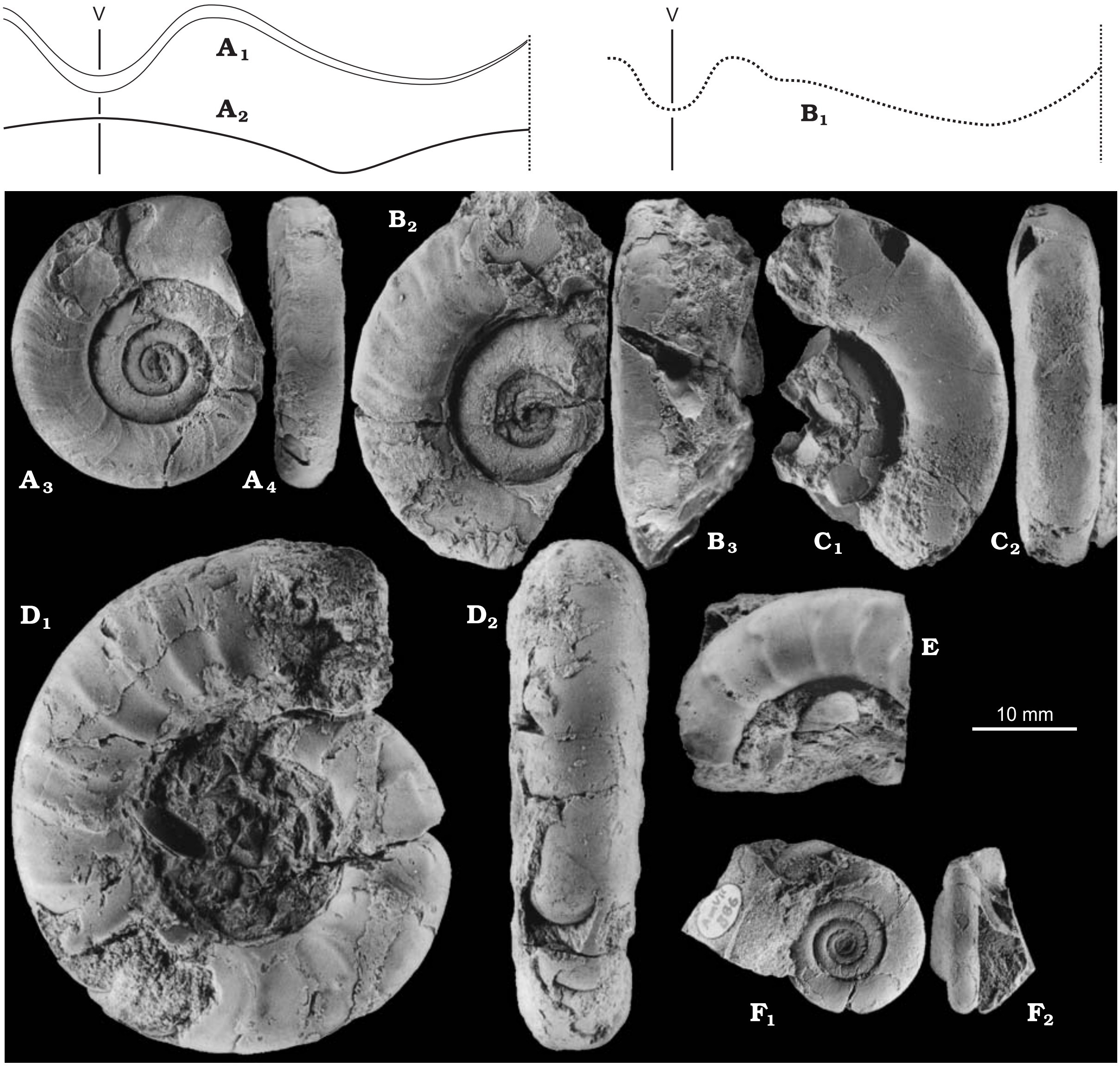


Fig. 187. Species of *Trigonoclymenia* from the *P. trachytera* Zone of the Holy Cross Mountains. **A**, **B**, **F**. *T. glabra* (Czarnocki, 1989) from Ostrówka; growth lines, suture, and views of IG 284.II.164 (A); internal shell thickening and views of IG 284.II.234 (B); views of juvenile specimen ZPAL AmVII/886 from Jabłonna probably belonging to this species (F; bed 25). **C**–**E**. *T. spinosa* (Münster, 1842); views of ZPAL AmVII/27 from Ostrówka (C, sample Ost-7), IG 284.II.155 from the same locality (D, bed 4 of Czarnocki 1989), and ZPAL AmVII/222 from Besówka (E).

Remarks. — Korn and Price (1987) suggested that the lineage of *Kosmoclymenia* originated from *Platyclymenia* with simple baloon-like septum. The new evidence on the earliest clymenias from the Holy Cross Mountains suggests rather that the marginal vaulting of the septum is an ancestral character inherited after the tornoceratids and that *Clymenia* and its probable successor *Kosmoclymenia* are less derived in this respect than *Platyclymenia*.

Genus ***Trigonoclymenia*** Schindewolf, 1934

Type species: *Clymenia spinosa* Münster, 1842 from Frankenwald.

Diagnosis. — Periodic expansions of the shell aperture produced funnel-like blades or ventrolateral parabolic nodes; septum with minute lateral vaulting; conch evolute.

Remarks. — The type species shows a simple septum and morphology closely similar to that in the species of *Platyclymenia*. Its affinities to *Clymenia* are suggested by the septal morphology and ornamentation of *T. glabra* (Czarnocki, 1989), that is, morphologically transitional rather between *Aktuboclymenia* and

Clymenia. The simple suture of advanced *Trigonoclymenia* may thus be an effect of simplification parallel to that at the origin of the *Platyclymenia* lineage, which may be otherwise closely related. *Spinoclymenia aculeata* Bogoslovsky, 1962, with its ventrolateral spines (Bogoslovsky 1962) may also represent this clade.

Trigonoclymenia glabra (Czarnocki, 1989)
(Figs 187A, B, F?, and 196)

Type horizon and locality: Lower part of *Platyclymenia* Stufe at Ostrówka (bed 4 of Czarnocki 1989), Holy Cross Mountains.

Material. — Two specimens.

Diagnosis. — Periodic blade-like expansion of the aperture.

Remarks. — Czarnocki (1989) classified this species in *Platyclymenia* but the septal morphology makes it close rather to *Clymenia*. An apparent tendency towards developing parabolic nodes points out its probable affinity to *Trigonoclymenia spinosa*.

Distribution. —Probably the early *P. trachytera* at Ostrówka (bed 4 of Czarnocki 1989).

Trigonoclymenia spinosa (Münster, 1842)
(Figs 187C–E and 196)

Type horizon and locality: Schübelhammer near Heinersreuth in Frankenwald?

Material. — Two specimens.

Diagnosis. — Ventrolateral parabolic nodes expressed on conch internal moulds as more or less apparent tubercles.

Remarks. — Czarnocki's (1989) *Platyclymenia unisulcata*, showing prominent ventrolateral tubercles, may belong here. Specimen ZPAL AmVII/027 from sample Ost-7 at Ostrówka shows a *Clymenia*-like septal morphology, although the suture is not suitable to prepare a camera lucida drawing. In fact, as the shell surface is not preserved, it cannot be excluded that this is a morph of *Nodosoclymenia distincta* Czarnocki, 1989.

Distribution. — Black limestone of probably the *P. trachytera* Zone at Ostrówka (bed 4) and Besówka, and grey limestone of the *L. styriacus* Zone (sample Ost-7).

Genus ***Clymenia*** Münster, 1834

Type species: *Planulites laevigatus* Münster, 1832 from Schübelhammer near Heinersreuth in Frankenwald?

Diagnosis. — Very evolute conch; septum with incipient lateral vaulting expressed in angulation of flank lobe of the suture, dorsal slope of which is more or less concave and ventral convex.

Clymenia primaeva (Czarnocki, 1989)
(Figs 189A and 196)

Type horizon and locality: Lower part of the *Platyclymenia* beds at Ostrówka, Holy Cross Mountains.

Material. — Three specimens.

Diagnosis. — Suture with relatively deep and angulate flank lobe; compressed whorls with tabulate venter.

Remarks. — *C. primaeva* was proposed by Czarnocki (1989) to be the type species of his genus *Eokosmoclymenia*. It is transitional between *Aktuboclymenia* and *Protoxyclymenia* and apparently represents a stage in the continuous lineage. One may doubt if so detailed subdivision is necessary.

From the same stratum the types of Czarnocki's (1989) *Eokosmoclymenia subacuta* originated, defined as developing ventrolateral furrows in mature stages, and *E. transitoria*, with slighly more acute venter. Their status seems questionable.

Distribution. — Probably the *P. trachytera* Zone at Jabłonna (well w52d dug by Żakowa *et al*. 1984) and Ostrówka (Czarnocki 1989).

Clymenia laevigata (Münster, 1839)
(Figs 188 and 196)

Type horizon and locality: Schübelhammer near Heinersreuth in Frankenwald?

Material. — Three specimens from Jabłonna, 23 specimens from Kowala, one from Ostrówka.

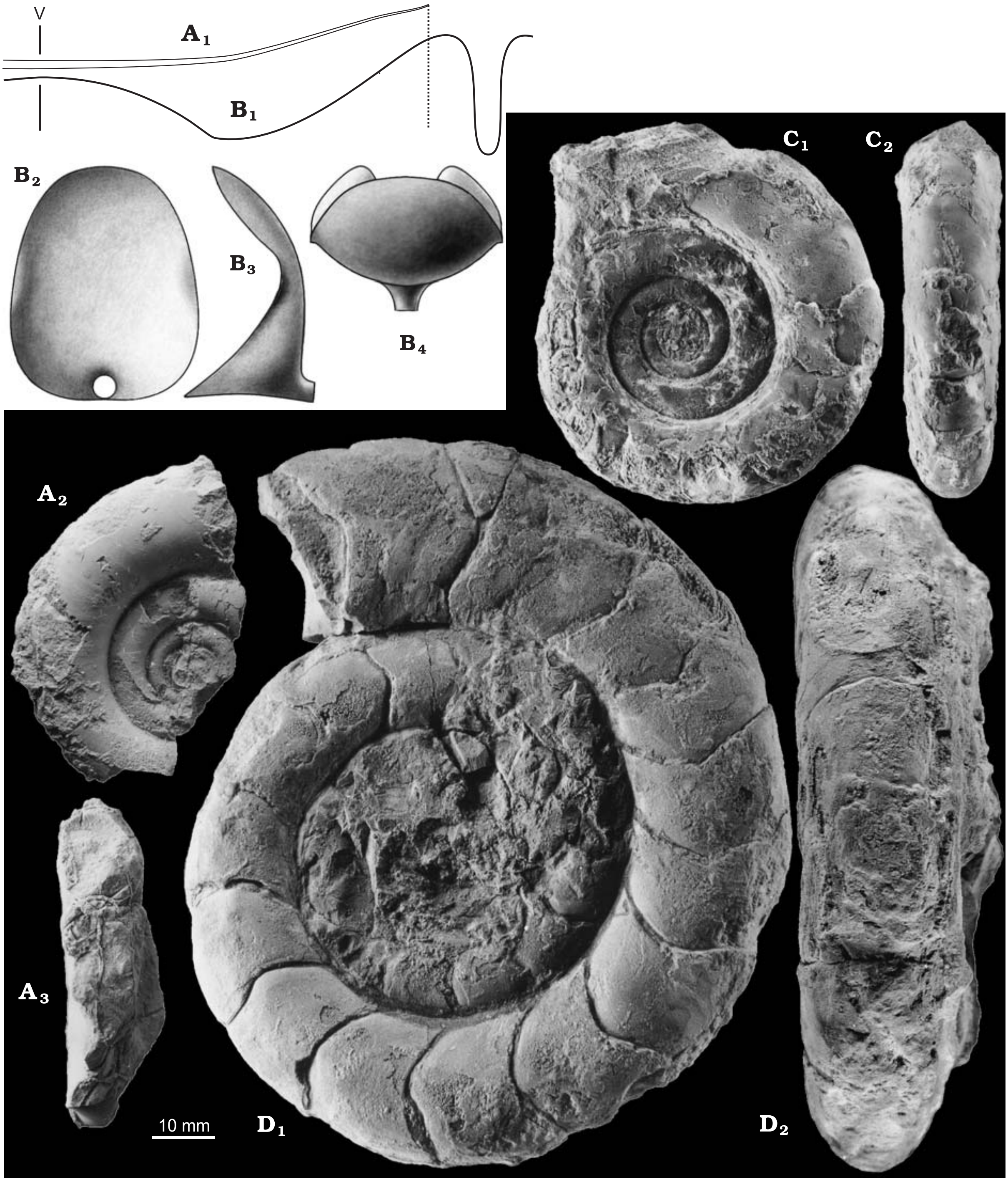


Fig. 188. *Clymenia laevigata* (Münster, 1839) from the early *P. jugosus* Zone of the Holy Cross Mountains; growth lines and views of ZPAL AmVII/303 from Jabłonna (A, sample J-51); suture and restoration of septum based on unnambered fragmentary specimens from Kowala (B); views of ZPAL AmVII/107 and IG 284.II.787 from Jabłonna (C, bed 28; D, beds with *Costaclymenia*).

Diagnosis. — Slight flank lobe angulation in the suture; aperture without ventral sinus.

Distribution. — The late *L. styriacus* Zone at Ostrówka (sample Ost-9) and Kowala, the early *P. jugosus* Zone at Jabłonna (bed 28 and sample J-51).

Genus ***Aktuboclymenia*** Bogoslovsky, 1979

Type species: *A. ancestralis* Bogoslovsky, 1979 from the Egedin Formation of the Urals.

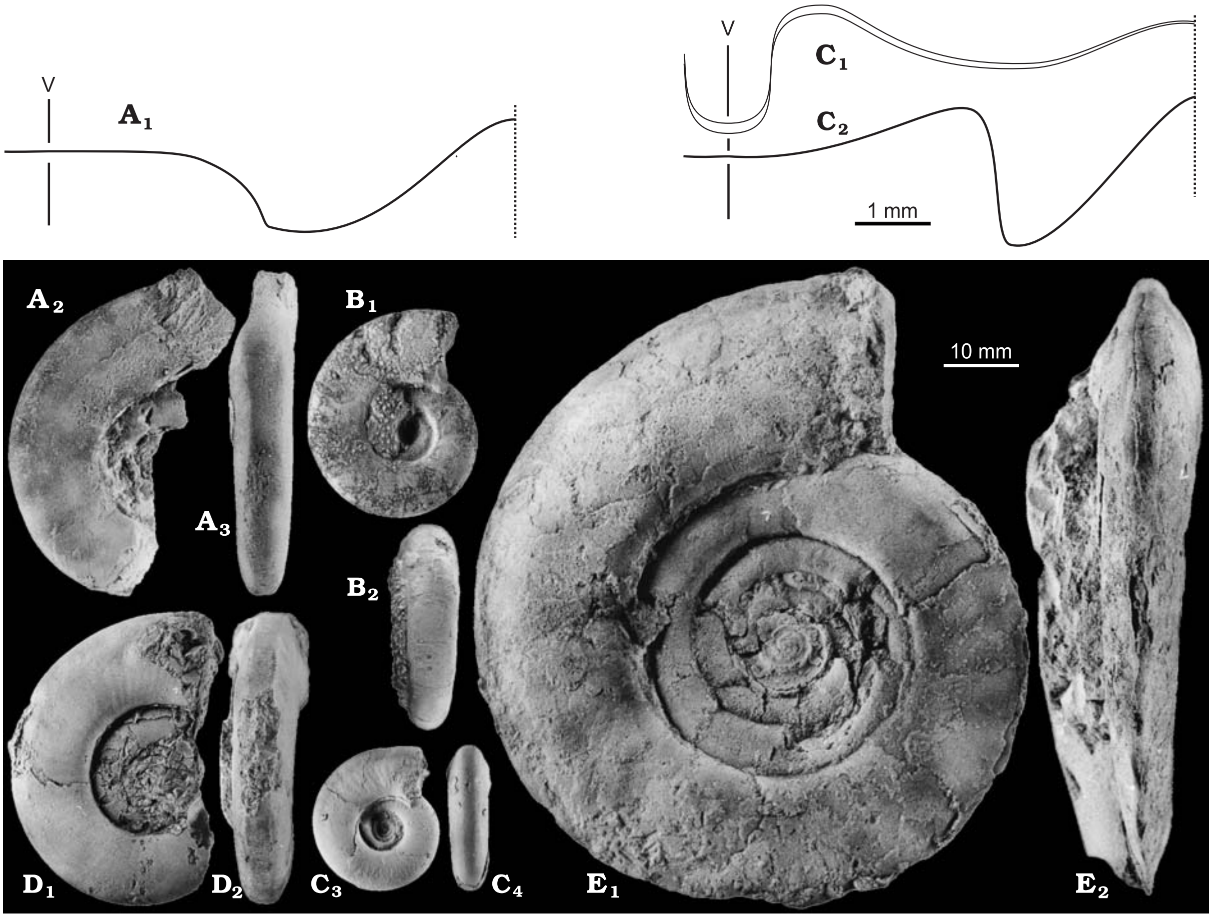


Fig. 189. Clymeniids from the *P. trachytera* Zone at Ostrówka in the Holy Cross Mountains. **A**. *Clymenia primaeva* Czarnocki, 1989; suture and views of ZPAL AmVII/708 from Jabłonna (well w52d of Żakowa *et al*. 1984). **B**. *Aktuboclymenia ancestralis* Bogoslovsky, 1979 from Sieklucki's brickpit in Kielce; suture and views of pyritic internal mould IG 284.II.182 (also Czarnocki 1989, pl. 21: 20). **C**, **D**. *Protoxyclymenia galezicensis* Czarnocki, 1989, growth lines, suture, and views of ZPAL AmVII/1117 (B, sample Ost-16); views of IG 284.II.219 (C, *Nodosoclymenia* bed). **E**. *Protoxyclymenia serpentina* (Münster, 1832); views of IG 284.II.216 (holotype of *Kosmoclymenia prima* Czarnocki, 1989; *Nodosoclymenia* bed).

Diagnosis. — Incipient septal vaulting expressed as an asymmetric angulation of the flank lobe, relatively involute conch with subtrapezoidal whorl cross section.

Remarks.— Bogoslovsky (1979) considered the type species of the genus ancestral to the branch of the Clymeniidae because its evolute conch and shallow flank lobe of the suture. The Polish species supports this interpretation. The incipient marginal vaulting of the septum seems to be inherited after a tornoceratid ancestor, preserved in the Cymaclymeniidae but apparently lost in the lineage of *Clymenia*.

Aktuboclymenia ancestralis Bogoslovsky, 1979
(Figs 189B, and 196)

Type horizon and locality: Egedin Formation at Kara Dzhar in the southern Urals.

Remarks. — The single pyritized specimen representing juvenile portion of the phragmocone and made the type of Czarnocki's *Flexiclymenia fundifera* shows conch evoluteness and suture making it indistinguishable from those of *A. ancestralis*. Obviously, until mature conchs are found in the Holy Cross Mountains, this species identification remains tentative.

Despite its small size, a true vaulting near the margin of the septum is developed, with the tip of the flank lobe extending significantly deeper than the nearby area of the septum. In this respect the species is transitional between *A. humboldti* and species of *Cymaclymenia*.

Distribution. — Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce.

Genus ***Protoxyclymenia*** Schindewolf, 1923

Type species: *Clymenia dunkeri* Münster, 1839 from Kirch-Gattendorf in Oberfranken.

Diagnosis. — Septum with lateral vaulting expressed in angulation of the flank lobe of the suture, the dorsal slope of which is almost straight and the ventral slightly angulated.

Protoxyclymenia galezicensis Czarnocki, 1989
(Figs 189C, D and 196)

Type horizon and locality: Lower part of the *Platyclymenia* beds at Ostrówka, Holy Cross Mountains.

Material. — Three specimens.

Diagnosis. — Ventral slope of the flank lobe of the suture almost parallel to the venter, delimited with slightly rounded angulation from the wide ventral lobe.

Remarks. — The septum is of almost hemispherical shape ventrally of the flank lobe, which makes tracing its contact with conch wall difficult.

Distribution. — The *P. trachytera* Zone at Ostrówka (sample Ost-16).

Protoxyclymenia serpentina (Münster, 1832)
(Figs 189E and 196)

Type horizon and locality: Schübelhammer near Heinersreuth in Frankenwald (Korn and Price 1987).

Remarks. — The only identifiable specimen collected by Czarnocki (1989) was made by him the type of *Kosmoclymenia prima*, although suture cannot be traced and generic affiliation remains uncertain. Restudy of the type material by Korn and Price (1987) removed objections against the proposed here identification of the specimen, although its preservation makes any determination tentative.

Distribution. — Probably the *P. trachytera* Zone at Ostrówka (lower *Platyclymenia* beds of Czarnocki 1989).

Genus ***Kosmoclymenia*** Schindewolf, 1949

Type species: *Planulites undulatus* Münster, 1832 from Försterei Reigern near Balve, Rhenish Slate Mountains (Korn and Price 1987).

Diagnosis. — Pointed flank lobe of the suture delimited ventrally by a narrow saddle giving it a zigzag appearance.

Remarks. — A great number of *Kosmoclymenia* species has been proposed and its taxonomy is rather complex (Korn and Price 1987). The differences between species result mostly from maturation of their conchs at various size. It remains to be determined with biometrics of large samples how strict was the control of ontogeny and how much variation is allowed for a species and its particular populations.

Kosmoclymenia kowalensis Czarnocki, 1989
(Figs 190 and 196)

Type horizon and locality: Lower part of the *Wocklumeria* beds at Kowala, Holy Cross Mountains (Czarnocki 1989).

Material. — 17 specimens.

Diagnosis. — Conch of generalized morphology and longiconic appearance at juvenile stages, developing ventrolateral furrows at diameter of 40–45 mm; delicate irregular growth lines.

Remarks. — The species shows much similarity to *K. bisulcata* (Münster, 1832), lacking its diagnostic lateral furrows at maturity (see Korn and Price 1987) and to *K. ademmeri* Korn *et* Price, 1987, but lacks any spiral ornament.

The holotype of *K. kowalensis* is a juvenile specimen, unidentifiable at the species level if taken alone. Probably the oldest true *Kosmoclymenia* in the Holy Cross Mountains occurs at Kowala in the grey limestone below the black Epinette Event shale. Along with several internal moulds collected by myself from there, two specimens with preserved shell showing growth lines were found and they fit the morphology of both the Czarnocki's type specimens of *K. kowalensis* from Ostrówka and those from the red limestone classified by him in *K. sedgwicki*. However, the lectotype of *Clymenia sedgwicki* Münster, 1840 has appeared to represent the tornoceratid *Pseudoclymenia* (Korn and Price 1987, p. 33).

Protoxyclymenia tenuissima Czarnocki, 1989 was based on a minute specimen considered mature by Czarnocki (1989) because of apertural modification of one specimen from Kowala (possible preservational artefact).

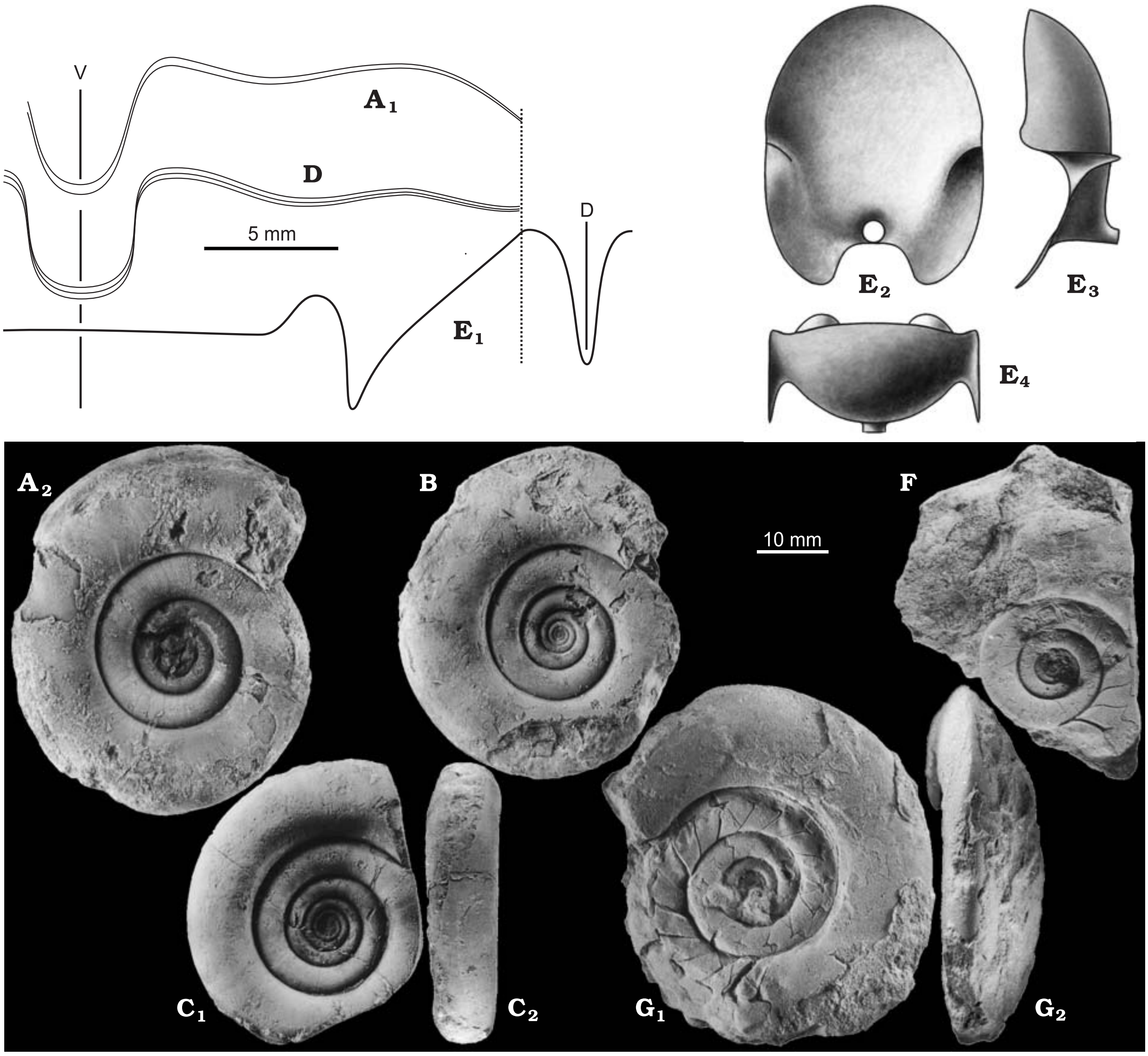


Fig. 190. *Kosmoclymenia kowalensis* Czarnocki, 1989 from Kowala in the Holy Cross Mountains; growth lines and views of mature specimens IG 284.II.457 and 457a, and juvenile specimen IG 284.II.465 from red limestone (A–C, *D. trigonica* Zone); suture growth lines of ZPAL AmVII/783, suture and restoration of septum based on unnambered specimens, and views of ZPAL AmVII/950 and 1615 from grey limestone immediately above the strata with *Clymenia* (D–G, *P. jugosus* Zone).

Distribution. — The *P. jugosus* and *D. trigonica* zones at Kowala and Ostrówka and Dzikowiec.

Kosmoclymenia sp. aff. *K. bisulcata* (Münster, 1832)
(Figs 191 and 196)

Material. — 36 specimens.

Diagnosis. — Conch of generalized morphology developing ventrolateral furrows at diameter of about 40 mm or later, ornamented with dense distinct growth lines.

Remarks. — The species is similar to *K. bisulcata* in general conch form but differs in underived shape of mature aperture and the lack of lateral furrows; probably also in distinctness of growth lines, a feature dependant on preservation. *K. adammeri* Korn *et* Price, 1987 is even more similar to the Dzikowiec form than that species in low whorl expansion rate, but its diagnostic character is a longitudinal striation. Such a striation sometimes developed in the Dzikowiec *Kosmoclymenia*, but rather on specimens of juvenile morphology resembling *K. undulata*.

Distribution. — The *D. trigonica* and possibly the late *P. jugosus* zones at Dzikowiec.

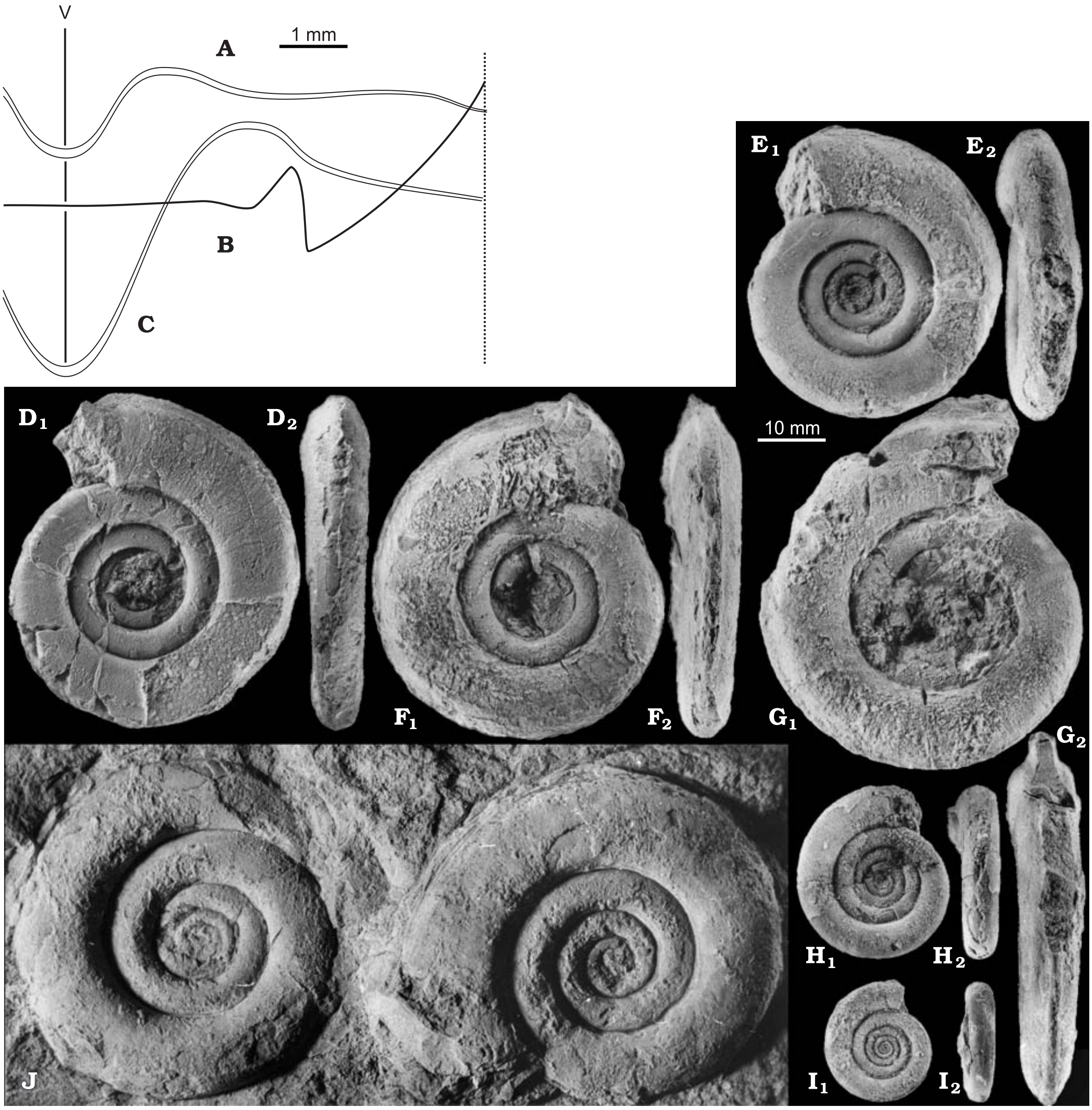


Fig. 191. *Kosmoclymenia* sp. aff. *K. bisulcata* (Münster, 1832) from the *D. trigonica* and the late *P. jugosus* zones at Dzikowiec in the Sudetes; growth lines of subadult specimen ZPAL AmVII/71 (A); suture of ZPAL AmVII/74 (B); growth lines of mature specimens ZPAL AmVII/156 (C); views of ZPAL AmVII/174, 163, 175, 153, 1029, and 170 (D–I), and Uwr 1776 (J).

Kosmoclymenia galeata (Wedekind, 1914)
(Figs 192 and 196)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes (Korn and Price 1987).

Material. — Two specimens.

Diagnosis. — Conch of generalized morphology developing ventrolateral furrows at diameter of about 70 mm, ornamented with regularly and densely distributed distinct growth lines.

Remarks. — The lectotype has poorly preserved growth lines and shows a rather early development of ventrolateral furrows, indicating conch maturity (Korn and Price 1987) but its evolute appearance suggests affinities to the topotype specimens included here in the same species. *K.* sp. aff. *K. bisulcata* shares a similar ornamentation and occurs at the same locality but not necessarily in the same stratum. *K. galeata* is distinct from it in ontogenetically later development of the ventrolateral furrows, but a somewhat higher growth expansion rate at earlier stages. The apertural lappets of the type specimen of *K. parundulata* Korn *et* Price, 1987 from Effenberg project forward, unlike the discussed specimens from Dzikowiec.

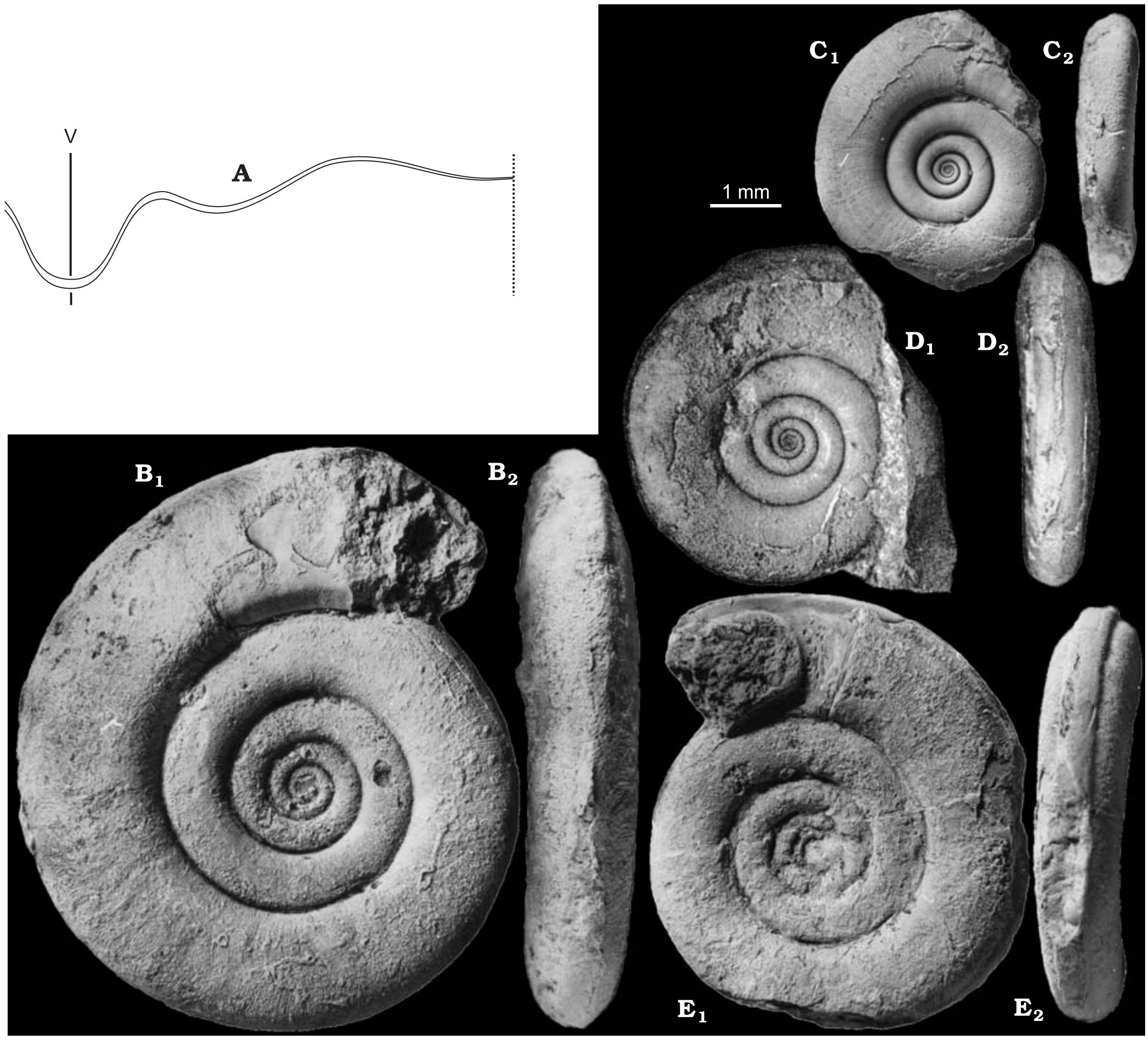


Fig. 192. *Kosmoclymenia galeata* (Wedekind, 1914) from the late *P. jugosus* zones at Dzikowiec in the Sudetes; suture of MB.C. 4285 (A), views of large immature specimen MB.C. 4046 and juvenile 4062 (B, C), the lectotype (D) reproduced from Korn and Price (1987), and small mature specimen MB.C. 4093 (E; note internal thickening near the aperture, similar to that in *Cymaclymenia silesiaca* on Fig. 185D).

Distribution. — Probably the late *P. jugosus* Zone at Dzikowiec.

Kosmoclymenia dzikowiecensis (Korn *et* Price, 1987)
(Figs 193A–E and 196)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes (Korn and Price 1987).

Material. — Three specimens.

Diagnosis. — Conch of generalized morphology and relatively breviconic appearance, developing ventrolateral furrows at diameter of about 25 mm, ornamented with regularly and densely distributed distinct growth lines.

Remarks. — The maturity at rather small conch size suggests that this species is ancestral to *K. similis*, occurring also at the same locality. No evidence on their stratigraphic relationship is available, however.

Distribution. — Probably the *P. jugosus* Zone at Dzikowiec.

Kosmoclymenia similis (Münster, 1832)
(Figs 193F–I and 196)

Type horizon and locality: Kirch-Gattendorf in Frankenwald (Korn and Price 1987).

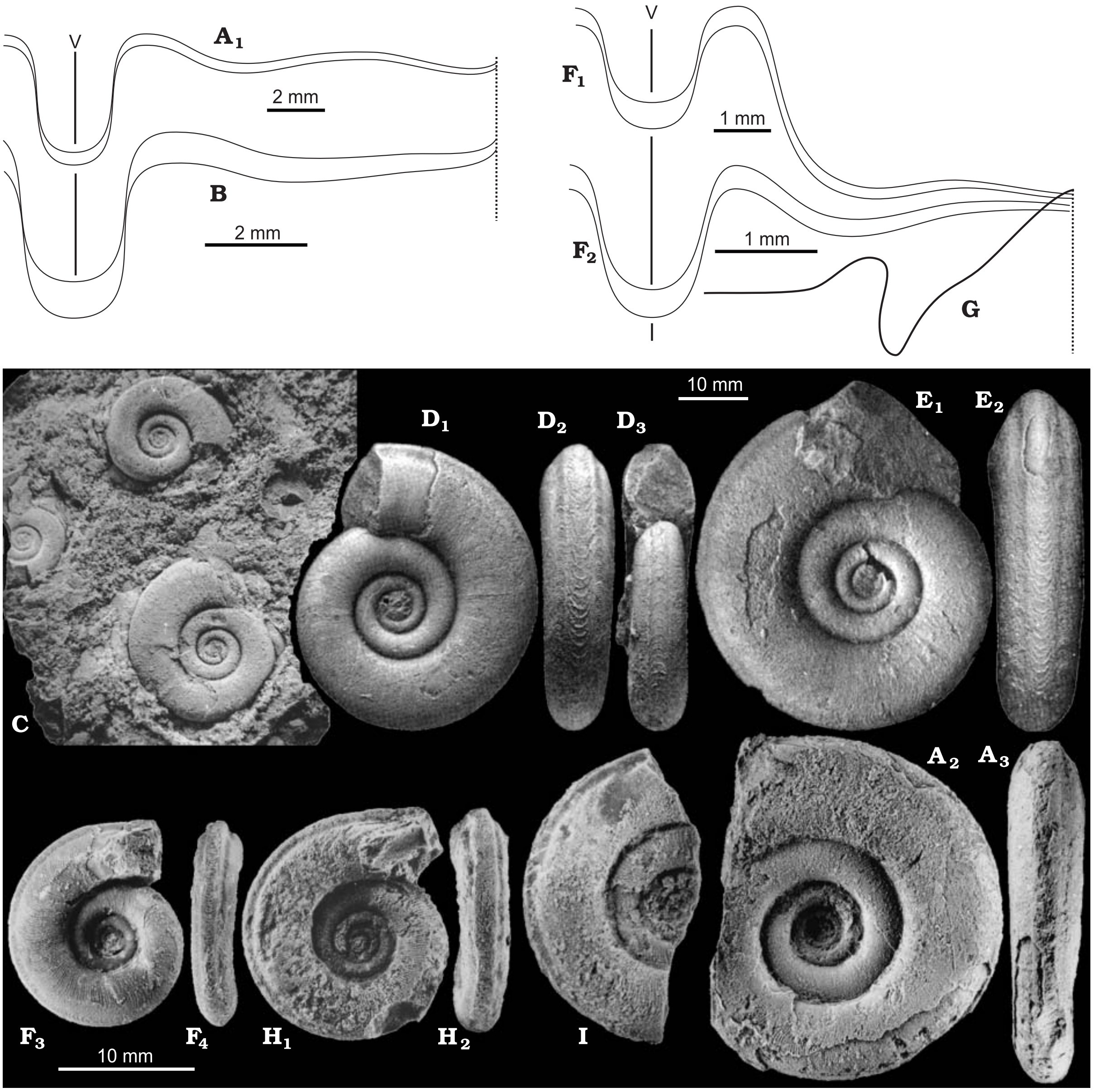


Fig. 193. Small size advanced *Kosmoclymenia* from Dzikowiec in the Sudetes. **A–E**. *Kosmoclymenia dzikowiecensis* (Korn *et* Price, 1987) probably from the late *P. jugosus* Zone; growth lines and views of specimen ZPAL AmVII/1026 (A); growth lines of ZPAL AmVII/1026 (B); view of specimen MB.C. 4043 (C); views of paratype and holotype (D, E, both reproduced from Korn and Price 1987, pl. 8: 58, 59). **F–I**. *Kosmoclymenia similis* (Münster, 1832) from the *D. trigonica* Zone; growth lines at maturity and prior to developing ventrolateral furrows and views of specimen ZPAL AmVII/117 (F); suture of ZPAL AmVII/43 (G); views of ZPAL AmVII/424 and 164 (H, I).

Material. — 23 specimens.

Diagnosis. — Minute conch developing ventrolateral furrows at diameter of about 12 mm.

Remarks. — This is probably the most characteristic and easy to determine species of *Kosmoclymenia* owing to its minute size at maturity.

Distribution. — The *D. trigonica* Zone at Kowala (sample Ko-107) and Dzikowiec (sample Dz-7 and loose blocks).

Kosmoclymenia xenostriata Korn *et* Price, 1987

(Figs 194 and 196)

Type horizon and locality: Probably Schübelhammer in Franconia (Korn and Price 1987).

Material. — 12 specimens.

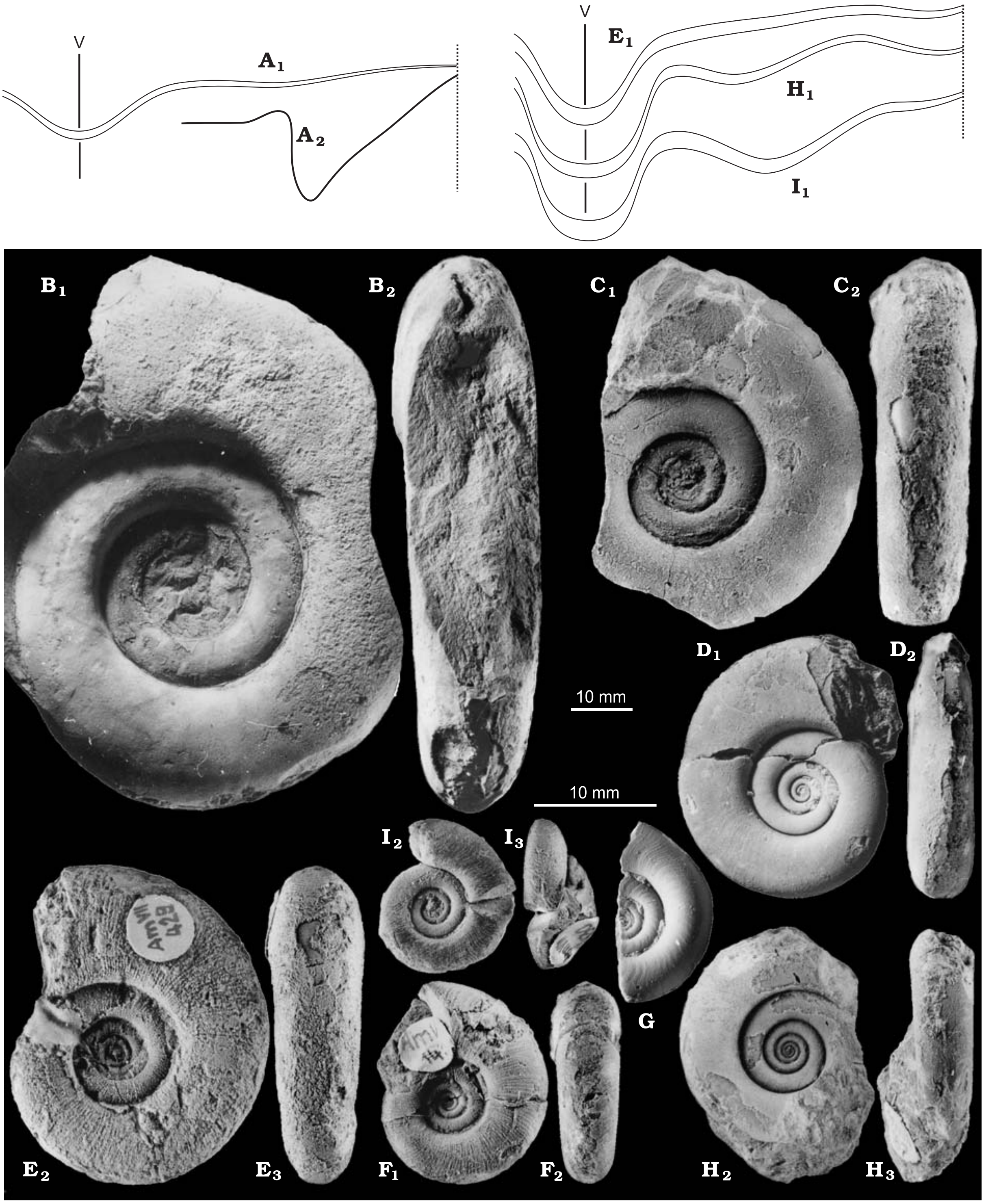


Fig. 194. *Kosmoclymenia xenostriata* Korn *et* Price, 1987 from the late *P. jugosus* Zone at Dzikowiec in the Sudetes (A–H) and Jabłonna in the Holy Cross Mountains (I); growth lines and suture of specimen ZPAL AmVII/428 (A); views of UWr 1769, ZPAL AmVII, 165, MB.C. 4076 (B–D); growth lines and views of of ZPAL AmVII/429 (E); views of ZPAL AmVII/143 and UWr 1760 (F, G); growth lines and views of of ZPAL AmVII/167 and 430 (H, I).

Diagnosis. — Oblique aperture of the conch with usually prominent growth lines and relatively breviconic appearance, umbonal wall rounded in profile.

Remarks. — The holotype is a juvenile specimen (Korn and Price 1987), but its oblique aperture profile is consistent with that of the Dzikowiec specimens at comparable stages of their ontogeny. In this respect

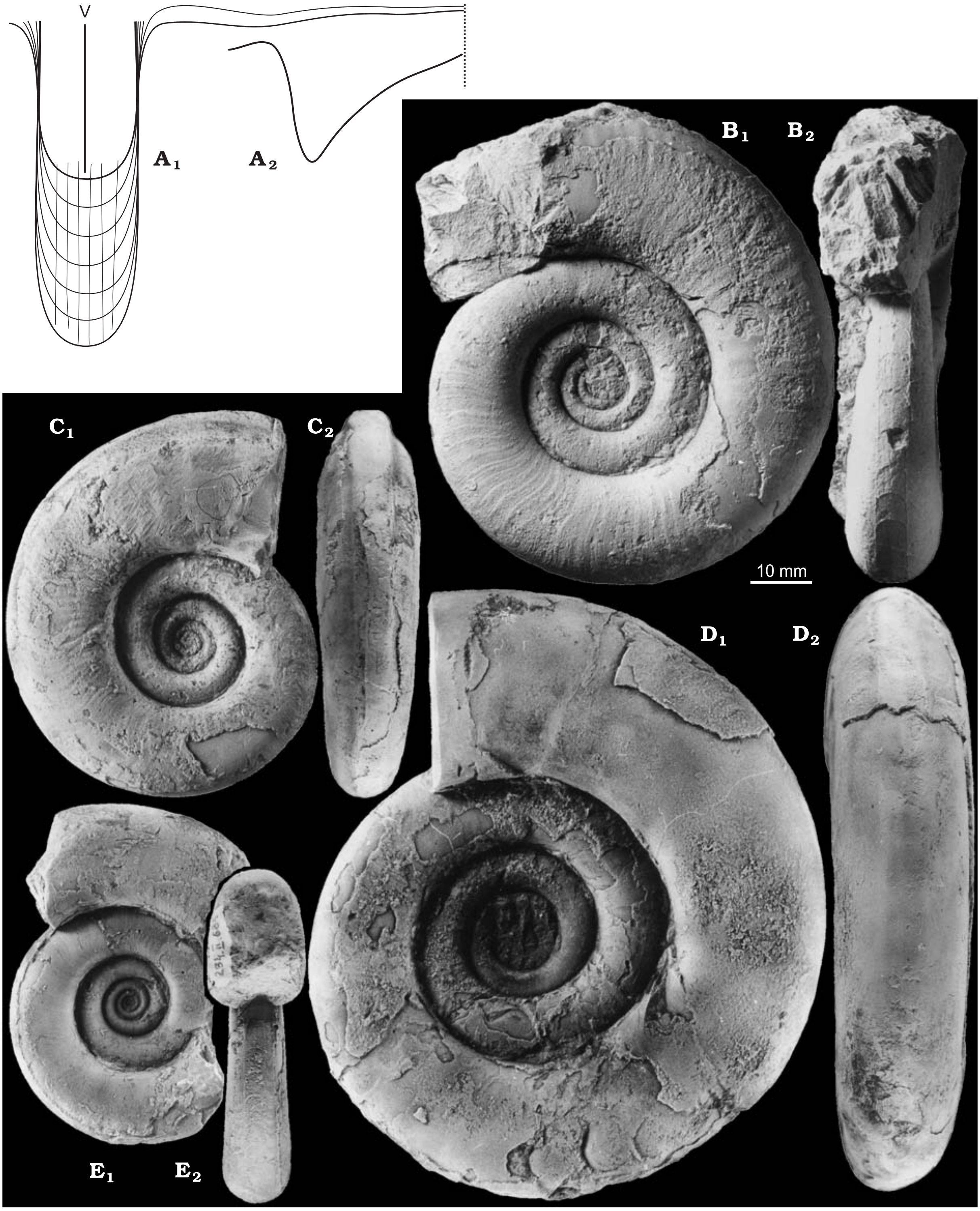


Fig. 195. *Kosmoclymenia undulata* (Münster, 1832) from the late *P. jugosus* Zone at Dzikowiec in the Sudetes (A, B) and at between Stokówka and Besówka in the Holy Cross Mountains (C–E); growth lines and suture of specimen ZPAL AmVII/416 (A); views of unnambered specimen Uwr (B), IG 284.II.367 (C; holotype of *K. venusta* Czarnocki, 1989), IG 284.II.363 (D), and 685 (E, paratype of *Eokosmoclymenia subacuta* Czarnocki, 1989).

they also resemble the lectotype of *Kosmoclymenia wocklumeri* (Wedekind, 1914) from the *P. paradoxa* Zone at Ense in Kellerwald, proposed by Korn and Price (1987), which differs, however, in an angular profile of the umbonal part of its umbo and in mature whorl lacking ventrolateral furrows despite the large conch size.

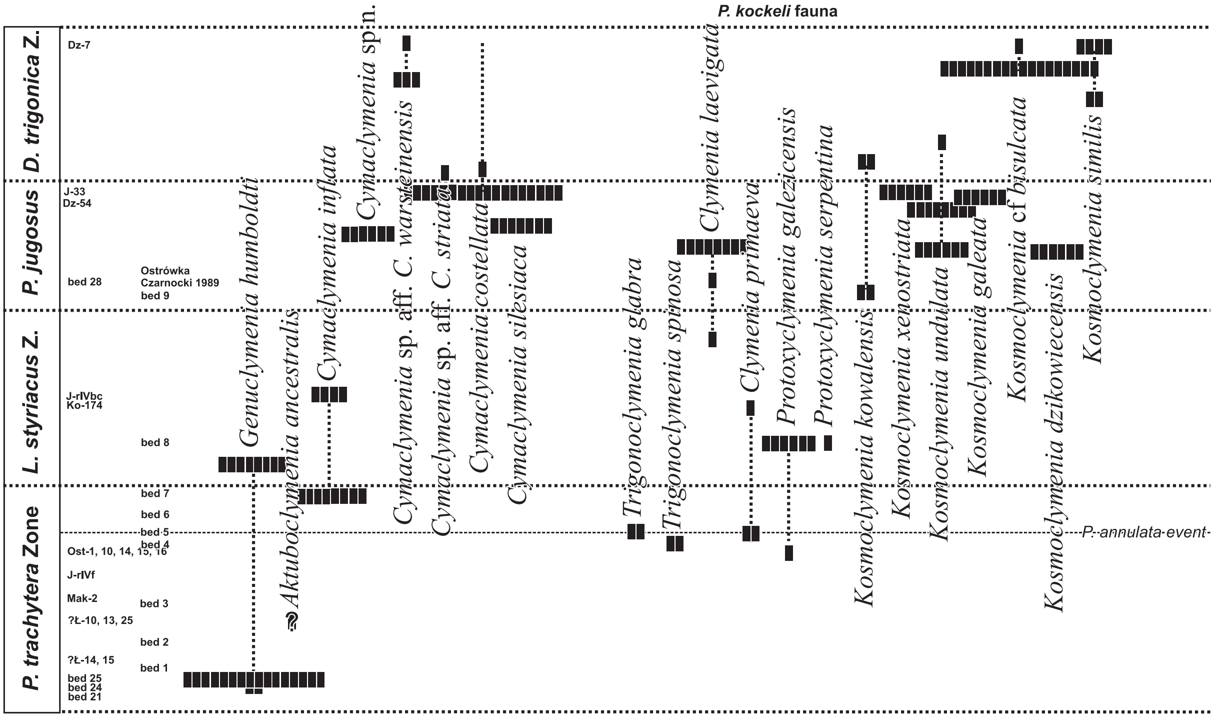


Fig. 196. Stratigraphic distribution of species of the Cymaclymeniidae and Clymeniidae in the Polish Famennian. Position of samples not included in Figs. 2 and 3 on the geochronological scale is hypothetical.

There is much variation in the prominence and regularity in distribution of growth lines among the Dzikowiec specimens showing their sinuous appearance. In a few specimens with prominent growth lines, lateral sinuses are not developed. They are thus more derived than *K. xenostriata* in this respect, which may place them within the range of variability of *K. wocklumeri*.

Distribution. — The late *P. jugosus* Zone at Dzikowiec and Jabłonna.

Kosmoclymenia undulata (Münster, 1832)
(Figs 195 and 196)

Type horizon and locality: Försterei Reigern near Balve, Rhenish Slate Mountains (Korn and Price 1987).

Material. — 12 specimens.

Diagnosis. — Serially distributed blade-like transverse expansions of the aperture ventrally prominent; deep infundibular sinus of the aperture; nearly circular whorl cross section until conch maturity.

Remarks. — The large specimen from Kowala attributed to *K. wocklumeri* by Czarnocki (1989) because of its angular umbo, is here transferred to *K. undulata*, as this is rather the character of this species. Also the material of *K. venusta* Czarnocki, 1989 from the locality between Besówka and Stokówka probably represents this species, as suggested by the appearance of fragmentarily preserved growth lines on one specimen (Czarnocki 1989, pl. 34: 7).

Distribution. — Red limestone of the late *P. jugosus* Zone at Ostrówka and grey limestone of probably the *D. trigonica* Zone at Kowala and Dzikowiec.

Family **Carinoclymeniidae** Bogoslovsky, 1975

Diagnosis. — Suture with clearly delimited semicircular flank lobe; more or less involute conch tending to develop acute venter.

Remarks. — Bogoslovsky (1975) introduced this family for clymenias with deeply involute conchs and acute venter. Advanced members of the clade developed periodic narrow "horns" along the ventral keel (Bogoslovsky 1982). Among species from the Holy Cross Mountains introduced by Czarnocki (1989), several are transitional between such forms and *Costaclymenia*. To preserve clarity of classification it seems necessary to extend the range of this family to encompass also those ancestral forms that are provisionally classified here in *Nanoclymenia*. It is only a matter of convenience whether to separate this clade from the family Costaclymeniidae, here restricted to forms with a tabulate venter, or not. An acute venter alone is a poor diagnostic character for high rank ammonoid taxa, and this feature appeared independently several times in the evolution of clymenias.

Genus ***Nanoclymenia*** Korn, 2002

Type species: *Clymenia nana* Münster, 1842 probably from the lower part of *Platyclymenia* Stufe at Schübelhammer near Heinersreuth in Frankenwald (Korn 2004b).

Diagnosis. — Suture with rounded flank lobe with gently sinuous dorsal and more steep ventral slope; moderately evolute conch with rounded subtrapezoidal whorl cross section.

Remarks. — This is a connecting link between early clymenias with angular flank lobe and *Costaclymenia* with distinctly developed semicircular lobe of the suture. It is assumed here that the specimens of *N. nana* described by Korn (2004b) and Korn and Klug (2002) are juveniles.

Nanoclymenia? *intermedia* (Czarnocki, 1989)
(Figs 197A–D and 218)

Type horizon and locality: *Prolobites* beds at Ostrówka, Holy Cross Mountains (Czarnocki 1989).

Remarks. — Suture of the species remains unknown. Czarnocki (1989) classified it in *Rectoclymenia* together with *Nanoclymenia retrusa*, although both lack the generically diagnostic ventral keel. He referred to some similarity in conch morphology, especially the shape of internal shell thickenings. In fact, the earliest keeled clymenia in the Ostrówka section, *Kiaclymenia polonica* (Czarnocki, 1989) occurs immediately above and shows much similarity in conch morphology to *N.*? *intermedia*. Another possible affinity of the species is among involute species of *Pleuroclymenia*.

Distribution. — The *P. trachytera* Zone, grey limestone of *Prolobites* beds at Ostrówka (bed 3? of Czarnocki 1989); several juvenile specimens from Jabłonna (trench rIVb dug by Żakowa *et al*. 1984) may also belong here.

Nanoclymenia retrusa (Czarnocki, 1989)
(Figs 197I, J and 218)

Type horizon and locality: Lower part of *Platyclymenia* beds at Ostrówka, Holy Cross Mountains.

Remarks. — Obliquely transverse internal shell thickenings make the species similar to *Pleuroclymenia intermedia* (Czarnocki, 1989) which may be ancestral both to it and the *Cteroclymenia* lineage of clymenias with acute venter but its exact evolutionary position remains questionable because of unknown suture.

Distribution. — Early *L. styriacus* Zone, lower part of the *Clymenia* beds (*Nodosoclymenia* bed) at Ostrówka (bed 8 of Czarnocki 1989) and probably the *P. trachytera* Zone at Jabłonna (bed 24).

Genus ***Cteroclymenia*** Bogoslovsky, 1979

Type species: *C. rozmanae* Bogoslovsky, 1979 from the Egedin Formation of Kara Dzhar in the southern Urals (Bogoslovsky 1979).

Diagnosis. — Conch with small umbilicus and parabolic venter developing a sharp keel at late ontogenetic stages; suture with small flank lobe located near umbilicus.

Cteroclymenia sp. n.
(Figs 197E, F and 218)

Remarks. — The species was determined by Czarnocki (1989) as *Rectoclymenia* aff. *arietina* (Sandberger, 1853) but the conch shape points rather to *Cteroclymenia rozmanae* Bogoslovsky, 1979 as its closest relative. The Polish species is less involute, which suggests its underived status. Unfortunately, the available evidence on suture and growth lines is insufficient to determine more precisely its relationships and to define new species.

Distribution. — The *P. trachytera* Zone, upper *Prolobites* beds at Ostrówka (bed 4? of Czarnocki 1989), juvenile specimen found in sample Ost-15.

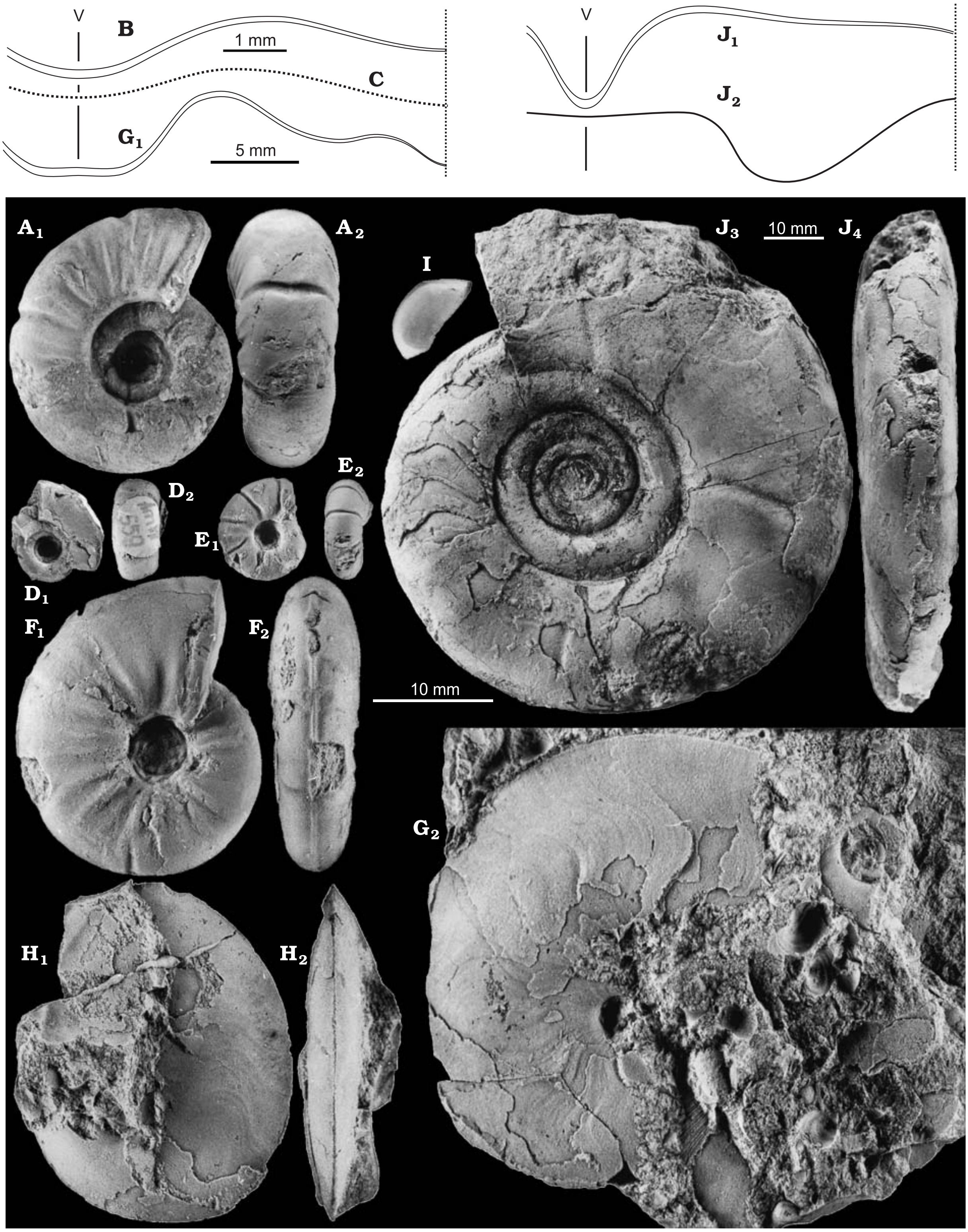


Fig. 197. Carinoclymeniids from the *P. trachytera* Zone of the Holy Cross Mountains. **A**–**E**. *Nanoclymenia*? *intermedia* (Czarnocki, 1989) from Ostrówka (A) and Jabłonna (B–D); views of specimen IG 284.II.39 (A, bed 1 of Czarnocki 1989); growth lines of ZPAL AmVII/557, internal thickening of 532, and views of 559 (B–D; trench rIVb of Żakowa *et al*. 1984). **E**, **F**. *Cteroclymenia* sp. n. from Ostrówka; views of specimen ZPAL AmVII/1677 (E, sample Ost-15) and IG 284.II.23 (F). **G**, **H**. *Carinoclymenia beulensis* (Lange, 1929) from the *P. trachytera* Zone at Ostrówka (lower *P. annulata* Zone according to label written in 1936 by Jan Czarnocki); growth lines and view of specimen IG 284.II.206 (G) and 206a (H). **I**, **J**. *Nanoclymenia retrusa* (Czarnocki, 1989) from Jabłonna (I, bed 24) and Ostrówka (J, *Nodosoclymenia* bed); a piece of the living chamber ZPAL AmVII/846 (I); growth lines, suture and views of IG 286.II.233 (J).

Genus *Carinoclymenia* Bogoslovsky, 1965

Type species: *?Tornoceras beulense* Lange, 1929 from the *P. annulata* Zone at Beul, in the Rhenish Slate Mountains.

Diagnosis. — Flat involute conch with a very sharp ventral keel.

Carinoclymenia beulensis (Lange, 1929).
(Figs 197G, H and 218)

Material. — Two specimens.

Remarks. — Growth lines reaching the margin of the ventral keel give it a characteristic serrated appearance (Müller 1956). Suture is not preserved; identification of the species as a clymenia is thus due only to data by Bogoslovsky (1965). *Clymenia subflexuosa* var. *acuta* of Perna (1914) with a wider umbilicus and less compressed conch may be the ancestor of this species.

Distribution. — The *P. trachytera* Zone, black crinoidal limestone with *Guerichia* of the lower *P. annulata* beds at Ostrówka (bed 5? of Czarnocki 1989).

Family **Costaclymeniidae** Schindewolf, 1920

Diagnosis. — Suture with flank lobe bordered by narrow saddles; evolute conch with more or less tabulate venter.

Genus *Costaclymenia* Schindewolf, 1920

Type species: *Goniatites binodosus* Münster, 1832.

Diagnosis. — Almost semicircular flank lobe dorsally delimited by distinct saddle and ventrally by angulation of the whorl.

Costaclymenia binodosa (Münster, 1832)
(Figs 198 and 218)

Material. — Three specimens.

Remarks. — Ventral and umbonal lobes of the suture are shallow; juvenile conch bears subventral tubercles. Czarnocki (1989) created species *C. limata* for the single large specimen from the red limestone of probable *Clymenia* Stufe strata at Ostrówka, referring to the completely smooth conch surface as the diagnostic character. Actually the conch shows indistinct tubercles, which usually disappear at the stage when the whorls increase their height (see Bogoslovsly 1981, pl. 3: 2b). I find thus this evidence insufficient to define a separate species.

Distribution. — Red limestone of the *Clymenia* beds at Ostrówka (bed 16 of Czarnocki 1989) and the earliest *P. jugosus* Zone at Jabłonna (bed 27), coeval strata at Kowala.

Genus *Trochoclymenia* Schindewolf, 1929

Type species: *Clymenia wysogorskii* Frech, 1902 from the clymeniid limestone at Dzikowiec, the Sudetes.

Diagnosis. — Very longiconic smooth evolute conch with shallow flank lobe of the suture.

Trochoclymenia wysogorskii (Frech, 1902)
(Figs 216A–C and 218)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

Material. — Three specimens.

Remarks. — The original from Dzikowiec is poorly preserved and offers little information on the conch morphology but its overall shape and suture (Frech 1902, fig. 3) strongly suggest species identity with the specimen from Kowala described by Czarnocki (1989). Among juvenile specimens from Dzikowiec there is one with a wide tabulate venter which potentially may also belong here. The suture, weel represented in the Kowala specimen, shows a pointed saddle on flanks without any correspondence to the whorl section. This is a feature of the *Costaclymenia* lineage.

Distribution. — The *D. trigonica* Zone at Kowala (lower *Wocklumeria* beds of Czarnocki 1989) and Dzikowiec (the highest clymeniid limestone according to Frech 1902, p. 33).

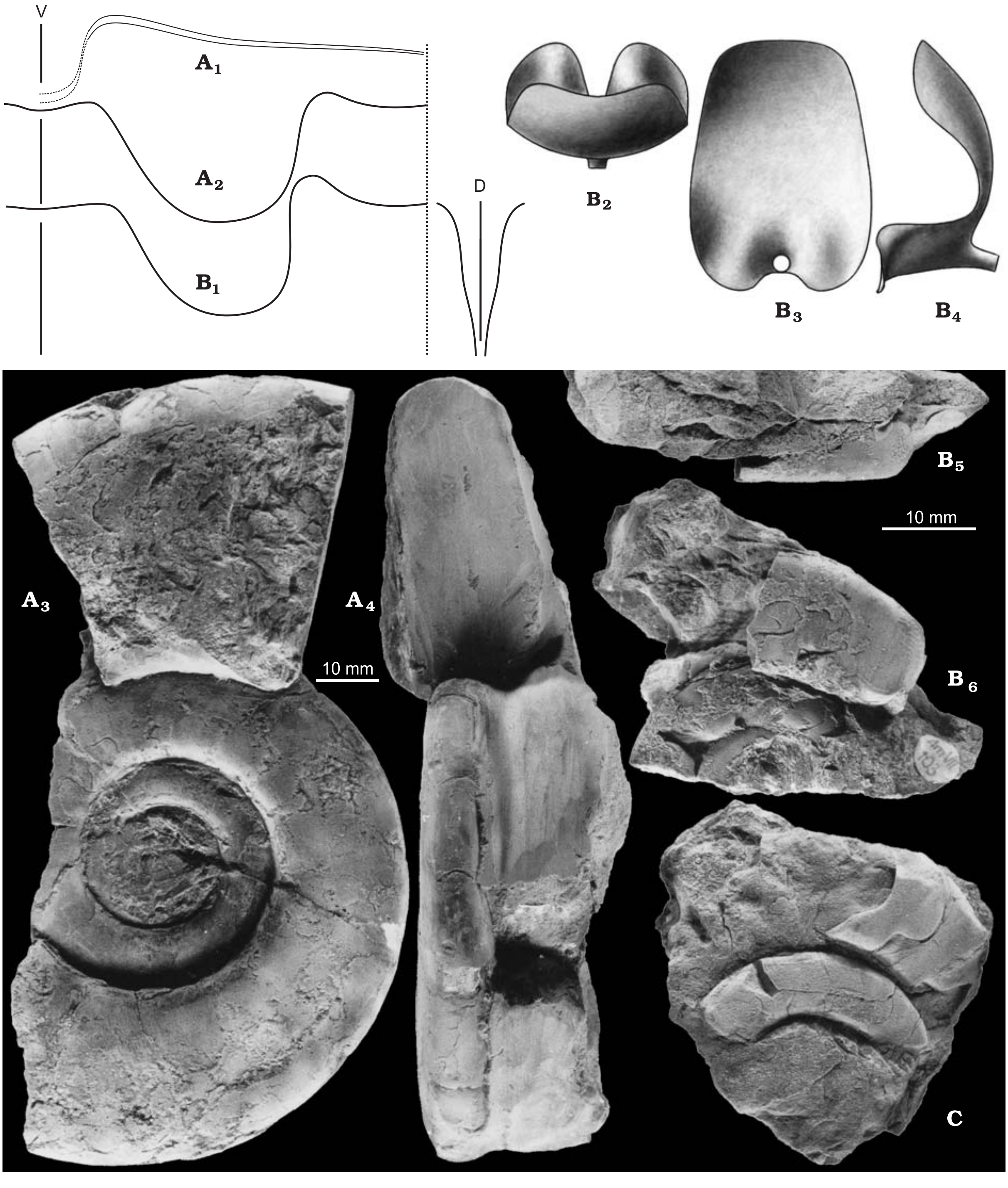


Fig. 198. *Costaclymenia binodosa* (Münster, 1832) from the Holy Cross Mountains; growth lines, suture, and views of specimen IG 284.II.231, from Ostrówka (A, probably the early *P. jugosus* Zone); suture, restored septum, and views of ZPAL AmVII/103 from the earliest *P. jugosus* Zone at Jabłonna (B, bed 27); view of ZPAL AmVII/945 from the early *P. jugosus* Zone at Kowala (C).

Family **Gonioclymeniidae** Hyatt, 1884

Diagnosis. — Suture with flank lobe bordered by narrow saddles; evolute conch with flat venter.

Remarks. — Probable ancestor of the gonioclymeniids is *Mesoclymenia nalivkinae* Bogoslovsky, 1981 from Kazakhstan, with acute ventral and flank lobes. Subsequent deepening of the umbonal lobe and subdivision of ventrolateral saddle apparently gave the situation known in *Gonioclymenia* (Bogoslovsky 1981).

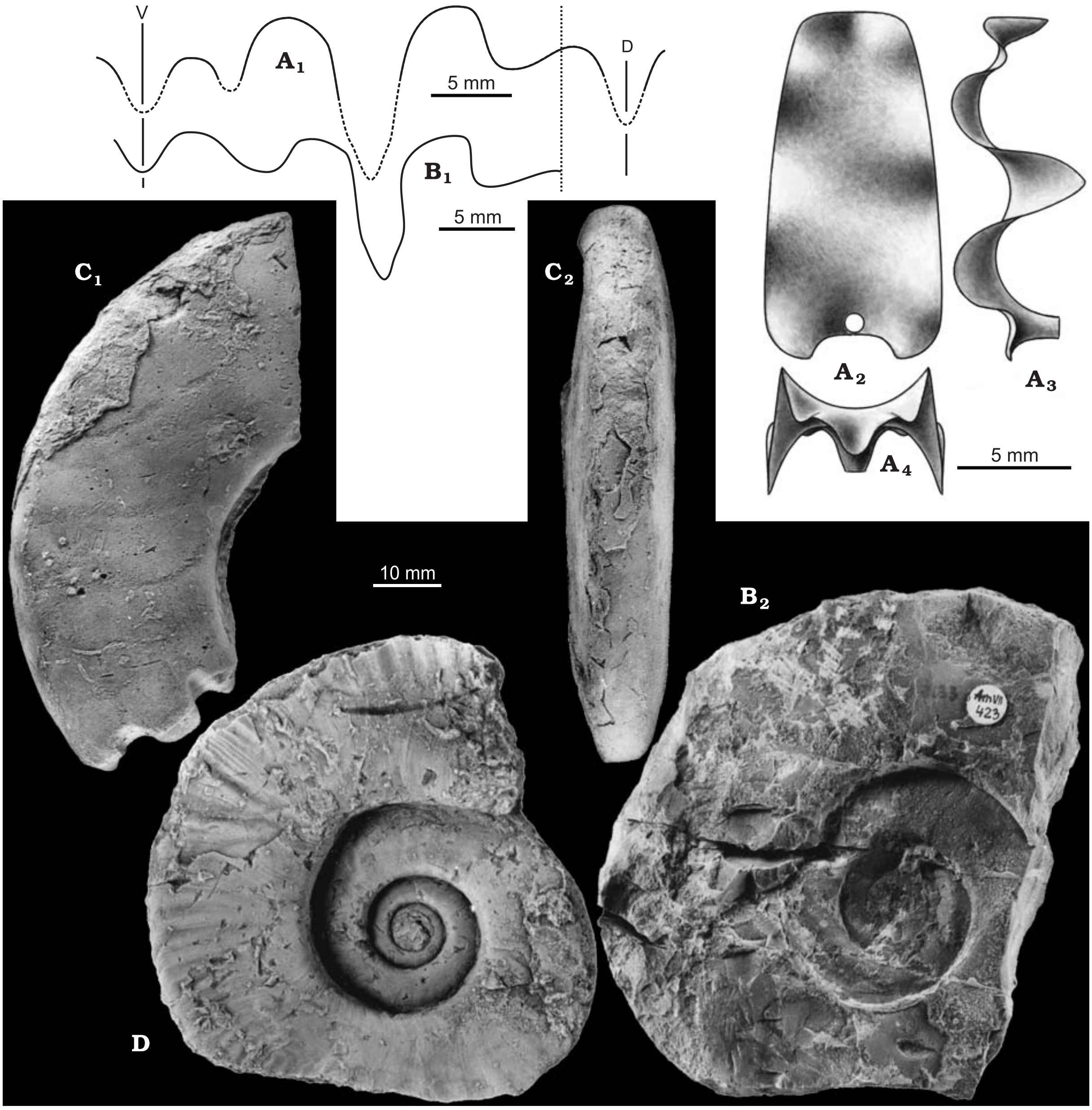


Fig. 199. *Finiclymenia wocklumensis* (Lange, 1929) from the *P. jugosus* Zone of the Holy Cross Mountains; suture, and restored septum of specimen IG 284.II.272, from Kowala (A); suture and view of ZPAL AmVII/423 from Jabłonna (B, C; bed 33); views of specimens IG 284.II. 852 and 635 from Kowala (C, D; D reproduced from Czarnocki 1989, pl. 4: 4).

Genus ***Finiclymenia*** Price *et* Korn, 1989

Type species: *Gonioclymenia (Kalloclymenia) wocklumensis* Lange, 1929 from *P. paradoxa* Zone, Burg near Balve, Rhenish Slate Mountains (Price and Korn 1989).

Diagnosis. — Suture with shallow rounded umbonal lobe; high trapezoidal whorls of the conch; ventrolateral tubercles.

Remarks. — Price and Korn (1989) defined their subgenus *Finiclymenia* of *Gonioclymenia*, on the V-shaped apperance of the flank lobe in the only available specimen. The specimens from Kowala (Czarnocki 1989) and Jabłonna, otherwise indistinguishable from the holotype, show a narrow flank lobe similar to that in species of *Kalloclymenia*. Otherwise the suture is significantly less derived in other lobes are shallow and round. This suggests that the lineage of *F. wocklumensis* is rooted deep in the branch of the Gonioclymeniidae being possibly transitional between *Costaclymenia* and *Kalloclymenia*. Future findings in strata older than the type horizon are predicted.

Finiclymenia wocklumensis (Lange, 1929)
(Figs 199 and 218)

Type horizon and locality: *P. paradoxa* Zone, Burg near Balve, Rhenish Slate Mountains (Price and Korn 1989)

Material. — One specimen.

Remarks. — The conch from Jabłonna is only partially exposed on a hard limestone block, but sections across ventrolateral spines (or tubercles) are visible in juvenile part up to about 10 mm diameter. At later stages the conch is virtually smooth, although in the probably conspecific specimen from Kowala described by Czarnocki (1989) numerous transverse riblets are developed near the venter. Suture is unexpectedly underived, which may suggest that the conch morphology is also primitive for the lineage, despite its stratigraphic location. The only other species of similar morphology are the more evolute *K. kozhimensis* Bogoslovsky *et* Kuzina, 1980 from the polar Urals (Bogoslovsky and Kuzina 1980; Bogoslovsky 1981) and K glabra Bogoslovsky, 1981 from the northern Urals.

Distribution. — The *P. jugosus* Zone at Jabłonna (bed 33) and Kowala (Czarnocki 1989).

Genus ***Kalloclymenia*** Wedekind, 1914

Type species: *Goniatites subarmatus* Münster, 1832 from Schübelhammer near Heinersreuth in Frankenwald (Price and Korn 1989).

Diagnosis. — Ventrolateral spines restricted to juvenile stages, convex venter of the conch.

Remarks. — The species of the genus differ mostly in the course of their ontogeny, with juvenile parabolic nodes or spines being replaced with ribs or ventrolateral tubercles and finally the whorls smoothen reaching maturity. Too little is known about their population variability to be sure of taxonomic identifications proposed below.

Kalloclymenia subarmata (Münster, 1832)
(Figs 200F, G and 218)

Type horizon and locality: Schübelhammer near Heinersreuth in Frankenwald (Price and Korn 1989).

Material. — Two specimens.

Diagnosis. — Somewhat compressed subquadrate whorls; laterally oriented parabolic nodes change into thick ribs terminating with robust ventrolateral tubercles at about 50 mm diameter.

Remarks. — Massive spines are preserved on inner whorls of specimen ZPAL Am VII/1075 from Dzikowiec. Immature, somewhat deformed specimen MB.C. 5462 from the same locality is about 20 cm in diameter.

Distribution. — The *P. jugosus* Zone at Dzikowiec and Ostrówka.

Kalloclymenia uhligi (Frech, 1902)
(Figs 200D and 218)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

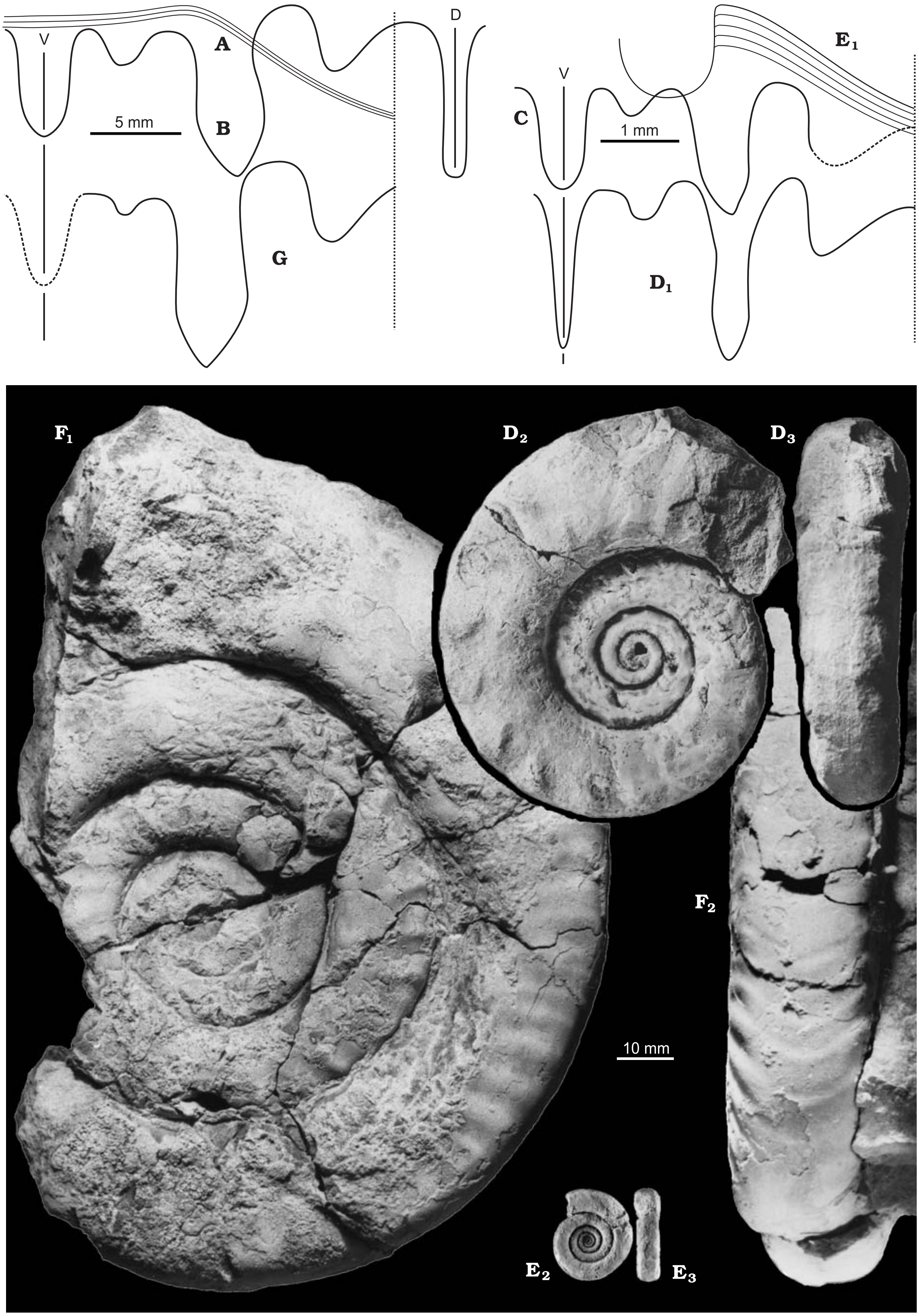
Material. — One specimen.

Diagnosis. — Lateraly oriented parabolic spines continue to at least 60 mm diameter; robust conch with high whorl expansion rate.

Remarks. — Korn and Price (1989, fig. 5f, g) gave wrong magnification of the lectotype picture, and this obliterated the difference in respect to *K. subarmata*. Whether this difference reflects only the population variability or species distinction remains to be determined.

Distribution. — Probably the late *P. jugosus* Zone at Dzikowiec.

Fig. 200. Underived species of *Kalloclymenia* from the *P. jugosus* Zone. **A**–**C**. *K. biimpressa* (von Buch, 1839); growth lines of subadult specimen ZPAL AmVII/224 (A); suture of IG 284.II.917 (B, for septum see Fig. 201A), ZPAL AmVII/223 (C, for views see Fig. 201E), and 1075 (D, for views see Fig. 201B) from Dzikowiec in the Sudetes. **D**. *Kalloclymenia uhligi* (Frech, 1902) from the late *P. jugosus* or *D. trigonica* Zone at Dzikowiec in the Sudetes; suture (from Price and Korn 1989) and views of the lectotype MB.C. 550. **E**. Undetermined juvenile of *Kalloclymenia* from Kowala in the Holy Cross Mountains (possibly the *D. trigonica* Zone); growth lines with parabolic node and views of specimen IG.284.II.851. **F**. *K. subarmata* (Münster, 1832); views of mature MD 16649 (5327) from Gałęzice in the Holy Cross Mountains (F, probably Ostrówka; collected by Jan Czarnocki) and suture of ZPAL Am VII/1075 from Dzikowiec (G). →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E2
10 mm
F1
F2
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Kalloclymenia biimpressa (von Buch, 1839)
(Figs 200A–C, 201, and 218)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

Material. — Six specimens.

Diagnosis. — Somewhat depressed subquadrate whorls, ribs parallel to aperture with ventrolateral tubercles disappearing gradually from about 50 mm diameter, laterally oriented parabolic nodes at juvenile stages.

Remarks. — The species differs from *K. subarmata* in somewhat more densely distributed and less massive ribs and wider whorl cross section. Probably it is more advanced. Parabolic nodes or massive spines are preserved on inner whorls of specimen ZPAL Am VII/224 from Dzikowiec and in ZPAL Am VII/1075.

Distribution. — The early *P. jugosus* Zone at Dzikowiec (sample Dz-9).

Kalloclymenia pessoides (von Buch, 1839)
(Figs 202A–E and 218)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

Material. — Eight specimens.

Diagnosis. — Compressed subquadrate whorls with smooth flanks; ribbing disappears at about 30 mm diameter.

Remarks. — The species is unique among those of *Kalloclymenia* in its virtually smooth adult conch. The parabolic nodes at juvenile stages disclose the close affinity to *K. subarmata*.

Distribution. — The *P. jugosus* Zone at Dzikowiec.

Kalloclymenia frechi (Lange, 1929)
(Figs 202F–H and 218)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

Material. — Two specimens.

Diagnosis. — Compressed subquadrate whorls with smooth flanks, ventrolaterally oriented spines disappearing at about 20 mm diameter.

Remarks. — In the conch form the species is closely similar to *K. pessoides* but prominent spines impressed in the umbonal wall of the successive whorls make it similar rather to *Sphenoclymenia*.

Distribution. — The early *P. jugosus* Zone at Dzikowiec.

Genus ***Gonioclymenia*** Hyatt, 1884

Type species: *Goniatites speciosus* Münster, 1831 from Schübelhammer near Heinersreuth in Frankenwald (Price and Korn 1989).

Diagnosis. — V-shaped lateral, umbonal, and subventral lobes of the suture, more or less concave venter with high trapezoidal whorls of the conch with smooth flanks.

Gonioclymenia speciosa (Münster, 1832)
(Figs 203 and 218)

Type horizon and locality: Schübelhammer near Heinersreuth in Frankenwald (Price and Korn 1989).

Material. — Four specimens.

Remarks. — These were probably the largest Famennian ammonoids as shown by an unlabeled IG exhibition specimens collected by Jan Czarnocki at Ostrówka, which is more than 30 cm in diameter.

Distribution. — The *P. jugosus* Zone at Kowala and Ostrówka (sample Ost-185).

Genus ***Sphenoclymenia*** Schindewolf, 1920

Type species: *Goniatites maximus* Münster, 1832 from Schübelhammer near Heinersreuth in Frankenwald (Price and Korn 1989).

← Fig. 201. *K. biimpressa* (von Buch, 1839) from the *P. jugosus* Zone at Dzikowiec in the Sudetes; septum of IG 284.II.917 (A, for suture see Fig. 200B); views of ZPAL AmVII/ 1075 (B, for suture see Fig. 200D); views of ZPAL AmVII/224 (C), Uwr 1768 (D), ZPAL AmVII/223 (E, for suture see Fig 200C), Uwr 1768 (F), and MB.C. 3216 (G).

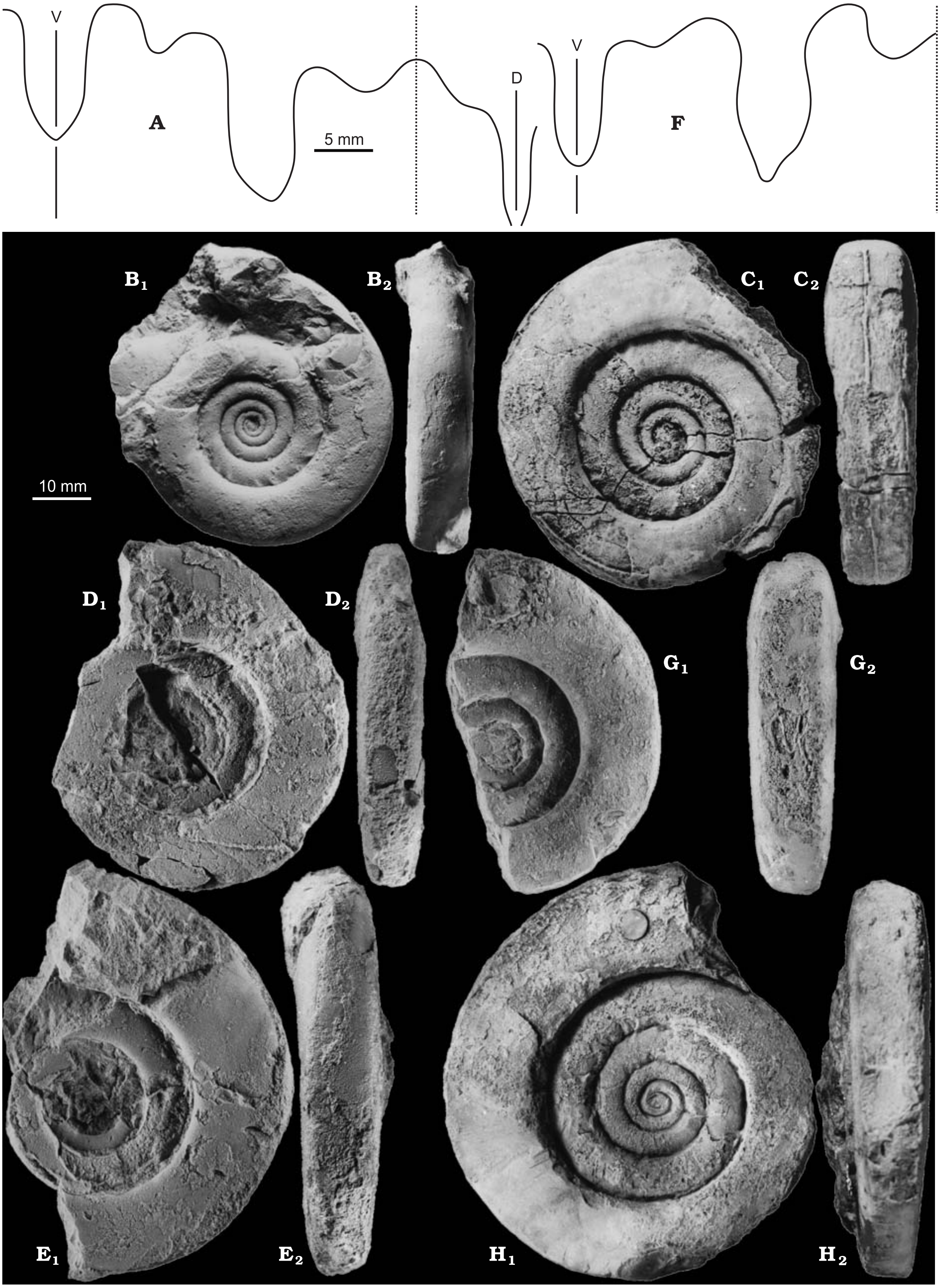


Fig. 202. Species of *Kalloclymenia* with tabulate venter from the *P. jugosus* Zone. **A**–**E**. *K. pessoides* (von Buch, 1839) from Kowala in the Holy Cross Mountains (A) and Dzikowiec in the Sudetes (B–E); suture of ZPAL AmVII/225 (A); views of UWR 2122s (B), MB.C. 4016 (C), ZPAL AmVII/1027, and 1584 (D, E). **F**–**H**. *K. frechi* (Lange, 1929) from Kowala (F, G) and Dzikowiec (H); suture of specimen IG.284.II.914 (F); views of 853 (G) and the holotype MB.C. 4029 (H).

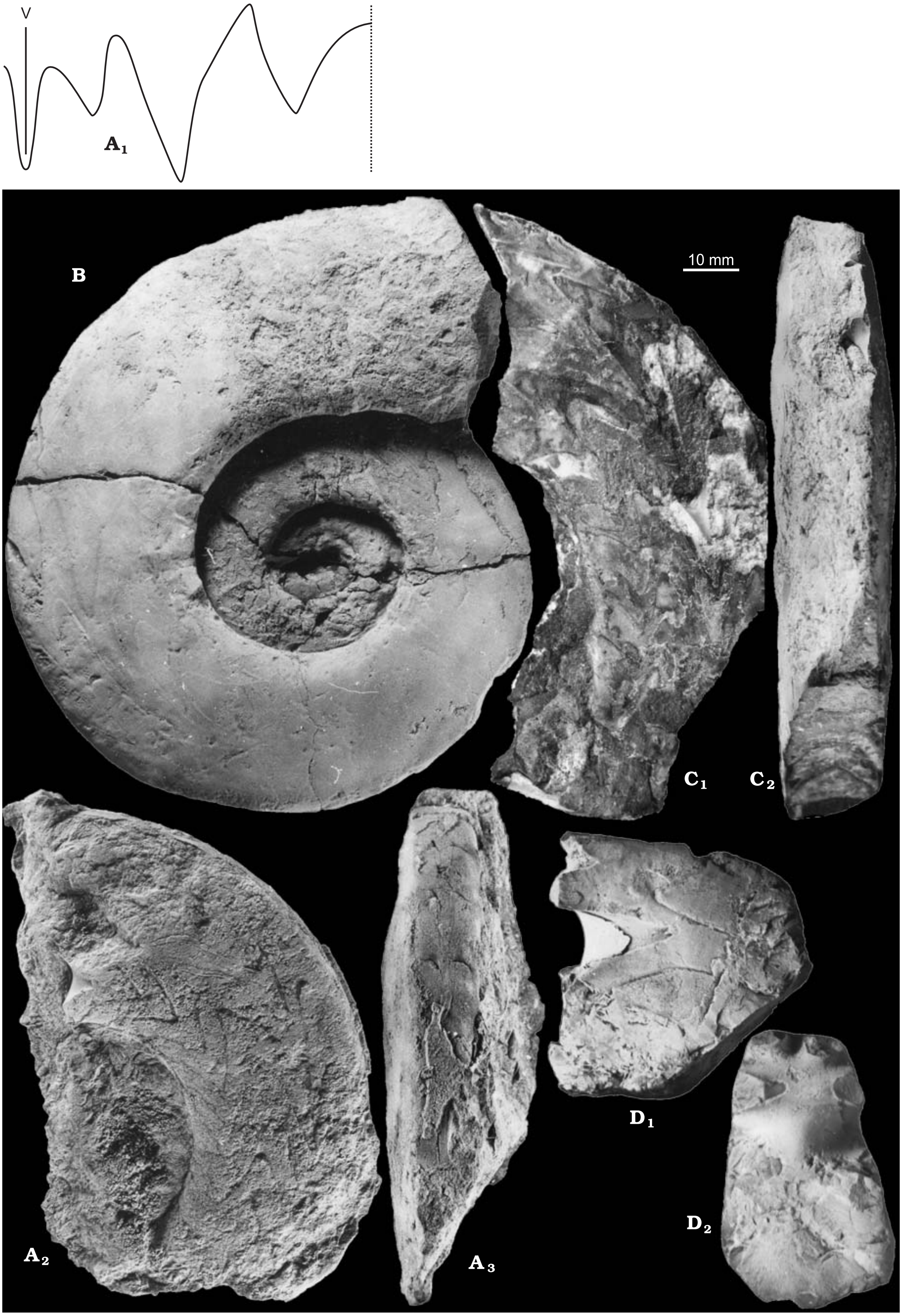


Fig. 203. *Gonioclymenia speciosa* (Münster, 1832) from the *P. jugosus* Zone at Ostrówka ina the Holy Cross Mountains (A) and Dzikowiec in the Sudetes (B–D); suture and views of ZPAL AmVII/185 (A); views of Uwr 1765 (B) and MB.C. 4021 (C, D).

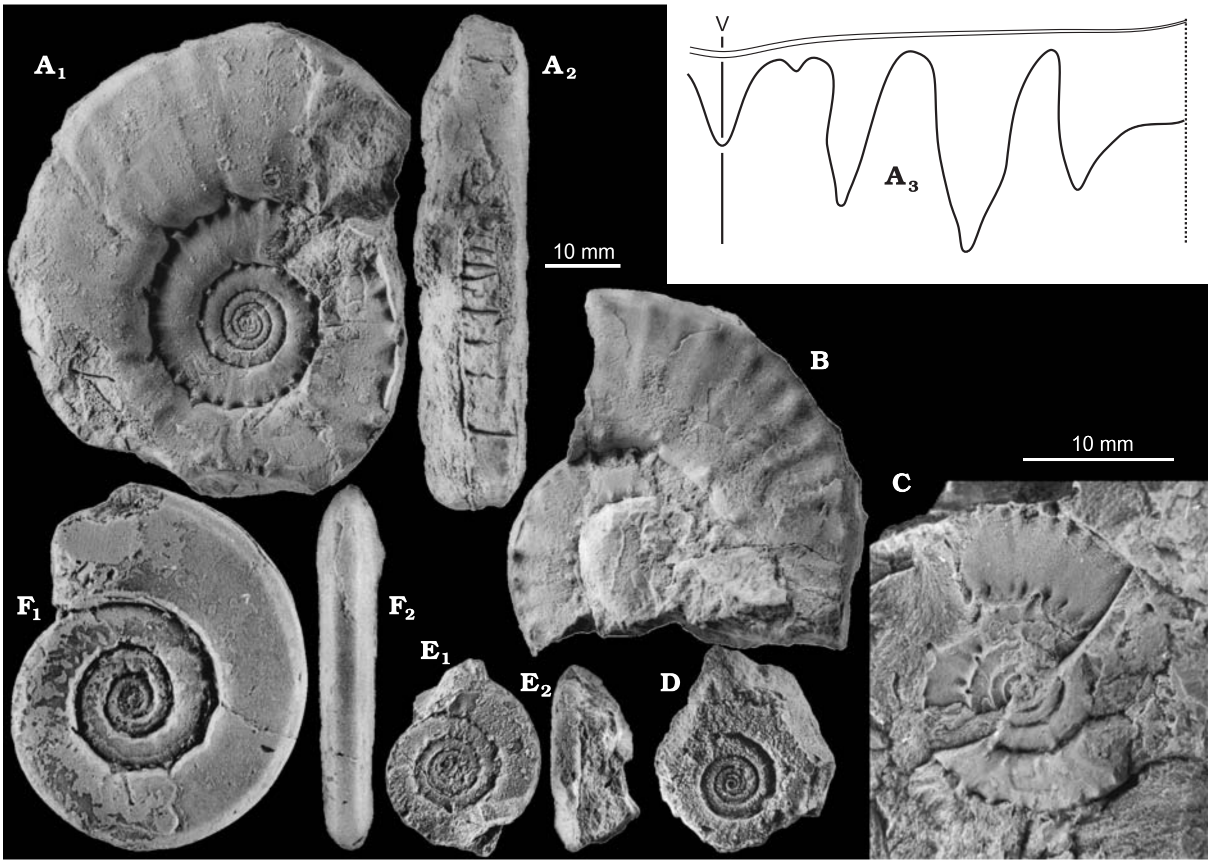


Fig. 204. Species of *Sphenoclymenia* from the *P. jugosus* Zone. **A**. *S. erinacea* Price *et* Korn, 1989 from Kowala in the Holy Cross Mountains; views and suture of specimen IG.284.II.772. **B**–**E**. *S. brevispina* (Lange, 1929) from Dzikowiec in the Sudetes; views of specimen ZPAL AmVII/194 (B), MB.C. 916 (C, also Frech 1902, pl. 2: 3a and Price and Korn 1989, fig. 5c, i, p), ZPAL AmVII/415, and 1581 (D, E). **F**. *S. plana* Bogoslovsky, 1981 from beds with *Gonioclymenia* between Besówka and Stokówka in the Holy Cross Mountains; views of specimen IG.284.II.381.

Diagnosis. — Two subventral lobes of the suture; compressed conch with ventrolaterally oriented spines at juvenile stages.

Remarks. — The suture of *Sphenoclymenia* is even more advanced in its subdivision than that in *Gonioclymenia*. On this basis Korn (1992) proposed to separate the genus in his family Sphenoclymeniidae.

Sphenoclymenia erinacea Price *et* Korn, 1989
(Figs 204A and 218)

Type horizon and locality: Base of bed 0 at Dasberg, Rhenish Slate Mountains (Price and Korn 1989).

Material. — One specimen.

Diagnosis. — The second subventral lobe incipient, at the tip of subventral saddle; spines dissappear at diameter about 20 mm, venter of mature specimens rounded.

Distribution. — Red limestone of the *D. trigonica* Zone at Kowala.

Sphenoclymenia brevispina (Lange, 1929)
(Figs 204B–E and 218)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

Material. — Four specimens.

Diagnosis. — The second subventral lobe deep and narrow; umbonal and ventrolateral tubercles occur up to late ontogenetic stages.

Remarks. — Suture has been traced by Korn and Price (1989) in a specimen from the Rhenish Slate Mountains.

Distribution. — Probably the *D. trigonica* Zone at Dzikowiec.

Sphenoclymenia plana Bogoslovsky, 1981
(Figs 204F and 218)

Type horizon and locality: Kia formation on the Kia River in the southern Urals (Bogoslovsly 1981)

Material. — One specimen.

Diagnosis. — Smooth conch with shallow ventrolateral furrows and spines disappering at diameter of about 20 mm.

Distribution. — Red limestone of the *Gonioclymenia* beds between Besówka and Stokówka in the Holy Cross Mountains, as labeled by Jan Czarnocki.

Family **Biloclymeniidae** Hyatt, 1884

Diagnosis. — Gently sinuous suture complicating ventrally in the course of evolution. Tendency to develop wide siphuncle and long septal necks reaching the preceding septum.

Remarks. — It is suggested here that families of the Devonian ammonoids represent clades in which gradual complication of septum geometry proceeds from the beginning of their emergence. In the case of the *Biloclymenia* clade, its evolution started from development of a wide ventral lobe. Therefore Pachyclymeniidae Korn, 1992 are included in the family. Both genera share also the higly unusual structure of siphuncle (Bogoslovsky 1981, p. 16, 17), analogous to that in *Aturia*.

Genus ***Pachyclymenia*** Schindewolf, 1937

Type species: *Pachyclymenia abeli* Schindewolf, 1937.

Diagnosis. — Moderately involute conch with rounded venter; suture with relatively narrow, rounded flank lobe and wide ventral lobe.

Remarks. — Despite some complication, the septum geometry was probably inherited by *Pachyclymenia* after the earliest *Protornoceras*-like clymenias. *P. kozlowskii*, with its internal shell constrictions and discoidal conch seems to be close to the ancestral condition.

Pachyclymenia kozlowskii (Czarnocki, 1989)
(Figs 205A and 218)

Type horizon and locality: Bed 16 of red limestone with *Costaclymenia* at Jabłonna, Holy Cross Mountains (Czarnocki 1989).

Diagnosis. — Moderately evolute conch with internal shell thickenings parallel to the aperture.

Remarks. — In the original description of the species the drawing of suture was reversed and this was probably the main basis to erect the genus *Borkowia* and compare it with *Kiaclymenia*. The morphologically closest species of *Pachyclymenia* seems to be *P. intermedia* Bogoslovsky, 1977 (Bogoslovsky 1977, 1981) which differs in a somewhat more involute conch with oblique internal thickenings. In the distribution of thickenings, *P. kozlowskii* resembles the more involute and discoidal *P. sinuconstricta* Bogoslovsky, 1977 from the *Clymenia–Gonioclymenia* Zone of the southern Urals. It seems that *P. kozlowskii* is the least derived of all species of the genus. Its ancestry is apparently within *Uraloclymenia* from the late *Prolobites–Platyclymenia* Zone of the southern Urals (Bogoslovsky 1977, 1981), which has the umbonal saddle restricted to the umbilicus. In fact this is hardly a generic level distinction.

Distribution. — Probably the early *P. jugosus* Zone at Jabłonna.

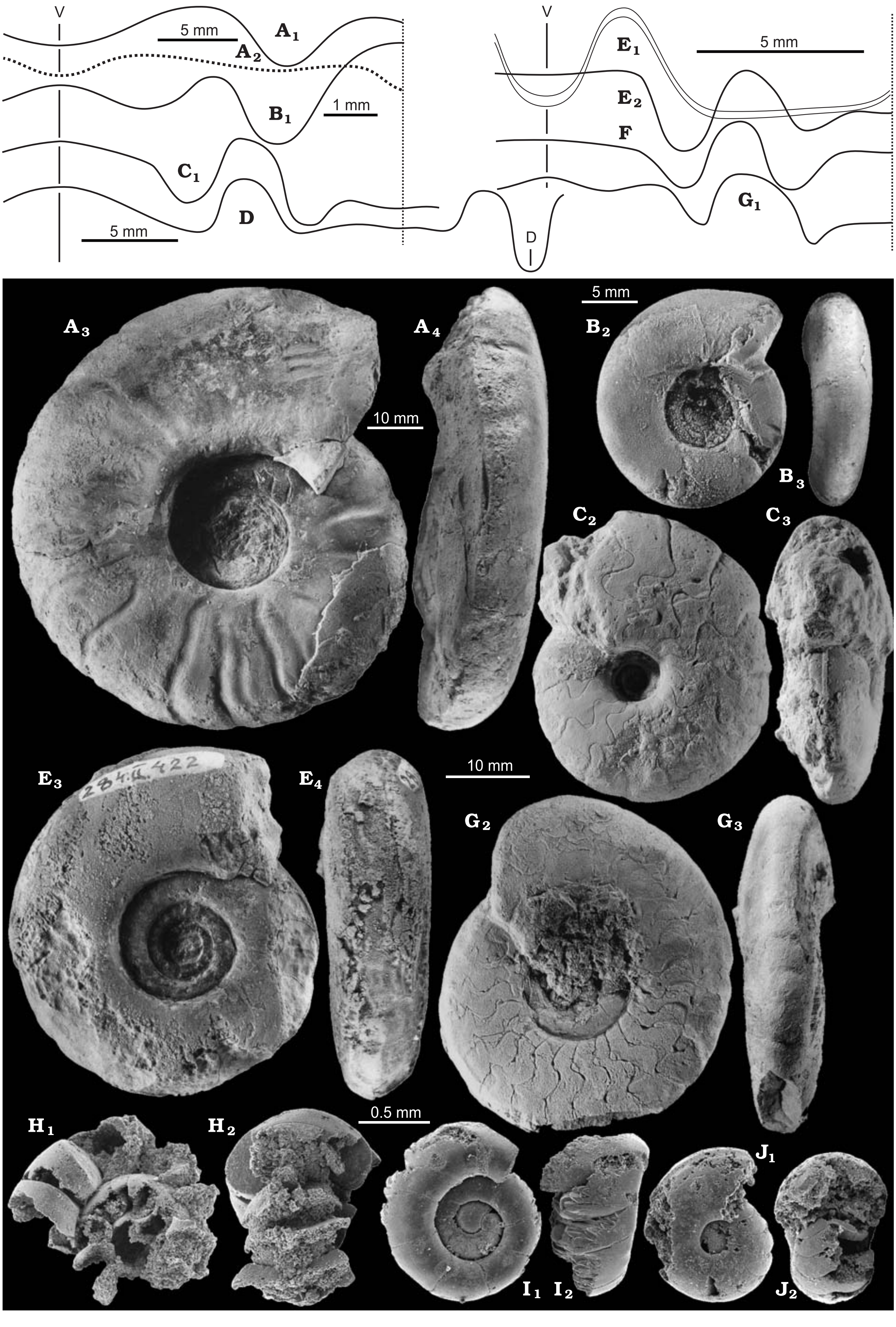
Genus ***Kiaclymenia*** Bogoslovsly, 1955

Type species: *Kiaclymenia uralica* Bogoslovsky, 1955 from the *Clymenia–Gonioclymenia* Zone at Kia, the southern Urals.

Diagnosis. — Suture with two rounded flank lobes on conch flanks and wide ventral saddle; moderately involute conch.

Kiaclymenia polonica (Czarnocki, 1989)
(Figs 205B and 218)

Type horizon and locality: *Prolobites* beds st Ostrówka (bed 5) in the Holy Cross Mountains (Czarnocki 1989).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J2

Diagnosis. — Gently rounded lateral and high umbonal saddles of the suture.

Remarks. — The species was originally referred to *Genuclymenia*, the type species of which has a basically different appearance of the suture and subtrapezoidal whorl section, pointing towards affinity with *Cymaclymenia* rather than *Kiaclymenia polonica*. Whatever is the generic affiliation of this species, it may serve as a good connecting link between *Uraloclymenia* and *Biloclymenia*.

Distribution. — *P. trachytera* Zone at Ostrówka (bed 5 of Czarnocki 1989).

Kiaclymenia laevis (Richter, 1848)
(Figs 205C, D, H, I, J? and 218)

Type horizon and locality: Saalfeld in Thuringia.

Material. — Two specimens.

Diagnosis. — Wide lateral saddle of the suture.

Remarks. — From *K. uralica* the species differs in a less prominent and wider flank lobe and somewhat angulate medially ventral lobe, probably resulting from the shape of the venter (Petter 1960; Bogoslovsky 1981). *Biloclymenia nebulosa* and *B. accessa* of Czarnocki (1989) apparently represent this species.

Distribution. — Grey limestone of the early *P. jugosus* Zone at Kowala; lower *Wocklumeria* beds at Ostrówka, Stokówka, and Besówka (Czarnocki 1989).

Genus ***Biloclymenia*** Schindewolf, 1923

Type species: *Clymenia bilobata* Münster, 1832 from Schübelhammer near Heinersreuth in Frankenwald.

Diagnosis. — Suture with two rounded flank lobes on conch flanks and shallow wide ventral lobe.

Remarks. — Czarnocki's (1989) concept of *Biloclymenia* corresponds rather to *Kiaclymenia* whereas his *Dimeroclymenia* is roughly the same as the former genus.

Biloclymenia pristina (Czarnocki, 1989)
(Figs 205E–G and 218)

Type horizon and locality: Lower *Wocklumeria* beds at Kowala, Holy Cross Mountains (Czarnocki 1989).

Material. — One specimen.

Diagnosis. — Second umbonal lobe of the suture not developed; moderately evolute conch.

Remarks. — The three species of *Dimeroclymenia* based by Czarnocki (1989) on the material from the same horizon at Kowala are probably conspecific.

Distribution. — Red limestone of the *D. trigonica* Zone at Kowala in the Holy Cross Mountains.

Family **Cyrtoclymeniidae** Hyatt, 1884

Diagnosis. — Simple septum in mature conchs lacking any vaulted areas; generalized conch morphology ranging from moderately involute to moderately evolute.

Remarks. — The only difference between *Cyrtoclymenia* and *Platyclymenia* I have been able to disclose is a more evolute conch of the latter. There is a complete gradation between these conch geometries and the conch evoluteness is hardly a character deserving distinction at the family rank. The family Platyclymeniidae Wedekind, 1914 is therefore not used here. It may be also a matter of dispute whether acute venter is enough to define the family Rectoclymeniidae Schindewolf, 1923.

← Fig. 205. Species of the Biloclymeniidae from the Holy Cross Mountains. **A**. *Pachyclymenia kozlowskii* (Czarnocki, 1989) from Jabłonna (probably the early *P. jugosus* Zone, bed 16 of Czarnocki 1989); suture, internal shell thickening and views of holotype IG 284.II.823. **B**. *Kiaclymenia polonica* Czarnocki, 1989 from the *L. styriacus* Zone at Ostrówka; suture and views of holotype IG 284.II.30. **C**, **D**. *Kiaclymenia laevis* (Richter, 1848) from the early *P. jugosus* Zone at Kowala; suture and views of specimen ZPAL AmVII/1802 (C) and suture of 947 (D). **E**–**G**. *Biloclymenia pristina* (Czarnocki, 1989) from the *D. trigonica* Zone at Kowala; growth lines, suture, and views of specimen IG 284.II.422 (E); suture of IG 284.II.912 (F); suture and views of specimen ZPAL AmVII/1803 (G). **H**, **I**. Juveniles of a species of an evolute biloclymeniid, probably *K. laevis*, from the late *L. styriacus* Zone at Kowala; internal pyritic moulds ZPAL AmVII/1829 and 1828 (sample Ko-187). **J**. Juvenile of a species of an involute biloclymeniid from the same sample; specimen ZPAL AmVII/1831.

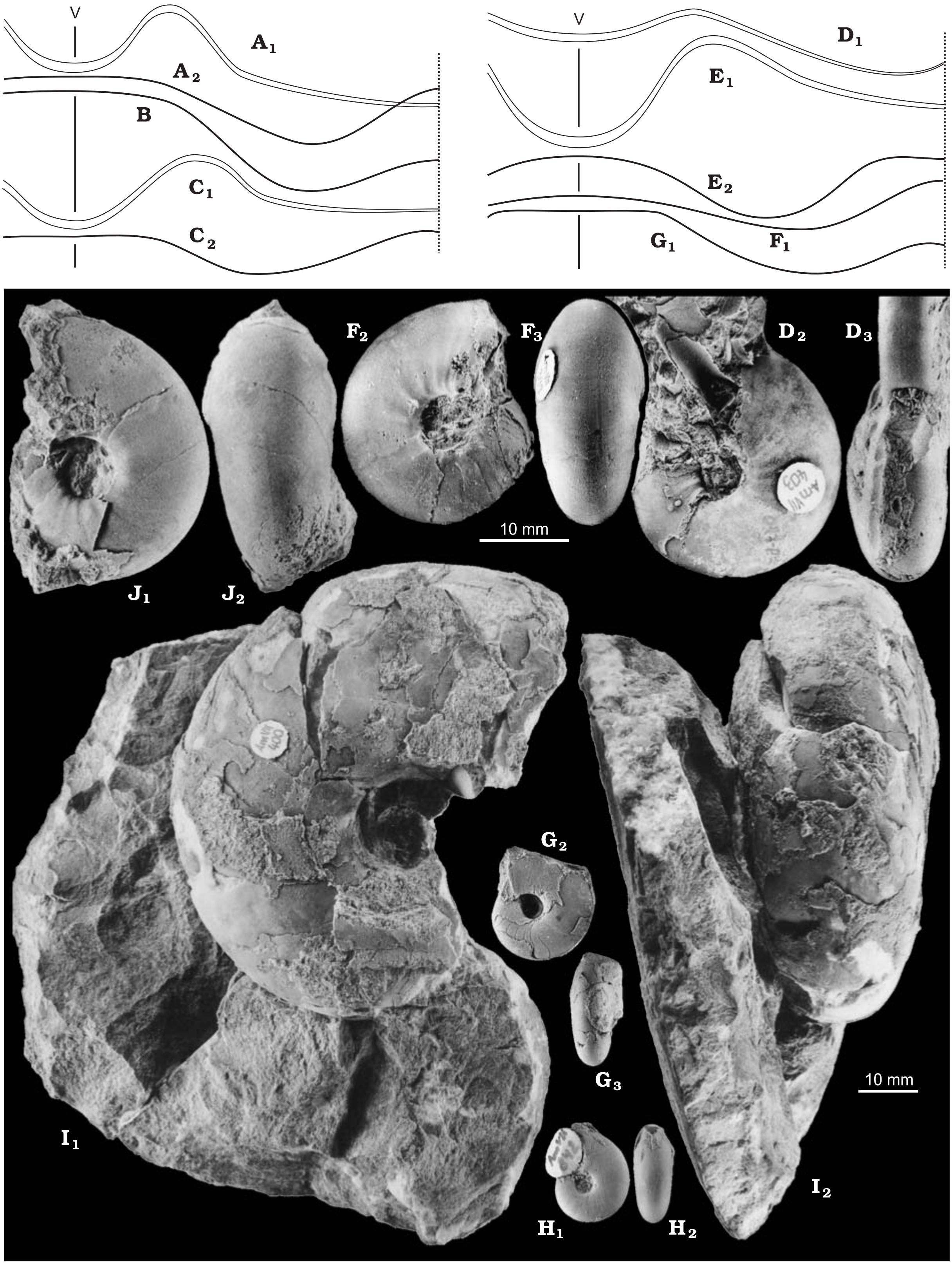

Fig. 206. *Cyrtoclymenia involuta* (Wedekind, 1908) from the Holy Cross Mountains; growth lines and sutures of specimens ZPAL AmVII/692 and 683 from Jabłonna (A, B, trench rIVc of Żakowa *et al*. 1984), and 694 (C, probably Ostrówka); suture and views of ZPAL AmVII/403 from Łagów (D); growth lines and suture of ZPAL AmVII/551 probably from Łagów (E); suture and views of ZPAL AmVII/399 from Łagów (F); suture and views of ZPAL AmVII/122 and 842 from Jabłonna (G, H, bed 24), and 400 (I, bed 27); views of ZPAL AmVII/160 from Ostrówka (J, sample Ost-7).

Genus ***Cyrtoclymenia*** Hyatt, 1884

Type species: *Planulites angustiseptatus* Münster, 1832 from Schübelhammer near Heinersreuth in Frankenwald.

Diagnosis. — Involute conch with small umbilicus and rounded venter.

Cyrtoclymenia involuta (Wedekind, 1908)
(Figs 206 and 223)

Type horizon and locality: Beds 13–10 at Enkeberg, Rhenish Slate Mountains.

Material. — 22 specimens.

Diagnosis. — Umbo covers somewhat more than one fourth of the whorl diameter, almost equal width and height of the whorl.

Remarks. — This is the oldest member of the *Cyrtoclymenia* lineage, *Praeflexiclymenia curvidorsata* being its possible relative. Sobolew's (1914) Gomi-monomeroclymenia *Humboldti subacuta*, known only from Sieklucki's brickpit, may be a connecting link between these species (or/and *C. acuta*).

Wedekind (1908) description refers to specimens showing much difference in the whorl width, exceeding that observed in the Holy Cross Mountains material. More information on the German topotype material is necessary to substantiate preliminary *Cyrtoclymenia* species identifications proposed here. Possibly, my specimens represent *Cyrtoclymenia ventriosa* Petter, 1960.

Distribution. — The *P. trachytera* to *L. styriacus* Zone at Jabłonna (beds 24, 25, 27, trenches rIVc and f dug by Żakowa *et al*. 1984) and Ostrówka (sample Ost-7); black clymeniid limestone at Łagów.

Cyrtoclymenia angustiseptata (Münster, 1832)
(Figs 207 and 223)

Type horizon and locality: Schübelhammer near Heinersreuth in Frankenwald.

Material. — Seven specimens.

Diagnosis. — Umbo covers almost half of the whorl diameter in mature specimens, much less in juveniles, smooth flattened flanks of the conch.

Remarks. — Distinction between this species and *C. plicata* (Münster, 1832) is rather doubtful on purely morphological grounds.

Distribution. — The late *P. jugosus* Zone at Dzikowiec, Ostrówka and Kowala (Czarnocki 1989).

Cyrtoclymenia sp.
(Figs 208A, B, E, F? and 223)

Remarks. — A single specimen in the Czarnocki's collection from a grey crinoidal limestone of his *Nodosoclymenia* beds at Ostrówka is unusual in having a parabolic section of the venter and gently curved septum also in the umbonal area. A similar specimens occur in the significantly younger strata with *Clymenia* at Kowala. Septum so steep dorsally resembles that in *Clymenia* and *Kosmoclymenia* and this may possibly be a vaulting-free member of that branch. In fact, in sample Ko-187 pyritized juvenile specimens occur closely resembling at this stage conchs of *Platyclymenia*, do not known so high in the Kowala section. They may belong to this species or to *Clymenia*.

Distribution. — Probably the early *L. styriacus* and earliest *P. jugosus* zones at Ostrówka and Kowala.

Cyrtoclymenia acuta Czarnocki, 1989
(Figs 208D and 223)

Type horizon and locality: *Prolobites* beds at Ostrówka, Holy Cross Mountains.

Remarks. — As usual in early species of *Cyrtoclymenia*, but unlike the late ones, the suture is sinuos in the umbonal area. In this respect the studied specimen differs from co-occurring *Cyrtoclymenia* sp. but resembles that from the upper *Wocklumeria* beds at Kowala classified by Czarnocki (1989) in *Falciclymenia falcifera* Münster, 1840. Because of its incomplete preservation and unexpectedly high stratigraphic origin I restrain from evaluating the phylogentic meaning of the latter.

The Czarnocki's (1989) name is a junior homonym of *Cyrtoclymenia acuta* Schmidt, 1925 but this species is now classified in the unrelated genus *Rectoclymenia* and too little material is available to make possible new name truly meaningful.

Distribution. — The *P. trachytera* and *L. styriacus* (sample Ost-7) zones, at Ostrówka.

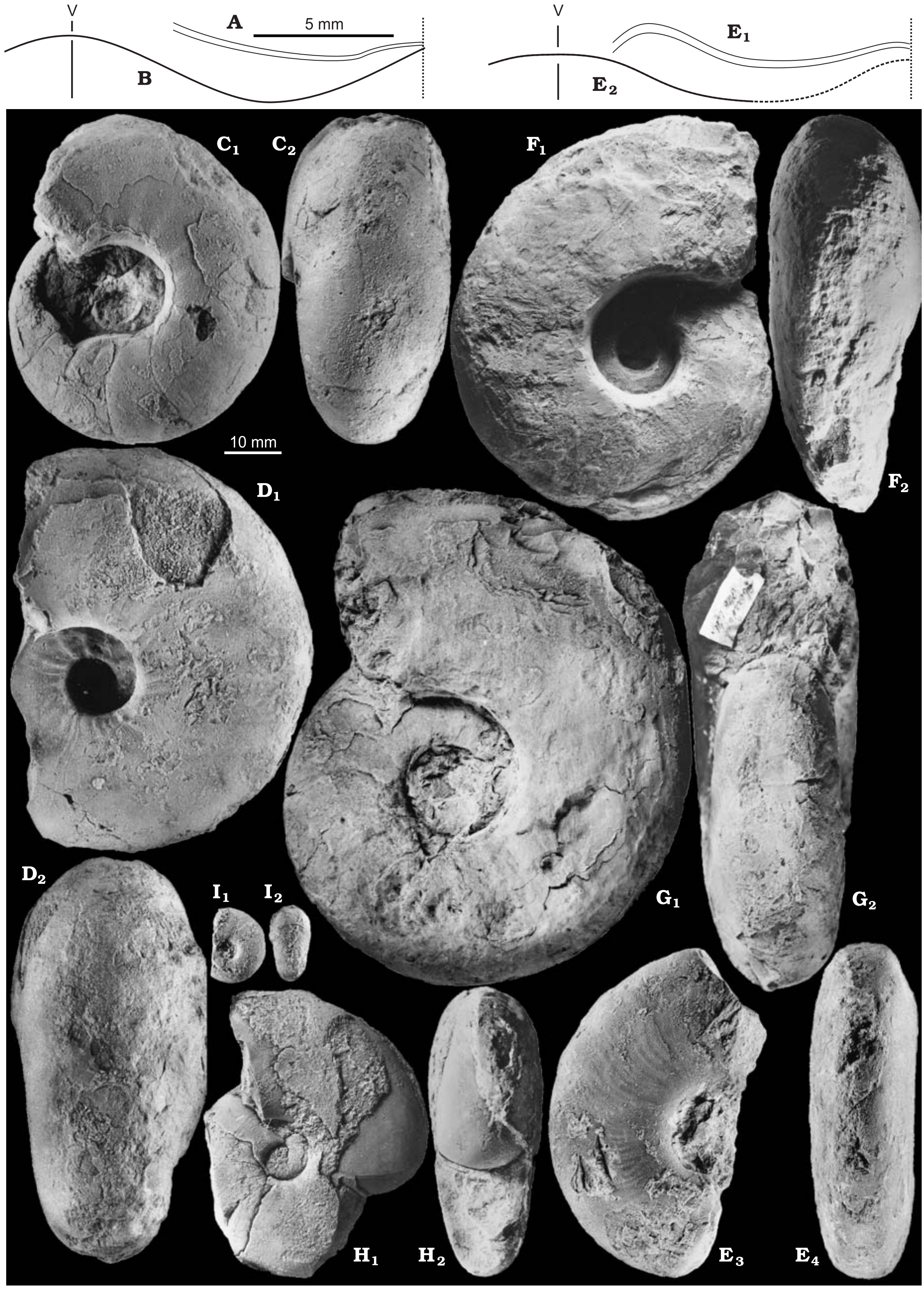

Fig. 207. *Cyrtoclymenia angustiseptata* (Münster, 1832) from the late *P. jugosus* (C) and *D. trigonica* (A, B, D) zones at Kowala (A–D) in the Holy Cross Mountains and Dzikowiec in the Sudetes (E–I); growth lines of specimen IG 284.II.982 (A); suture of 895 (B); views of ZPAL AmVII/1047 (C, sample Ko-86) and IG 284.II.868 (D); growth lines, suture, and views of ZPAL AmVII/152 (E); views of MB.C. 1761, 4209, and 4205 (F–H), and ZPAL AmVII/119 (I).

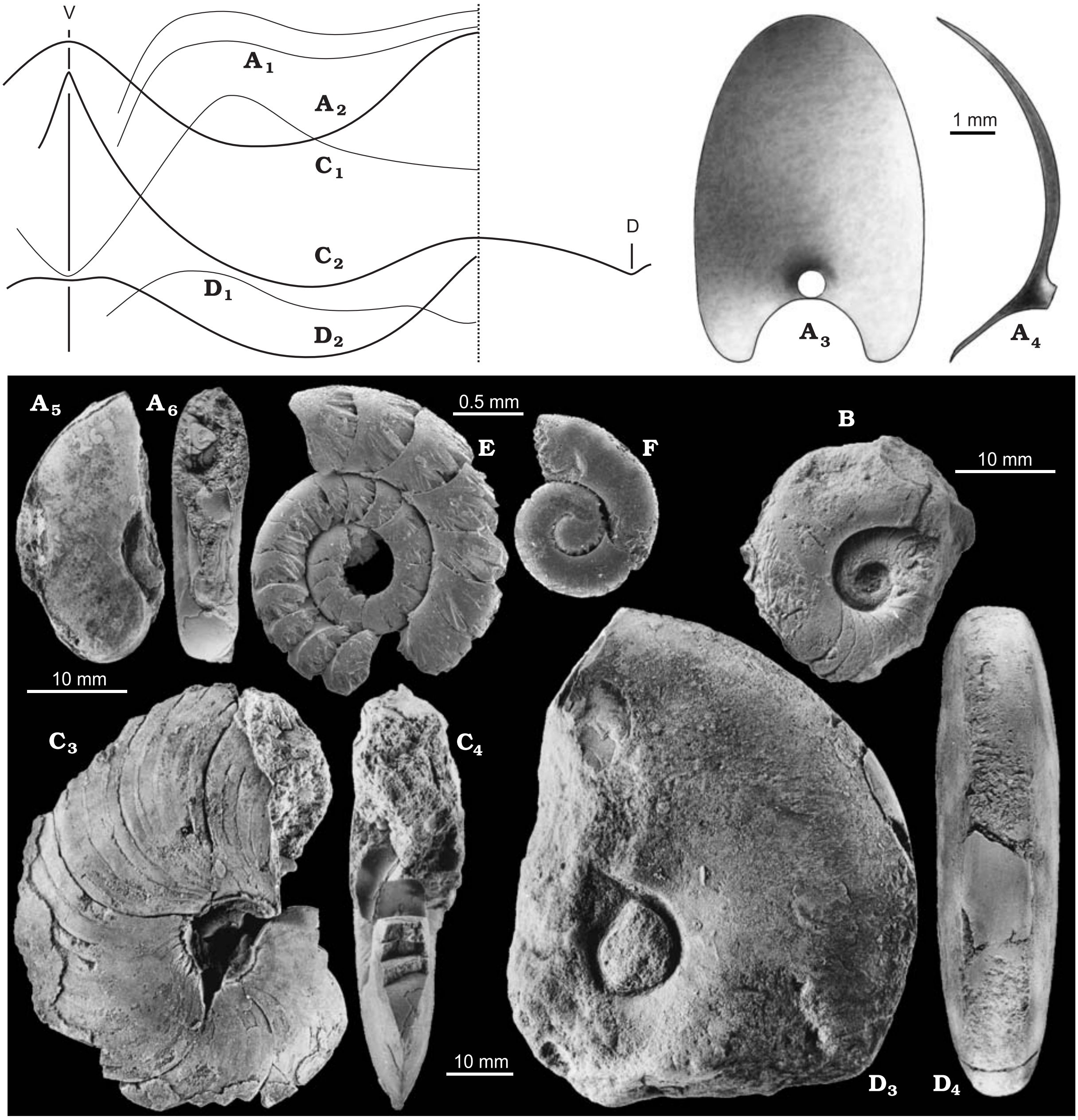

Fig. 208. Aberrant *Cyrtoclymenia* species from the Holy Cross Mountains. **A**, **B**. *Cyrtoclymenia* sp. from the early *P. jugosus* Zone at Ostrówka (A; *Nodosoclymenia* bed) and Kowala (B); growth lines, suture, restored septum, and views of specimen IG.284.II.269 (A); view of ZPAL AmVII/939 (B). **C.** *C. acuta* Czarnocki, 1989 from the *P. styriacus* Zone at Ostrówka; growth lines, suture, and views of specimens ZPAL AmVII/186 (sample Ost-7; *Nodosoclymenia* bed?). **D**. *C.*? *procera* Czarnocki, 1989 from the *P. jugosus* Zone at Kowala; growth lines, suture, and views of specimen IG 284.II.679. **E**, **F**. Juvenile *Cyrtoclymenia* or *Clymenia* from the *L. styriacus* Zone at Kowala; pyritic internal moulds ZPAL AmVII/1830 and 1832 (sample Ko-187).

Cyrtoclymenia? *procera* Czarnocki, 1989
(Figs 208E and 223)

Type horizon and locality: Upper *Wocklumeria* beds at Kowala, Holy Cross Mountains.

Remarks. — This is an enigmatic cephalopod, all specimens being too poorly preserved and fragmentary to be certain that this is actually a clymenia. The tabulate venter and thickening of the umbonal part of the conch resemble the situation in the centroceratid nautiloids (see Dzik 1984).

Distribution. — Probably the *D. trigonica* Zone at Kowala (Czarnocki 1989).

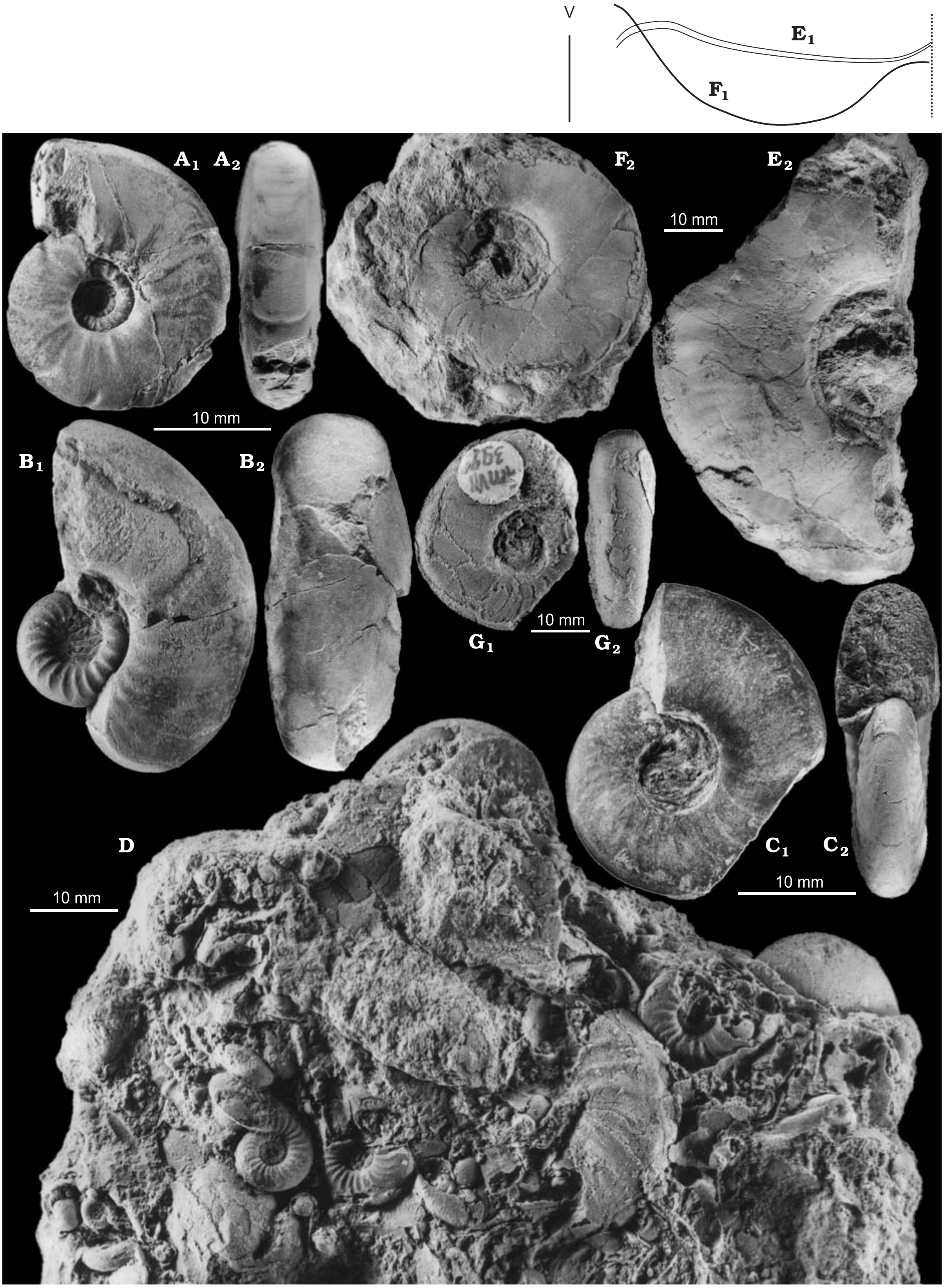

Fig. 209. Early involute *Platyclymenia* species from the *P. trachytera* Zone of the Holy Cross Mountains. **A**–**D**. *P. implana* (Czarnocki, 1989) from Łagów (A) and Ostrówka (B–D); views of specimens IG.284.II.5 (A) and 166 (B; holotype of *P. inflata* Czarnocki, 1989), 184 (C), and a block with mass occurrence of the species ZPAL AmVII/15 (D). **E**–**G**. *P. puschi* (Czarnocki, 1989) from Jabłonna (well w92b of Żakowa *et al*. 1984); growth lines (inferred from irregularities on the conch internal mould) and views of specimens ZPAL AmVII/390 (E); suture and views of 631 (F); views of 399 (G).

Genus ***Platyclymenia*** Hyatt, 1884

Type species: *Goniatites annulatus* Münster, 1832 from Kirch Gattendorf in Upper Franconia (Price and Korn 1989).

Diagnosis. — More or less evolute conchs with roundedly subquadrate whorl section.

Platyclymenia implana (Czarnocki, 1989)
(Figs 209A–D and 223)

Type horizon and locality: Lower part of the *Platyclymenia* beds at Ostrówka, Holy Cross Mountains.

Diagnosis. —Mature whorls significantly higher than wide; umbilicus covering less than one third of the conch diameter; juvenile whorls with sharp ribs on flanks.

Remarks. — Czarnocki (1989) classified this species in *Cyrtoclymenia*, but it is so close to *P. lagowiensis* that it remains uncertain whether it does not fall in the range of its population variability. *Platyclymenia inflata* Czarnocki, 1989 probably also represents this species.

Distribution. — The *P. trachytera* Zone at Łagów and Ostrówka (sample Ost-11).

Platyclymenia puschi (Czarnocki, 1989)
(Figs 209E–G and 223)

Type horizon and locality: *Prolobites* beds at Ostrówka, Holy Cross Mountains.

Material. — Four specimens.

Diagnosis. — Narrow umbilicus covering about one third of mature conch diameter, smooth surface.

Remarks. — As discussed above, Czarnocki (1989) introduced this species in replacement of *Clymenia humboldti* sensu Gürich, 1896 but I believe that his choice of holotype from Ostrówka changed the original meaning of the species and made his *Flexiclymenia puschi* a distinct species. In having a simple septum and relatively wide venter, it resembles some species of *Platyclymenia* and may be considered its earliest member, with some affinities to *Cyrtoclymenia*. Perhaps also the single specimen from the upper *Platyclymenia* beds at Ostrówka, on which *P. laxata* Czarnocki, 1989 is based, belongs also to this species.

Distribution. — The early *P. trachytera* Zone at Jabłonna (well w 92b dug by Żakowa *et al*. 1984) and Ostrówka (Czarnocki 1989).

Platyclymenia lagowiensis (Sobolew, 1912)
(Figs 210 and 223)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains.

Material. — 25 specimens.

Diagnosis. — Mature whorls somewhat higher than wide; umbilicus covering less than half of the conch diameter; juvenile whorls with sharp ribs on flanks.

Remarks. — From *Platyclymenia annulata* (Münster, 1832), the population variability of which was presented by Korn (2002), the Polish species differs in higher, more angular whorls and narrower umbilicus. *Cyrtoclymenia laxata* and *P. intracostata* of Czarnocki (1989) are probably mature specimens of the same species.

Distribution. — The *P. trachytera* Zone at Łagów (samples Ł-10, 13, and Mak-2), Jabłonna (beds 23 and 24), and Ostrówka (sample Ost-11).

Genus ***Nodosoclymenia*** Czarnocki, 1989

Type species: *N. distincta* Czarnocki, 1989 from Ostrówka, Holy Cross Mountains.

Diagnosis. — Subrectangular whorls tending to develop strong ribs and ventrolateral tubercles.

Nodosoclymenia distincta Czarnocki, 1989
(Figs 211 and 223)

Type horizon and locality: Lower part of the *Clymenia* beds (*Nodosoclymenia* bed) at Ostrówka, Holy Cross Mountains.

Remarks. — The material assembled by Czarnocki and split into several species of his genus *Nodosoclymenia* comes from a single bed (except for *N. variabilis* from a layer probably immediately above). It is interpreted here as representing a single very variable species. The conch surface ranges from virtually smooth to bearing irregularly distributed and variably expressed lateral ribs. In some specimens the ribs terminate

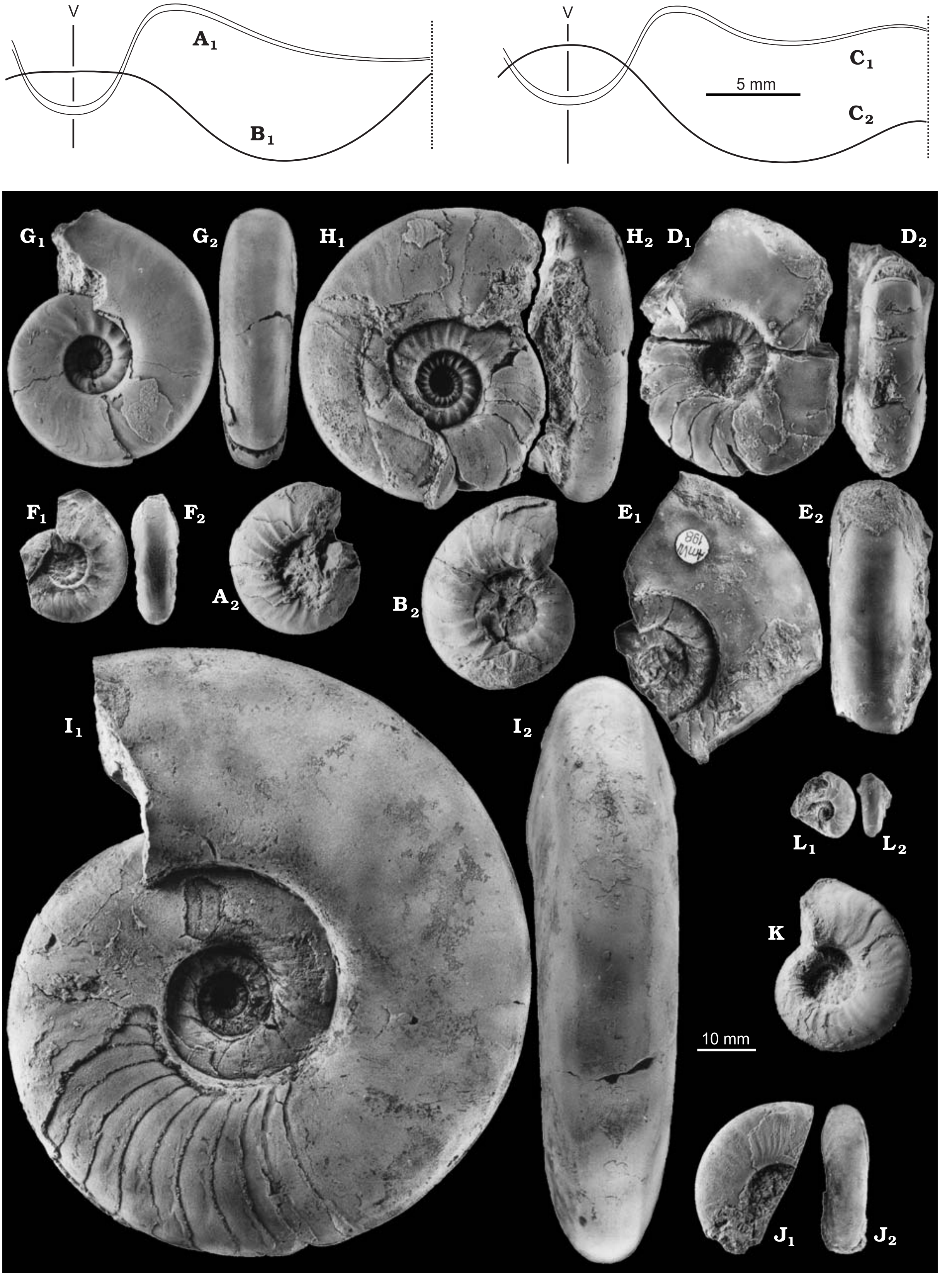

Fig. 210. *Platyclymenia lagowiensis* (Sobolew, 1912) from the *P. trachytera* Zone at Łagów (A–F), Ostrówka (G–J), and Jabłonna (K, L) in the Holy Cross Mountains; growth lines and view of specimen ZPAL AmVII/710 (A); suture and view of 715 (B); growth lines and suture of ZPAL AmVII/753 (C, sample Ł-10); views of ZPAL AmVII/196, 188, and 195 (D–F), IG.284.II.114, 62, 139 (G–I, black matrix), 134 (J, grey matrix), and ZPAL AmVII/709 and 116 (K, L, bed 24).

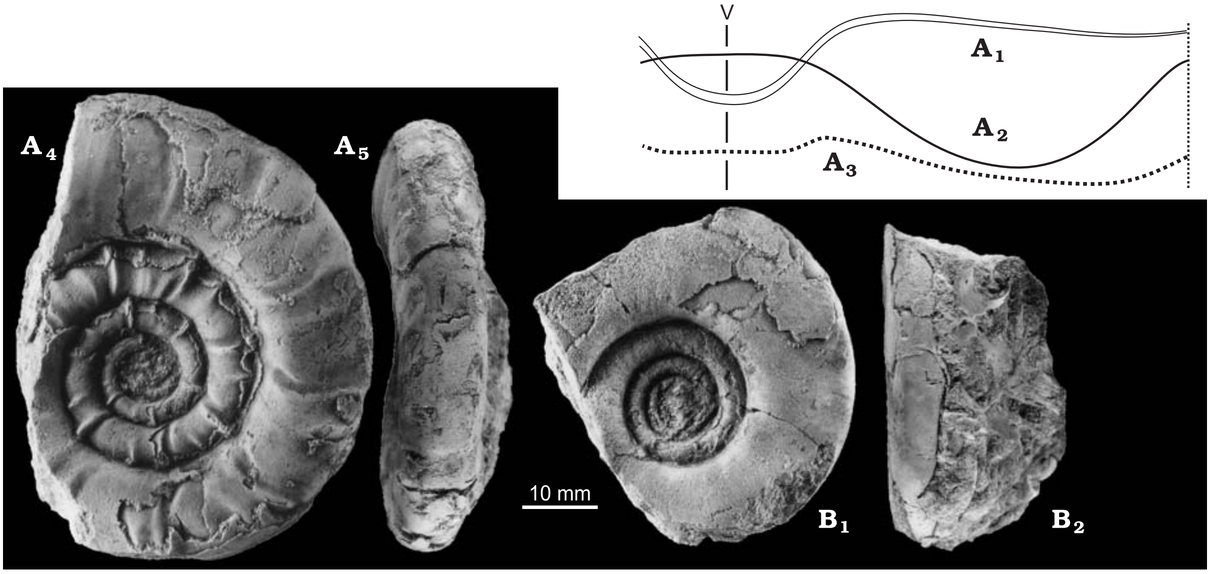

Fig. 211. *Nodosoclymenia distincta* (Czarnocki, 1989) from the *P. trachytera* (or early *L. styriacus*) Zone at Ostrówka in the Holy Cross Mountains (*Nodosoclymenia* bed of Czarnocki 1989); growth lines, suture, ribs and constrictions, and view of holotype IG.284.II.250 (A) and extreme, smooth morphotype specimen 724 (B, holotype of *Stenoclymenia elliptica* Czarnocki, 1989).

ventrally in prominent tubercles, in others flanks are almost smooth but ventrolateral tubercles of almost spinose appearance emerge. Although the variability is remarkable, it only slightly exceeds that presented by Korn (2002) for a population of *Platyclymenia annulata* (Münster, 1832) taken from a single bed at Kattensiepen. Almost smooth specimen were probably arbitrarily separated by him in *P. subnautilina* (Sandberger, 1855) to keep variability in reasonable limits.

Stenoclymenia elliptica Czarnocki, 1989 is based on a single specimen from grey crinoidal limestone of unknown stratigraphic provenace but not different from the *Nodosoclymenia* bed. It shows low massive ribs on the external whorl and fits in the population variablity of *N. distincta*. Juvenile specimen of *Nodosoclymenia* has been identified by Korn (2004b) who also pointed out synonymy of Czarnocki's (1989) *N. lupata* and *M. distincta*.

Distribution. — Probably early *L. styriacus* Zone at Ostrówka.

Genus ***Pleuroclymenia*** Schindewolf, 1934

Type species: *Platyclymenia crassissima* Schindewolf, 1955 (= *Cycloclymenia costata* Lange, 1929) from Beul in the Rhenish slate Mountains (Korn 2002).

Diagnosis. — Widely oval cross section of the conch whorls ornamented with periumbonal ribs at early stages of ontogeny.

Remarks. — Czarnocki (1989) introduced new genus *Gyroclymenia*, believing that its species are ancestral Hexaclymeniidae, being just homeomorphic to those of *Pleuroclymenia*. Becker (2000) proposed *Pleuroclymenia* to be ancestral to the lineage leading to the wocklumeriids.

Pleuroclymenia costata (Lange, 1929)
(Figs 212A–D and 223)

Type horizon and locality: *Platyclymenia annulata* Zone at Beul near Balve, Rhenish Slate Mountains (Korn 2002).

Material. — Three specimens.

Diagnosis. — Umbilicus covering about half of the conch diameter.

Remarks. — I believe that *Gyroclymenia cyclocostata* Czarnocki, 1989, the type species of *Gyroclymenia*, belongs to this species. Czarnocki's (1989) *G. angulata* and *G. evoluta* may fall in the range of its variability.

Distribution. — The *P. trachytera* Zone at Łagów Dule (sample Ł-13), Jabłonna (bed 20), and *Prolobites* beds at Ostrówka (beds 1–2 of Czarnocki 1989).

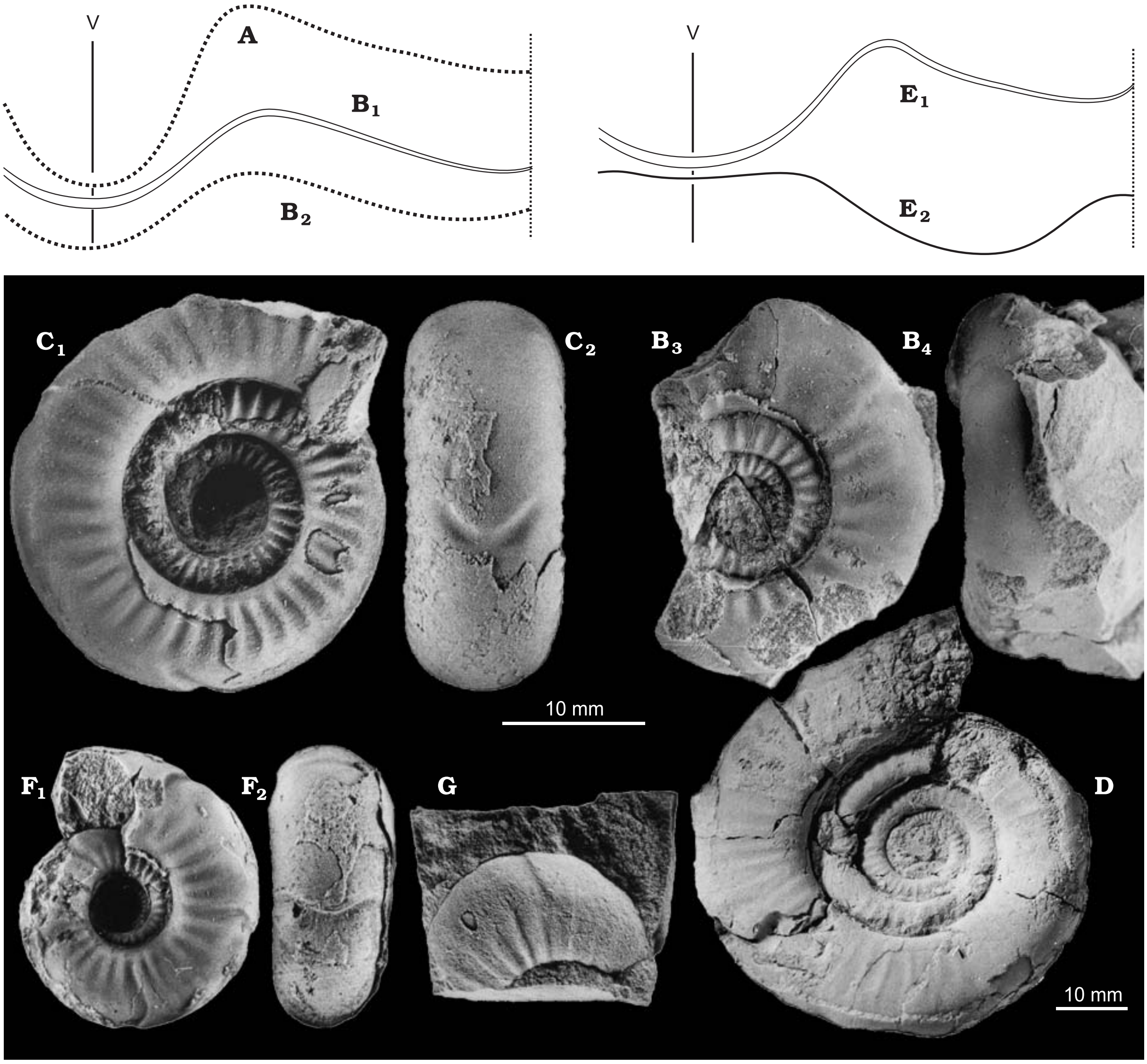

Fig. 212. Species of *Pleuroclymenia* from the Holy Cross Mountains. **A**–**D**. *P. costata* (Lange, 1929) from the *P. trachytera* Zone at Jabłonna (A), Łagów (B), and Ostrówka (B–D); internal thickening of specimen ZPAL AmVII/706 (A, bed 20); growth lines, internal thickening, and views of specimen 716 (B, sample Ł-13); views of IG.284.II.120 (C, bed 1? of Czarnocki 1989) and unnambered MD (D). **E**–**G**. *P. varicata* (Sobolew, 1914) from the early *L. styriacus* Zone ta Ostrówka (E, F) and Kowala (G); growth lines and suture of specimen ZPAL AmVII/754 (E); views of IG.284.II.188 (F, holotype of *Gyroclymenia mutabilis* Czarnocki, 1989), and ZPAL AmVII/372 (G).

Pleuroclymenia varicata (Sobolew, 1914)
(Figs 212E–G and 223)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — One specimen.

Diagnosis. — Umbilicus covering about one third of the conch diameter.

Remarks. — The species is close to *P. costata* but seems to represent the next stage of its evolution towards more and more involute conchs. Czarnocki's (1989) *Gyroclymenia mutabilis* and *G. rotundata* seem to represent the same species, and the type of *G. sophiae* apparently is mature.

Distribution. — The early *L. styriacus* Zone, lower *Clymenia* beds (*Nodosoclymenia* bed) at Ostrówka (bed 8 of Czarnocki 1989), reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains (Sobolew 1914).

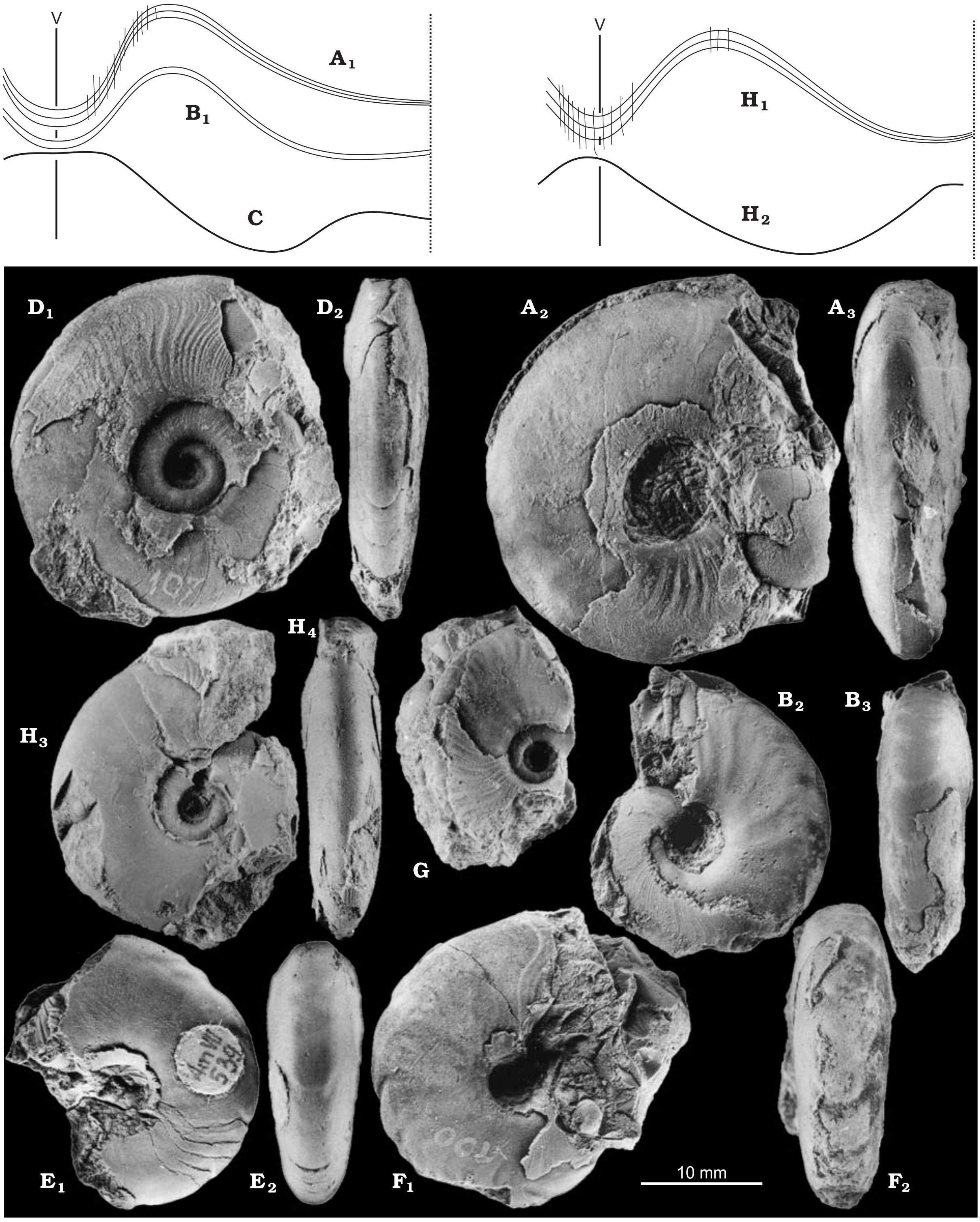

Fig. 213. *Praeflexiclymenia curvidorsata* (Sobolew, 1912) from the *P. trachytera* Zone at Łagów (A–G) and Jabłonna (H) in the Holy Cross Mountains; growth lines and views of specimens ZPAL AmVII/704 and 711 (A, B); suture of ZPAL AmVII/359 (C); views of IG.284.II.107 (D), ZPAL AmVII/539 (E), IG.284.II.100 (F), and ZPAL AmVII/705 (G); growth lines, suture and views of ZPAL AmVII/703 (H, bed 24).

Family **Hexaclymeniidae** Lange, 1929

Diagnosis. — Extremely evolute conch with tabulate venter; simple septum in mature conchs lacking any vaulted areas.

Remarks. — These are clymenias of simplified morphology, thus difficult to diagnose with any newly acquired character (synapomorphy). Despite still incomplete fossil record of their evolution, they seem to represent a rather well-defined clade changing the conch morphology towards being more and more evolute. At least in the lineage of *Soliclymenia*, some amount of paedomorphism is involved, with diminished size of mature conchs and depressed whorl cross section.

Genus ***Praeflexiclymenia*** Czarnocki, 1989

Type species: *Clymenia tenuis* Sobolew, 1912 from the clymeniid limestone at Łagów-Dule, Holy Cross Mountains.

Diagnosis. — Narrow tabulate venter of moderately evolute conch.

Remarks. — The type species of the genus is actually located at the extremity of the morphologic diversity of species included in it, probably related to *Stenoclymenia*. Unfortunately, there seems to be no other generic name available to encompass these early clymenias. *Hexaclymenia* Schindewolf, 1923, with widened whorl cross section but still relatively narrow tabulate venter seems to be a derivative of *Praeflexiclymenia*. Its origin from *Pleuroclymenia*, advocated by Becker (2000, p. 50), is a possible alternative.

Praeflexiclymenia curvidorsata (Sobolew, 1912)
(Figs 213 and 223)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains.

Material. — 23 specimens.

Diagnosis. — Relatively involute conch, frequently developing numerous internal thickenings at the venter, parallel to the apertural sinus.

Remarks. — The holotype (Sobolew 1912, pl 4: 5; Czarnocki 1989, pl 21: 12) is an internal mould of a relatively evolute conch hardly distinguishable from the holotype of *Praeflexiclymenia obliqua* Czarnocki, 1989 (Czarnocki 1989, pl. 9: 8). Typical specimens from Łagów Dule are significantly more involute (like the paratype of Sobolew 1912, pl. 4: 6) whereas another specimen included in *P. obliqua* by Czarnocki (1989, pl 21: 17; here Fig. 213F) is much more evolute. Generally, mature specimens are significantly more evolute than juveniles and some specimens show a change in conch geometry during the ontogeny. It seems thus that this is an extremely variable species both in respect to the conch evoluteness and the development of internal thickenings. The specimens from Jabłonna with extremely narrow venter are also included here.

Distribution. — The *P. trachytera* Zone at Łagów Dule (sample Ł-14 and 15) and Jabłonna (beds 20, 24, and 26).

Praeflexiclymenia tenuis (Sobolew, 1912)
(Figs 214A–C and 223)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains.

Material. — 14 specimens.

Diagnosis. — Small evolute conch with gently concave flank lobe of the mature, and *Clymenia*-like juvenile, suture.

Remarks. — The specimens from Jabłonna are of generally poor preservation and only the juvenile whorls, with a subcircular cross section, show sutures. They exhibit the suture angulation and minute marginal vaulting of the septum virtually undistiguishable from that in *Clymenia laevigata*. Mature whorls of the Jabłonna specimens are closely similar to those of the Łagów specimens. Probably this is a case of recapitulation of the ancestral features in the ontogeny, pointing to *Aktuboclymenia* as another close relative.

Distribution. — The *P. trachytera* Zone at Jabłonna (beds 24, 25, and 26) and black clymeniid limestone at Łagów Dule (Sobolew 1912; Czarnocki 1989).

Praeflexiclymenia flexilobata (Sobolew, 1914)
(Figs 214D and 223)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Diagnosis. — Evolute conch with sinuous umbilical saddle of the suture.

Remarks. — Sobolew (1914b, fig. 2) illustrated a specimen from Sieklucki's brickpit closely similar to the holotype of *Flexiclymenia mariae* (Czarnocki 1989, pl. 23: 13) referring to it as "*Gomi-monomeroclymenia Humboldti flexilobota* Sob.", apparently having in mind the earlier proposal by himself [Sobolew

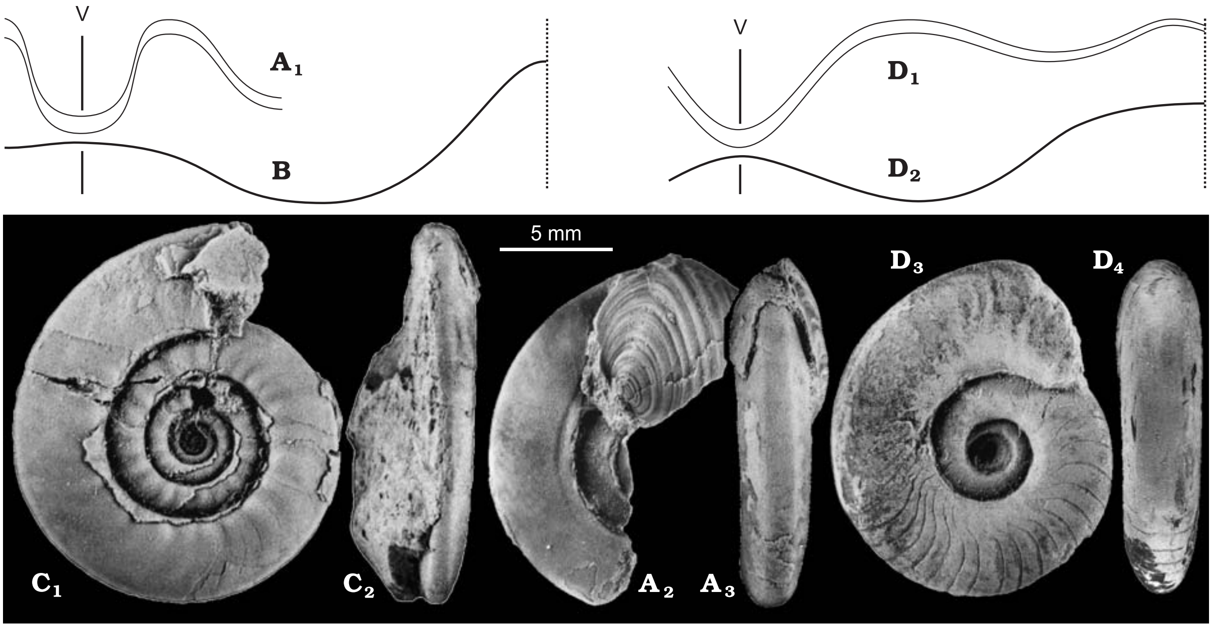

Fig. 214. Small-size species of *Praeflexiclymenia* from the Holy Cross Mountains. **A**–**C**. *P. tenuis* (Sobolew, 1912) from the *P. trachytera* Zone at Jabłonna (A, B) and Łagów-Dule (C); growth lines and views of specimen ZPAL AmVII/578 (A, bed 26); suture of ZPAL AmVII/576 (B, bed 26); views of IG.284.II.3 (C). **D**. *P. flexilobata* (Sobolew, 1914) from Sieklucki's brickpit in Kielce; growth lines (inferred from irregularities on the internal mould of the living chamber), suture, and views of IG.284.II.104, the holotype of *Flexiclymenia mariae* Czarnocki, 1989.

1914a, p. 64, spelled there "*Gomi-monomeroclymenia Humboldti* (Pusch. em. Gürich) *flexilobata* n. nom."]. The original description is followed by schematic suture drawings and photographs (Sobolew 1914a, pl. 9: 33) of two specimens with the umbilicus somewhat narrower than in Sobolew (1914b, fig. 2) and resembling rather Czarnocki's (1989) *P. obliqua* (here classified in *P. curvidorsata*). It is unclear whether all the specimens referred to by Sobolew (1914a, b) are conspecific but I propose to accept the most informative of them (Sobolew 1914b, fig. 2) as the type.

Distribution. — Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce.

Genus ***Stenoclymenia*** Lange, 1929

Type species: *Platyclymenia stenomphala* Lange, 1929 from Enkenberg, Rhenish Slate Mountains.

Diagnosis. — Tabulate venter of evolute conch with sharp edges.

Stenoclymenia sandbergeri (Wedekind, 1908)
(Figs 215A–G and 223)

Type horizon and locality: Bed 12 at Enkenberg, Rhenish Slate Mountains

Material. — 19 specimens.

Remarks. — Specimens with ribs, considered typical for *S. sandbergeri*, are rare in the Holy Cross Mountains material, as pointed out by Czarnocki (1989, p. 53). The prominence and distribution of ribs is higly variable and this suggests that these are extreme morphotypes of the species. Specimens that do not bear ribs are usually classified in *Platyclymenia prorsostriata* Schindewolf, 1920. *S. stenomphala* is less evolute. Do not having enough information on the variability in the type populations I am not able to decide which of those names should be applied to the Polish material.

Distribution. — The *P. trachytera* Zone at Łagów Dule (sample Ł-10) and Jabłonna (beds 23 and 26; wells w92b and c dug by Żakowa *et al.* 1984), and Ostrówka (samples Ost-14 and 16).

Stenoclymenia? spp.
(Figs 215H, I and 223)

Material. —Two specimens.

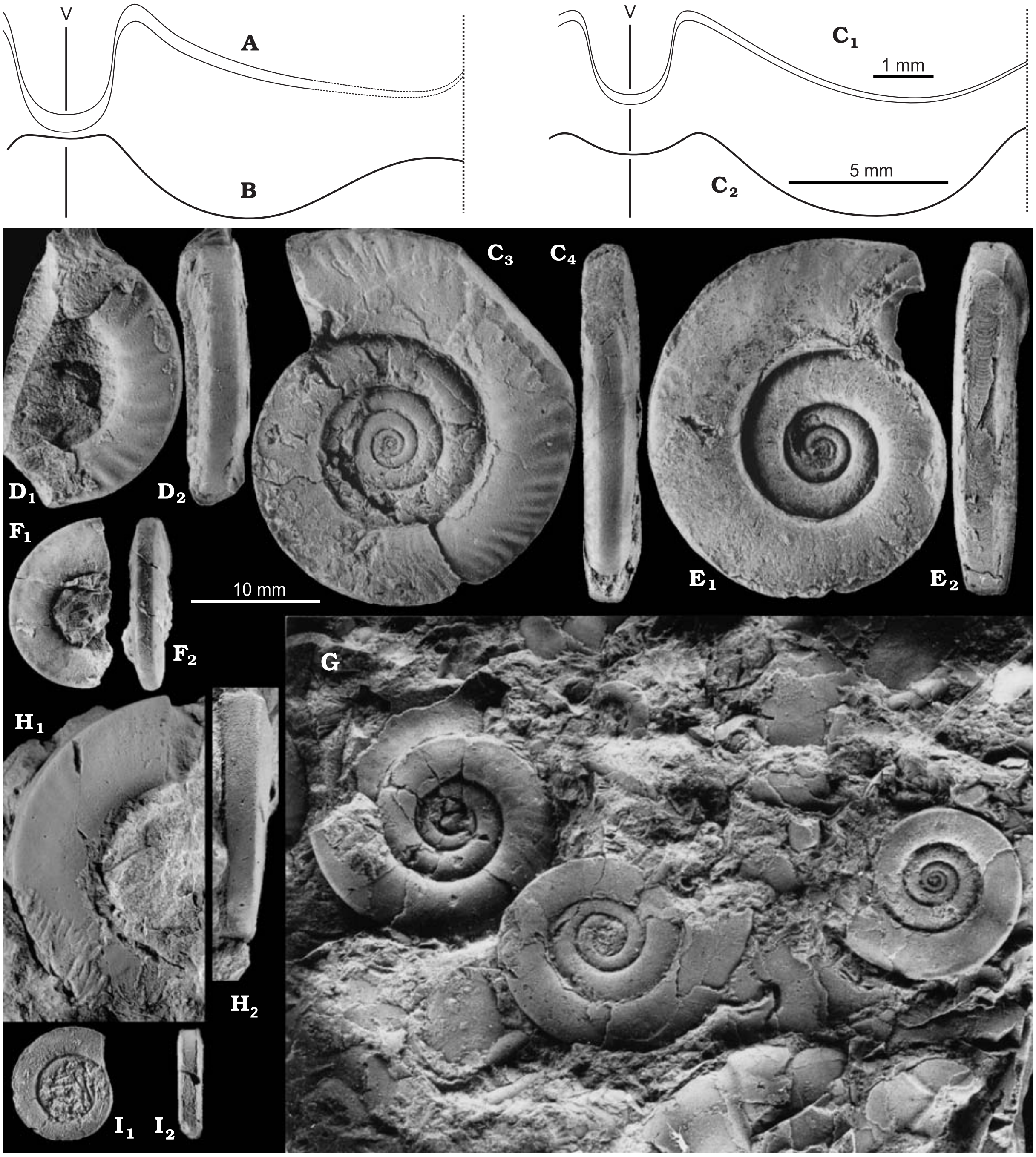

Fig. 215. Species of *Stenoclymenia*. **A**–**G**. *S. sandbergeri* (Wedekind, 1908) from the *P. trachytera* Zone at Ostrówka (A–E) and Jabłonna (F) in the Holy Cross Mountains; growth lines of specimen ZPAL AmVII/189 and suture of 567 (A, B); growth lines, suture and views of IG.284.II.854 (C); views of ZPAL AmVII/573 (D), IG.284.II.813 (E), ZPAL AmVII/115 (F, bed 24), and of virtually monospecific accumulation ZPAL AmVII/184 (G). **H**. *Stenoclymenia* sp. from the *P. jugosus* Zone at Kowala in the Holy Cross Mountains; views of specimen ZPAL AmVII/. **I**. *Stenoclymenia* sp. from the *D. trigonica* Zone at Dzikowiec in the Sudetes; views of specimen ZPAL AmVII/1670 (sample Dz-7).

Remarks. — Suture cannot be traced in available specimens which makes their classification only tentative. In general conch form they can be compared only with the much older *S. sandbergeri* and this may sugegst continuation of the lineage almost to the end of the Famennian. Relationship to gonioclymeniids cannot be excluded, however.

Distribution. — The early *P. jugosus* Zone at Kowala in the Holy Cross Mountains; the *D. trigonica* Zone at Dzikowiec in the Sudetes (sample Ł-7).

Genus ***Soliclymenia*** Schindewolf, 1937

Type species: *Goniatites solarioides* von Buch, 1840 from the clymeniid limestone at Dzikowiec, the Sudetes.

Diagnosis. — Very longiconic evolute conch with wide tabulate venter and ribs on flanks.

Soliclymenia aegoceras (Frech, 1902)
(Figs 216D–F and 223)

Type horizon and locality: Probably *Clymenia* Stufe at Kleiner Pal in the Carnic Alps (Price and Korn 1989).

Material. — Three specimens.

Diagnosis. — Smooth concave venter and strong regular ribs on flanks of slightly compresses subquadrate whorls.

Remarks. — Price and Korn (1989) have chosen the neotype for the type species of *Progonioclymenia*, *P. acuticostata* (Münster, 1842) with juvenile ventrolateral spines and ribbing similar to those in the gonioclymeniids. This makes it fundamentally different from *Clymenia aegoceras* Frech, 1902 (Price and Korn 1989; Korn and Klug 2002), believed to be a junior synonym of *P. acuticostata* by Bogoslovsky (1981). It is here transferred to *Soliclymenia* as the earliest member of the lineage. The specimen from the *Prolobites–Platyclymenia* Zone of the Ishikay River determined as *S. solarioides* by Bogoslovsky (1981) has been made the type of *Borisiclymenia ishikayensis* by Korn and Klug (2002), whereas that from the *Clymenia–Gonioclymenia* Zone of the Kia River section originally referred to *P. acuticostata* has been named *P. bogoslovskyi*. They may represent the same lineage.

Distribution. — The early *P. jugosus* Zone (grey *Clymenia* limestone) at Kowala.

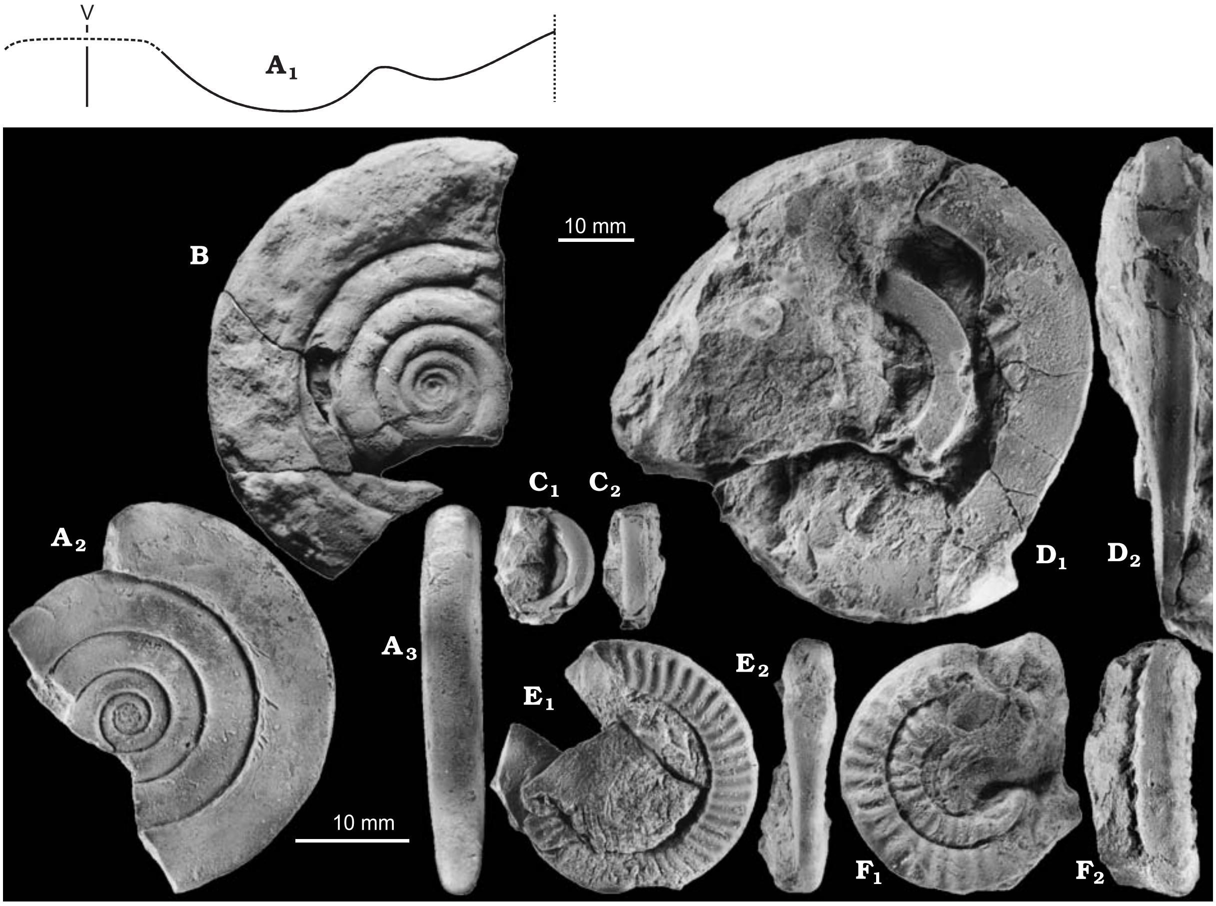

Fig. 216. Late Famennian extremely evolute clymenias. **A**–**C**. *Trochoclymenia wysogorskii* (Frech, 1902) from the early *P. jugosus* Zone at Kowala in the Holy Cross Mountains (A) and Dzikowiec in the Sudetes (B, C); suture and views of specimen IG.284.II.824 (A); views of unnambered specimen UWr (B); juvenile ZPAL AmVII/189 probably belonging to this species (C). **D**–**F**. *Soliclymenia aegoceras* (Frech, 1902) from the early *P. jugosus* Zone at Kowala in the Holy Cross Mountains; views of specimens ZPAL AmVII/10, 942 and 940.

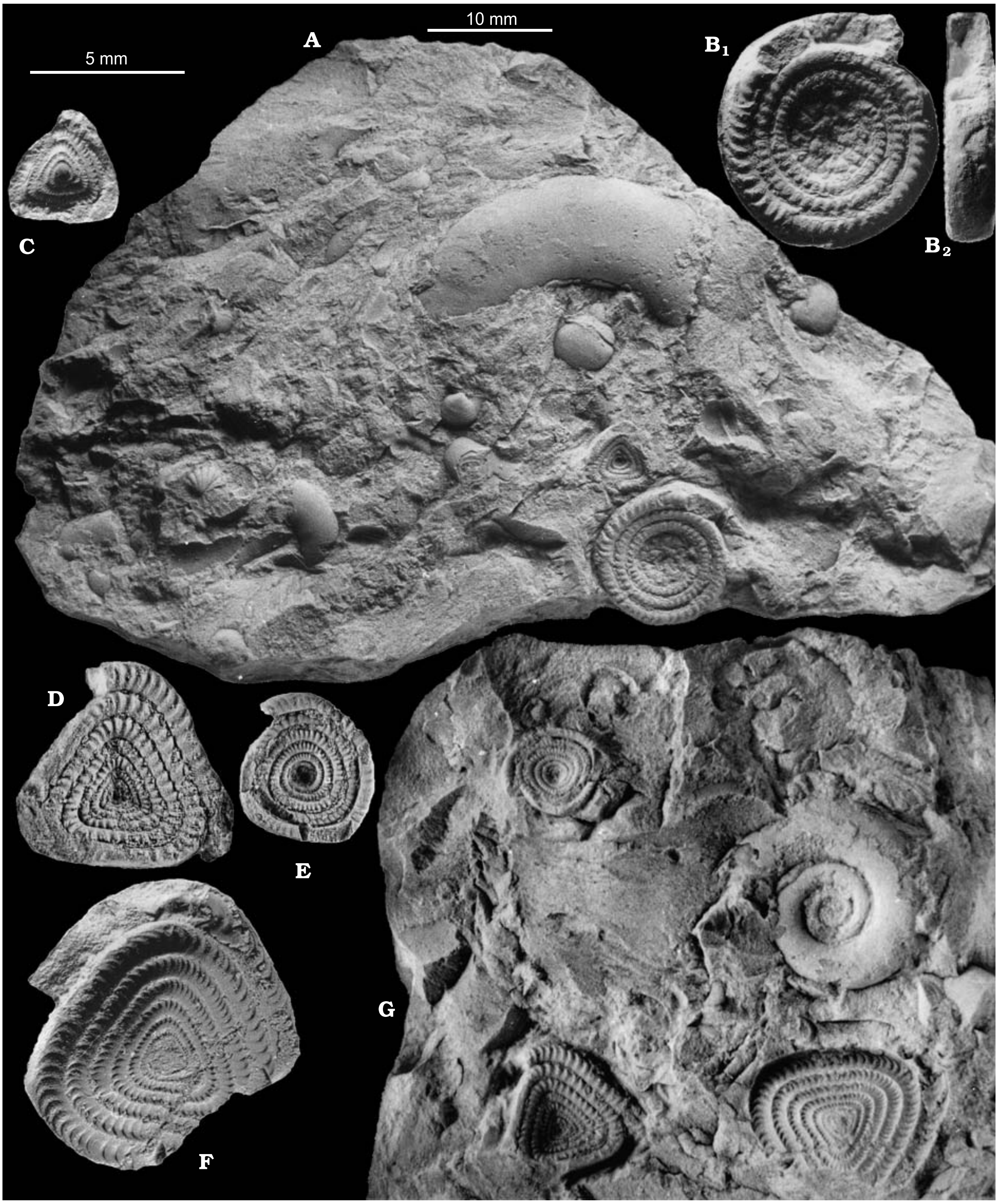

Fig. 217. Limestone blocks with associations of *Soliclymenia* from the late *P. jugosus* Zone at Dzikowiec Uwr 1760 (A) and Göttingen unnambered (G; see also Korn and Klug 2005) and magnified views of their conchs (B–F). **B**. *S. solarioides* (von Buch, 1840). **C**–**F**. *S. paradoxa* (Münster, 1839).

Soliclymenia solarioides (von Buch, 1840)
(Figs 217A, B and 223)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

Material. — Eight specimens.

Diagnosis. — Strongly depressed whorls with rounded flanks.

Distribution. — The late *P. jugosus* Zone at Dzikowiec (Korn *et al*. 2005).

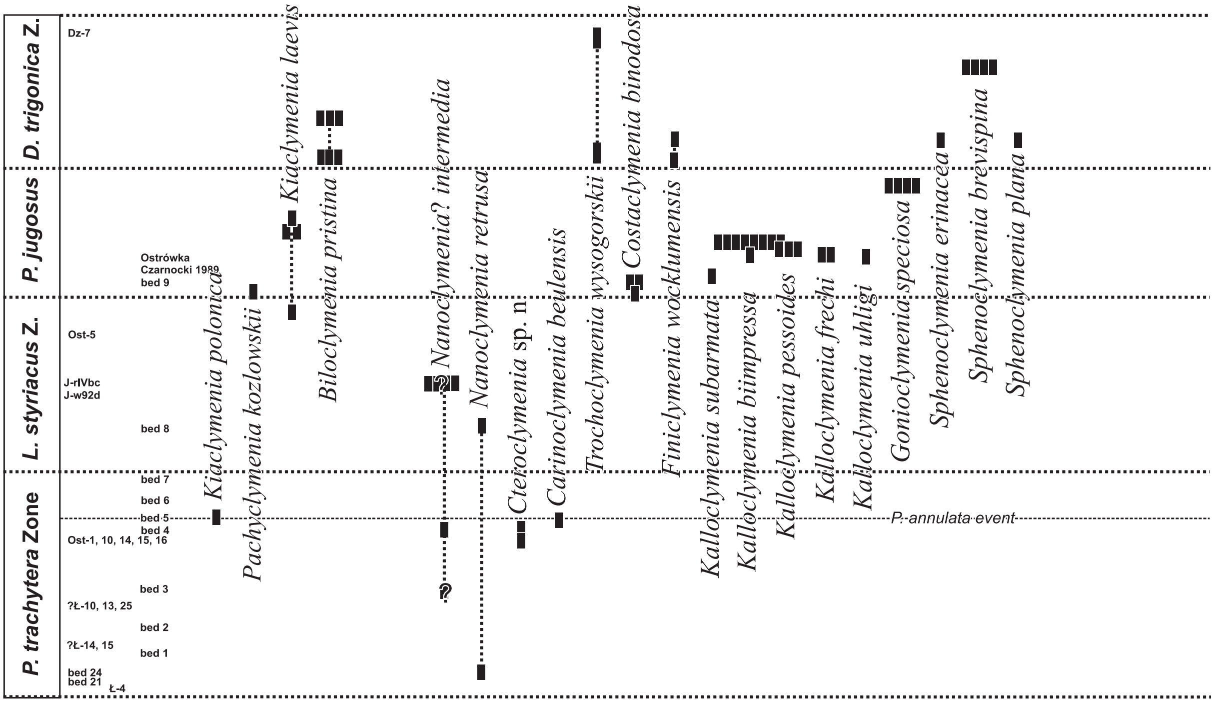

Fig. 218. Stratigraphic distribution of species of the Carinoclymeniidae, Costaclymeniidae, Gonioclymeniidae, and Biloclymeniidae in the Polish Famennian. Position of samples not included in Figs. 2 and 3 on the geochronological scale is hypothetical.

Soliclymenia paradoxa (Münster, 1839)
(Figs 217A, C–G and 223)

Type horizon and locality: Schübelhammer near Heinersreuth in Frankenwald (Schindewolf 1937).

Material. — Ten specimens.

Diagnosis. — Roundedly triangular conch outline.

Remarks. — *S. paradoxa* co-occurs with *S. solarioides* on the same bedding planes (Fig. 209A, G; Korn *et al.* 2005). There is also a great variation in the conch outline among triangular specimens found together, although the sample size is too small to enable reasonable statistics (Korn *et al*. 2005). The single more roundedly triangular specimen described by Schindewolf (1937) as his *S. semiparadoxa* (Fig. 209E) may belong to the same species as an extreme morphology. There seems to be, however, a bimodality in frequency distribution of conch morphologies covering ranges of *S. solarioides* and *S. paradoxa*; these thus seem to be biologically meaningful. Because the triangular or regularly spiral coiling starts from almost the beginning of the conch growth, it is unlikely that this is a case of sexual dimorphism.

Distribution. — The late *P. jugosus* Zone at Dzikowiec.

Family **Glatziellidae** Schindewolf, 1928

Diagnosis. — Evolute conch ribbed on flanks, with subventral furrows.

Genus ***Rhiphaeoclymenia*** Bogoslovsky, 1981

Type species: *Rhiphaeoclymenia canaliculata* Bogoslovsky, 1981 from *Kalloclymenia–Wocklumeria* Zone at Kia in the southern Urals.

Diagnosis. — Evolute conch with depressed juvenile, and furrowed mature, whorls; suture with deep subventral lobes and shallow acute flank lobes.

Remarks. — The external morphology of juvenile conch makes it similar to those of *Pleuroclymenia* (relationship proposed for the Glatziellidae by Becker 2000) or even *Soliclymenia* but suture points out rather towards *Kiaclymenia*.

Rhiphaeoclymenia canaliculata Bogoslovsky, 1981 (Figs 219A and 223)

Type horizon and locality: *Kalloclymenia–Wocklumeria* Zone of the Kia Formation at Kia in the southern Urals.

Fig. 219. Species of the Glatziellidae from Kowala (A, K, L) and Karczówka (G, I) in the Holy Cross Mountains and Dzikowiec (B–F, J) in the Sudetes. **A**. *Rhiphaeoclymenia canaliculata* Bogoslovsky, 1981 from the *P. jugosus* Zone at Kowala; photograph of lost specimen (reproduced from Czarnocki 1989, pl. 3: 11). **B**–**G**. *Glatziella helenae* (Renz, 1914) probably from the late *P. jugosus* or early *D. trigonica* Zone at Dzikowiec (B–F) and Karczówka (G); views of specimens ZPAL AmVII/806, 426, 1583, 796, and 1582 (B–F; all probably from the same level at the southern end of the quarry), and specimen IG 284.II.821a (G, in red haematitic shale). **H**, **I**. *G. minervae* (Renz, 1914) probably from the early *D. trigonica* Zone at Dzikowiec (H) and Karczówka (I); views of specimens ZPAL AmVII/161 (H) and mature conch IG 284.II.821b (I, in red haematitic shale). **J**–**L**. *G. glaucopis* (Renz, 1914) from the *D. trigonica* Zone at Dzikowiec (J) and Kowala (K, L); views of specimen ZPAL AmVII/944 (J, sample Dz-180 with *Parawocklumeria paradoxa*), 1043, and 1040 (K, L, both from a bed near sample Ko-102).

Remarks. — *Liroclymenia fundifera* Czarnocki, 1989 seems to represent this species (Becker 1997), although the single original specimen is lost and cannot be studied. The description of its suture (Czarnocki 1989, p. 47), indicating presence of two deep acute lobes on flanks, is consistent with this identification.

Distribution. — Probably the *P. jugosus* Zone at Kowala (lower *Wocklumeria* beds of Czarnocki 1989).

Genus ***Glatziella*** Renz, 1914

Type species: *Glatziella helenae* Renz, 1914 from the clymeniid limestone at Dzikowiec in the Sudetes.

Diagnosis. — Minute conch with very low whorls.

Remarks. — Suture of *Glatziella helenae* illustrated by Schindewolf (1937, fig. 15) shows two lobes on the flanks, thus a situation similar to that in *Rhiphaeoclymenia*. Lobes are, however, much shallower, which may be related to a secondary simplification in result of the paedomorphic nature of the genus.

Glatziella helenae (Renz, 1914)
(Figs 219B–G and 223)

Type horizon and locality: Clymeniid limestone at Dzikowiec in the Sudetes.

Material. — Four specimens.

Diagnosis. — Evolute conch with whorls height similar to width.

Remarks. — Each of the studied specimens is unique in the whorl cross section. No doubt that this is a highly variable species. Still, the extend of variability approaches, but does not reach the more *Rhiphaeoclymenia*-like morphology of the oldest species of the lineage, *G. lethmathensis* Becker, 1997 from the Rhenish Slate Mountains (1997). There seems to be also a gap separating this species from the equally variable *G. minervae* (Renz, 1913). A possibility remains that these are actually members of a single continuous lineage. Unfortunately, all the specimens studied were collected from the scree in blocks too small to provide conodont samples of size enabling precise age determination.

Distribution. — The early *D. trigonica* Zone at Dzikowiec and Karczówka.

Glatziella minervae (Renz, 1914)
(Figs 219H, I and 223)

Type horizon and locality: Clymeniid limestone at Dzikowiec in the Sudetes.

Material. — Three specimens.

Diagnosis. — Moderately involute conch; wide whorls with distinct ribbing on flanks.

Remarks. — Particular specimens differ from each other mostly in having more or less apparent ribbing on flanks and in the width of the umbilicus. Schindewolf (1937; also Becker 2000) introduced *G. diensti* and *G. tricincta* from the same locality, the species transitional in the conch geometry between *G. helenae* and *G. minervae*. It remains to be documented with more material whether these are stages in the evolutionary development of the lineage, end-members of population variability, or truly separate species.

Distribution. — The early *D. trigonica* Zone at Dzikowiec.

Glatziella glaucopis (Renz, 1914)
(Figs 219J–L and 223)

Type horizon and locality: Clymeniid limestone at Dzikowiec in the Sudetes.

Material. — Two specimens.

Diagnosis. — Globose, relatively involute conch; wide whorls with smooth flanks.

Remarks. — This is probably the end-member of the *Glatziella* lineage. No sign of ribbing is visible on internal moulds and also the areas with preserved shell visible in sections seem to be smooth. Suture can be traced only in the umbonal part of specimen ZPAL AmVII/1040 and septa in a section across the inner whorl of the holotype. It was apparently of simple geometry and does not differ substantially from the sutures of related species from Dzikowiec, traced by Schindewolf (1937).

Distribution. — The late *D. trigonica* Zone at Kowala, probably somewhat older stratum at Dzikowiec (Renz 1914; Schindewolf 1937).

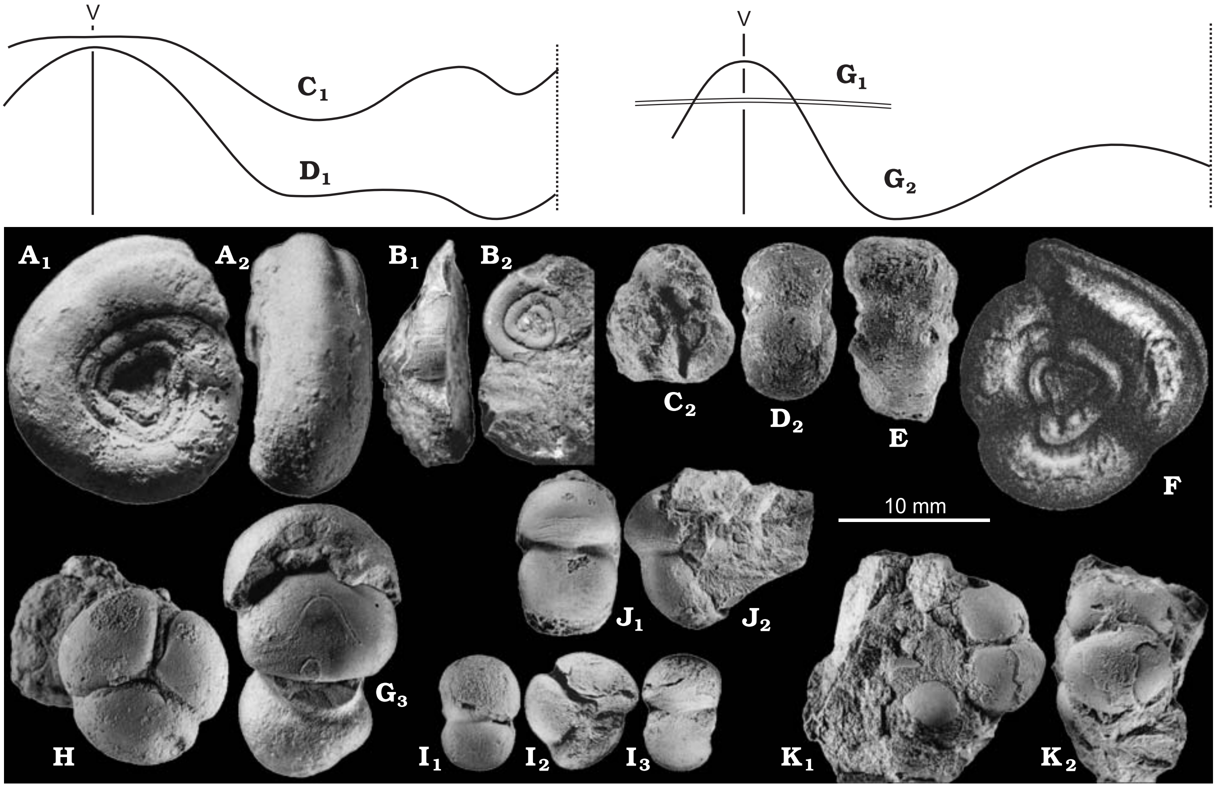

Fig. 220. Species of the *Parawocklumeria* lineage from Dzikowiec (A–F, I–L) in the Sudetes and Kowala (G, H) in the Holy Cross Mountains. **A**, **B**. *Kamptoclymenia trivaricata* Schindewolf, 1937 probably from the *P. jugosus* Zone at Dzikowiec; views of the holotype UWr 1772 (A) and unnambered MfN (B, 0.1 m below the top of the Famennian, illustrated also in Schindewolf 1937, pl. 3: 16). **C**–**F**. *Parawocklumeria distorta* (Tietze, 1870) from the late *P. jugosus* or early *D. trigonica* Zone at Dzikowiec; suture and view of specimens ZPAL AmVII/108 and 109 (C, D); view of 110 (E) and mature specimen (F, holotype of *Parawocklumeria patens*, reproduced from Schindewolf 1937, pl. 4: 5). **G**–**K**. *Parawocklumeria paradoxa* (Wedekind, 1918) from the *D. trigonica* Zone at Kowala (G, H) and Dzikowiec (I–K); growth lines, suture, and view of specimen ZPAL AmVII/954 (G); views of 1046, 800 (H, I), 936, and 938 (J, K, sample Dz-180).

Family **Wocklumeriidae** Schindewolf, 1937

Diagnosis. — Conch with three constrictions per whorl at least early in the ontogeny.

Remarks. — It was convincingly shown by Becker (2000) that, contrary to the original idea of Schindewolf (1937), the lineages of *Wocklumeria* and *Parawocklumeria* are closely related to each other, and their similarity is not a case of homeomorphy but the result of common descend. It does not seem necessary to distinguish the separate family Parawocklumeriidae Schindewolf, 1937; at the best it deserves the subfamily rank.

Genus ***Kamptoclymenia*** Schindewolf, 1937

Type species: *K. endogona* Schindewolf, 1937 from beds 7–9 at Hönnental, Rhenish Slate Mountains (Schindewolf 1937).

Diagnosis. — Evolute conch with adult stages bearing ventrolateral furrows and juvenile conch of trigonal shape.

Kamptoclymenia trivaricata Schindewolf, 1937
(Figs 220A, B and 223)

Type horizon and locality: Clymeniid limestone at Dzikowiec in the Sudetes.

Material. — Two specimens.

Diagnosis. — Trigonal conch form reaches in ontogeny the stage with ventrolateral furrow.

Remarks. — The species seems to be confined to the upper part of the clymeniid limestone at Dzikowiec (Schindewolf 1937). Also the juvenile whorls attributed by Schindewolf (1937, pl. 3: 16; here Fig. 220B) to his *K. trigona* (the holotype being an adult conch from Hönnental) seem indistinguishable from corresponding whorls of the holotype of *K. trivaricata*.

Probable ancestor of this species is *K. endogona* from Hönnental (co-occurring there in the same beds with the closely similar *K. trigona*) which differs in a more evolute spiral conch, the trigonal appearance being restricted to early stages (Schindewolf 1937; Becker 2000).

Distribution. — The *D. trigonica* Zone at Dzikowiec (0.1 m below the top of the Famennian in the quarry according to Schindewolf 1937).

Genus ***Parawocklumeria*** Schindewolf, 1926

Type species: *Wocklumeria paradoxa* Wedekind, 1918.

Diagnosis. — More or less involute conch, with three deep constrictions on each whorl.

Parawocklumeria distorta (Tietze, 1870)
(Figs 220C–F and 223)

Type horizon and locality: Clymeniid limestone at Dzikowiec in the Sudetes.

Material. — Three specimens.

Diagnosis. — Relatively evolute conch with ventrolateral furrows on the mature living chamber.

Remarks. — The holotype of *P. patens* from the same strata (Schindewolf 1937; Becker 2000) may represent mature stage of the same species. Unfortunately, being originally housed in Wrocław, it was probably lost during World War II, together with the holotype of *P. distorta*. *P. distributa* Czarnocki, 1989 from Kowala closely resembles the Dzikowiec specimens of *P. distorta* in the conch form but differs from the specimen illustrated by Schindewolf (1937, fig. 26) in a wider and mory distinctly bilobate ventral saddle of the suture. Becker (2000) introduced the separate genus *Tardewocklumeria* for it, hypothesizing that this is the ancestral member of the Wocklumeriidae.

Distribution. — The *D. trigonica* (perhaps also the late *P. jugosus*) Zone at Dzikowiec (Schindewolf 1937), probably the late *P. jugosus* Zone at Kowala (Czarnocki 1989).

Parawocklumeria paradoxa (Wedekind, 1918)
(Figs 220G–K and 223)

Type horizon and locality: Burg near Balve in the Rhenish Slate Mountains (Wedekind, 1918).

Material. — Five specimens.

Diagnosis. — Involute conch with ventrolateral furrows on the mature living chamber.

Remarks. — The ontogeny of suture was studied by Czarnocki (1989). *P. paprothae* Korn, 1989 from Grünen Schneid in the Carnic Alps is intermediate between *P. distorta* and *P. paradoxa* in having an open umbilicus. Specimens of such morphology occur also in Dzikowiec and Kowala and it remains to be shown whether they represent a separate stage in the evolutionary development of the lineage (Becker 2000) or only an extreme in the population variability.

Distribution. — The *D. trigonica* Zone at Dzikowiec, Miedzianka and Kowala (Czarnocki, 1989).

Genus ***Epiwocklumeria*** Schindewolf, 1937

Type species: *Wocklumeria paradoxa* var. *applanata* Wedekind, 1918 from Burg near Balve in the Rhenish Slate Mountains.

Diagnosis. — Involute discoidal conch; suture with deep ventral and flank lobes, and shallow umbonal lobe.

Epiwocklumeria bohdanowiczi (Czarnocki, 1989)
(Figs 221A–D and 223)

Type horizon and locality: Burg near Balve in the Rhenish Slate Mountains (Wedekind, 1918).

Material. — One specimen.

Diagnosis. — Discoidal conch; rounded ventral and acute flank lobes of the suture.

Remarks. — The mature living chamber in this species lacks constrictions and is evolute. Its venter is acute. Czarnocki (1989) introduced genus *Kielcensia* for the species (developed further by Becker 2000) but it seems more likely to me that this is rather a connecting link between *Parawocklumeria* and the type species of *Epiwocklumeria*.

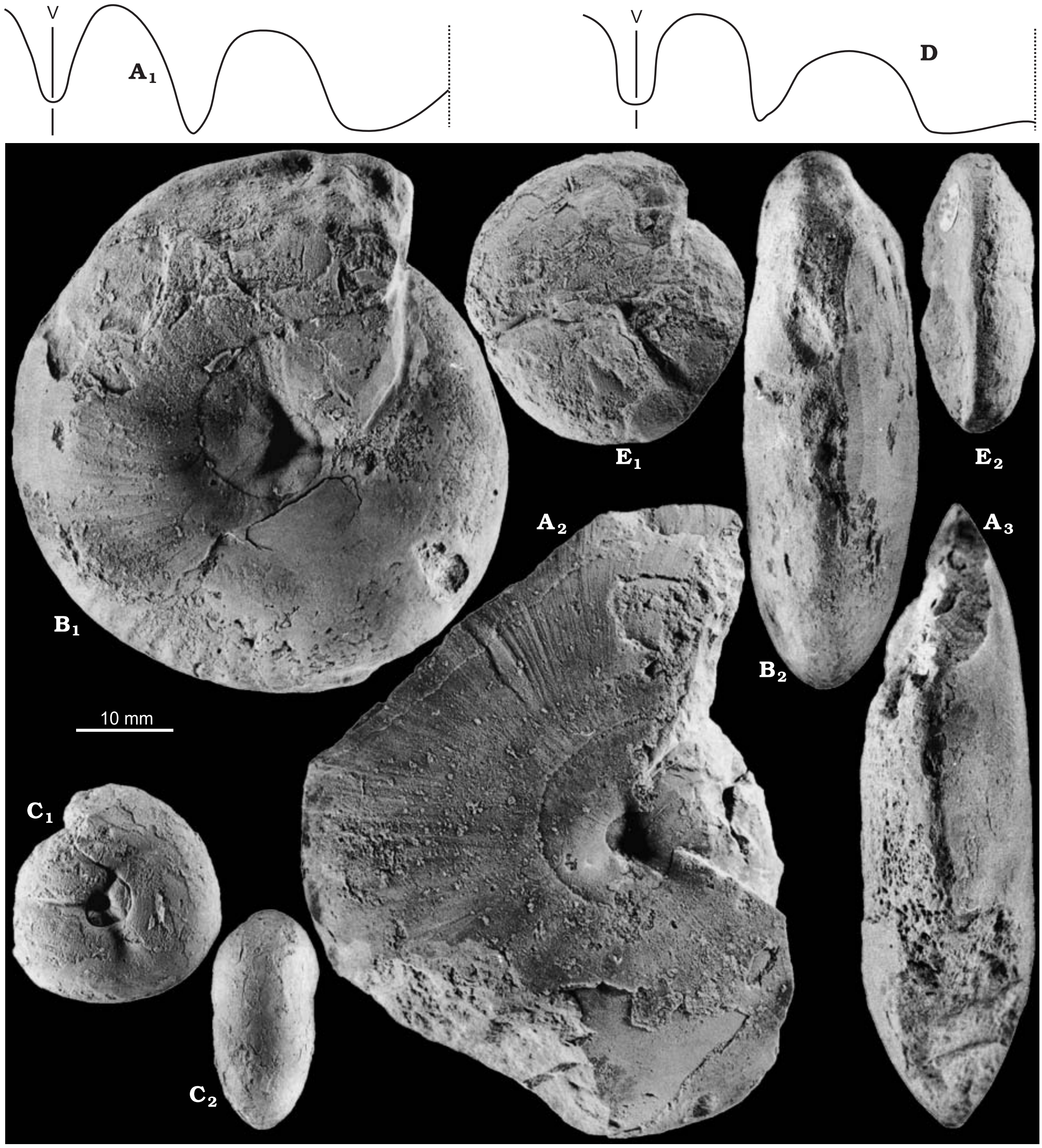

Fig. 221. Species of the *Epiwocklumeria* from Kowala in the Holy Cross Mountains. **A**–**D**. *Epiwocklumeria bohdanowiczi* (Czarnocki, 1989) probably from the *P. jugosus* Zone at Kowala (A–C) and Jabłonna (D); suture and views of mature specimen ZPAL AmVII/183 (A); views of mature IG 284.II.443 (B, trench III, bed 2 of Jan Czarnocki) and juvenile IG 284.II.431 (C); suture of ZPAL AmVII/448 (D, bed 33). **E**. *Epiwocklumeria applanata* (Wedekind, 1918) probably the *D. trigonica* Zone; views of specimen IG 284.II.875.

Distribution. — Probably the late *P. jugosus* Zone at Kowala in the Holy Cross Mountains. According to Czarnocki (1989, p. 27), *Kielcensia* occurs throughout his 5.54 m thick *Wocklumeria* beds, starting from below the red marly limestone. This is a mysterious notion as no single specimen of this clymenia was found by myself in these strata. *Epiwocklumeria* and *Wocklumeria* is reported by him from the base of 1.85 m thick upper unit of the beds. He also reports a mass occurrence of Kielcensia from the “cuboidally breaking shale” immediately below the bituminous black shale (equivelent to the Hangenberg Shale; Dzik 1997), which obviously refers to *Acutimitoceras*. It seems thus that only the report of *E. bohdanowiczi* from the stratum below the red limestone is likely to be correct.

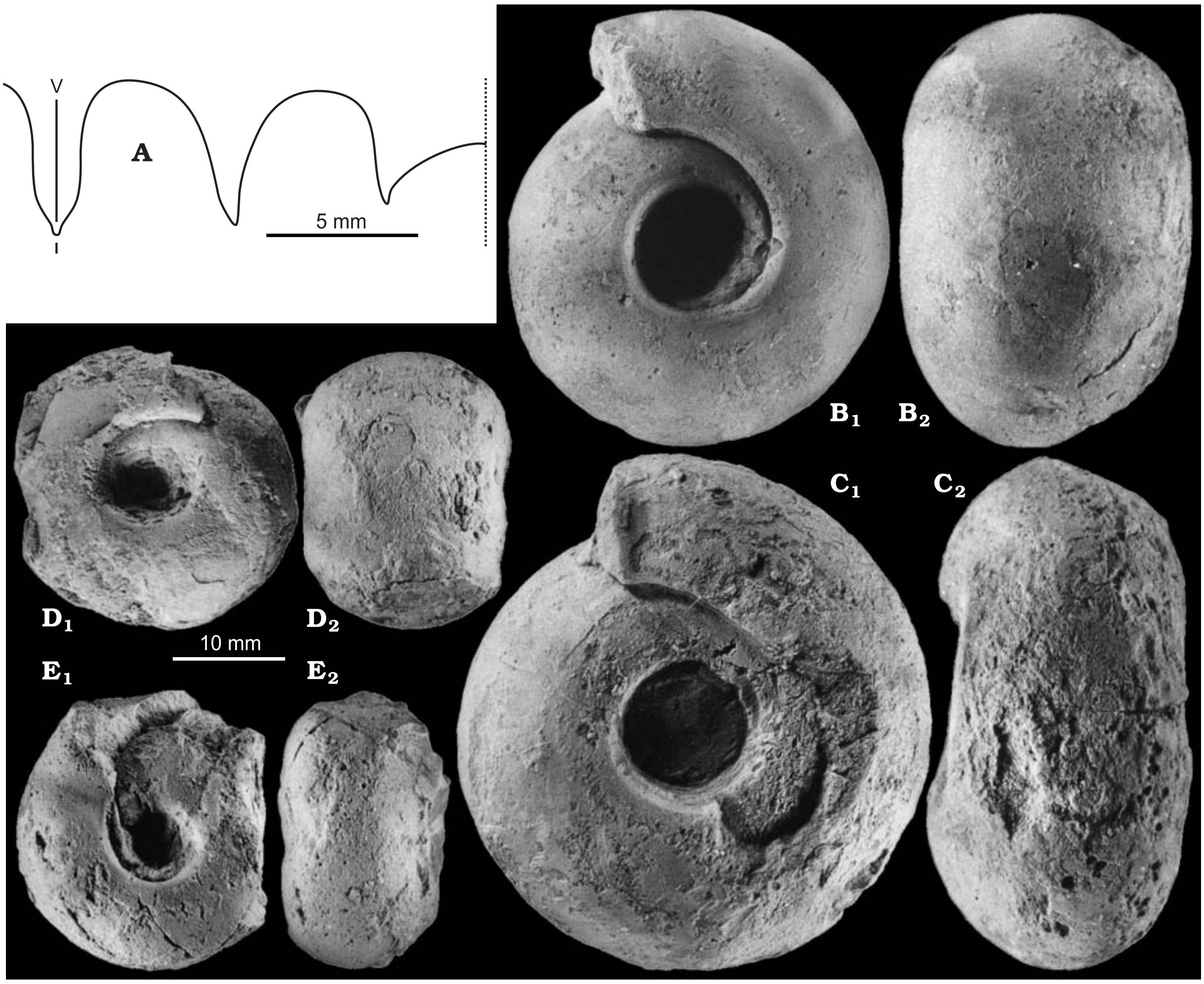

Fig. 222. W*ocklumeria sphaeroides* (Richter, 1848) probably from the *D. trigonica* Zone at Kowala in the Holy Cross Mountains; suture of specimen IG 284.II.874 (A); views of mature specimens IG 284.II.622, 775 (B, C), subadult ZPAL AmVII/1045, and 1042 (D, E).

Epiwocklumeria applanata (Wedekind, 1918)
(Figs 221E and 223)

Type horizon and locality: Burg near Balve in the Rhenish Slate Mountains (Wedekind, 1918).

Diagnosis. — Flat discoidal conch with ventrolateral furrows on the mature living chamber.

Remarks. — It is unclear whether among available specimens there are adults and whether constrictions developed truly until the maturity.

Distribution. — The *D. trigonica* Zone at Kowala in the Holy Cross Mountains (Czarnocki, 1989).

Genus ***Wocklumeria*** Wedekind, 1918

Type species: *Goniatites sphaeroides* Richter, 1848 from Bohlen near Saalfeld in Thuringia (Becker 2000).

Diagnosis. — Evolute smooth globose conch; suture with acute ventral, lateral, and umbonal lobes.

Wocklumeria sphaeroides (Richter, 1848)
(Figs 222 and 223)

Type horizon and locality: Burg near Balve, Rhenish Slate Mountains (Wedekind, 1918).

Material. — Two specimens.

Distribution. — Probably the late *D. trigonica* Zone at Kowala in the Holy Cross Mountains (Czarnocki, 1989).

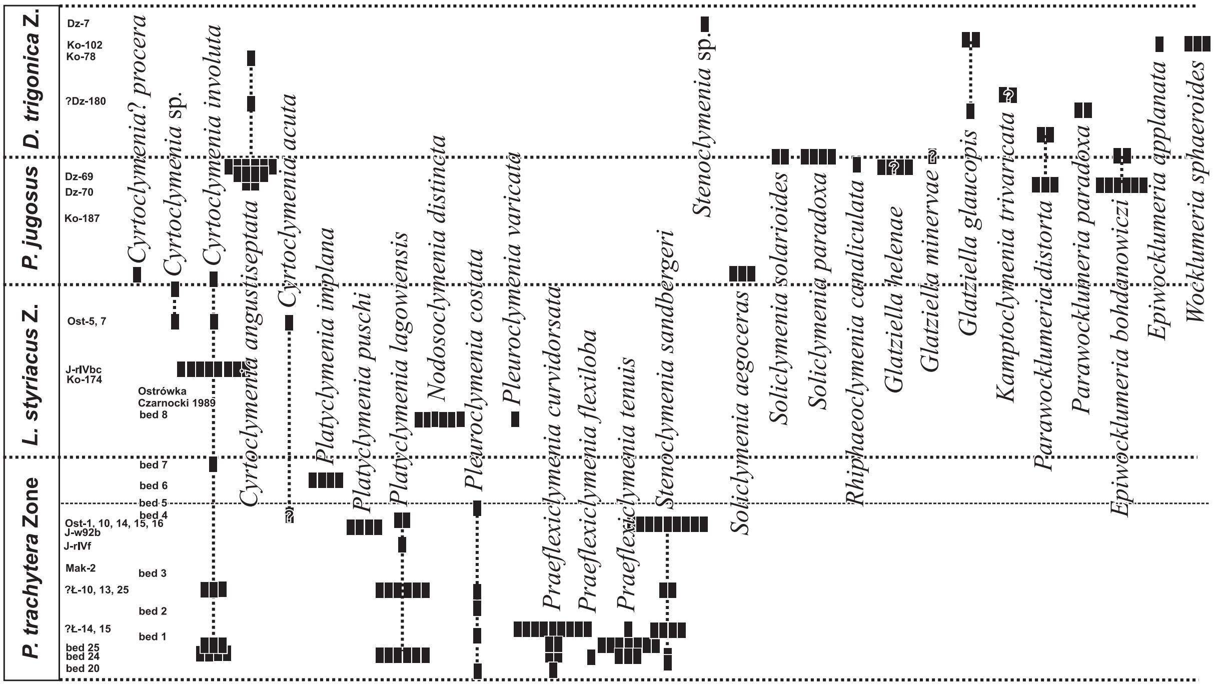

Fig. 223. Stratigraphic distribution of species of the Cyrtoclymeniidae, Hexaclymeniidae, Glatziellidae, and Wocklumeriidae in the Polish Famennian. Position of samples not included in Figs. 2 and 3 on the geochronological scale is hypothetical.

SUCCESSION OF THE FAMENNIAN AMMONOID FAUNAS IN POLAND

The fossil record of the ammonoid faunal dynamics is much more complete in the Famennian of the Holy Cross Mountains than in the Frasnian of the same area (Dzik 2002). Still, it remains highly punctuated and incomplete. Even in the most fossiliferous localities (Jabłonna, Łagów), cephalopod conchs occur only in few horizons. Their stratigraphic relationship is usually hard to determine because the strata were accessible to exploitation for a limited time and most of the material collected by myself is derived from the scree of exposures no longer accesible. Even in cases of the bed-by-bed collecting by previous authors (Sobolew 1912; Czarnocki 1989), the original descriptions and most of the specimens were lost as a result of historical turbulencies in this part of Europe. The review of the evolution of ammonoid faunas presented below has to be thus taken with caution, as based on limited evidence and tentative stratigraphic attribution of many findings.

Biogeographic affinities. — Perhaps the most surprising aspect of the Holy Cross Mountains Famennian ammonoid assemblages is their rather remote similarity to those from the Rhenish Slate Mountains in Germany. Polish assemblages are generally more diverse, as acutely shown by comparison of the species contents of the *Platyclymenia annulata* Zone fossil assemblages from Ostrówka (Czarnocki 1989) with the classic Kattensiepen, quantitatively studied by Korn (2002), or Enkenberg (Korn 2004a). Perhaps the most striking is the apparent lack of *P. annulata* in Poland! This has not only faunistic but also biostratigraphic implications. It turns out that geographic and ecologic ranges of the Famennian ammonoids were rather restricted, as compared with conodonts. The pattern of change in the studied area does not need to be the same as in western Europe. Therefore the process should be seen also in its geographic dimension.

A similar distinction characterizes also the southern Urals Famennian, as can be estimated on the basis of Perna (1914) and numerous papers by Bogoslovsky (e.g., 1960, 1981). Despite its location on the opposite, western *versus* eastern, side of the East European Platform, the South Urals faunas seem more alike than those from the Rhenish Massif. This is well exemplified by the protornoceratid and earliest clymenias assemblages, apparently having an eastern provenance.

Changes at the Frasnian–Famennian boundary. — The question of the nature of the Frasnian–Famennian transition in the Holy Cross Mountains has been already discussed by myself (2002) and little new evidence emerged since that time in respect to ammonoids (although a lot of new data has been published on other faunal groups and the local stratigraphy: Racki and House 2002; Baliński *et al*. 2002). Similarly as in, e.g., Timan (Becker *et al*. 2000), the only tornoceratid ammonoid lineage that reaches the end of the Frasnian in the area is *Linguatornoceras*. The lack of well-defined evolutionary novelties (apomorphies) in the conch of this tornoceratid and its earliest Famennian successors makes identification of the exact ancestry and the course of evolution difficult. It remains thus to be convincingly shown whether all the post-Frasnian goniatites diversified from a single survivor or, as suggested by Becker (1993a) at least two separate lineages crossed the boundary. Most probably, the underived morphology is a reflection of their opportunistic ecology. No doubt, however, that tremendous shifts in the geographic distribution of ammonoid species at the boundary was connected with environmental changes, as it was the case also with conodonts. It is thus unlikely that the change from ancestors to successors can be traced in any single section representing the Devonian equatorial environment.

Famennian faunas. — The stratigraphically oldest occurrence of the Famennian goniatites in the Holy Cross Mountains is the now not accessible cephalopod layer at Karczówka (Gürich 1896, 1901) with mass occurrence of probably *Tornoceras typum*. Mature macroconchs of this species in somewhat younger strata at Jabłonna and Janczyce reach 12 cm of the conch diameter and it was the largest ammonoid of its time. A local outshoot of the lineage initiated a fast evolutionary change towards the oxyconic conch shape. This is probably the most convincing case of the phyletic evolution among the Devonian ammonoids, best recognizied at Janczyce (Makowski 1991), but apparent also at Jabłonna and Kowala.

While *Tornoceras* evolved so directionally, the fossil goniatite assemblage was enriched with the first member of the *Polonoceras* lineage and a few sympatric species of the cheiloceratids. All these lineages entered as immigrants from an unknown source region with no signs of any evolutionary change at place. The best fossil record of their diversity is from the mid *K. crepida* Zone, with few findings from strata of younger age until the late *C. quadrantinodosa* Zone. Then, a very rich assemblage of the protornoceratids, cheiloceratids, dimeroceratids, and early sporadoceratids emerges, together with the black shale and limestone facies, at Kowala and Łagów, the latter being the subject of the large monograph by Sobolew (1914a). The faunas of the *C. quadrantinodosa* and *C. marginifera* are different in that underived tornoceratids were replaced by more advanced posttornoceratids as a result of another wave of immigrants. The largest ammonoid of the *C. quadrantinodosa* was the dimeroceratid *Dimeroceras* cf. *petterae* Petersen, 1975, whereas in the *C. marginifera* Zone time it was the posttornoceratid *Maeneceras lagoviense* Gürich, 1896, both reaching about 11 cm in their conchs diameter.

The high diversity of fossil assemblages continued to the early *P. trachytera* zones, but with a dramatic change in its composition meanwhile. The cheiloceratids disappeared completely, only a few dimeroceratids survived, and sporadoceratids reduced their diversity. A number of clymenias entered the area. They co-occured for some time with their close phylogenetic and ecological relatives, the protornoceratids.

These are clymenias that dominate all the younger assemblages. In the late *P. trachytera* Zone they are supplemented, apart of the ubiquitous *Sporadoceras varicatum*, by the prolobitids, represented probably by two long-ranging but ecologically sensitive lineages. In the *L. styriacus* Zone, large clymeniids emerged for the first time, with *Clymenia laevigata* (Münster, 1839) reaching 15 cm in diameter. The largest Famennian ammonoid was probably *Gonioclymenia speciosa* (Münster, 1832) of 30 cm diameter.

The *Prionoceras* clade, rooted in underived cheiloceratids, increased gradually its importance during the late Famennian, near its end being the dominant goniatites, associated with the morphologically conservative *Cymaclymenia*, evolute *Kosmoclymenia*, and aberrant involute wocklumeriid clymenias. More or less the same assemblage occurs in the Sudetes, different only in including several species of the minute prionoceratid *Balvia*, elsewhere known from the Rhenish Slate Mountains (Korn 1994) and England (Selwood 1960). The roots of all the post-Devonian ammonoids were within the prionoceratids (Korn *et al*. 2003).

EVOLUTION OF THE FAMENNIAN AMMONOIDS

Although little changed in the morphology of the adult conch of the earliest Famennian tornoceratids prior to their diversification into the main clades, their larval conch (referred to as such because of reasons explained at the beginning of the ammonoid part of this work) underwent a profound transformation. The change was comparable with that during formation of the tightly coiled ammonoid larval conch in the Mid Devonian (e.g., Klofak *et al*. 1999). The larval conch was clearly demarkated, from both the spherical embryonic protoconch and the differently ornamented teleoconch, and bore 2–3 septa already in the Silurian ancestors of the ammonoids (Dzik 1981) and in bactritids (Doguzhaeva 2002). Its tight coiling was actually the only substantial modification until the origin of the tornoceratids. Near the origin of the clade in the Givetian, the first larval septum developed a deep concavity, which made tornoceratids different from all other ammonoids (Ruzhentcev 1962; Bogoslovsky 1969). As speculated above, this could have been a result of delayed secretion of the septal tissue in respect to the cameral liquid.

A limited evidence from the Holy Cross Mountains (Fig. 140) suggests that during the early Famennian this tendency was reversed and the tornoceratid ancestor of the clymenias had the first septum of underived morphology. Whether this happened prior to derivation of the cheiloceratid lineage, or the cheiloceratids originated from a Frasnian ancestor lacking the bulbous first septum, has to be shown.

GONIATITES

According to House and Price (1985) at least five lineages of the tornoceratids crossed the Frasnian–Famennian. Even if this undervalues the change, data from regions outside the equatorial Devonian has to be obtained before the monophyly of all the post-Frasnian ammonoids is accepted. Anyway, morphologic similarities among the earliest Famennian tornoceratids and cheiloceratids from the Holy Cross Mountains are so close that their origin from the single lineage of *Tornoceras typum* cannot be excluded. From the earliest Famennian *K. triangularis* Zone only poorly preserved juvenile specimens probably representing this species are known to me. In the *P. crepida* Zone mature *Tornoceras* conchs show bimodal size frequency distribution, interpreted by Makowski (1991) as the evidence of sexual dimorphism. That this was truly the case is supported by a similar size differences in the lineage of the oxyconic tornoceratids, but the supposed macroconchs are there two times smaller in diameter. At present it cannot be excluded that actually two generalized species of *Tornoceras* occur in the early Famennian of the Holy cross Mountains, different only in mature conch size. The small-size species gave rize to the local phyletic lineage of tornoceratids with acute conch venter (Fig. 224).

Oxyconic tornoceratids. — The change from the roundedly discoidal *Tornoceras typum* to the oxyconic *T. sublentiforme* was probably a case of fast phyletic evolution (Makowski 1991) restricted to the Holy Cross Mountains. It has its counterpart in the probably coeval Rhenish lineage of *Oxytornoceras* (Becker 1993a). Acute whorls developed several times also in other unrelated ammonoids known from the Holy Cross Mountains. Apparently, a selection pressure on developing this kind of conch geometry was frequently released and a response to it from developmental mechanisms was easy and fast. As a result the origin of most such short-living lineages is cryptic, having little chance to be recorded in strata.

The ancestral lineage of *T. typum* continued its occurrence in the area and it is not clear how the genetic isolation allowing the divergent evolutionary change developed.

Protornoceratid conch geometry. — The early tornoceratids had a virtually closed umbilicus throughout their ontogeny, with exception of the larval stage. Frequently a callus developed (Fig. 141A). The first tornoceratid with open (although still narrow) umbilicus emerges from the fossil record in the Holy Cross Mountains area very early, almost together with *T. typum* (Fig. 159) and it may have Frasnian roots. The virtual lack of goniatite fossils immediately above the Frasnian and during the whole the *K. triangularis* Zone is hardly any evidence, as throughout the whole Frasnian only three horizons with ammonoid are reported from the Holy Cross Mountains (Dzik 2002). No doubt that they occurred also in epochs without any fossil record. To be preserved, the ammonoid conchs require extraordinary sedimentary conditions, preventing degradation of aragonite (almost instanteous covering with the sediment).

Despite the punctuated fossil record, it seems that the phyletic evolution towards the tabulate venter in the *Polonoceras* lineage took place in the area (Fig. 204). It reached the level of *P. dorsoplanum* in the late *C. quadrantinodosa* zone. The enigmatic *P. sudeticum* from the latest Famennian of the Sudetes seems to be a continuation of the lineage after a great gape in the record, as suggested by the very characteristic arcuate depressions on the conch flanks and conical umbilicus slopes. It is different from the early Famennian *Polonoceras* in its rounded venter, suggesting a reversal in the evolution. The *C. marginifera* Zone was a

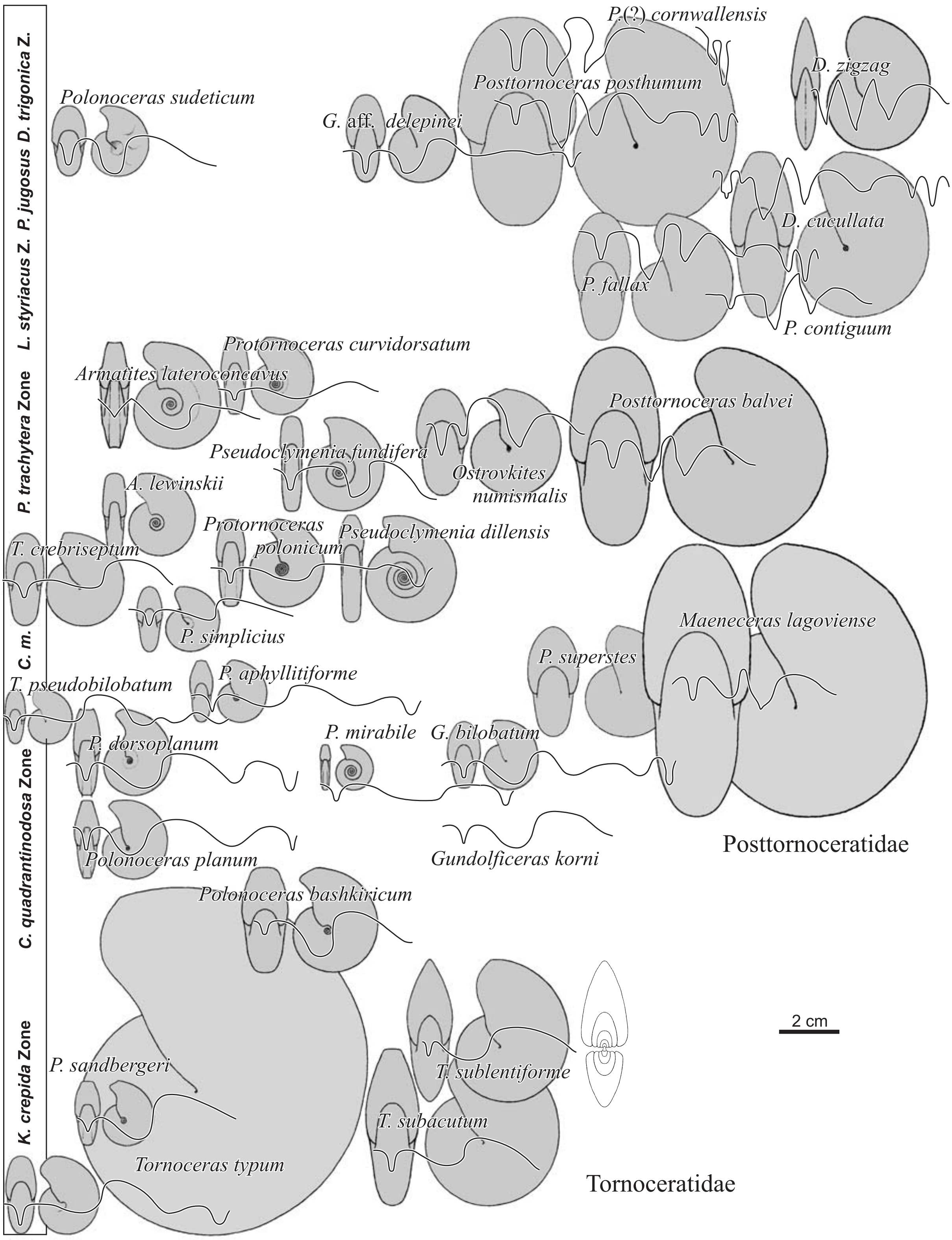

Fig. 224. Chronomorphoclines identifiable in the tornoceratid and posttornoceratid goniatites in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 159). Contours of probably mature specimens in scale and suture lines are given.

time of migrations and the lack of record of the lineage in this time span may be meaningful. The open umbilicate *Armatites*, which emerged in the *P. trachytera* Zone is evidently a successor of *Polonoceras* but, being known also in the Rhenish Massif (Becker 1993a), may have originated there.

A somewhat tabulate venter associated with the evoluteness of the conch developed independently in *Protornoceras*, an early offshoot of *Polonoceras*. Species of the *Polonoceras–Protornoceras* clade all had a very small mature conchs, which may be an expression of their position in the community different from theat of the main lineage of the tornoceratids. There are many sympatric species of *Protornoceras*, each unusually variable in the conch morphology. Their ability to contribute new and new sympatric species to the assemblage must have have been connected with their biology, but its nature remains unknown. In the most derived of the protornoceratids, the evolute *Pseudoclymenia*, an *Aturia*-like morphology of the septum developed.

Complex septa of the posttornoceratids. — The marginal concavities in the protornoceratid septa were probably of little functional meaning, as the most of the septum surface was still concave and not adapted to withstand the increased hydraulic pressure from the living chamber. The functional meaning of further undulation of the septal margin in the *Gundolficeras* lineage is also unclear, although it is represented by a virtually continuous series of morphologies in the local fossil record (Fig. 224). Whatever was its original cause, this change initiated a profound modification of the conch geometry characterizing the important branch of the posttornoceratids. In this lineage, most of the complication of the septum geometry originated near umbo.

The succession of increasing septal complexity from *Posttornoceras superstes*, through species of the genus with increasingly acute lobes of the suture, then *Discoclymenia cucullata*, and finally *D. zigzag* with acute lobes and saddles, is consistent with stratigraphic superposition of findings (Fig. 224). It is likely to be a true phyletic change but the record is too punctuated and the distribution of particular taxa to separate geographically to have a good control of migrations and evolution. A completely vaulted septum developed near the end of the lineage. The origin of the lineage remains cryptic, although *Gundolficeras* is the likely ancestor and the origin of *P. superstes* required only a further deepening of the septal undulations.

A separate lineage evolving towards similarly complicated septa is represented by *Maeneceras* that possibly replaced the *Tornoceras* in the niche of large-sized ammonoids (Fig. 224). Too little evidence has been gathered to be sure that it is rooted in *Tornoceras* and not in *Felisporadoceras*. The problem is in a rather labile apertural shapes in these Famennian goniatites. Possibly, shallow and wide auricles could reappear as a result of a reversal in the evolution of cheiloceratids.

Proterogeny in the cheiloceratid-dimeroceratid branch. — Such changes in the profile of the aperture did not occur in the early evolution of the cheiloceratid clade. It seems that after the derivation of the *Nehdenites* lineage from *Tornoceras* (this required only a reduction of the shallow apertural auricles) the shape of aperture remained rather stable until the late Famennian. Interestingly, also in the *Nehdenites* lineage a trend towards the oxyconic shape of the conch developed (Fig. 225).

There was little change in septal geometry of the cheiloceratids, until derivation of the sporadoceratids. Like in the protornoceratids, a small indentation of the suture tended to develop and the final outcome was a rather deep, pointed flank lobe. Together with various combinations of internal conch thickenings, originally parallel to aparture but in derived forms attaining quite unexpected arrangements, this help in distinguishing species. The main change was, however, in the early ontogeny of the conch and vaulting of the internal part of the septum.

The septum is baloon-shaped aslo in its dorsal part in *Nehdenites* and generalized *Cheiloceras*, developing at the best a minute dorsal indentation. The trifid dorsal lobe is apparently the best marker of the origin of the prionoceratid and dimeroceratid lineages (Becker 1993a) but the exact sequence of events cannot be traced at present.

The evoluteness characteristic of the larval conch expanded to a few further coils in the dimeroceratid clade. Several juvenile whorls developed a very wide, cadiconic appearance (Becker 1993a). Mature *Dimeroceras* reached large size similar to that of somewhat younger *Maeneceras* and the geologically older, large-sized *Tornoceras*, being transitional between them in the septal complexity. Despite the globose conch shape and relatively little complication of the suture, the septum of derived *Dimeroceras* was completely vaulted. This suggest an adaptation to open sea environment, allowing high hydrostatic resistance of the conch but a low investment of deficit calcium in its construction. Possibly, these three large-sized early famennian goniatites were adapted to operate at different water depths.

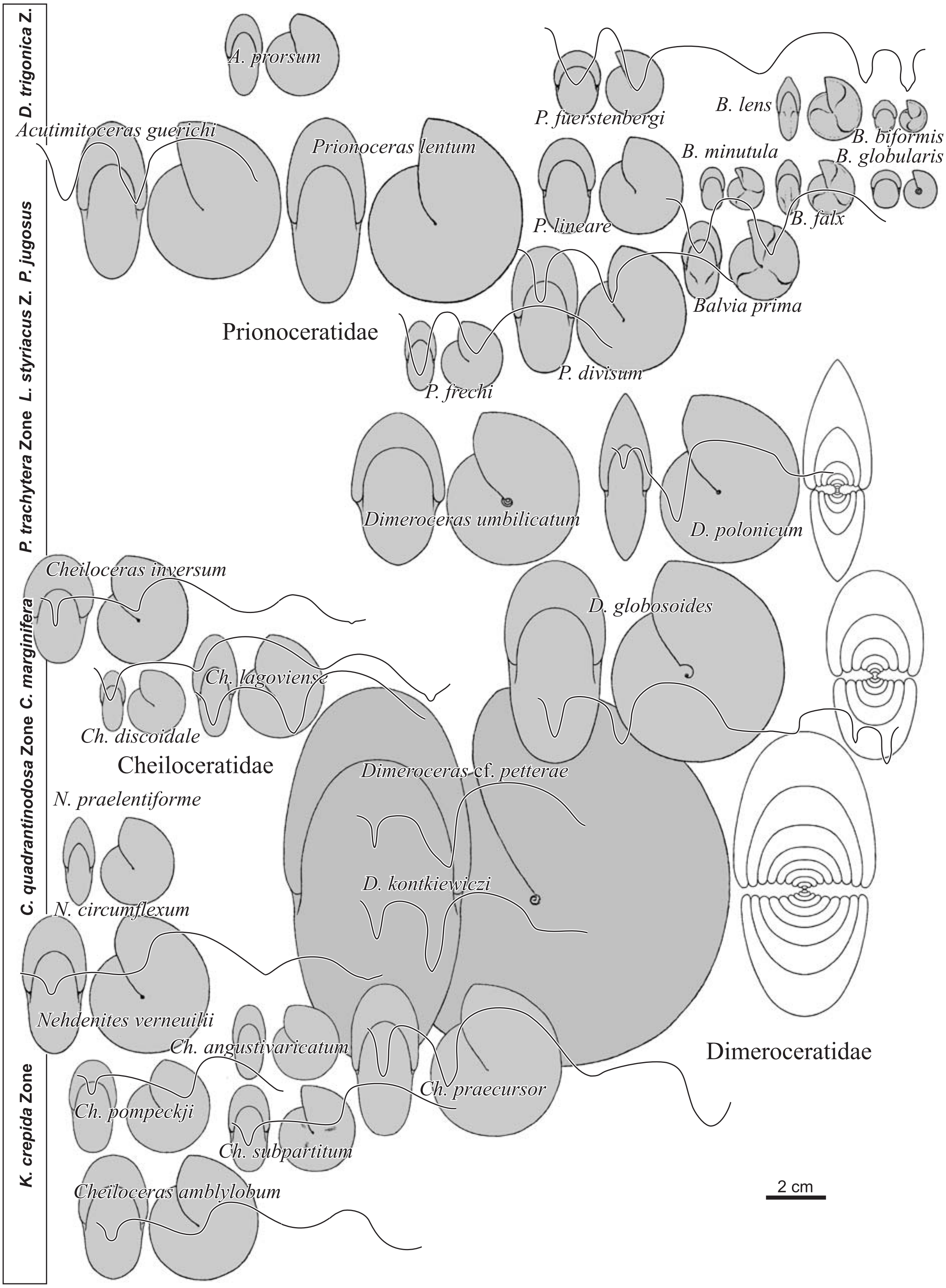

Fig. 225. Chronomorphoclines identifiable in the cheiloceratid, prionoceratid, and dimeroceratid goniatites in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 181). Contours of probably mature specimens in scale and suture lines are given.

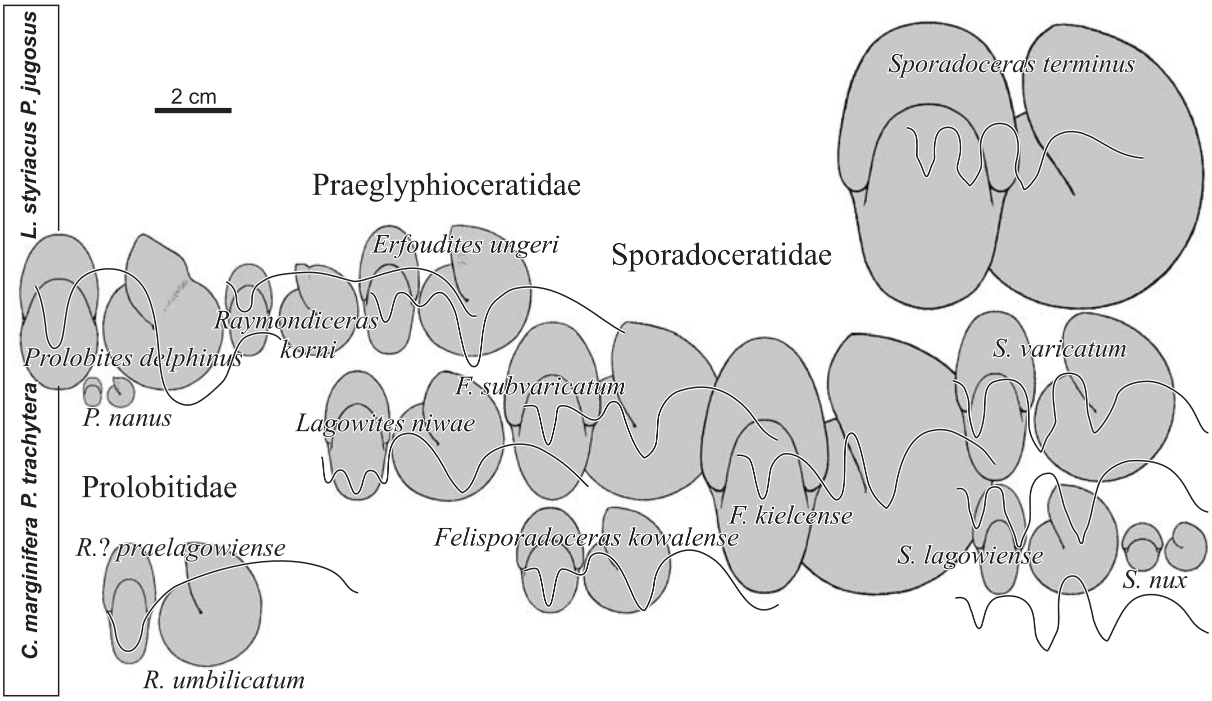

Fig. 226. Chronomorphoclines identifiable in the prolobitid, praeglyphioceratid, and sporadoceratid goniatites in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 181). Contours of probably mature specimens in scale and suture lines are given.

There are many cheiloceratid species in the Holy Cross Mountains (Sobolew 1914a) but in no single case their phyletic evolution is determined. Similarly chaotic seems the distribution of *Dimeroceras* species tending to develop oxyconic conchs (*D. polonicum*). This may be a result of the punctuated fossil record.

Diminutive prionoceratids. — A profound change in the embryonic morphology, of an extent similar to that in the *Tornoceras* larvae, took place at the origin of the prionoceratids. Their conchs and septa are rather indifferent, closely resembling those of *Cheiloceras*, from which the lineage apparently emerged. Their most characteristic aspect is the barrel-like protoconch, attaining remarkable sizes as for the ammonoids (Dzik 1997, p. 109). Such protoconchs emerge in the fossil record in the Holy Cross Mountains together with the first prionoceratids. Ironically, the increase in egg size is connected there with a decrease in size of mature conch. Advanced members of the clade, numerous species of *Balvia* known from the Sudetes, are among the smallest Devonian ammonoids (Korn 1992, 1995). Although their characteristic conchs can be easily arranged in a morphocline (Fig. 225), there is no evidence of any phyletic evolution and their distribution seems controlled mostly by migration.

Near the end of the Devonian a lineage evolving towards oxyconic conchs emerged, of much importance in the Tournaisian (Korn 1994). Another prionoceratid lineage, in which the evoluteness of early stages expanded towards the mature stages, gave origin to the evolute prolecanitid ammonoids of the Carboniferous (Korn 1994).

Simplified septa and controlled ontogeny in *Prolobites*. — The morphological simplicity of the prolobitids forced Bogoslovsky (1969) to look for their ancestry among the most underived Middle Devonian agoniatitids. But this is definitely a case of secondary simplification. There seems to be a chronomorphocline connecting the simplest cheiloceratid *Nehdenites* with *Prolobites* (Fig. 226). The change was in simplification of septa connected with evolute or even cadiconic juvenile conch geometry and in a far-reaching ontogentic regulation of mature conch features. First, the internal conch thickening was restricted to near the base of the terminal aperture, being associated there with a constriction in the living chamber. By analogy with Recent snails this may be interpreted as protective against predation. In the most derived species, the terminal aperture attained a hood-like appearance. Except for a brief time immediately before the *P. annulata* event, these goniatites were rare. Probably they occupied a rather narrow ecological niche, requiring a special and rfarely occurring environment.

Complex septa of the sporadoceratids. — Unlike protornoceratids, in the series leading from *Lagowites* through *Felisporadoceras* to *Sporadocaras*, an additional complication (fluting) of the septum occurred near its venter. This is why the "tornoceratid" *Maeneceras* may be a member of this group despite auriculate aperture. Transitional morphology of the aperture in *Erfoudites* further strenghtens this idea. Unlike the *Posttornoceras* lineage, sporadoceratids developed the complete vaulting of the septa rather late and only in the most globose species.

The most primitive sporadoceratid, *F. kowalense*, shows some similarity in its ventral septal geometry to that of the praeglyphioceratids (Fig. 226). This low-diversity branch of the Famennian goniatites has its homeomorph in the tornoceratid *Ostrovkites*. It was probably a short-lived side branch of the sporadoceratids of little importance to the phylogeny of the goniatites.

CLYMENIAS

There is little doubt that clymenias originated from *Protornoceras* (House 1970) and that the South Urals *Kirsoceras* is the connecting link. Yet, the exact course of the transition at the ordinal boundaries has not been determined. The protornoceratids form a whole plexus of species differing in the evoluteness of the conch and usually showing remarkable population variability. They continue their occurrence throughout the *C. quadrantinidosa*, *C. marginifera*, and the early *P. trachytera* zones, probably represented by lineages evolving (and speciating?) at place. Their diversity gradually increased and the immigration of the first clymenias at the beginning of the *P. trachytera* Zone is hardly discernible in the spectrum of the ammonoid conch forms. This is only the location of the siphuncle (and replacing the ventral lobe with dorsal one) which makes the difference.

The origin of clymenias. — The first clymenias emerged in the fossil record in the Holy Cross Mountains as a remarkable number of obout ten sympatric species. These were small-size ammonoids probably occuppying niches in the ecosystem closely similar to those of their relative, the protornoceratids. The beginning of the *P. trachytera* Zone is marked by a sedimentary discontinuity level (Łagów) or at least a change in facies to the predominance of black shale (e.g., Kowala) and obviously a whole new biota invaded the area together with this environmental change. Perhaps the migration route was from the east (the South Urals) to

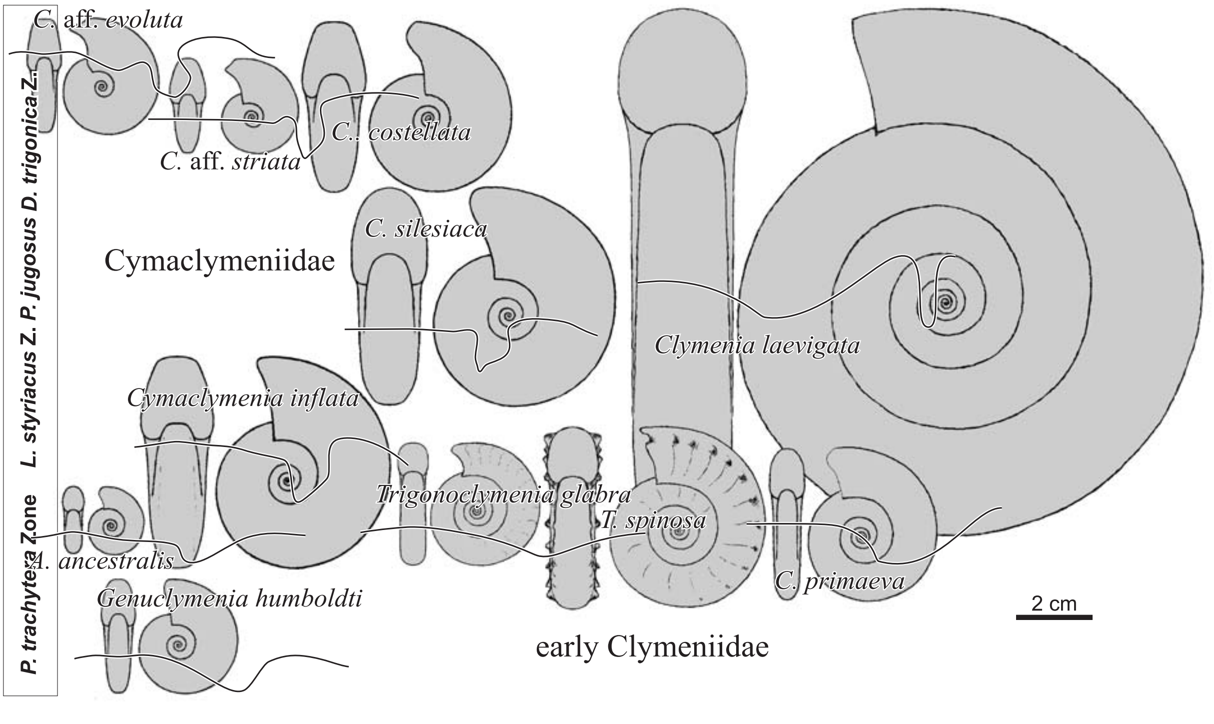

Fig. 227. Chronomorphoclines identifiable in the cymaclymeniid and early clymeniid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 196). Contours of probably mature specimens in scale and suture lines are given.

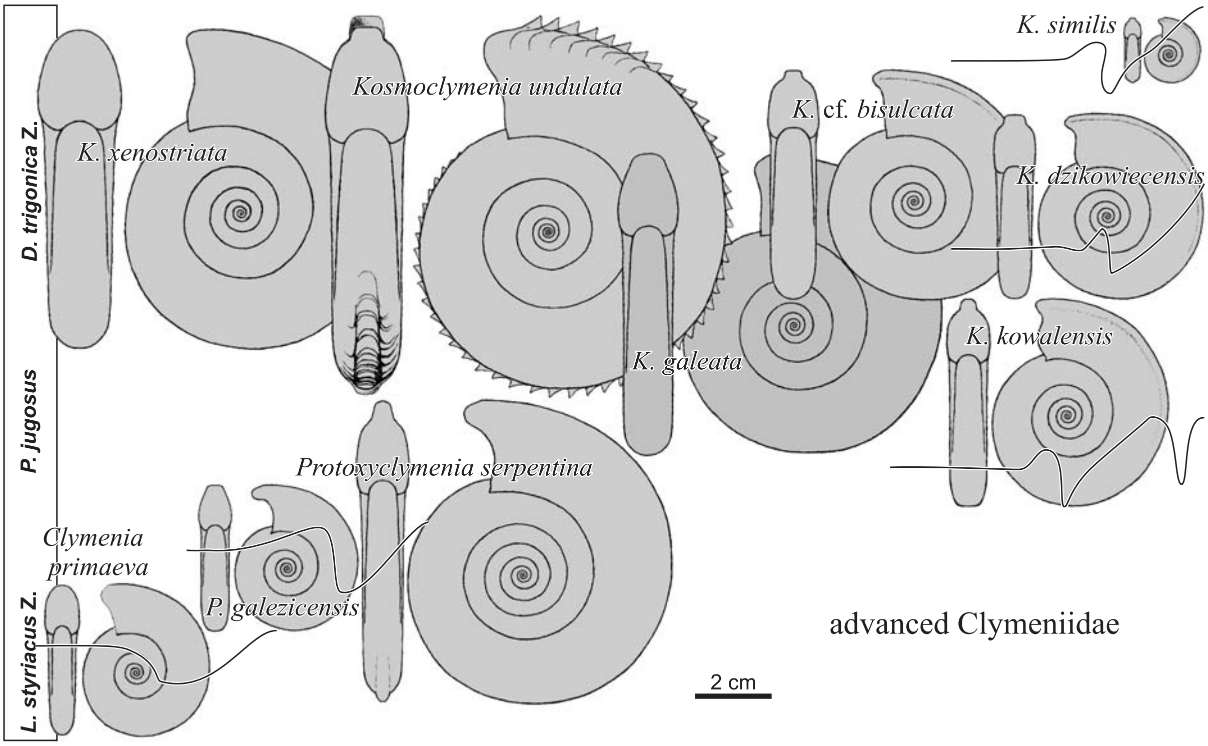

Fig. 228. Chronomorphoclines identifiable in the advanced clymeniid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 196). Contours of probably mature specimens in scale and suture lines are given.

west (the Rhenish Massif). This pattern of faunal change precludes any precise phylogenetic studies of the origin and early diversification of clymenias in the Holy Cross Mountains. The clymenias do not have any local roots there.

It seems to be of importance that among the earliest clymenias species with the conch geometry closely resembling *Protornoceras* dominate (Fig. 227). Among them there are species (of *Aktuboclymenia*) with the septal geometry of tornoceratid aspects (except for the location of siphuncle). This conch morphology has appeared highly conservative and continued their occurrence, with some minor modifications, to the end of the occurrence of the order (in the *Cymaclymenia* lineage). Paradoxically, the relatively complex suture and rather involute conchs, rather untypical for the clymenias, appear to be ancestral (plesiomorphic features).

Secondary evoluteness of the clymeniids. — Taking this point of view, the subsequent steps of the evolution was apparently simplification of the septum, which attained the baloon geometry. It can be inferred from the distribution of characters among the first Polish clymeniids, that this happened in the common ancestor of the cyrtoclymeniids (*Cyrtoclymenia*, *Pleuroclymenia*, *Platyclymenia*) and hexaclymeniids (*Praeflexiclymenia*, *Stenoclymenia*), after separation of its lineage from the ancestral cymaclymeniids (*Aktuboclymenia*). Interestingly, in the subsequent independent evolution of each of these branches, the evolute conch geometry developed. A similar increase in the spectrum of conch geometry took place earlier in the *Protornoceras* clade. In all these cases, the probable developmental mechanism of the process was an extension of the early postlarval conch geometry to later stages of the ontogeny.

Platyclymenia and *Cyrtoclymenia* were first clymenias with conch size comparable to that of the stratigraphically preceding them goniatites (Fig. 231). Even larger sizes have been achieved some time later by *Clymenia*.

Thus, from the early branch of the clymeniids with *Protornoceras*-like suture the lineage of *Trigonoclymenia* developed. This led to probably the most evolute and geometrically simple conch morphology of *Clymenia*, generally (but not quite correctly) believed to be typical of the clymenias. Despite simplified conch morphology, the septum of *Trigonoclymenia* is primitively complex. One may guess that *Kosmoclymenia* is its descendant (Fig. 228). Its septal geometry is somewhat more complex and the tendency to a periodic expansion of aperture developed further, resulting in various funnel-like structures. *Kosmoclymenia*

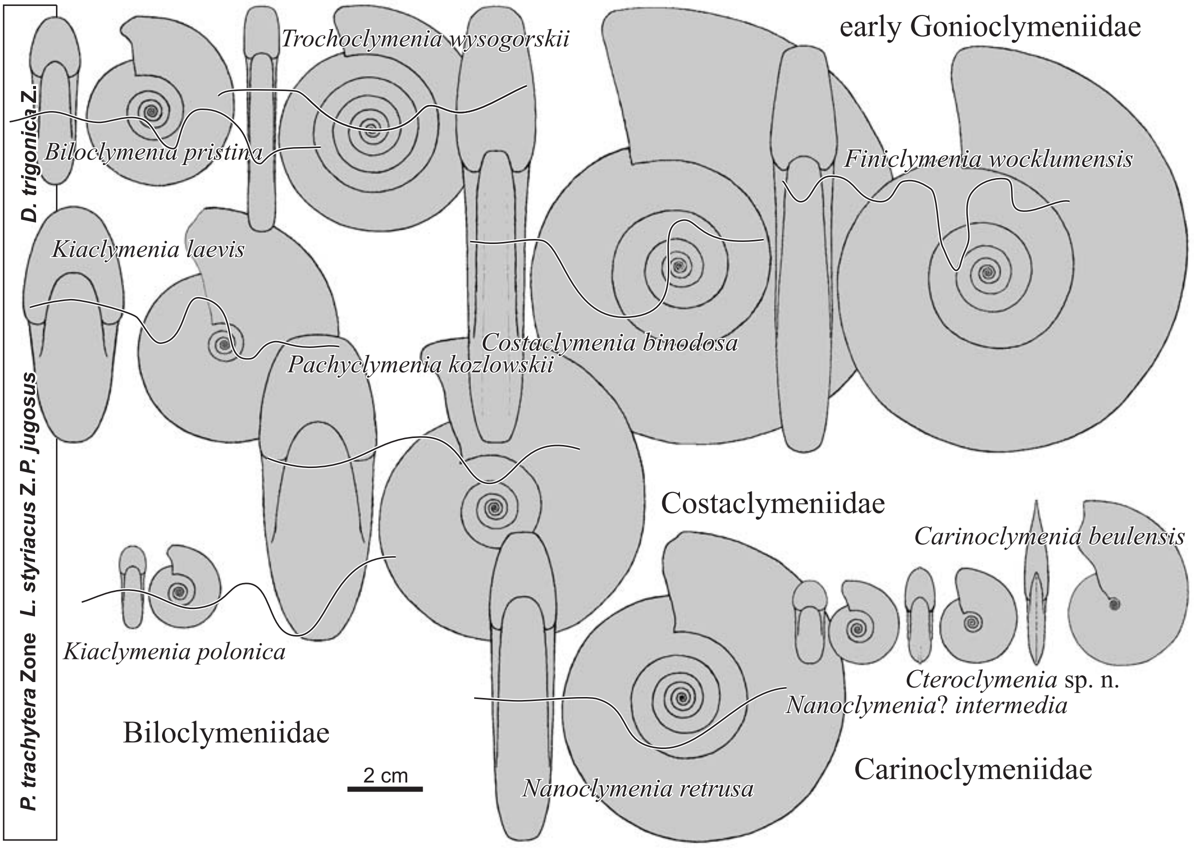

Fig. 229. Chronomorphoclines identifiable in the carinoclymeniid, biloclymeniid, costaclymeniid, and early gonioclymeniid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 218). Contours of probably mature specimens in scale and suture lines are given.

is among the most speciose genera of the clymenias. Probably the most significant aspect of its evolution is the rather advanced control of the course of ontogeny. The adult living chamber of *Kosmoclymenia* has a ventral tabulate keel, in many species with periodic apertural funnels protruding (Korn and Price 1987). The maturity was achieved at very different sizes. In some species with minute conch, the ventral keel continues throughout most of the ontogeny. Attempts to restore the course of evolution show a rather complex picture (Korn and Price 1987) and no continuos series of samples showing the phyletic evolution has been assembled until now.

Biloclymeniid septal geometry. — A highly specific mode of modification of the septal geometry was initiated in the late *P. trachytera* Zone (immediately before the *P. annulata* Event) in the lineage of *Genuclymenia*. A relationship to the geologically older *Nanoclymenia* is suggested by the transitional morphology of both the conch and suture of *Pachyclymenia*, known from significantly younger strata and probably relict. In the course of evolution, the septum attained quite a complex appearance but lobes remained smoothly sinuous until the disappearance of the lineage in the early *D. trigonica* Zone (Fig. 229).

Complex septa of the gonioclymeniids. — The tornoceratid septa and evolute conchs are shared by *Nanoclymenia* and *Costaclymenia*, the probable ancestors also of the carinoclymeniid and gonioclymeniid clades. There is a series of progressive complication of the septal geometry, proceeding in the periumbonal, ventrolateral and ventral parts of the septum, and leading to acute tips of lobes and finally of saddles (Fig. 229). *Gonioclymenia*, with its acute saddles is apparently younger geologically than the less derived *Kalloclymenia*. It was also the largest ammonoid of the Famennian. The most complex suture characterizes *Sphenoclymenia* from the *D. trigonica* Zone, but otherwise the stratigraphic distribution of morphologies does not help in deciphering the course of evolution (Fig. 230). These clymenias were apparently ecologically specific and their distribution was controlled more by changes in environment than by their evolution.

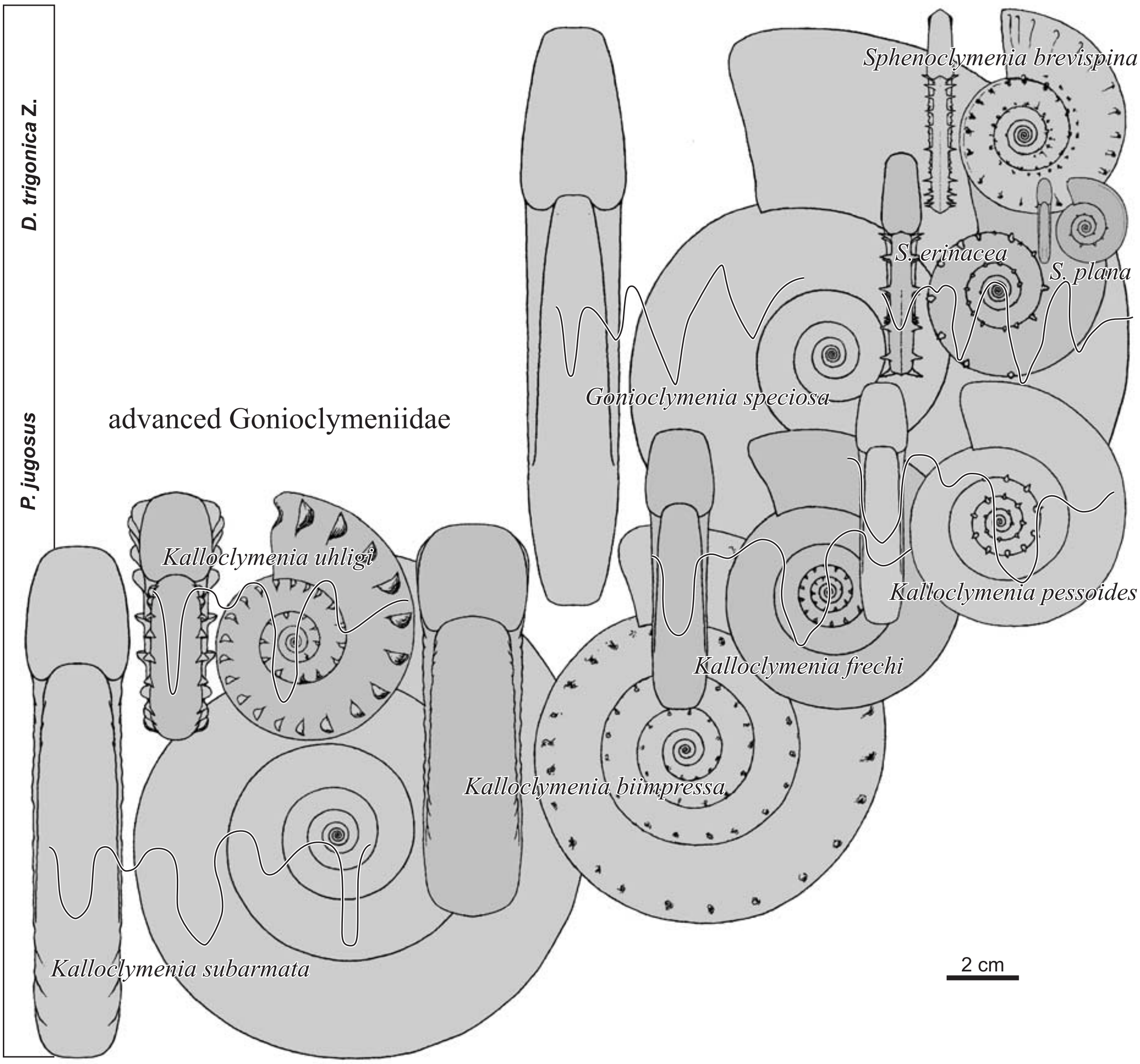

Fig. 230. Chronomorphoclines identifiable in the advanced gonioclymeniid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 218). Contours of probably mature specimens in scale and suture lines are given.

Acutely discoidal clymeniids. — Among the early clymenias with a tornoceratid septum, a tendency towards developing a discoidal conch shape, ventral ridge, and then extremely oxyconic conch was quite early initiated (Fig. 229). The succession of morphologies, with *Carinoclymenia* at the end, is consistent with stratigraphy in the Holy Cross Mountains and it is likely that the lineage evolved phyletically at the place.

Carinoclymenia was parallelled in its evolution by the unrelated conservative lineage of *Cyrtoclymenia* (Fig. 231), perhaps having something to do with more advanced in the septal geometry, geographically widespread *Falciclymenia*.

Proterogenetic lineage. — One of the most celebrated cases of the proterogenetic expansion of juvenile morphology to adult stages of the conch development in the ammonoids (Schindewolf 1937; Korn 1992, 1995; Becker 2000) can be supported and extended backward with the data from the Holy Cross Mountains. Specimens of *Soliclymenia aegoceras* from the early *P. jugosus* at Kowala (older than the minute Dzikowiec species), showing a narrow sharp-edged venter of the mature living chamber, point out towards *Stenoclymenia* as the ancestor of the lineage (Fig. 232). Even less derived member of the lineage seems to be *Praeflexiclymenia*, species of which are among the first clymenias in the Holy Cross Mountains. The evolution there was first towards simplification of septa, then increase in the conch evoluteness and tabulation of

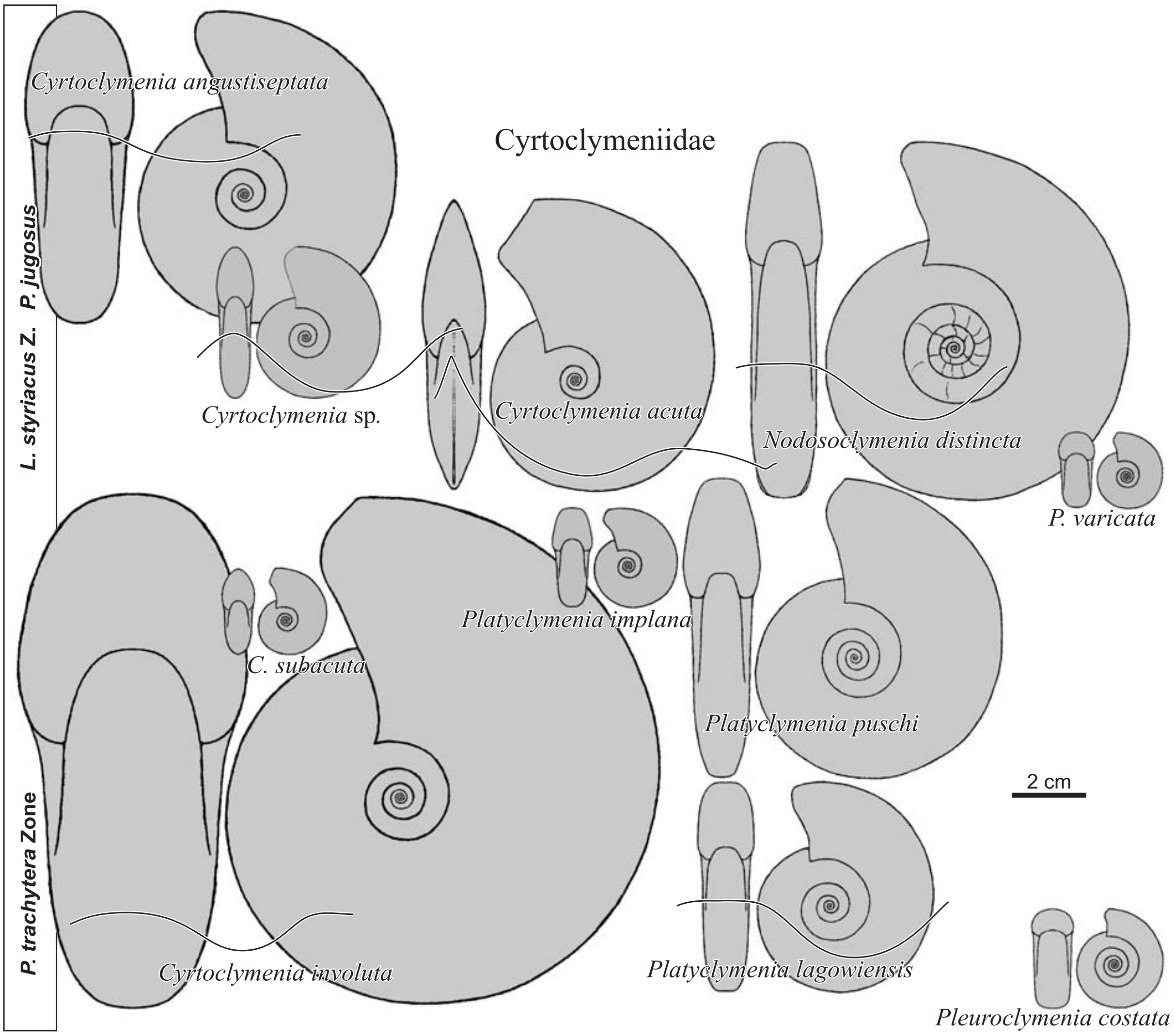

Fig. 231. Chronomorphoclines identifiable in the cyrtoclymeniid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 223). Contours of probably mature specimens in scale and suture lines are given.

the venter, and finally diminution in size and domination of ribbing on flanks of low whorls, earlier occurring only in juveniles.

Trigonal and involute wocklumeriid conchs. — This is the second case of proterogenesis and development of trigonal conch shape presented by Schindewolf (1937). The relationships within and the origin of the wocklumeriids was a matter of controversy until the subject was reopened in recent times (Korn 1992, 1995; Becker 2000). It seems now that both *Parawocklumeria* and *Epiwocklumeria* are related to *Glatziella* and have their roots in *Rhiphaeoclymenia*. The sequence of events started from formation of two ventrolateral furrows in *Rhiphaeoclymenia* inherited by its successors. In the lineage of *Glatziella* a cadiconic conch morphology developed, retaining the lateral ribbing until it was lost in *G. glaucopis*. Near the end of the Famennian the tendency to size decrease was partially reversed in the lineage of *Glatziella*, the last member of which is of medium size, typical for most of the Late Devonian ammonoids.

In the *Kamptoclymenia–Parawocklumeria* lineage, the ribbing disappeared, being replaced by constrictions at early ontogenetic stages, three per whorl. Mature living chamber preserved ventrolateral furrows until they were lost in *P. distorta*. Furrows are also missing in *Epiwocklumeria* and *Wocklumeria*. These latest Famennian lineages evolved divergently, developing involute oxyconic conch in *E. bohdanowiczi* (with complex ontogeny) and cadiconic conch do not showing significant ontogenetic changes in *Wocklumeria*

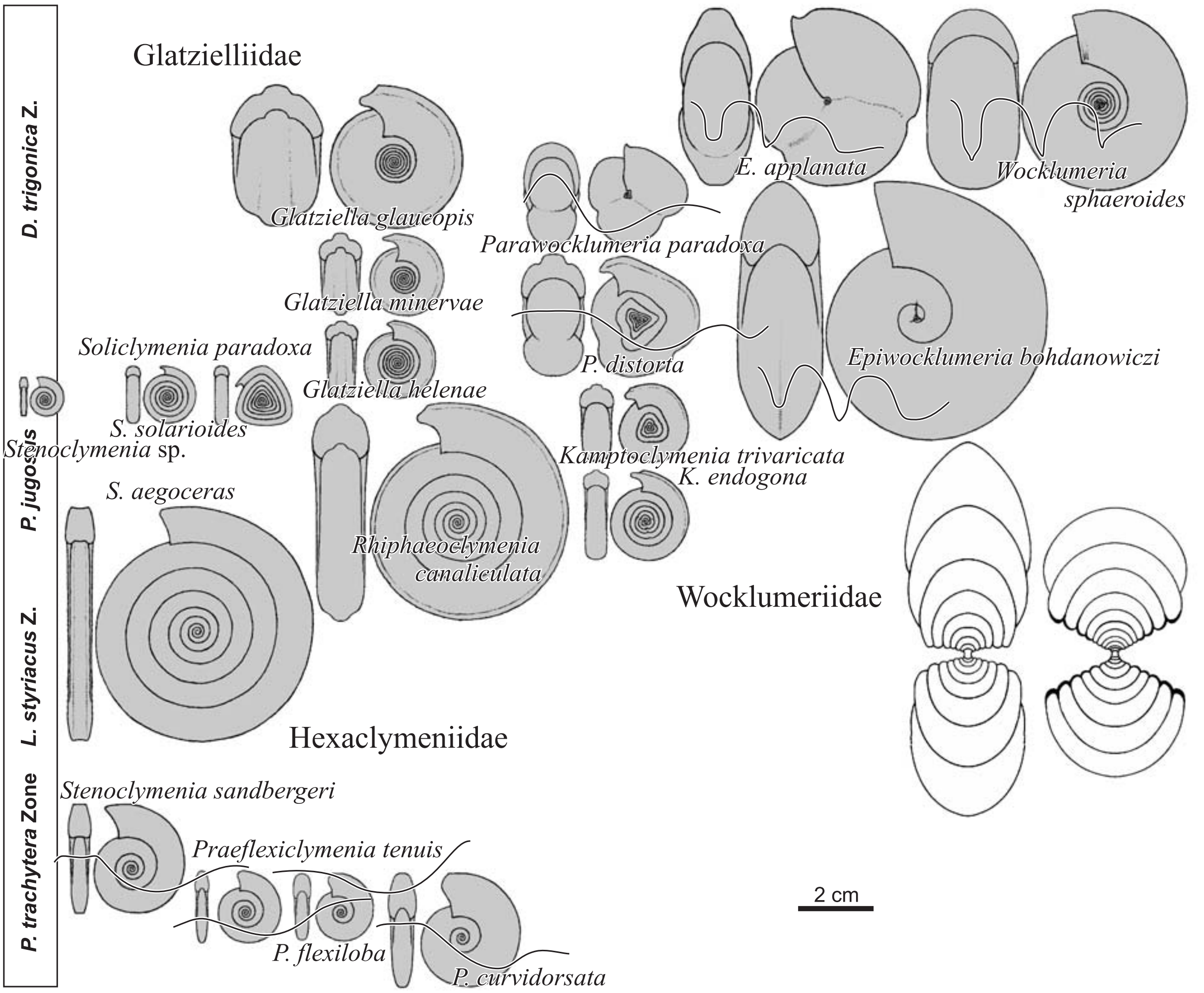

Fig. 232. Chronomorphoclines identifiable in the hexaclymeniid, glatziellid, and wocklumeriid clymenias in the Polish Famennian (for details of stratigraphic distribution of species see Fig. 223). Contours of probably mature specimens in scale and suture lines are given.

sphaeroides. The stratigraphic distribution of these clymenias in the Holy Cross Mountains and Sudetes does not help in deciphering the precise pattern of phylogeny (Fig. 232).

Even more problematic is the origin of the glatziellids and wocklumeriids. Their narrow tabulate venter and prominent juvenile whorls ribbing suggests that *Hexaclymenia* may be their ancestor. A significant time and morphologic gap separates these taxa, so much research is necessary to solve the question.

FAUNAL DYNAMICS OF OTHER FAMENNIAN PELAGIC ANIMALS

In most attempts to interprete profound changes in the Devonian living world abiotic factors tend to be invoked as the only motor of evolutionary change, frequently even of extraterrestrial nature. This is despite the at least equally obvious influence of the evolution of organisms on the environment (e.g., Algeo *et al*. 2001). No doubt that the evolutionary expansion of some ecologically important group of organisms to environments earlier not inhabited by them, or appearance of completely new modes of exploitation of the environment, had a significant influence on fates of the Devonian biota. The fossil record is awfully incomplete in respect to the main producers of biomass in the Devonian, mostly lacking any mineral skeleton and known from very few fossils from rare localities with soft-bodied organisms preservation. But even the available limited evidence provides a remarkable list of high-rank taxa that emerged and expanded in diversity during the Devonian. Among them are the largest pelagic predators of the Famennian: the open-sea sharks, crossopterygian and ganoid fishes, concavicarid and angustidontid crustaceans, and ammonoid cephalopods. The Devonian was the time of emergence and diversification of the eumalacostracan crustaceans.

At least some of the conodonts seem to be ecological analogues of the recent chaetognaths, feeding on small crustaceans. It remains unknown which of the planktonic filter-feeding crustaceans inhabited the Famennian seas. their weakly sclerotized body covers had little chance to fossilize. Among the planktonic crustaceans only ostracodes offer a reasonable fossil record of their faunal dynamics and evolution.

Entomozoacean ostracodes. — Faunal changes in planktonic ostracodes across the Frasnian–Famennian boundary has been described by Olempska (2002). Interestingly, the earliest Famennian assemblage of entomozoaceans has appeared to be of very low diversity with single dominant species of *Franklinella*, supplemented with rare *Nehdentomis* in higher part of the section at Płucki. This contrasts with the high diversity latest Frasnian assemblage. Pyritized entomozoid carapaces are common in black shale or limestone facies throughout the Famennian.

Concavicarid thylacocephalans and *Angustidontus*. — Phosphatized crustacean carapaces and grasping appendages are abundand on some bedding planes in the early Famennian laminated limestone at Wietrznia and Kowala. The strongly sclerotized carapaces with reticulate surface pattern up to 5 cm in length represent an unnamed species of *Concavicaris*. These were relatively large predators with large compound eyes and long but rather weakly sclerotized grasping appendages emerging from the ventral opening of the carapace, but except for carapaces nothing convincingly attributable to the concavicarids has been identified in the Holy Cross Mountains material. No doubt, however, that they were common in the pelagic environment during the Famennian playing an important role in the ecosystem.

Strongly sclerotized, secondarily phosphatized appendages and mandibles (Dzik 1980) of *Angustidontus* co-occur with concavicarids in great number throughout most of the early Famennian in the Holy Cross Mountains. These were eumalacostracans with the first postoral appendage pair transformed into a mantis-like grasping apparatus (Rolfe and Dzik 2007). Ironically, opposite to the situation in *Concavicaris*, the appendages of *Angustidontus* preserve well in the fossil record but the carapace was weakly sclerotized and no remnats of it has been found in the Holy Cross Mountains material. Although pelagic, *Angustidontus* may be related also to the stomatopods, predatory benthic crustaceans with reduced carapace, known since the Early Carboniferous. The alternately toothed grasping parts of the *Angustidontus* appendages closely resemble “hindeodella” type of conodont elements but are of an order of magnitude larger. It is likely that they fed on conodonts.

Nautiloids. — Nautiloids co-occur with ammonoids in all localities of cephalopod limestone or black shale of the Frasnian and Famennian of the Holy Cross Mountains and the Sudetes. The terminal Frasnian linguiformis Zone cephalopod limestone occurs in Wietrznia and Płucki. Nautiloid fossil assemblages of these sites differ dramatically, despite their age and similar conodont assemblages. In Płucki, numerous orthoconic bactritids and *Plagiostomoceras*-like orthoceratids co-occur with small-size oncoceratids probably representing an unnamed species of *Pachtoceras* (Dzik 1985). At Wietrznia, oncoceratids dominate, with large extremely breviconic undescribed form and *Lysagoraceras*-like slender conchs. The only nautiloid shared by both sites is a large orthocerati resmbling the Famennian *Plagiostomoceras*? *cardiolae* (Gürich, 1896). The only locality with cephalopod limestone of the *K. triangularis* Zone is Psie Górki. The assemblage is composed almost exclusively of crushed indeterminable oncoceratids. Diverse assemblages of nautiloids has been identified in the *K. crepida* Zone at Kadzielnia and *C. marginifera* Zone at Łagów-Dule (Dzik 1985). In the latter locality also the clymeniid limeston of the *P. trachtera* Zone yielded nautiloids, but the fossils were collected from loose blocks and it is rarely possible to be confident with its exact stratigraphic location The only reliable source of stratigraphic information on Łagów-Dule remains the study by Sobolew (1912b). Anyway, all those faunal assemblages appear to be rather different from each other but not as a result of different age, but rather of different environment. The oncoceratid nautiloids species were apparently very sensitive on the local condition. The overall spectrum of their morphologies in the Famennian is the same as in the latest Frasnian and there is hardly any reason to see termination of a substantial potrion of their lineages at the Frasnian–Famennian boundary.

The mode of life of the orthoceratid and oncoceratid nautiloids, as well as their trophic preferences, remain a mystery. They were hardly efficient swimmersand even their predatory abilities may be questioned. The only unquestionable large predators of the late Devonian remain the vertebrates.

Fishes. — In the Late Devonian three groups of vertebrates are already well established in the open sea pelagic environment: ganoid fishes, sharks, and the acanthodians (e.g., Blieck *et a*l. 2000; Ginter 2001). They all have Silurian roots in near-shore marine environments and in the late Silurian they rarely co-occur with conodonts in pelagic sediments.The difference in facies distribution of early vertebrates and conodonts was probably a reflection of their physiology. The conodont's kidneys, similarly to Recent myxinoids, apparently lacked renal tubuli enabling osmotic regulation of sodium content in their blood and could not enter waters of lowered salinity (Dzik 2000). This was opposite to the early agnathans and fishes easily entering brackish waters and in the Devonian (like Recent petromyzontids) expanding both to rivers and to the ocean.

The most complete record of the stratigraphic and geographic distribution of fishes is offered by acid resistant residues of limestone samples. The biological productivity of fishes was a small fraction of that of the conodonts. Only in samples from stratigraphically condensed sections, where winnowing enriched the lime mud in phosphatic debris, more than a few specimens per a few kilogram weight sample can be collected. Teeth and scales of the chondrichthyans are known from both the Frasnian and Famennian, and there is no special reason to propose any dramatic change in fish faunas at the boundary in the Holy Cross Mountains (Ginter 1992, 1995, 1999, 2000, 2002). Also placoderms, known mostly after isolated large bones show a phyletic continuity across the boundary (Ivanov and Ginter 1997). Acanthodians, known mostly after their scales, also occur on both sides of the boundary.

The Famennian fishes represent various levels in the trophic pyramid of their ecosystem. The shark *Cladoselache* from the Cleveland shale (Cleveland Member of the Ohio Shale Formation) of Ohio is known to prey on the ganoid fish *Kentuckia* (found in the stomach contents of 65% of 53 specimens; Williams 1990), but also on the crustacean *Concavicaris* (28%), and conodonts (9%). Other fishes probably were more inclined to benthic animals as their food, as suggested by coprolites from the underlying Chagrin Member of the same Formation (Hannibal *et al*. 2005). Most probably, the sharks in the Polish Famennian played a similar role as those in Ohio, as all these groups of pelagic animals are abundantly represented there in acid-resistant residues.

The characteristic feature of the early Famennian *K. triangularis* Zone fish assemblages from Karczówka and Jabłonna is the relative abundance of scales and teeth of the protoacrodontid sharks (cf., Ginter and Piechota 2004) and the acanthodians, thus a composition closely similar to the assemblage from the latest Frasnian at Miedzianka. Remnants of crossopterygian fishes are also known from the early Famennian of Karczówka (scales) and Kowala (onychodontid skull; Dzik 1992, fig. 1.6C). Interestingly, in the earliest Famennian of Dębnik near Kraków the same species of the crossopterygian *Strunius* occurs (Ginter 2002) as in the latest Frasnian of Miedzianka and Kowala. The similarity in local environment (near shore in both cases) were apparently more important than the difference in age.

The change in composition of the fish assemblages during the Famennian is mostly connected with facies changes, and only to some degree a result of evolutionary transformations. In the black limestone of the *C. marginifera* Zone at Łagów, where fish skeletal remains are relatively common, teeth of the phoebodontid sharks dominate in number over the acanthodian and ganoid fish scales. Near the *Platyclymenia annulata* Event black shale (*P. trachytera* Zone) at Kowala and limestone at Ostrówka, the ganoid? fish teeth and scales dominate associated by acanthodians, with minor contribution of shark teeth.

The general pattern of the fish distribution in the Famennian of the Holy Cross Mountains is towards reduction in their diversity (Fig. 233). This is most apparent in case of sarcopterygian fishes, known only in the earliest Famennian *P. triangularis* Zone. Chondrichthyan scales, probably partially belonging to placoderms, occur mostly in the late part of the Zone and in the *K. crepida* Zone. They disappear from the record after the *P. trachytera* Zone. The ganoid fish scales and conical minute teeth seem to be restricted to two episodes of high sea-level stand, in the *K. crepida* and *P. trachytera* zones. These were apparently open-sea pelagic species. Also acanthodians are common in most of the succession but are rare in the late Famennian. The most uniform is distribution of shark teeth. Rare teeth of advanced phoebodontid *Thrinacodus*, less derived sharks and ganoid scales occur throughout the late Famennian. They continued to the Carboniferous in the region.

Possible cause of the diversity changes. — It is generally accepted that taxonomic diversity of marine communities is a function of the heterogeneity of the environment, competition between individuals of various species, and predation pressure (Paine 1966; Connell 1975; Menge and Sutherland 1976, 1987). The pelagic environment of the Famennian Variscan Sea, located in low latitudes and opened to the ocean, the heterogeneity factor was probably of minor importance. One may thus wonder whether there were changes in predation or rather in competition that made the diversity of conodonts and ammonoids to change so dramatically (Fig. 233).

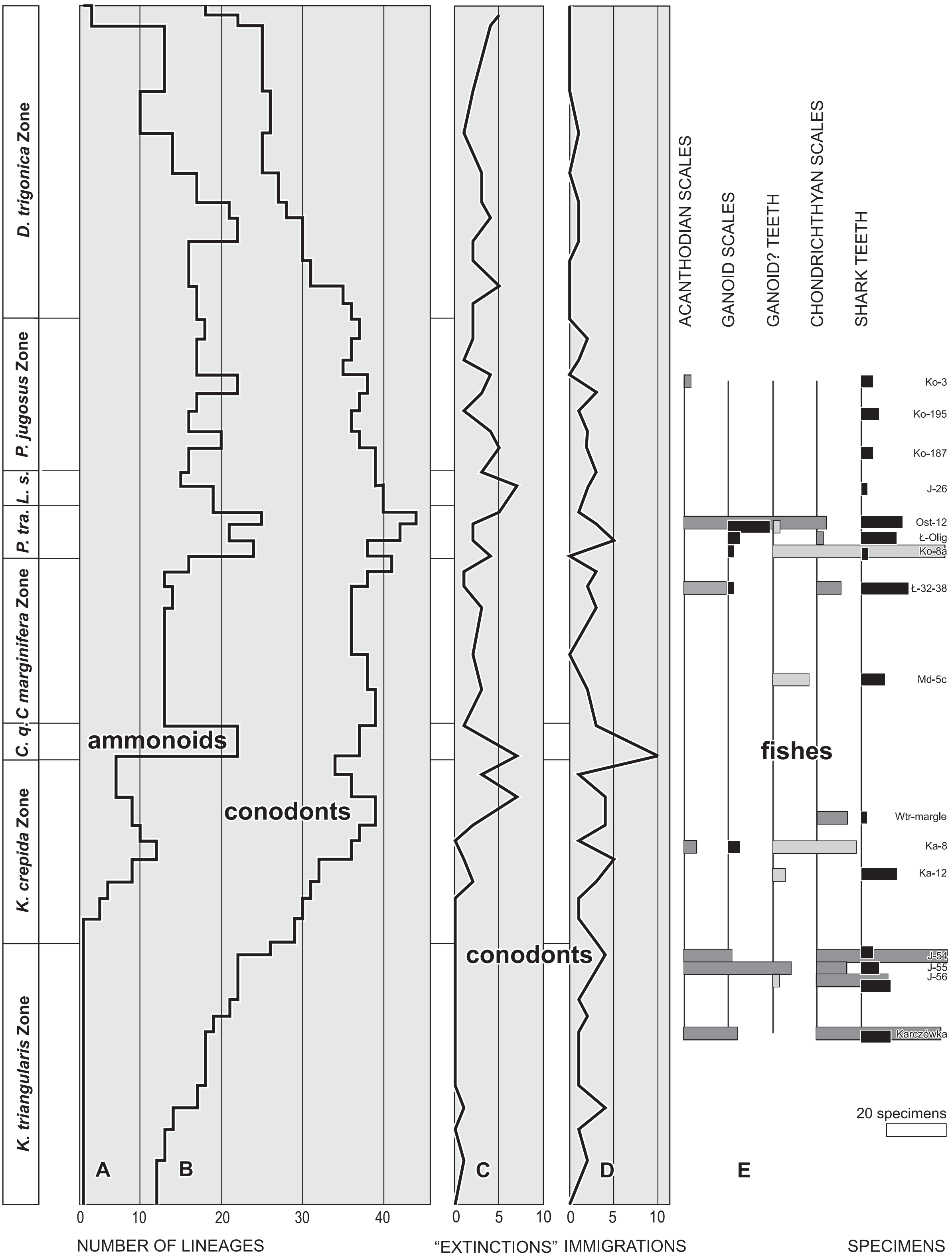

Fig. 233. Dynamics of the Famennian pelagic faunas in the Polish part of the Variscan sea. Number of lineages has been inferred from the punctuated fossils record of conodonts and ammonoids by connecting the known occurrences by hypothetical lineages. Note that the age correlation of particular sections is not precise enough to be distinguish sympatric occurrences from successive occurences. The time segments within particular zones are arbitrary. Numbers of lineages disappearing from the record or immigrating to the area are counted for each of those units. Fish remains (ichthyoliths) are rare in most conodont samples and their number is given only for the most productive samples to show horizons with their greatest abundance and contribution of particular high-rank taxa to samples.

The conodonts were small predators with a 3–7 cm long lamprey-like bodies. They most probably occupied niches similar to those of the present-day chaetognaths and fed on small planktonic arthropods (e.g., Sweet 1988). They were almost certainly a prey to co-occurring predatory concavicarid crustaceans and possibly also to the ammonoids. Both these groups of Devonian animals had body volume at least an order of magnitude larger than the conodonts. However, in the Devonian the fishes entered pelagic environments and their contribution to fossil assemblages with conodonts and ammonoids gradually increased. It is thus tempting to check whether there was a correlation between the productivity and diversity of conodonts, ammonoids, and fishes in the course of the evolution of the Famennian ecosystem of the Variscan Sea.

The available data are unavoidably incomplete and biased, as usual in paleontology, so it would be premature to expect that a rigorous statistical work can be done based on the evidence assembled in this work. Anyway, some preliminary observations may be useful as suggestion to future research. However incomplete is the fossil record in the Famennian of the Holy Cross Mountains, it is apparent that the species diversity of conodonts dramatically, although gradually increased to reach a plateau in the *K. crepida* Zone (Fig. 233). Ammonoids show a similar pattern, but they did the same with a significant delay. They were also delayed in respect to conodonts in reducing their diversity in the late Famennian. Both groups suffered equally near the end of the Famennian, however. The pattern of distribution of skeletal elements of fishes (ichthyoliths) is completely different. The peak in their taxonomic diversity and abundance of fossils was in the earliest Famennian and there was apparently a continuity from the Frasnian, even at the species level. The dominant chondrichthyan probably gradually decreased abundance and perhaps also species diversity and only the distribution of the ganoid fishes seems correlated with eustacy, their occurrence reaching the highest level during the *K. crepida* and *P. trachytera* zones high stands of the sea level. These peaks are identifiable also in the pattern of diversity of conodonts and ammonoids, but in both cases are not so dramatic.

It can thus be hypothesized that it was probably not the predation pressure from fishes that caused conodonts and ammonoids to increase their diversity in the early Famennian. It is also unlikely that the ammonoids were the source of factors governing the distribution of taxonomic diversity of the conodonts. We have thus to return to the factor of the environment instability to explain the observed pattern of the conodont and ammonoid faunal dynamics in the Famennian of the Polish part of the Variscan Sea. However, it was probably not the instability in the ecological time terms. The source of diversity was probably provided rather by several climate and sea level changes, which forced the pelagic to change their large-scale geographic distribution (?progressive cooling and glaciation; Streel *et al.* 2000; Brand *et al.* 2004).

This could have been a factor promoting allopatric speciation and subsequent mixing of geographically distant communities. Much more research based on dense sampling in different regions of the world is necessary to identify exact sequence of events in their time and space dimensions.

CONCLUSIONS

Pelagic organisms with mineral skeleton offer the best fossil record of evolution. Among them the phosphatic teeth of conodonts are especially abundant, easy to be extracted from rock samples, and rich in information of taxonomic value. Ammonoid conchs can compete with them as a subject of evolutionary research. Although not so easily fossilizing, they attract collectors and after more than two hundred years of their professional studies by geologists and paleontologists over the whole world, one may expect that knowledge of their evolution is reasonably complete. Yet, having an opportunity to study a large collection of conodonts and ammonoids and compare it with a tremendous amount of published data I am hardly able to present a convincing picture of the evolution of pelagic biota in the Famennian of central Europe. Two aspects of the fossil record of their evolution makes this so difficult.

The first obstacle is that almost all the available evidence is restricted to the equatorial climatic zone of the Late Devonian (compare Racki 2005). As a result, the geographic dimension of their evolution remains out of reach of their students. With data from thousands of conodont samples and hundreds of localities along the equatorial zone, the evolving lineages should be traced whenever they enter the tropics. Unfortunately, taxonomic resolution seems to be too low to see all the important differences and identify affinities at sufficiently low taxonomic level. This is because virtually all the published data is on typologically defined forms of one element type in the oral apparatus, which is composed of many elements representing usually six or seven different morphologies. The apparatus reconstructions presented in this and a few other published works help in removing this limitation. They still are too few and from not enough numerous regions to enable understanding of their evolution in time and space. Much more apparatus research is necessary to achieve this.

The second difficulty is caused by the punctuated distribution of fossiliferous strata, controlled by eustacy and changing climate, so profound in the Famennian (Johnson *et al.*, 1985, Walliser 1996; Streel *et al*. 2000). In cases when the record is complete enough to record evolution, as is the case with the palmatolepidid conodont *Tripodellus* or oxyconic goniatite *Tornoceras* lineages, its gradualistic nature is obvious. In other cases the evolution was probably of the same nature and only punctuation of the record prevents its presentation. Anyway, the sections with potentially accessible record of the phyletic evolution are rare as compared with those clearly showing geographic migrations. No doubt that migration was the most important factor controlling distribution of the equatorial Devonian faunas of pelagic organisms.

A good record of evolution appears to be more difficult to find near the paleoequator than in regions located in high paleolatitudes. No doubt that in purely physical terms the environment is less stable in high latitudes, whereas there is no special reason to believe that conditions of sedimentation differed between latitudes, in respect to possible preservation of continuous fossil record. What exactly caused this distinction remains to be determined but one may speculate, that the equatorial organisms are sensitive to even minor differences in environment, to which they immediately respond by changing their spatial distribution. It may be enough that cold deeper waters enter, or retreat from, shallow oligotrophic seas, changing either their temperature or primary productivity, to cause a dramatic rebuilding of assemblages. Perhaps what we observe in the pelagic Famennian of the Holy Cross Mountains and the Sudetes is an illustration of numerous such changes.

REFERENCES

Aboussalam, Z.S. 2003. Das “Taghanic-Event” in höheren Mittel-Devon von West-Europa und Marokko. *Münstersche Forschungen zur Geologie und Paläontologie* **97**, 1–332.

Algeo, T.J., Scheckler, S.E., and Maynard, J.B. 2001. Effectes of the Middle to Late Devonian spread of vascular land plants on weathering regimes, marine biotas, and global climete. *In*: P.G. Gensel and D. Edwards (eds) *Plants Invade the Land. Evolutionary and Environmental Perspectives*. 213–253. Columbia University Press, New York.

Austin, R.L., Orchard, M.J., and Stewart, I.J. 1985. Conodonts of the Devonian System from Great Britain. *In*: A.C. Higgins and R.L. Austin (eds) *A Stratigraphical Index of Conodonts*. 93–166. Ellis Horwood Limited, Chichester.

Baliński, A. 1995. Brachiopods and conodont biostratigraphy of the Famennian from the Dębnik Anticline, southern Poland. *Palaeontologia Polonica* **54**, 1–88.

Baliński, A., Olempska, E., and Racki, G. (eds) 2002. Biotic responses to the Late Devonian global events. *Acta Palaeontologica Polonica* **47**, 185–404.

Bambach, R.K., Knoll, A.H., and Wang, S.C. 2004. Origination, extinction, and mass depletions of marine diversity. *Paleobiology* **30**, 522–542.

Baranowski, Z. Haydukiewicz, A., Kryza, R., Lorenc, S., Muszyński, A., Solecki, A., and Urbanek, Z. 1990. Outline of geology of the Góry Kaczawskie (Sudetes, Poland). *Neues Jahrbuch fur Geologie und Palaontologie, Abhandlungen* **179**, 223–257.

Bardashev, I.., Weddige, K., and Ziegler, W. 2002. The phylomorphogenesis of some Early Devonian platform conodonts. *Senckenbergiana lethaea* **82**, 375–451.

Becker, R.T. 1993*a*. Anoxia, eustatic changes, and Upper Devonian to lowermost Carboniferous global ammonoid diversity. *In*: M.R. House (ed.) The Ammonoidea: Environment, Ecology, and Evolutionary Change. *Systematic Association Special Volume* **47**, 115–163.

Becker, R.T. 1993*b*. Stratigraphische Gliederung und Ammonoideen-Faunen im Nehdenium (Oberdevon II) von Europa and Nord-Afrika. *Courier Forschungsinstitut Senckenberg* **155**, 1–405.

Becker, R.T. 1995. Taxonomy and evolution of late Famennian Tornocerataceae (Ammonoidea). *Berliner geowissenschaftliche Abhandlungen E* **25**, 31–41.

Becker, R.T. 1997. Eine neue and älteste *Glatziella* (Clymeniida) aus dem höheren Oberdevon des Nordsauerlandes (Rheinisches Schiefergebirge). *Berliner geowissenschaftliche Abhandlungen E* **16**, 607–643.

Becker, R.T. 2000. Taxonomy, evolutionary history and distribution of the middle to late Famennian Wocklumeriina (Ammonoidea, Clymeniida). *Miiteilungen der Museum für Naturkunde, Geowisseschaftliche Reihe* **3**, 27–75.

Becker, R.T. 2002. *Alpinites* and other Posttornoceratidae (Goniatitida, Famennian). *Mitteilungen der Museum für Naturkunde, Geowisseschaftliche Reihe* **5**, 51–73.

Becker, R.T., House, M.R., Menner, V.V., and Ovnatanova, N.S. 2000. Revision of ammonoid biostratigraphy in the Frasnian (Upper Devonian) of the southern Timan (northeast Russian Platform). *Acta Geologica Polonica* **50**, 67–97.

Becker, R.T. and House, M.R. 1994a. Kellwasser Events and goniatite successions in the Devonian of the Montagne Noire with comments on possible causations. *Courier Forschungsinstitut Senckenberg* **169**, 45–77.

Becker, R.T., Ashouri, A.R., and Yazdi, M. 2004. The Upper Devonian *Annulata* Event in the Shotori Range (eastern Iran). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **231**, 119–143.

Beinert, R.J., Klapper, G., Sandberg, C.A., and Ziegler, W. 1971. Revision of *Scaphignathus* and description of *Clydagnathus*? *ormistoni* n. sp. (Conodonta, Upper Devonian). *Geologica et Palaeontologica* **5**, 81–91.

Belka, Z. 1998. Taxonomy, phylogeny and biogeography of the late Famennian conodont genus *Mashkovia*. *Journal of Micropalaeontology* **17**, 119–124.

Belka, Z., Klug, C., Kaufmann, B., Korn, D., Döring, S., Feist, R., and Wendt, J. 1999. Devonian conodont and ammonoid succession of the eastern Tafilalt (Ouidane Chebbi section), Anti-Atlas, Morocco). *Acta Geologica Polonica* **49**, 1–23.

Berkowski, B. 2002. Famennian Rugosa and Heterocorallia from southern Poland. *Palaeontologia Polonica* **61**, 1–52.

Biernat, G. and Szulczewski, M. 1992. The Famennian brachiopod *Zilimia polonica* (Gürich) and its paleoenvironmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* **100**, 37–46.

Bischoff, G. 1956. Oberdevonische Conodonten (toId) aus dem Rheinischen Schiefergebirge. *Notizblatt der hessischen Landesamt für Bodenforschung* **84**, 115–157.

Blieck, A., Turner, S., and Young G.C. 2000. Devonian vertebrate biochronology and global marine/non marine correlation. *Courier Forschungsinstitut Senckenberg* **220**, 161–193.

Bockwinkel, J., Beker, R.T., and Ebbighausen, V. 2002. Morphometry and taxonomy of lower Famennian Sporadoceratidae (Goniatitida) from southern Morocco. *Abhandlungen der Geologischen Bunesanstalt* **57**, 279–297.

Bogoslovsky, V.I. [Богословский, В.И.] 1960. Новые представители некоторых малоизвестных родов девонских аммоноидеи из фаменских отложении Урала [New representatives of some poorly known genera of the Devonian ammonoids from the Famennian deposits of the Urals]. *Палеонтологический журнал* **1960** (4), 69–73.

Bogoslovsky, V.I. [Богословский, В.И.] 1962. Редкий тип скулптуры у климении [A rare kind of sculpture in the clymeniids]. *Палеонтологический журнал* **1962** (1), 166–168.

Bogoslovsky, V.I. [Богословский, В.И.] 1965. *Carinoclymenia* – новый род семеиства Rectoclymeniidae [*Carinoclymenia* – a new genus of the family Rectoclymeniidae]. *Палеонтологический журнал* **1965** (4), 88–91.

Bogoslovsky, V.I. [Богословский, В.И.] 1969. Девонские Ammonoidei. I. Агониатиты [Devonian ammonoids. I. Agoniatitids]. *Труды Палеонтологического Института АН СССР* **124**, 1–339.

Bogoslovsky, V.I. [Богословский, В.И.] 1971. Девонские Ammonoidei. II. Гониатиты [Devonian ammonoids. II. Goniatitids]. *Труды Палеонтологического Института АН СССР* **127**, 1–228.

Bogoslovsky, V.I. [Богословский, В.И.] 1975. Novoye semeistvo klimenii [A new family of the clymeniids]. *Палеонтологический журнал* **1975** (3), 35–41.

Bogoslovsky, V.I. [Богословский, В.И.] 1976. Ранний онтогенез и происхождение климении [The early ontogeny and origin of the clymeniids]. *Палеонтологический журнал* **1976** (2), 41–50.

Bogoslovsky, V.I. [Богословский, В.И.] 1977. О семействие Miroclymeniidae Schindewolf, 1924 [On the family Miroclymeniidae Schindewolf, 1924]. *Палеонтологический журнал* **1977** (4), 47–58.

Bogoslovsky, V.I. [Богословский, В.И.] 1979. Новый род семейства Rectoclymeniidae [A new genus of the family Rectoclymeniidae]. *Палеонтологический журнал* **1979** (1), 140–143.

Bogoslovsky, V.I. [Богословский, В.И.] 1981. Девонские Ammonoidei. III. Климении (подотряд Gonioclymeniina) [Devonian Ammonoids. III. Clymeniids (suborder Gonioclymeniina)]. *Труды Палеонтологического Института АН СССР* **191**, 1–123.

Bogoslovsky, V.I. [Богословский, В.И.] 1982. Интересная форма приустевых образовании на раковине климении. [An interesting kind of periapertural modifications in the clymeniid shell] *Доклады Академии Наук СССР* **264**, 1483–1486.

Bogoslovsky, V.I. and Kuzina, L.F. [Богословский, В.И. и Кузина, Л.Ф.] 1980. Позднедевонские аммоноидеи бассеина реки Кожим на приполярном Урале [Late Devonian ammonoids of the Kozhim River basin in the subpolar Urals]. *Палеонтологический журнал* **1980** (2), 67–73.

Bond, D. and, Zatoń, M. 2003. Gamma-ray spectrometry across the Upper Devonian basin succession at Kowala inthe Holy Cross Mountains (Poland). *Acta Geologica Polonica* **53**, 93–99.

Boogaard, van den, M. 1983. Conodont faunas from Portugal and southwestern Spain. *Scripta Geologica* **69**, 1–17.

Boogaard, van den, M. 1992. The recurrence of *Vogelgnathus campbelli*-dominated conodont faunas in the Viséan and early Namurian of the Cantabrian Mts (Spain): a reflection of sea level fluctuations? *Scripta Geologica* **99**, 1–33.

Boogaard, van den, M. and Kuhry, B. 1979. Statistical reconstruction of the *Palmatolepis* apparatus (Late Devonian conodontophorids) at the generic, subgeneric, and specific level. *Scripta Geologica* **49**, 1–57.

Bouckaert, J. and Groessens, E. 1976. *Polygnathus paprothae*, *Pseudopolygnathus conili*, *Pseudopolygnathus graulichi*: espèces nouvelles a la limite Dévonien–Carbonifère. *Annales de la Société Géologique de Belgique* **99**, 587–599.

Brand, U., Legrand-Blain, M., and Streel, M. 2004. Biochemostratigraphy of the Devonian–Carboniferous boundary Global Stratotype Section and Point, Griotte Formation, La Serre, Montagne Noire, France. *Palaeogeography, Palaeoclimatology, Palaeoecology* **205**, 337–357.

Branson, E.B. and Mehl, M.G. 1934. Conodonts from the Grasy Creek Shale of Missouri. *The University of Missouri Studies* **8**, 171–259.

Bratton, J.F., Berry, W.B.N., and Morrow, J.R. 1999. Anoxia pre-dates Frasnian–Famennian boundary mass extinction horizon in the Great Basin, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* **154**, 275–292.

Buch, von, L. 1839. Über Goniatiten und Clymenien in Schlesien. *Physikalische Abhandlungen der königlichen Akademie der Wissenschaften, Berlin* **1838**, 149–169.

Bultynck, P. 2003. Devonian Icriodontidae: biostratigraphy, classification and remarks on paleoecology and dispersal. *Rivista Española de Micropaleontología* **35**, 295–314.

Casier, J.-G., Devleeschouwer, X., Lethiers, F., Preat, A., and Racki, G. 2000. Ostracods and sedimentology of the Frasnian–Famennian boundary beds in the Kostomłoty section (Holy Cross Mountains, Poland). *Bulletin de l'Institute Royal des Sciences Naturelles de Belgique, Sciences de la Terre* **70**, 53–74.

Casier, J.-G., Lethiers, F., and Baudin, F. 1999. Ostracods, organic matter and anoxic events associated with the Frasnian/Famennian boundary in the Schmidt quarry (Germany). *Geobios* **32**, 869–881.

Chauff, K.M. and Price, J. 1980. *Mitrellataxis*, a new multielemet genus of Late Devonian conodont. *Micropaleontology* **26**, 177–188.

Clark, D.L., Sweet, W.C., Bergström, S.M., Klapper, G., Austin, R.L., Rhodes, F.H.T., Müller, K.J., Ziegler, W., Lindström, M., Miller, J.F., and Harris, A.G. 1981. Conodonta. *In*: R.A. Robison (ed.) *Treatise on Invertebrate Paleontology, Part W, Supplement 2*. 202 pp. The University of Kansas, Boulder.

Clarke, J.M. 1882. New phyllopod crustaceans from the Devonian of western New York. *American Journal of Sciences, series 3* **23**, 476–478.

Clausen, C.-D. 1969 Oberdevonische Cephalopoden aus dem Rheinischen Schiefergebirge. II. Gephyroceratidae, Beloceratidae. *Palaeontographica* **A132**, 95–178.

Closs, D. 1967. Goniatiten mit Radula und Kieferapparat in der Itararé Formation von Uruguay. *Paläontologische Zeitschrift* **41**, 19–36.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. *In*: M.L. Cody and J.M. Diamond (eds) *Ecology and Evolution of Communities*. 460–490. Belknap Press, Cambridge, Ma.

Cooper, C.L. 1931. New conodonts from the Woodford Formation of Oklahoma. *Journal of Paleontology* **5**, 230–243.

Czarnocki, J. 1928. Przegląd stratygrafii famenu i karbonu dolnego (kulmu) w zachodniej i środkowej części Gór Świętokrzyskich. *Posiedzenia Naukowe Państwowego Instytutu Geologicznego* **21**, 55–59.

Czarnocki, J. 1933. Stratygrafia warstw granicznych między dewonem i karbonem w okol. Kowali. *Posiedzenia Naukowe Państwowego Instytutu Geologicznego* **35**, 31–34.

Czarnocki, J. 1989. Klimenie Gór Świętokrzyskich. *Prace Państwowego Instytutu Geologicznego* **127**, 1–91.

Czarnocki, J. and Samsonowicz, J. 1911. O górnym dewonie na górze Miedziance. *Sprawozdania z posiedzeń Towarzystwa Naukowego Warszawskiego* **4**, 316–321.

Czarnocki, J. and Sujkowski, Z. 1931. O fosforytach z warstw granicznych między dewonem i karbonem w górach Świętokrzyskich. *Posiedzenia Naukowe Państwowego Instytutu Geologicznego* **31**, 109–110.

Doguzhaeva, L. Mapes, R.H., and Mutvei, H. 1997. Beaks and radulae of Early Carboniferous goniatites. *Lethaia* **30**, 305–314.

Doguzhaeva, L. 2002. Adolescent bactritoid, orthoceroid, ammonoid and coleoid shells from the Upper Carboniferous and Lower Permian of the South Urals. *Abhandlungen der Geologischen Bundesanstalt* **57**, 9–55.

Donoghue, P.C.J. 2001. Conodonts meet cladistics: Recovering relationships and assessing the completeness of the conodont fossil record. *Palaeontology* **44**, 65–93.

Dreesen, R. and Dusar, M. 1974. Refinement of conodont-biozonation in the Famenne-type area. *In*: J. Bouckaert and M. Streel (eds) *International Symposium on Belgian Micropaleontological Limits from Emsian to Visean, Namur* **13**, 1–36.

Dreesen, R. and Orchard, M. 1974. "Intraspecific" morphological variation within *Polygnathus semicostatus* Branson & Mehl. *In*: J. Bouckaert and M. Streel (eds) *International Symposium on Belgian Micropaleontological Limits from Emsian to Visean, Namur* **21**, 1–8.

Dreesen, R. 1976. Interspecific morphological relations within the "*quadrantinodosa*-stock" (Branson & Mehl, 1934) (*marginifera*-Zone, Upper Devonian). *Annales de la Société Géologique de Belgique* **99**, 511–529.

Dreesen, R., Dusar, M. and Groessens, E. 1976. Biostratigraphy of the Yves-Gomez road section (uppermost Famennian). *Service Geologique de Belgique, Professional Paper* **1976** (6), 1–20.

Drevermann, F. 1901. Die Fauna der oberdevonischen Tuffbreccie von Langenaubach bei Haiger. *Jahrbuch der Preussischen geologischen Landesanstalt* **21**, 99–207.

Drygant, D.M. [Дрыгант, Д.М.] 1986. Новыые конодонты рода *Polygnathus* Hinde, 1879 из среднего и верхнего девона Львовского прогиба [New conodonts of the genus *Polygnathus* Hinde, 1879 from the Middle and Upper Devonian of the Lviv deformation]. *Палеонтологический сборник* **23**, 47–52.

Dybczyński, T. 1913. Amonity górnego dewonu Kielc. Wiadomość tymczasowa. *Kosmos* **38**, 510–525.

Dzik, J. 1980. Isolated mandibles of early Palaeozoic phyllocarid Crustacea. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1980**, 87–106.

Dzik, J. 1981. Origin of the Cephalopoda. *Acta Palaeontologica Polonica* **26**, 161–191.

Dzik, J. 1985. Phylogeny of the Nautiloidea. *Palaeontologia Polonica* **45**, 1–219.

Dzik, J. 1991. Evolutian of oral apparatuses in the conodont chordates. *Acta Palaeontologica Polonica* **36**, 265–323.

Dzik, J. 1992. *Dzieje życia na Ziemi. Wprowadzenie do paleobiologii.* 447 pp. Państwowe Wydawnictwo Naukowe. Warszawa.

Dzik, J. 1994. Evolution of "small shelly fossils" assemblages of the early Paleozoic. *Acta Palaeontologica Polonica* **39**, 247–313.

Dzik. J. 1995. Range-based biostratigraphy and evolutionary geochronology. *Palaeopelagos Special Publication* **1**, 121–128.

Dzik, J. 1997. Emergence and succession of Carboniferous conodont and ammonoid communities in the Polish part of the Variscan sea. *Acta Palaeontologica Polonica* **42**, 57–170.

Dzik, J. 1999. Relationship between rates of speciation and phyletic evolution: Stratophenetic data on pelagic conodont chordates and benthic ostracods. *Geobios* **32**, 205–221.

Dzik, J. 2000. The origin of the mineral skeleton in chordates. *Evolutionary Biology* **31**, 105–154.

Dzik, J. 2002. Emergence and collapse of the Frasnian conodont and ammonoid communities in the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* **47**, 565–650.

Dzik, J. 2005. The chronophyletic approach: stratophenetics facing an incomplete fossil record. *Special Papers in Palaeontology* **73**, 159–183.

Ebbinghausen, V., Becker, R.T., and Bockwinkel, J. 2002. Morphometric analyses and taxonomy of oxyconic goniatites (Paratornoceratinae n. subfam.) from the Early Famennian of the Tafilalt (Anti-Atlas, Morocco). *Abhandlungen der Geologischen Bundesanstalt* **57**, 167–180.

Filipiak, P. and Racki, G. 2005. Unikatowy zapis dewońskich zdarzeń beztlenowych w profilu kamieniołomu Kowala k. Kielc. *Przegląd Geologiczny* **53**, 846–847.

Frech, F. 1902. Über devonische Ammoneen. *Beiträge zur Paläontologie und Geologie des Österreich-Ungarns und des Orients* **14**, 27–112.

Frye, C.J. and Feldmann, R. M. 1991. North American Late Devonian cephalopod aptychi. *Kirtlandia* **46**, 49–71.

Garcia-López, S. 1986. Basis for the establishment of a new phylogeny of the genus *Ancyrodella. Revista Española de Micropaleontologia* **18**, 443–456.

Garcia-López, S. 1987. Los conodontos y su aplicacion al estudio de la divisiones cronostratigraficas mayores del Devonico Asturleones (España). *Boletin Geológico y Minero* **97**, 1–112.

Ginter, M. 1995. Ichthyoliths and Late Devonian events in Poland and Germany. *Ichthyolith Issues Special Publication* **1**, 23–30.

Ginter, M. 1999. The early Famennian recovery of phoebodont sharks. *Acta Geologica Polonica* **49**, 105–117.

Ginter, M. 2000. Late Famennian pelagic shark assemblages. *Acta Geologica Polonica* **50**, 369–386.

Ginter, M. 2002. Chondrichthyan fauna of the Frasnian–Famennian boundary beds in Poland. *Acta Palaeontologica Polonica* **47**, 329–338.

Ginter, M. 2001. Chondrichthyan biofacies in the Late Famennian of Utah and Nevada. *Journal of Paleontology* **21**, 714–7129.

Ginter, M. and Ivanov, A. 1992. Devonian phoebodont shark teeth. *Acta Palaeontologica Polonica* **37**, 55–75.

Ginter, M. and Piechota, A. 2004. The first Devonian holocephalian tooth from Poland. *Acta Palaeontologica Polonica* **49**, 409–415.

Girard, C. and Feist, R. 1997. Eustatic trends in conodont diversity across the Frasnian–Famennian boundary in the stratotype area, Montagne Noire, southern France. *Lethaia* **29**, 329–337.

Girard, C., Klapper, G., and Feist, R. 2005. Subdivision of the terminal Frasnian *linguiformis* conodont Zone, revision of the correlative interval of Montagne Noire Zone 13, and discussion of stratigraphically significant associated trilobites. *In*: D.J. Over, J.R. Morrow., and P.B. Wignall (eds) *Understanding Late Devonian and Permian–Triassic Biotic and Climatic Events: Towards and Integrated Approach. Developments in Palaeontology and Stratigraphy, Vol. 20,* 181–198. Elsevier, Amsterdam.

Glenister, B.F. and Klapper, G. 1966. Upper Devonian conodonts from the Canning Basin, western Australia. *Journal of Paleontology* **40**, 777–842.

Gong Y.-M., Li B.-H., Wang C.-Y., and Wu Y. 2001. Orbital cyclostratigraphy of the Devonian Frasnian–Famennian transition in South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* **168**, 237–248.

Gottobrio, W.E. and Saunders, W.B. 2005. The clymeniid dilemma: functional implications of the dorsal siphuncle in clymeniid ammonoids. *Paleobiology* **31**, 233–252.

Gouwy, S. and Bultynck, P. 2000. Graphic correlation of Frasnian sections (Upper Devonian) in the Ardennes, Belgium. *Bulletin de l'Institute Royal des Sciences Naturelles de Belgique, Sciences de la Terre* **70**, 25–52.

Göddertz, B. 1987. Devonische Goniatiten aus SW-Algerien und ihre stratigraphische Einordnung in die Conodonten-Abfolge. *Palaeontographica* **197A**, 127–220.

Gürich, G. 1896. Das Paläozoicum im polnischen Mittelgebirge. *Verhandlungen der Russisch-kaiserlichen mineralogischen Gesellschaft zu St. Petersburg Serie 2* **32**, 1–539.

Gürich, G. 1901. Nachträge zum Paläozoicum des polnischen Mittelgebirge. *Neues Jahrbuch für Geologie und Paläontologie, Beilage Band* **13**, 331–387.

Habetín, V. and Knobloch, E. 1981. *Kapesní atlas zkamenělin. Druhé vydání*. 285 pp. Státní Pedagogické Nakladatelství, Praha.

Hallam, A. and Wignall, P.B. 1999. Mass extinctions and sea-level changes. *Earth-Science Reviews* 48, 217–250.

Hannibal, J.T., Janevski, G.A., and O'Connor, G. M. 2005. Tales from the digestive tract: coprolites, including strands of fecal pellets, and stacked lingulids interpreted as having been excreted by a lingulid-eating organism, from the Chagrin shale (Famennian) of northeastern Ohio. *Geological Society of America North-Central Section – 39th Annual Meeting (May 19–20, 2005), Abstracts and Programs, Paper No*. 17-7.

Haydukiewicz, J. 1981. Pelagiczne utwory turneju w południowo zachodniej części Gór Bardzkich. *Geologia Sudetica* **16**, 219–225.

Helms, J. 1959. Conodonten aus dem Saalfelder Oberdevon (Thüringen). *Geologie* **8**, 634–677.

Helms, J. 1961. Die "*nodocostata*-Gruppe" der Gattung *Polygnathus*. Oberdevonische Conodonten. *Geologie* **10**, 674–711.

Helms, J. 1963. Zur „Phylogenese" und Taxionomie von *Palmatolepis* (Conodontida, Oberdevon). *Geologie* **12**, 449–485.

Helms, J. and Wolska, Z. 1967. New Upper Devonian conodonts from Poland and Germany. *Acta Palaeontologica Polonica* **12**, 227–238.

Holmes, G.B. 1928. A bibliography of the conodonts with descriptions of Early Mississippian species. *Proceedings of the United States Museum* **72** (5), 1–38.

House, M.R 1965. A study in the Tornoceratidae: the succession of *Tornoceras* and related genera in the North American Devonian. *Philosophical Transactions of the Royal Society of London* **B250**, 79–130.

House, M.R 1970. On the origin of the clymeniid ammonoids. *Palaeontology* **13**, 664–676.

House, M.R 1971. The goniatite wrinkle-layer. *Smithsonian Contribution of Paleobiology* **3**, 23–32.

House, M.R. 1978. Devonian ammonoids from the Appalachians and their bearing on international zonation and correlation. *Special Papers in Palaeontology* **21**, 1–70.

House, M.R. 2002. Strength, timing, setting and cause of mid-Palaeozoic extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* **181**, 5–25.

House, M.R., Becker, R.T., Feist, R., Girard, C., and Klapper, G. 2000. The Frasnian/Famennian boundary GSSP at Coumiac, southern France. *Courier Forschungsinstitut Senckenberg* **225**, 59–75.

House, M.R and Price, J.D. 1985. New Late Devonian genera and species of tornoceratid goniatites. *Palaeontology* **28**, 159–188.

House, M.R and Ziegler, W. 1977. The goniatite and conodont sequences in the early Upper Devonian at Adorf, Germany. *Geologica et Palaeontologica* **11**, 69–108.

Huddle, J.W. 1968. Redescription of Upper Devonian conodont genera and species proposed by Ulrich and Bassler in 1926. *U.S. Geological Survey Professional Paper* **578**, 1–55.

Ivanov, A. and Ginter, M. 1997 Comments on the Late Devonian placoderms from the Holy Cross Mountains. *Acta Palaeontologica Polonica* **42**, 413–426.

Ji, Q. 1989. On the Frasnian–Famennian mass extinction event in South China. *Courier Forschungsinstitut Senckenberg* **117**, 275–301.

Joachimski, M.M., Ostertag-Henning, C., Pancost, R.D., Strauss, H., Freeman, K.H., Littke, R., Damste, J.S.S., and Racki, G. 2001. Water column anoxia, enhanced productivity and concomitant changes in delta C-13 and delta S-34 across the Frasnian–Famennian boundary (Kowala Holy Cross Mountains/Poland). *Chemical Geology* **175**, 109–131.

Joachimski, M.M. and Buggisch, W.S. 2002. Conodont apatite δ^{18}O signatures indicate climatic cooling as a trigger of the Late Devonian mass extinction. *Geology* **30**, 711–714.

Joachimski M.M., Van Geldern R., Breisig S., Buggisch W., and Day, J.S. 2004. Oxygen isotope evolution of biogenic calcite and apatite during the Middle and Late Devonian. *International Journal of Earth Sciences* **93**, 542–553.

Johnson, J.G., Klapper, G., and Sandberg, C.A. 1985. Devonian eustatic fluctuations in Euramerica. *Geological Society of America Bulletin* **96**, 567–587.

Klapper, G, Feist R., Becker, R.T., and House, M.R. 1994. Definition of the Frasnian/Famennian Stage boundary. *Episodes* **16**, 433–441.

Klapper, G. 1989. The Montagne Noire Frasnian (Upper Devonian) conodont succession. *In*: N.J. McMillan, A.F. Embry, and D.J. Glass (eds) Devonian of the World Volume III: Paleontology, Paleoecology and Biostratigraphy. *Canadian Society of Petroleum Geology Memoir* **14**, 449–468.

Klapper, G. 1990. Frasnian species of the Late Devonian conodont genus *Ancyrognathus. Journal of Paleontology* **64**, 998–1025.

Klapper G., Feist R., Becker R.T., and House, M.R. 1993. Definition of the Frasnian/Famennian stage boundary. *Episodes* **16**, 433–441.

Klapper, G. and Foster, C.T., Jr. 1993. Shape analysis of Frasnian species of the Devonian conodont genus *Palmatolepis*. *The Paleontological Society Memoir* **32**, 1–35.

Klapper, G. and Philip, G.M. 1971. Devonian conodont apparatuses and their vicarious skeletal elements. *Lethaia* **4**, 429–452.

Klapper, G. and Philip, G.M. 1972. Familial classification of reconstructed Devonian conodont apparatuses. *Geologica et Palaeontologica* **SB 1**, 97–114.

Klapper, G. and Ziegler, W. 1967. Evolutionary development of the *Icriodus latericrescens* group (Conodonta) in the Devonian of Europe and North America. *Palaeontographica* **127A**, 68–83.

Klapper, G., Uyeno, T.T., Armstrong, D.K., and Telford, P.G. 2004. Conodonts of the Williams Island and Long Rapids Formations (Upper Devonian, Frasnian–Famennian) of the Onakawana B drillhole, Moose River Basin, northern Ontario, with a revision of Lower Famennian species. *Journal of Paleontology* **78**, 371–387.

Klofak, S.M., Landman, N.H., and Mapes, R.H. 1999. Embryonic development of primitive ammonoids and the monophyly of the Ammonoidea. *In*: F. Oloriz and F.J. Rodriguez-Tovar (eds) *Advancing Research on Living and Fossil Cephalopods*. 23–45.

Klug, C. and Korn, D. 2004. The origin of ammonoid locomotion. *Acta Palaeontologica Polonica* **49**, 235–242.

Klug, C., Korn, D., Richter, U., and Urlichs, M. 2004. The black layer in cephalopods from the German Muschelkalk (Triassic). *Palaeontology* **47**, 1407–1425.

Korn, D. 1979. Mediandornen bei *Kosmoclymenia* Schindewolf (Ammonoidea, Cephalopoda). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1979**, 399–405.

Korn, D. 1981. *Cymaclymenia*, eine besonders langlebige Clymenien-Gattung (Ammonoidea, Cephalopoda). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **161**, 172–208.

Korn, D. 1985. Runzelschicht und Ritzstreifung bei Clymenien (Ammonoidea, Cephalopoda). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1985**, 533–541.

Korn, D. 1988. Oberdevonische Goniatiten mit dreieckigen Innenwindungen. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1988**, 605–610.

Korn, D. 1989. Paläontologischer Anhang: Die Clymenien aus der Schichtenfolge an der Nordostwand des östlichen Provinzialsteinbruches Drewer. *Fortschritte in der Geologie der Rheinlande und Westfalen* **35**, 220–222.

Korn, D. 1991. Threedimensionally preserved clymeniids from the Hangenberg Black Shale of Drewer (Cephalopoda, Ammonoidea; Devonian–Carboniferous boundary; Rhenish Massif). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1991**, 553–563.

Korn, D. 1992. Heterochrony in the evolution of Late Devonian Ammonoids. *Acta Paleontologica Polonica* **37**, 21–36.

Korn, D. 1992. Relationship between shell form, septal construction and suture line in clymeniid cephalopods (Ammonoidea; Upper Devonian). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **185**, 115–130.

Korn, D. 1994. Oberdevonische und unterkarbonische Prionoceraten aus dem Rheinischen Schiefergebirge. *Geologie und Paläontologie in Westfalen* **30**, 1–85.

Korn, D. 1995. Paedomorphosis of ammonoids as a result of sealevel fluctuations in the Late Devonian *Wocklumeria* Stufe. *Lethaia* **28**, 155–165.

Korn, D. 1999. Septal projections – a method for the illustration of septa in early ammonoids. *In*: А.Ю. Розанов и А.А. Шевырев [A.Yu. Rozanov and A.A. Shevyrev] (eds) *Ископаемые цефалоподы: новейшие достижения в их изучении* [*Fossil Cephalopods: New Achievements in their Studies*], 62–67. Палеонтологический Институт РАН, Москва.

Korn, D. 2000. Mantle expansion upon the conch in the Late Devonian ammonoid *Erfoudites*. *Acta Geologica Polonica* **50**, 21–27.

Korn, D. 2002*a*. Historical subdivisions of the Middle and Late Devonian sedimentary rocks in the Rhenish Mountains by ammonoid faunas. *Senckenbergiana lethaea* **82**, 545–555.

Korn, D. 2002*b*. Die Ammonoideen-Fauna der *Platyclymenia annulata*-Zone vom Kattensiepen (Oberdevon, Rheinisches Schiefergebirge). *Senckenbergiana lethaea* **82**, 557–608.

Korn, D. 2004*a*. The mid-Famennian cephalopods from the Refrath 1 Borehole (Bergisch Gladbach-Paffrath Syncline; Ardennes-Rhenish Massif. *Geological Quarterly* **48**, 245–252.

Korn, D. 2004b. Late Famennian ammonoid succession in the Rhenish Mountains: the "*annulata* Event" reconsidered. *Courier Forschungsinstitut Senckenberg* **251**, 175–183.

Korn, D., Belka, Z., Frohlich, S., Rucklin, M., and Wendt, J. 2004. The youngest African clymeniids (Ammonoidea, Late Devonian) – failed survivors of the Hangenberg Event. *Lethaia* **37**, 307–315.

Korn, D., Ebbighausen, V., Bockwinkel, J., and Klug, C. 2003. The A-mode sutural ontogeny in prolecanitid ammonoids. *Palaeontology* **46**, 1123–1132.

Korn, D. and Klug, C. 2001. Biometric analyses of some Paleozoic ammonoid conchs. *Berliner geowissenschaftliche Abhandlungen E* **36**, 173–187.

Korn, D. and Klug, C. 2002. Ammoneae Devonicae. *In*: W. Riegraf (ed.) *Fossilium Catalogus I: Animalia, Pars 138.* 1–374. Backhuys Publishers, Leiden.

Korn, D. and Luppold, F.W. 1987. Nach Clymenien und Conodonten gegliederte Profile des oberen Famennium im Rheinischen Schiefergebirge. *Courier Forschungsinstitut Senckenberg* **92**, 199–223.

Korn, D., Niedźwiedzki, R., and Posieczek, J.B. 2005. Age, distribution, and phylogeny of the peculiar Late Devonian ammonoid *Soliclymenia*. *Acta Geologica Polonica* **55**, 99–108.

Korn, D. and Price, J. 1987. Taxonomy and phylogeny of the Kosmoclymeniinae subfam. nov. (Cephalopoda, Ammonoidea, Clymeniida). *Courier Forschungsinstitut Senckenberg* **92**, 5–75.

Korn, D., Price, J. and Ademmer, F. 1984. *Prolobites aktubensis* Bogoslovskiy – eine devonische Goniatiten-Art (Ammonoidea) mit irregulärem Mundrand. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1984**, 66–76.

Korn, D. and Titus, A. 2006. The ammonoids from the Three Forks Shale (Late Devonian) of Montana. *Fossil Record* **9**, 198–212.

Korn, D. and Ziegler, W. 2002. The ammonoid and conodont zonation at Enkenberg (Famennian, Late Devonian; Rhenish Mountains). *Senckenbergiana lethaea* **82**, 453–462.

Kullmann, J., Korn, D., and Petersen, M.S. 1994. *GONIAT V2.41. Paleozoic Ammonoids Database*. Universität Tübingen.

Kulicki, C., Landman, N.H., Heaney, M.J., Mapes, R.H., and Tanabe, K. 2002. Morphology of the early whorls of goniatites from the Carboniferous Buckhorn Asphalt (Oklahoma) with aragonitic preservation. *Abhandlungen der Geologischen Bundesanstalt* **57**, 205–224.

Lange, F.G. 1968. Conodonten-Gruppenfunde aus Kalken des tieferen Oberdevon. *Geologica et Palaeontologica* **2**, 37–57.

Lewowicki, S. 1959. Fauna wapieni klimeniowych z Dzikowca Kłodzkiego. *Biuletyn Instytutu Geologicznego* **146**, 73–118.

Lindsay, E. 2003. Chronostratigraphy, biochronology, datum events, land mammal ages, stage of evolution, and appearance event ordination. *Bulletin of the American Museum of Natural History* **279**, 212–230.

Lindström, M. and Ziegler, W. 1965. Ein Conodontentaxon aus vier morphologisch verschiedenen Typen. *Fortschritte der Geologie Rheinland und Westfalen* **9**, 209–218.

Makowski, H. 1962. Recherches sur le dimorphisme sexuel chez les Ammonoïdés (Note préliminaire). *In*: E. Passendorfer (ed.) *Księga pamiątkowa ku czci profesora Jana Samsonowicza* 32–55. Wydawnictwa Geologiczne, Warszawa.

Makowski, H. 1963. Problem of sexual dimorphism in ammonites. *Palaeontologia Polonica* **12**, 1–92.

Makowski, H. 1991. Dimorphism and evolution of the goniatite *Tornoceras* in the Famennian of the Holy Cross Mountains. *Acta Palaeontologica Polonica* **36**, 241–254.

Matern, H. 1931. Oberdevonische Anaptychen in situ und über die Erhaltung von Chitin-Substanzen. *Senckenbergiana* **13**, 160–167.

Matyja, H. 1972. Biostratygrafia dewonu górnego z profilu wiercenia Chojnice 2 – Pomorze Zachodnie. *Acta Geologica Polonica* **22**, 735–750.

Matyja, H. 1974. A new conodont species from the Famennian of Poland. *Bulletin de l'Academie Polonaise des Sciences, Série des sciences biologiques* **22**, 785–787.

Matyja, H. 1993. Upper Devonian of western Pomerania. *Acta Geologica Polonica* **43**, 27–94.

Matyja, H. and Narkiewicz, M. 1992. Conodont biofacies succession near the Frasnian/Famennian boundary, some Polish examples. *Courier Forschungsinstitut Senckenberg* **154**, 125–147.

Matyja, H. and Narkiewicz, M. 1995. Conodont stratigraphy of the Upper Devonian in the Janczyce I borehole section, eastern Holy Cross Mts. *Geological Quarterly* **39**, 177–206.

Matyja, H. and Żbikowaka, B. 1985. Stratygrafia dewońskiej sekwencji węglanowej w wierceniach regionu lubelskiego. *Przegląd Geologiczny* **33**, 259–263.

McGhee, G.R. 1996. *The Late Devonian Mass Extinction: The Frasnian/Famennian Crisis*. Columbia University Press, New York.

Menge, B.A. and Sutherland, J.P. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* **110**, 351–369.

Menge, B.A. and Sutherland, J.P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* **130**, 730–757.

Metzger, R.A. 1989. Upper Devonian (Frasnian–Famennian) conodont biostratigraphy in the subsurface of north-central Iowa and southeastern Nebraska. *Journal of Paleontology* **63**, 503–524.

Metzger, R.A. 1994. Multielement reconstructions of *Palmatolepis* and *Polygnathus* (Upper Devonian, Famennian) from the Canning Basin, Australia, and Bactrian Mountains, Nevada. *Journal of Paleontology* **68**, 617–647.

Mound, M.C. 1968. Upper Devonian conodonts from southern Alberta. *Journal of Paleontology* **42**, 444–524.

Müller, K.J. 1956. Cephalopodenfauna und Stratigraphie des Oberdevons von Schleiz und Zeulenroda in Thüringen. *Beiheft der Geologisches Jahrbuch* **20**, 1–94.

Müller, K.J. and Müller, E.M. 1957. Early Upper Devonian (Independence) conodonts from Iowa, part I. *Journal of Paleontology* **31**, 1069–1108.

Narkiewicz, M. 1978. Stratygrafia i rozwój facjalny górnego dewonu między Olkuszem a Zawierciem. *Acta Geologica Polonica* **28**, 415–470.

Narkiewicz, M. 1989. Turning points in sedimentary development in the Late Devonian in southern Poland. *In*: N.J. McMillan, A.F. Embry, and D.J. Glass (eds) Devonian of the World. *Canadian Society of Petroleum Geology Memoir* **14-II**, 619–635.

Narkiewicz, M. and Racki, G. 1987. Korelacja i rozwój sedymentacji dewonu górnego między Dębnikiem i Zawierciem. *Kwartalnik Geologiczny* **31**, 241–256.

Nehring, M. 1967. Konodonty dolnego famenu z profilu Winowno w okolicach Siewierza (Wyżyna Śląsko-Krakowska). *Biuletyn Instytutu Geologicznego* **209**, 113–169.

Nehring-Lefeld, H. 1990. Biostratygrafia famenu z otworu wiertniczego Kowala 1 na podstawie konodontów. *Kwartalnik Geologiczny* **34**, 271–290.

Nicoll, R.S. 1980. The multielement genus *Apatognathus* from the Late Devonian of the Canning Basin, Western Australia. *Alcheringa* **4**, 133–152.

Nicoll, R.S. 1985. Multielement composition of the conodont species *Polygnathus xylus* Stauffer 1940 and *Ozarkodina brevis* (Bischoff and Ziegler 1957) from the Upper Devonian of the Canning Basin, western Australia. *BMR Journal of Australian Geology and Geophysics* **9**, 133–147.

Norby, R.D. and Rexroad, C.B. 1985. *Vogelgnathus*, a new Mississippian conodont genus. *Department of Natural Resources Indiana Geological Survey Occasional Paper* **50**, 1–14.

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

Orchard, M.J. 2005. Multielement conodont apparatuses of Triassic Gondolelloidea. *Special Papers in Palaeontology* **73**, 73–101.

Osmólska, H. 1962. Famennian and lower Carboniferous Cyrtosymbolinae (Trilobita) from the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* **7**, 53–204.

Over, D.J. 1992. Conodonts and the Devonian–Carboniferous boundary in the upper Woodford Shale, Arbuckle Mountains, south-central Oklahoma. *Journal of Paleontology* **66**, 293–311.

Over, D.J. and Rhodes, M.K. 2000. Conodonts from the Upper Olentangy Shale (Upper Devonian, central Ohio) and stratigraphy across the Frasnian–Famennian boundary. *Journal of Paleontology* **74**, 101–112.

Paine, R.T. 1966. Food web complexity and species diversity. *American Naturalist* **100**, 65–75.

Pajchlowa, L., Malinowska, M., Miłaczewski, L., Sarnecka, E., and Woroncowa-Marcinowska, T. 2003. *Budowa geologiczna Polski. Tom III, Atlas skamieniałości przewodnich i charakterystycznych, cz. 1b Dewon (z. 1, z. 2).* 786 pp. Państwowy Instytut Geologiczny, Warszawa.

Perri, M.C. and Spalletta, C. 1990. Famennian conodonts from climenid pelagic limestone, Carnic Alps, Italy. *Palaeontographia Italica* **77**, 55–83.

Perri, M.C. and Spalletta, C. 1991. Famennian conodonts from Cava Cantoniera and Malpasso sections, Carnic Alps, Italy. *Bolletino della Società Paleontologica Italiana* **30**, 47–78.

Perna, E. [Перна, Е.] 1914. Аммонеи верхниего неодевона восточного склона Урала [Ammonoids of the upper Neodevonian of the eastern slope of the Urals]. *Труды Геологического Комитета, Новая Серия* **99**, 1–86.

Petersen, M.S. 1975. Upper Devonian (Famennian) ammonoids from the Canning Basin, western Australia. *The Paleontological Society Memoir (supplement to Journal of Paleontology vol. 49, No. 5)* **8**, 1–55.

Petter, G. 1959. Clymènies du du Sahara. *Publications du Service de la Carte Géologique de l'Algérie (nouvelle Série), Paléontologie, Mémoire* **6**, 1–58.

Petter, G. 1960. Goniatites Dévoniennes du Sahara. *Publications du Service de la Carte Géologique de l'Algérie (nouvelle Série), Paléontologie, Mémoire* **2**, 1–313.

Philip, G.M. and McDonald, L. 1975. A provisional phylogeny for some reconstructed Late Devonian polygnathid conodont apparatuses. *Alcheringa* **1**, 97–107.

Poty, E. 1999. Famennian and Tournaisian recoveries of shallow water Rugosa following late Frasnian and late Strunian major crises, southern Belgium and surrounding areas, Hunan (South China) and the Omolon region (NE Siberia). *Palaeogeography, Palaeoclimatology, Palaeoecology* **154**, 11–26.

Price, J. and Korn, D. 1989. Stratigraphically important clymeniids from the Upper Devonian. *Courier Forschungsinstitut Senckenberg* **110**, 257–294.

Puchkov, V.N., Klapper, G., and Mashkova, T.V. 1981. Natural assemblages of *Palmatolepis* from the Upper Devonian of the northern Urals. *Acta Palaeontologica Polonica* **26**, 281–298.

Purnell, M.A. 1993. The *Kladognathus* apparatus (Conodonta, Carboniferous): homologies with ozarkodinids, and the prioniodinid Bauplan. *Journal of Paleontology* **67**, 875–882.

Purnell, M.A., Donoghue, P.C.J., and Aldridge, R.J. 2000. Orientation and anatomical notation in conodonts. *Journal of Paleontology* **74**, 113–122.

Pusch, G.G. 1837. *Polens Paläontologie oder Abbildung und Beschreibung der vorzüglichsten und der noch unbeschriebenen Petrefakten aus den Gebirgsformationen in Polen, Volhynien und den Karpathen nebst einigen allgemainen Beiträgen zur Petrefaktenkunde und einem Versuch zur Vervollständigung der Geschichte des Europäischen auer-Ochsen*. 218 pp. E. Schweizerbart's Verlagshandlung, Stuttgart.

Racki, G. 1990. Frasnian/Famennian event in the Holy Cross Mts., central Poland: Stratigraphical and ecologic aspects. *In*: E.G. Kauffman and O.H. Walliser (eds) *Extinction Events in Earth History*. 169–181. Springer (Lecture Notes in Earth Sciences 30), Berlin.

Racki, G. 1993. Evolution of the bank to reef complex in the Devonian of the Holy Cross Mountains. *Acta Palaeontologica Polonica* **37**, 87–182.

Racki, G. 1998. Frasnian–Famennian biotic crisis: undervaluated tectonic control? *Palaeogeography, Palaeoclimatology, Palaeoecology* **141**, 177–198.

Racki, G. 2005. Toward understanding Late Devonian global events; few answers, many questions. *In*: D.J. Over, J.R. Morrow, and P.B. Wignall (eds), *Understanding Late Devonian and Permian–Triassic biotic and climatic events; towards an integrated approach. Developments in Palaeontology and Stratigraphy, Vol. 20*, 5–3. Elsevier, Amsterdam.

Racki, G. and Baliński, A. 1998. Late Frasnian Atrypida (Brachiopoda) from Poland and the Frasnian–Famennian biotic crisis. *Acta Palaeontologica Polonica* **43**, 273–304.

Racki, G. and House, M.R. (eds) 2002. Late Devonian biotic crisis: ecological, depositional and geochemical records. *Palaeogeography, Palaeoclimatology, Palaeoecology* **181**, 1–374.

Renaud, S. and Girard, C. 1999. Strategies of survival during extreme environmental perturbations: evolution of conodonts in response to the Kellwasser crisis (Upper Devonian). *Palaeogeography, Palaeoclimatology, Palaeoecology* **146**, 19–32.

Renz, C. 1914. Neue Arten aus dem Clymenienkalk von Ebersdorf in Schlesien. *Jahrbuch der Königlichen Preußischen geologischen Landesanstalt* **34**, 99–125.

Rexroad, C.B. and Merrill, G.K. 1996. Conodonts from the Reelsville Limestone (Chesterian, Lower Carboniferous) in Indiana and adjacent Kentucky, U.S.A. *Geologica et Palaeontologica* **30**, 225–238.

Rexroad, C.B. and Varker, W.J. 1992. The new Mississippian conodont genus *Synclydognathus*. *Journal of Paleontology* **66**, 165–170.

Richter, U. 2001. Spuren der Weichkörper verlangerung auf Pyritsteinkernen von Ammonoideen. *Berliner geowissenschaftliche Abhandlungen E* **36**, 157–167.

Richter, U. 2002. Gewebeansatz-Strukturen auf pyritisierten Steinkernen von Ammonoideen. *Geologische Beiträge Hannover* **4**, 1–113.

Richter, U. and Fischer, R. 2002. Soft tissue attachment structures on pyritized internal moulds of ammonoids. *Abhandlungen der Geologischen Bundesanstalt* **57**, 139–149.

Roemer, F. 1866. Geognostische Beobachtungen im Polnischen Mittelgebirge. *Zeitschrift der Deutsche geologische Gesselschaft* **18**, 667–690.

Rolfe, W.D.I. and Dzik, J. 2006. *Angustidontus*, a Late Devonian pelagic predatory crustacean. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **97**, 1 (in press).

Romanek, A. and Rup, M. 1990. Podział litostratygraficzny dewonu w profilu otworu wiertniczego Kowala 1. *Kwartalnik Geologiczny* **34**, 221–242.

Ruzhentcev, V.E. [Руженцев, В.Е.]1962. Надотряд Ammonoidea. Аммоноидеи. Общая часть. *In*: В.Е. Руженцев (ed.) *Основы палеонтологии. Справочник для палеонтологов и геологов СССР. Моллюски – Головоногие. I. Агониатиты, Гониатиты, Климении* [*Superorder Ammonoidea. Ammonoidea. General Part. Fundamentals of Palaeontology. A Handbook for Palaeontologists and Geologists of the USSR. Cephalopod Molluscs. I. Nautiloidea, Endoceratoidea, Actinoceratoidea, Bactritoidea, Ammonoidea*], 243–424. Издательство Академии Наук СССР, Москва.

Rzehak, A. 1910. Der Brünner Clymenienkalk. *Zeitschrift der Mährischen Landesmuseum* **10**, 149–216.

Sandberg, C.A. and Dreesen, R. 1984. Late Devonian icriodontid biofacies models and alternative shallow-water conodont zonation. *Geological Society of America Special Paper* **196**, 143–178.

Sandberg, C.A., Hasenmueller, N.R., and Rexroad, C.B. 1994. Conodont biochronology, biostratigraphy, and biofacies of Upper Devonian part of New Abany Shale, Indiana. *Courier Forschungsinstitut Senckenberg* **168**, 227–253.

Sandberg, C.A. and Ziegler, W. 1979. Taxonomy and biofacies of important conodonts of Late Devonian *styriacus*-Zone, United States and Germany. *Geologica et Palaeontologica* **13**, 173–212.

Sannemann, D. 1955a. Oberdevonische Conodonten (to IIα). *Senckenbergiana lethaea* **36**, 123–156.

Sannemann, D. 1955b. Beitrag zur Untergliederung des Oberdevons nach Conodonten. *Neues Jahrbuch fur Geologie und Palaontologie, Abhandlungen* **100**, 324–331.

Sanz-López, J., García-López, S., Montesinos, J.R., and Arbizu, M. 1999. Biostratigraphy and sedimentation of the Vidrieros Formation (middle Famennian-lower Tournaisian) in the Gildar-Montó unit (northwest Spain). *Bolletino della Società Paleontologica Italiana* **37**, 393–406.

Schäfer, W. 1976. Einige neue Conodonten aus dem höheren Oberdevon des Sauerlandes (Rheinisches Schiefergebirge). *Geologica et Palaeontologica* **10**, 141–152.

Schindewolf, O.H. 1923. Beiträge zur Kenntnis des Paläozoikums in Oberfranken, Ostthüringen und dem Sächsischen Vogtlande. I. Stratigraphie und Ammoneenfauna des Oberdevons von Hof a. S. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band* **49**, 250–357, 393–509.

Schindewolf, O.H. 1937. Zur Stratigraphie und Paläontologie der Wocklumer Schichten (Oberdevon). *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge* **178**, 1–132.

Schülke, I. 1995. Evolutive Prozesse bei *Palmatolepis* in der frühen Famenne-Stufe (Conodonts, Ober-Devon). *Göttinger Arbeiten zur Geologie und Paläontologie* **67**, 1–108.

Schülke, I. 1996. Evolution of early Famennian ancyrognathids (Conodonta, Late Devonian). *Geologica et Palaeontologica* **30**, 33–47.

Schülke, I. 1998. Conodont community structure around the "Kellwasser mass extinction event" (Frasnian/Famennian boundary interval). *Senckenbergiana lethaea* **77**, 97–99.

Schülke, I. 1999. Conodont multielement reconstructions from the early Famennian (Late Devonian) of the Montagne Noire (southern France). *Geologica et Palaeontologica SB* **3**, 1–123.

Schindewolf, O.H. 1944. *Grundlagen und Methoden der paläontologischen Chronologie*. 139 pp. Berlin.

Schindewolf, O.H. 1950. *Grundfragen der Paläontologien*. 506 pp. Schweizerbart, Stuttgart.

Schindler, E., Schülke, I., and Ziegler, W. 1998. The Frasnian/Famennian boundary at the Sessacker Trench section near Oberscheld (Dill Syncline, Rheinisches Schiefergebirge, Germany). *Senckenbergiana lethaea* **77**, 243–261.

Seilacher, A. 1975. Mechanische Simulation and funktionelle Evolution des Ammoniten-Septums. *Paläontologische Zeitschrift* **49**, 268–286.

Selwood, E.B. 1960. Ammonoids and trilobites from the Upper Devonian and lowest Carboniferous of the Launceston area of Cornwall. *Palaeontology* **3**, 153–185.

Serpagli, E. 1982. The conodont apparatus of *Icriodus woschmidti woschmidti* Ziegler. *Fossils and Strata* **15**, 155–161.

Sobolew, D. [Соболев, Д.] 1911. О фаменском ярусие Келецко-Сандомирского кряжа [On the Famennian stage of the Kielce-Sandomierz upland]. *Ежегодник по Геологии и Минералогии России* **12**, 24–41.

Sobolew, D. [Соболев, Д.] 1912a. О верхнем неодевоне окрестностей Келец [On the upper Neodevonian of the vicinities of Kielce]. *Известия Варшавского Политехнического Института* **1912** (1), 1–14.

Sobolew, D. [Соболев, Д.] 1912b. О верхнем неодевоне Лагоша [On the upper Neodevonian of Łagów]. *Известия Варшавского Политехнического Института* **1912** (3), 1–20.

Sobolew, D. [Соболев, Д.] 1914a. Наброски по филогении гониатитов [Comments on the phylogeny of the goniatites]. *Известия Варшавского Политехнического Института* **1914** (1), 1–193.

Sobolew, D. 1914b. Über Clymenien und Goniatiten. *Paläontologische Zeitschrift* **1**, 348–378.

Stauffer, C.R. 1938. Conodonts of the Olentangy Shale. *Journal of Paleontology* **12**, 48–53.

Streel, M., Caputo, M.V., Loboziak, S., and Melo, J.H.G. 2000. Late Frasnian–Famennian climates based on palynomorph analyses and the question of the Late Devonian glaciations. *Earth-Science Reviews* **52**, 121–173.

Sweet, W.C. 1988. *The Conodonta: Morphology, Taxonomy, Paleoecology, and Evolutionary History of a Long-Extinct Animal Phylum*. 212 pp. Clarendon Press, Oxford.

Szulczewski, M. 1971. Upper Devonian conodonts, stratigraphy and facial development of the Holy Cross Mts. *Acta Geologica Polonica* **21**, 1–129.

Szulczewski, M. 1972. Interspecific relation of some Upper Devonian polygnathid conodonts. *Acta Geologica Polonica* **22**, 449–458.

Szulczewski, M. 1978. The nature of unconformities in the Upper Devonian–Lower Carboniferous condensed sequence in the Holy Cross Mts. *Acta Geologica Polonica* **25**, 283–298.

Szulczewski, M. 1989. Światowe i regionalne zdarzenia w zapisie stratygraficznym pogranicza franu z famenem. *Przegląd Geologiczny* **37**, 551–557.

Szulczewski, M. 1992. Ekologiczne uwarunkowania zespołów faunistycznych w śródszelfowych basenach fameńskich Gór Świętokrzyskich. *Przegląd Geologiczny* **40**, 610.

Szulczewski, M. 1995. Depositional evolution of the Holy Cross Mts. in the Devonian and Carboniferous – a review. *Kwartalnik Geologiczny* **39**, 471–488.

Szulczewski, M., Bełka, Z., and Skompski, S. 1996. The drowning of a carbonate platform: an example from the Devonian–Carboniferous of the southwestern Holy Cross Mountains, Poland. *Sedimentary Geology* **106**, 21–49.

Szulczewski, M. and Żakowa, H. 1976. Nowe dane o famenie synkliny gałęzickiej. *Biuletyn Instytutu Geologicznego* **296**, 51–73.

Thomas, L.A. 1949. Devonian-Mississippian formations of southeast Iowa. *Bulletin of the Geological Society of America* **60**, 403–438.

Tietze, E. 1870. Über die devonischen Schichten von Ebersdorf unweit Neurode in der Grafschaft Glatz, eine geognostisch-paläontologische Monographie. *Palaeontographica* **19**, 103–158.

Veevers, J.L. and Powell, C.M. 1987. Late Paleozoic glacial episodes in Gondwanaland reflected in transgression-regresion depositional sequences in Euramerica. *Geological Society of America Bulletin* **98**, 475–487.

von Bitter, P.H. and Merrill, G.K. 1998. Apparatus composition and structure of the Pennsylvanian conodont genus *Gondolella* based on assemblages from the Desmoinesian of northeastern Illinois, USA. *Journal of Paleontology* **72**, 112–132.

von Bitter, P.H. and Norby, R.D. 1994. Fossil epithelial cell imprints as indicators of conodont biology. *Lethaia* **27**, 193–198.

Vorontzova, T.N. [Воронцова, Т.Н.] 1993. Род *Polygnathus* sensu lato (конодонты): филогения и ситематика [Genus *Polygnathus* sensu lato (conodonts): phylogeny and systematics]. *Палеонтологический журнал* **1993** (3), 66–78.

Vorontzova, T.N. [Воронцова, Т.Н.] 1996. Род *Neopolygnathus* (конодонты): филогеня и ниекоторые вопросы систематики [Genus Neopolygnathus (conodonts): phylogeny and some questions of the systematics]. *Палеонтологический журнал* **1996** (2), 82–84.

Walliser, O.H. 1996. Global events in the Devonian and Carboniferous. *In*: O.H. Walliser (ed.) *Global Events and Event Stratigraphy in the Phanerozoic,* 225–250. Springer Verlag, Berlin.

Walliser, O.H., Groos-Uffenorde, H., Schindler, E., and Ziegler, W. 1989. On the Upper Kellwasser Horizon (boundary Frasnian/Famennian). *Courier Forschungsinstitut Senckenberg* **110**, 247–256.

Wang, C. 1989. Devonian Conodonts of Guangxi. *Memoirs of Nanjing Institute of Geology and Palaeontology, Academia Sinica* **25**, 1–152.

Wang, C. and Wang, Z. 1978. Upper Devonian and Lower Carboniferous conodonts from southern Guizhou. *Memoirs of the Nanjing Institute of Geology and Palaeontology, Academia Sinica* **11**, 51–91.

Wang, C.-y. and Ziegler, W. 2002. The Frasnian–Famennian conodont mass extinction and recovery in South China. *Senckenbergiana lethaea* **82**, 463–493.

Wang, S. and Turner, S. 1985. Vertebrate microfossils of the Devonian–Carboniferous boundary, Muhua section, Guizhou Province. *Vertebrata Palasiatica* **23**, 223–234.

Wedekind, R. 1908. Die Cephalopodenfauna des höheren Oberdevon am Enkeberge. *Neues Jahrbuch fur Geologie und Paläontologie, Beilage Band* **26**, 565–634.

Wedekind, R. 1918. Die Genera der Palaeoammonoidea (Goniatiten). *Palaeontographica* **62**, 85–184.

Wendt, J. and Belka, Z. 1991. Age and depositional environment of Upper Devonian (Early Frasnian to Early Famennian) black shales and limestones (Kellwasser Facies) in the eastern Anti-Atlas, Morocco. *Facies* **25**, 51–90.

Williams, M.E. 1990. Feeding behaviour in Cleveland Shale fishes. *In*: A.J. Boucot (ed.) *Evolutionary Paleobiology of Behaviour and Coevolution*. 273–287. Elsevier, New York.

Wolska, Z. 1967. Górno-dewońskie konodonty z południowo-zachodniego regionu Gór Świętokrzyskich. *Acta Palaeontologica Polonica* **12**, 363–435.

Woroncowa-Marcinowska, T. 2003. Górnodewońskie goniatyty Gór Świętokrzyskich (z kolekcji muzeum PIG) i ich pozycja stratygraficzna w skali konodontowej. *Przegląd Geologiczny* **51**, 982.

Woroncowa-Marcinowska, T. and Szrek, P. 2004. Zbiory Jana Czarnockiego w Muzeum Geologicznym PIG – nieustające źródło badań. *Przegląd Geologiczny* **52**, 638.

Yazdi, M. 1999. Late Devonian–Carboniferous conodonts from eastern Iran. *Rivista Italiana di Paleontologia e Stratigrafia* **105**, 1–13.

You Xing Li 2000. Famennian tentaculitids of China. *Journal of Paleontology* **74**, 969–975.

Youngquist, W.L. 1945. Upper Devonian conodonts from the Independence Shale(?) of Iowa. *Journal of Paleontology* **19**, 355–367.

Youngquist, W. and Peterson, R.F. 1947. Conodonts from the Sheffield Formation of north-central Iowa. *Journal of Paleontology* **21**, 242–253.

Żakowa, H. and Radlicz, K. 1990. Makro- i mikrofauna oraz petrografia famenu z otworu wiertniczego Kowala 1. *Kwartalnik Geologiczny* **34**, 243–270.

Żakowa, H., Nehring-Lefeld, H., and Malec, J. 1985. Devonian–Carboniferous boundary in the borehole Kowala 1 (southern Holy Cross Mts, Poland): nacro- and microfauna. *Bulletin of the Polish Academy of Sciences, Earth Sciences* **33**, 87–95.

Zalasiewicz, J., Smith, A., Brenchley, P., Evans, J., Knox, R., Riley, N., Gale, A., Gregory, F.J., Rushton, A., Gibbard, P., Hesselbo, S., Marshall, J., Oates, M., Rawson, P., and Trewin, N. 2004. Simplifying the stratigraphy of time. *Geology* **32**, 1–4.

Ziegler, P.A. 1990. *Geological Atlas of Western and Central Europe*. 239 + 56 pp. Shell, Avon.

Ziegler, W. 1962. Taxionomie und Phylogenie Oberdevonischer Conodonten und ihre stratigraphische Bedeutung. *Abhandlungen des Hessischen Landesamtes für Bodenforschung* **38**, 1–166.

Ziegler, W. 1971. Conodont stratigraphy of the European Devonian. *Geological Society of America Memoir* **127**, 227–284.

Ziegler, W. (ed.) 1975. *Catalogue of Conodonts. Volume II*. 404 pp. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Ziegler, W. (ed.) 1977. *Catalogue of Conodonts. Volume III*. 573 pp. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Ziegler, W. and Sandberg, C.A. 1984. *Palmatolepis*-based revision of upper part of standard Late Devonian conodont zonation. *Geological Society of America Special Paper* **196**, 179–194.

Ziegler, W. and Sandberg, C.A. 1990. The Late Devonian standard conodont zonation. *Courier Forschungsinstitut Senckenberg* **121**, 5–115.

Ziegler, W. Sandberg, C.A., and Austin, R.L. 1974. The *Bispathodus* group (Conodonta) in the Upper Devonian and Lower Carboniferous. *In*: J. Bouckaert and M. Streel (eds) *International Symposium on Belgian Micropaleontological Limits from Emsian to Visean, Namur* **20**, 1–8.

Żakowa, H., Szulczewski, M., and Chlebowski, R. 1984. Górny dewon i karbon synkliny borkowskiej. *Biuletyn Instytutu Geologicznego* **345**, 5–134.

Table 1. Frequencies of conodont elements in samples from the earliest Famennian of Płucki, the Holy Cross Mountains. In this and following tables elements which cannot be safely attributed to particular species on morphologic grounds are listed under generic headings. In cases when even such determinantion was not possible, they are attributed arbitrarily to one of species to which they may belong, as a rule to that of highest contribution to the sample.

PŁUCKI		Pł-36	Pł-42	Pł-41	Pł-40	Pł-32	Pł-33	Pł-34	Pł-14	Pł-13	Pł-11	Pł-10	Pł-9	Pł-1	Pł-6	Pł-5	Pł-2
Icriodus	P_1	429	105	9	15	710	23	21	5	3	2		2	267			
alternatus	P_2-M	372	89	6	12	47	17	1	10	3	1		5	215	1		
Pelekysgnathus	P_1		1	2				1						2			42
Ligonodina	P_2					1											
pectinata	S_0					1											
	S_1					1											
	S_{3-4}				2	3			1					1			
	M				1									1			
Pluckidina	P_1	2	1?											1			
lipperti	P_2	4	3			2								1			
	S_1	3												1			
	S_2	2	1?			1								3			
	S_{3-4}	3	2											1			
	M	1	5			1											
Vogelgnathus	P_2													1			
variabilis	S_0													3			
	S_2													1			
	S_{3-4}													3			
Mehlina	P_1	3	10	4		1	2		1					5			1
kielcensis	P_2		10														
	S_0			1										1			
	S_2		3														
	S_{3-4}		5	2													
	M			1		1											1
Ctenopolygnathus	P_1	11			1	14								28			
brevilamina	P_2	3				3								3			
	S_0					6								1			
	S_1	6												4			
	S_2	1				3											
	S_{3-4}	6				6								3			
	M					5								3			
P. praecursor	P_1	188	28	3	15	122	8	6	4	1	3	1	1	21	1		
P. procerus	P_1																2
Polygnathus	P_2	77	10	5	2	52	4	7				3	2	8			1
spp.	S_0	25	1	1	1	7		1				1	1	17			
	S_1	38	3			12		1						24			
	S_2	10	3		1	13	2	1			2			75			
	S_{3-4}	96	27	9	13	47	7	5	3	2	2			28			
	M	86	9	1	3	28	3	1	1					76			
K. ultima	P_1	660															
K. triangularis	P_1		36	4	8	194	28	17									
Klapperilepis	P_2	111	26	5		32	8				2			8			
spp.	S_0	10	2				1				1			3			
	S_1	14	6	3		1	1				1			5			
	S_2	20	4			4	3							7			
	S_{3-4}	43	7	4		5	4							12			
	M	40	4	2		6	4										
K. delicatula	P_1		23		3	22	8	3						82			
K. schuelkei	P_1		17														
Klapperilepis	P_1										3						8
spathula	P_2																1
Klapperilepis	P_1													2?		1	4
wolskae	P_2																1
K. protorhomb.	P_1										2						
K. robusta?	P_1																7

Table 1 – continued		Pł-36	Pł-42	Pł-41	Pł-40	Pł-32	Pł-33	Pł-34	Pł-14	Pł-13	Pł-11	Pł-10	Pł-9	Pł-1	Pł-6	Pł-5	Pł-2
Palmatolepis	P_1								5	6	6		3	210	1	7	14
sandbergi	P_2								2					35	1		2
	S_0													2			
	S_1									1				5			
	S_2								1					8			
	S_{3-4}								3					10	2		
	M								1					3			
Tripodellus	P_1		51	15	49	56	25	21	11	3	7	4	2	96	1		
clarki	P_2				5				1		1			3	1		
	S_0													1			
	S_1				1									4			
	S_{3-4}				4									5			
	M		1		2									4			
T. variabilis	P_1																17
C. lobicornis?	P_1																20

Table 2. Frequencies of conodont elements in samples from the early Famennian of Łagów, Wietrznia, and Jabłonna, the Holy Cross Mountains.

JABŁONNA Wietrznia		ŁPł-1	Wtr-27	J-53	J-37	J-38	J-53a	J-54	J-55	J-56	J-57	J-58	J-59	J-60	J-61	J-62	J-67
Latericriodus sp.	P_1			1													
Icriodus	P_1		264	650	108	19	1779	316	723	319	77	650	60	16	3	94	2
alternatus	P_2-M		547	122	15	3	359	157	307	78	35	535	20	11		23	1
Pelekysgnathus	P_1	1	36	4	1		30		4	1	3	5	1		1		
planus	P_2-M	9					13										
M. conoidalis	P-M				3												
M. circularis	P-M												11	7	5		
Pluckidina	P_1			1			1										
lipperti	P_2			2													
	S_0			3													
	S_2			2				1									
	S_{3-4}			4			4										
	M			2													
Ligonodina	P_1					1											
pectinata	P_2			1									1	1			
	S_0		1						2								
	S_1					1	1										
	S_2													1		1	
	S_{3-4}		1	3?		3	3		2				1	4?			
	M			1		2	5	1	4				2	1			
Ligonodina	P_1											4					
albidens?	P_2									1		1					
	S_0									1		4					
	S_1											4					
	S_2											4					
	S_{3-4}	3								1		13					
	M									2		7					
Vogelgnathus	P_1	2	1	7	2		139	1	3	7	7	15	4	1			
variabilis	P_2	17	4	4	3		96	4	2	9	7	12		1			
	S_0	4	2	1	1		26	1	2	5	2	15	1				
	S_1	2					8										1
	S_2	4	2	3			29	2		2	1	4	1				2
	S_{3-4}	23	5	7	5		98	4	2	9	8	4	1	5			1
	M	14	5	1	1		32	1	2	3	7	30					3
Francodina	P_1		1														
franconica	P_2		2														
	S_{3-4}		1														
Mehlina	P_1	2			3	1	13			2				1			
kielcensis	P_2						4			2							
	M													1			

Table 2 – continued		ŁPł-1	Wtr-27	J-53	J-37	J-38	J-53a	J-54	J-55	J-56	J-57	J-58	J-59	J-60	J-61	J-62	J-67
Ctenopolygnathus	P_1		6	8	4	1	11	6	10	10	2	3					
brevilamina	P_2			4	3	5	14	2	2	1	5	2					
	S_0				2	2	5	2	2	2					1?		
	S_1				1	1	8	3	1		2	1					
	S_2	2		1			4	4	1	1	1	1	1?				
	S_{3-4}	4	2	3			19	4	2	1	3	4	1?		3?		
	M	1	3	1	1	2	36	5	2	1	2	2					
I. streeli	P_1						2										
Polygnathus	P_1	18	193	161	31	19	330	33	61	32	51	49	22	11		9	1
praecursor	P_2	28	78	44	5	5	131	14	13	12	16	44	36	18	1	5	1
	S_0	6	12	26	3	3	23	6	2	6	6	18	3	10	4		
	S_1	8	5	14		2	7	1	2	1	7	21	3	4		1	
	S_2	10	14	28		3	17	4		2	4	14	3	7			
	S_{3-4}	35	28	48	8	5	86	12	2	11	28	43	20	47	8	5	1
	M	3	32	30	3	2	35	4	7	7	7	20	8	16	2	2	
P. procerus	P_1												77				
Ancyrognathus	P_1		1									1					
sinelamina	P_2	1										1					
	S_1	1															
	S_2		2														
	M		2														
K. delicatula	P_1	8															
K. spathula	P_1		117	29	7	17	303	84	62	29	29	3	27			6	7
Klapperilepis spp.	P_2	5	13	9		1	137	10	8	1	6	1	6	8	1		1
	S_0	2	1				1										
	S_1	3	1				1			1				3			1
	S_2	6	2				2							2		1	1
	S_{3-4}	5	2	2			2							3			
	M		2	2		1	25	1	1	2	5			2			
K. protorhomb.	P_1		5			2		28			2						
K. regularis	P_1		3														
Klapperilepis	P_1		11														
wolskae	P_2		1														
K. robusta	P_1		52													1	
P. initialis	P_1	38		118	36	27											
P. sandbergi	P_1		28				212	105	41	25	28	132	57	58	5	6	18
Palmatolepis spp.	P_2	2	9	54	1		39	10	15	3	8	18	7	2		2	5
	S_0			5			2										
	S_1	1	2	14			10		2			1		1			
	S_2	8		12			6		1				1				
	S_{3-4}	4	6	12	1	1	11	1	2	1	3			2			2
	M	1		11			13	1			1	2		2			
T. clarki	P_1	13	102	72													
T. variabilis	P_1						1376	112	83	59	77	159	59	27	4	11	6
Tripodellus spp.	P_2	15	20	5			64	20	7	4	4	28	10	2	2	1	
	S_0	2	6				9	1	1	2		9		1			1
	S_1	4	3				15	1	2	1		10		3			1
	S_2	3	17	3			34	3	1	2	1	13	1	2	1		2
	S_{3-4}	12	11	1			49	3	1	7	3	37	2	1	3		
	M	4	6	2			42			2	2	33	3	9	1		
C. lobicornis	P_1		32														
C. linguiloba	P_1											1					5
Conditolepis spp.	P_2		6														3

Table 3. Frequencies of conodont elements in samples from the early Famennian of Jabłonna and Łagów, the Holy Cross Mountains.

JABŁONNA ŁAGÓW		J-3	J-4	J-63	J-68	J-5	J-6	J-7	J-8	J-9	J-12	J-13	J-14	J-15	J-16	Ł/Pl -2	Ł-Mec
J. erectus	P-M										1	1			2		
Icriodus cornutus	P_1							2	1								

Table 3 – continued		J-3	J-4	J-63	J-68	J-5	J-6	J-7	J-8	J-9	J-12	J-13	J-14	J-15	J-16	Ł/Pl -2	Ł-Mec
Pelekysgnathus	P_1	169	7	1	1	132	22	19	17							3	1
planus	P_2-M	20	1		1	21		4	2								
M. conoidalis	P-M				8	7		1									
M. circularis	P-M	?			5		3	2							2		
Ligonodina	P_1						2	1	1				1				
albidens	S_0							1									
	S_{3-4}	1			4	2	3	5	2	2			1	1	1		
	M	1			1		2		2	2							
Ligonodina	P_2													1			
latibasalis	S_{3-4}														1		1
Pluckidina	P_1						1										
lipperti	P_2	1						1									
	S_1						1	1									
	S_2	1															
	S_{3-4}	2					3	2									
	M						3										
Uncadina unca	S_{3-4}				1			4					2	4			1
Synclydognathus	S_2														1		
ancestralis	S_{3-4}														1		
A. provarians	S						2					1		1	1		
G. dinodontoides	S_0										1						
Pandorinellina?	P_1				7												
vogelgnathoides	P_2				3												
	S_2				1												
	S_{3-4}				4												
	M				1												
Vogelgnathus	P_1								3	1		1			1		
proclinatus	P_2				1				3	1	1	1			1		
	S_0								1								
	S_2						1					1					
	S_{3-4}						1		3	1	1	1		1	1		1
	M				3		3		2	2		2					1
Francodina	P_1	6			1	2	43	19	68								3
santacrucensis	P_2	4				10	21	18	36								3
	S_0	8				4	13	5	14								
	S_1	6		1		11	9	7	23								1
	S_2	7				12	11	3	17								2
	S_{3-4}	20			2	11	33	24	41								3
	M	10			1	1	29	21	39								1
Francodina	P_1						1	1	7	3	2	1					
franconica	P_2				1		6	3	15	6		1			1		
	S_0						2	3	5	4							
	S_1				1		3	5	12	3							
	S_2				3		11	3	18	2	1	1					
	S_{3-4}			1	7		30	7	40	14	1	1		1	1		1
	M				3		11	8	23	11	1	2					1
M. kielcensis	P_1	8			1												
M. robustidentata	P_1						2	4	2			2					
Mehlina spp.	P_2	2			1			1				2	1				
	S_{3-4}				1						1				2	1	
	M	1			2				2						1	1	
Ctenopolygnathus	P_1	13				4	3	4									
brevilamina	P_2	4				1	8	2									
	S_0	1				2	1										
	S_1						1	1									
	S_2					1	2	1									
	S_{3-4}	3						2									
	M	3		3	1	1	2	2									
Polygnathus	P_1					2	7		18	3		1	1		1		1
procerus	P_2		2			1	9		15	4	2	2	3	3	5		1
	S_0						6		2	2		1	2	1			
	S_1		2			1	1		2								
	S_2		1				13		6						1		
	S_{3-4}		2		1	1	5		10	7		8	1	4	3		
	M		4				6		22	2		1	5	5	1		1

Table 3 – continued		J-3	J-4	J-63	J-68	J-5	J-6	J-7	J-8	J-9	J-12	J-13	J-14	J-15	J-16	Ł/Pl-2	Ł-Mec
Lagovignathus	P_1	5						4									
glaber	P_2	4						6									
	S_0	4						2									
	S_1							1									
	S_2	2						2									
	S_{3-4}	14						4									
	M	2						1									
P. pergyrata	P_1		1	2	1		2	13	13					1	1		3
Ancyrognathus	P_1	4				1		1	1								
sinelamina	P_2	2					1										
	S_0					1											
	S_2														1		
	S_{3-4}							1									
	M						1	2	1								
K. quadrantinodo-	P_1	137	5	13	14	83	112	189	130	2			4	4		1	16
solobata	P_2	34		1	7	6	4	12	8				1			3	
	S_0	1							1			2					
	S_1	1			1				1								
	S_2	4			1	2	2										
	S_{3-4}	1	2						2					1		1	
	M	2			1		1										
Klapperilepis	P_1	2			7		11		16	3	1						
regularis	P_2									2							
Klapperilepis	P_1	23	1	9		15											
wolskae	P_2	1		1													3
	S_0	1				2											
	S_2								1								1
	S_{3-4}					1											
	M	1															
K. circularis	P_1						11	47	4								13
Klapperilepis	P_1			6	25		29	3	37	2		5		1		3	2
termini	P_2				1				5	1	1						
	S_1									1							
	S_2									1							
Klapperilepis	P_1	17	2		7	2	30	50	14	4		2	4	3	1		
crepida	P_2						1		2				1				
Palmatolepis	P_1	293	23			35		6	1								2
aff. *sandbergi*	P_2	14	3			6	3	2									
sandbergi	S_1	1															
	S_{3-4}					4											
Tripodellus	P_1	152	4	20	58	59	73	102	98	11	9	28	5	20	20	1	26
variabilis	P_2	17	2		7	5	9	12	23	1	1	2	3	3	1		3
	S_0					2	2	3	3	1	1						
	S_1	5						2			2		1				
	S_2	6			2	3	6	2	2			1		1	2		
	S_{3-4}	9			3	2	8	5	20	2		2	3	2	3	1	
	M	12	1		9	8	6	8	24	2	2	1	1			3	
T.? subtilis	P_1									2							
C. linguiloba	P_1	3															
C. tenuipunctata	P_1			52	42	42	151	208	166	17	11	32	14	7	7	17	21
C. prima	P_1													1	2		
C. klapperi	P_1														1		
Conditolepis spp.	P_2				3			8	1			2	1	2			3
	S_{3-4}				3				1								
	M						1		3								

Table 4. Frequencies of conodont elements in samples from the early Famennian of Jabłonna, Wietrznia, and Miedzianka, the Holy Cross Mountains.

JABŁONNA Wietrznia Miedzianka		J-65	J-40	J-41	J-42	J-43	J-44	J-45a	J-45	J-46	J-47	J-48	J-50	Wtr-32	Wtr-21	Wtr-33	Md-1
Icriodus	P_1	11			1				1					11	1		3
cornutus	P_2-M	81			6				2					36			2

Table 4 – continued		J-65	J-40	J-41	J-42	J-43	J-44	J-45a	J-45	J-46	J-47	J-48	J-50	Wtr-32	Wtr-21	Wtr-33	Md-1
Pelekysgnathus	P_1	1	1					9		1		1	1	5	1	3	59
planus	P_2-M							12		3							6
M. conoidalis	P-M					8											
M. circularis	P-M							2	1	53	8	5	5		67		5
Ligonodina	P_1				4		4	24						3	6		6
albidens	P_2				2			2							1		1
	S_0					2	1	25						2		1	
	S_1				2	3		3							7		
	S_2														9		
	S_{2-4}				8	4	18	108		2		1		2	23		1
	M				4	2	1	14		2				4	6		
Ligonodina	S_2																5
multidens	S_{3-4}																1
	M														1		10
Ligonodina	P_1						3	8	1					2	9		
latibasalis	P_2						3	20						11	3		
	S_0						2	8	4					8	2		
	S_1							12						4	3		
	S_{3-4}		1				8	58	13					15	16		
	M		1				1	4	3					2			
Uncadina unca	S	39				32	49	562	30					107	97	17	
Guizhoudella	P_1							1									
dinodontoides	P_2							2									
	S_0							1		1							
	S_1						1	6					1				
	S_2							4					1				
	S_{3-4}	1						1					1				
Branmehla	S_0														1		
aff. *bohlenana*	M														1		
Synclydognathus	P_1							1						18			
ancestralis	P_2							1						14			
	S_0													3			
	S_2													6			
	S_{3-4}													37			
	M													27			
Apatognathus	P						1										
provarians	S_{1-2}							59						5	10		
	S_{3-4}				2			20		7	1	3	4	6	3		
Vogelgnathus	P_1	24		1	46	11	26	342	4	13			10	157	82	1	
proclinatus	P_2	33			23	14	34	442	14	14			11	134	79	1	
	S_0				3		1	135	6	1			6	39	14	1	
	S_1				1			51						25	10		
	S_2				1	1		129	6				3	54	19	1	
	S_{3-4}	2			9	14	19	418	13	4			7	151	51	4	
	M	3			7	6	10	234	17				15	81	41		
Vogelgnathus	P_1										4	8	1				
unicus	P_2				1	1		2				4	1				
	S_0					3				1	1	1	1				
	S_1				1		1		1		1						
	S_2				2	2	3	1	1		1	4	8				
	S_{3-4}				2	2					4	8	2				
	M				1	2		6		1	1	4	6				
Vogelgnathus	P_1													1			3
arcuatus	P_2													3	1		2
	S_0													3			
	S_2														1		1
	S_{3-4}													3	6		3
	M													17	2		1

Table 4 – continued		J-65	J-40	J-41	J-42	J-43	J-44	J-45a	J-45	J-46	J-47	J-48	J-50	Wtr-32	Wtr-21	Wtr-33	Md-1
Francodina	P_1									3							15
santacrucensis	P_2									4							12
	S_0									1							1
	S_1							1		2							2
	S_2													1	1		4
	S_{3-4}							1		5					1		5
	M									3	1						5
Francodina	P_1	2	1		1									2	5	2	
franconica	P_2	7	5		2			8	1					3	13	2	
	S_0	6	1		2			14	1						1	1	
	S_1	1					1	23							13		
	S_2	7						13						5	2	1	
	S_{3-4}	29	6		5	3	6	50	1					8	18	1	
	M	16	1		1	2	2	30	1					11	13	3	
Mehlina	P_1	2			5	1	6	64	1				1		9		
robustidentata	P_2							22									
	S_1							9									
	S_2							11									
	S_{3-4}	1						18									
	M	3						9									
C. brevilamina	P_1													5			11
Immognathus	P_1	5		1	8		8	28		2				27	37	5	1
streeli	P_2				2	1	14	13	3					10	17		5
	S_0	1			1	2	1	15	2					1	4		2
	S_1					1	1	20	4					2	6		2
	S_2					1	4	14	1					5	9		
	S_{3-4}			2	2	8	8	64	6					15	27	1	6
	M				3		1	30						9	15		2
P. semicostatus	P_1					1		12									
Polygnathus	P_1	1	2							3				7	10	2	381
procerus	P_2		2							2			1	3	6	5	38
	S_0	3								1			2	2	3	1	5
	S_1		2											4	2	2	7
	S_2	2	1							2			2	6	4	2	7
	S_{3-4}	1	2							2			1	21	20	1	28
	M	1	4											5	5	4	11
Ancyrognathus	P_1	3															
sp. n.	P_2	2															
	S_{3-4}	1															
	M	1															
Ancyrognathus	P_1																11
sinelamina	S_2													1			
	M													1			
Polylophodonta	P_1				2		15	16	6					6	25	2	4
ovata	P_2						10	10	5					1	17	2	2
	S_0						1	6						2	6		
	S_1						1	13							9		
	S_2						3	13	1						8		
	S_{3-4}						4	16							12		
	M							23						1	6		
Lagovignathus	P_1							1		2	1	2					
glaber	P_2									4	4	5					
	S_0									1		3					
	S_2										1	2					
	S_{3-4}									1	6	7					
	M									3	2	9					
K. delicatula	P_1																1
K. quadrantinodo-	P_1	86	3	2	20	5	52	297	25	18		1	2	86	65	14	87
solobata	P_2	2			9		2	7				1	1	3			18
	S_0																2
	S_1							3		1				5			
	S_2						1	2		2			2	13	3		
	S_{3-4}							4		1				14	2		4
	M						13	37						9	8		2
Klapperilepis	P_1	5	2		1	2	2	12		5	1		1		8	2	
regularis	P_2	2					1			1			1				1
	S_2											2					
	S_{3-4}											1					
Klapperilepis	P_1																8
circularis	P_2																7
	S_1																1
	S_{3-4}																1
K. termini	P_1				10	1											13
Klapperilepis	P_1	106	1	1	11	6	82	241	24	9		3		125	239	11	15
crepida	P_2	2	1			2		5	2					12	4		
	S_0													1			
	S_1													3			
	S_2	1							1					1			
	S_{3-4}									2				4	1		
	M							1	1	1				2			
P. sandbergi	P_1	122				17								11	8	4	
P. perlobata	P_1		2		39		19	37	1	9		3	11				
Palmatolepis	P_2	18			1	5	2	5		2			1			1	
spp.	S_1													1			
	S_2													1			
	S_{3-4}	1				1	3	1						1			
	M	2				1											
Tripodellus	P_1	239	2	1	89	29	185	2007	96	37	2	8	16	760	293	38	76
variabilis	P_2	13			3	2	9	141	38	11		4	8	63	24	2	8
	S_0	3			1	1	1	66	21	5		3	7	10	3	1	
	S_1	1	1		1		7	78	8	1	1	1	2	12	3		2
	S_2	2			2	2	4	102	21	2	2	9	10	23	3		2
	S_{3-4}	5	1	1	2	4	5	132	30	9	2	11	11	73	9	2	2
	M	5	3		8	6	7	153	19	10	2	7	15	58	19	1	7
T. lobus	P_1	26	1	1	2	3	26	85	5	1	2		1		244		
T.? subtilis	P_1					1	3	18						2	2		
T. subgracilis	P_1							3									
Conditolepis	P_1														13		
linguiloba	P_2														1		
C. tenuipunctata	P_1		9	14	95	29	304	540	24					240	305	66	141
C. lobicornis	P_1	303															
C. prima	P_1									83	18	13	31			6	
Conditolepis	P_2	26			5		9	89	2	5		1	4	63	23	39	3
spp.	S_0	1						5						2		4	
	S_1							1						1			1
	S_2							2	1					3	1		1
	S_{3-4}						1	14						13	1	1	
	M					1	1	23		1			2	27			2

Table 5. Frequencies of conodont elements in samples from the mid Famennian of Jabłonna and Ściegnia, the Holy Cross Mountains.

JABŁONNA ŚCIEGNIA		J-23	J-20	J-24	J-26a	J-26b	J-27	J-51	J-52	J-64	J-66	J-r.IVc	Wzd -10	Wzd -7	Wzd -2	Wzd -9	Wzd -13
Jablonnodus	P_1			15													
oistodiformis	P_2	1		20	1												
	S_0	1		41													
	S_{1-2}	1	1	87													
	S_{3-4}		1	127													
	M			35	1												
Jablonnodus	P_1						17	2	6	1							7
erectus	P_2						6										9
	S_0						26		2								7
	S_{1-2}						27		2								29
	S_{3-4}						80	15	2	2							26
	M						14										6

Table 5 – continued		J-23	J-20	J-24	J-26a	J-26b	J-27	J-51	J-52	J-64	J-66	J-r.IVc	Wzd-10	Wzd-7	Wzd-2	Wzd-9	Wzd-13
M.? asymmetr.	P_1-M			4													4
M. circularis	P-M			86	1		94	7	8	22	3		5	3	1		119
Pluckidina	P_1			9				2									
purnelli	P_2			15									1				
	S_0			1				1									
	S_1			22				1									
	S_2			14													
	S_{3-4}			42				4			1						
	M			5													
Idioprioniodus	P_1			3									3				
ruptus	P_2			5	1	1				2	2		8				6
	S_0	1		15		1		1	2	1	1						1
	S_1			10				2	2		1						
	S_2			20	2					2							1
	S_{3-4}	1		19	2			2	1	1	3		3			1	9
	M			21				1			1					1	3
Idioprioniodus	P_2						3										
uncadinoides	S_0						1										
	S_{3-4}						13										
B. bohlenana	P_1		4			1	5						58	1			169
B. inornata	P_1			22	6	8	242	140	55	84	20	1					
B. suprema	P_1											9					
Branmehla spp.	P_2			4		1	28	5	3	5	3		5			1	24
	S_0			37		1	1	1	4	2	1		1				1
	S_1			7			2	2	2				3			1	1
	S_2			6			9	8	8	6	1		2				7
	S_{3-4}			6		4	11	13	11	14	2		7				9
	M			36			15	6	7	8	1		5				16
Guizhoudella	S_{3-4}						2										
triangularis	M						2										
G. dinodontoides	M										1						
Synclydognathus	P_1			4													
triramosus	P_2			4													
	S_0			1													
	S_2			3													
	M			2													
Apatognathus	P_1			2													1
varians	S_{1-2}			1			1						1				3
	S_{3-4}	2		2					1				3				2
	M			2													
V. unicus	P_1												1				
Vogelgnathus	P_1			169			185										
branmehloides	P_2			53			26				1						
	S_0			24			6										
	S_1						2										
	S_2			17	1		11										
	S_{3-4}			40			10										
	M			60			15										
Vogelgnathus	P_1			370													8
werneri	P_2			9													2
	S_0			2													
	S_1																2
	S_2			1													2
	S_{3-4}			7													
Sweetodina	P		1	12			10	2	1		1		5	3		1	52
monodentata	S_2			1													
	S_{3-4}			1									2			1	16
	M			1			2						1	1			25
Planadina	S_0						2					1					3
plana	S_{1-2}			3			25						2	4			3
	S_{3-4}			11	1		8	1	1	1	1	3		1	1		2
	M			2						1		2	2				5
P. vulgaris	P_1			873	18							8					
P. bituberculata	P_1							108	62	74	7		1	39	3	4	

Table 5 – continued		J-23	J-20	J-24	J-26a	J-26b	J-27	J-51	J-52	J-64	J-66	J-r.IVc	Wzd-10	Wzd-7	Wzd-2	Wzd-9	Wzd-13
Pandorinellina	P_2			327	5			18	14	24	2	4	1	11	1		
spp.	S_0			180					1	5	2	1		3			
	S_1			217					4			3		2			
	S_2			153				3	6	4		5		8		1	
	S_{3-4}			679	6			23	35	29	3	8		8	1	3	
	M			305	3				10	7	4	1		5			
Mehlina	P_1	8	1				55	56	29	26	4	1					
strigosa	P_2	5					9	7	2	9	1						
	S_0	1															
	S_1	1					11										
	S_2						9			1							
	S_{3-4}	5					23			3							
	M	1					19										
P. transitus	P_1			263	2	1	41						22				10
	P_2			152													3
	S_0			64													
	S_1			77													
	S_2			44													
	S_{3-4}			245													
	M			57													
P. lauriformis	P_1													26			
C. brevilamina	P_1	3		84													
I. streeli	P_1													8			
P. semicostatus	P_1		23	506		3						5	32	2			
P.? experplexus	P_1						118	3	2	1							
P. extralobatus	P_1						335	16	10	15							25
P. znepolensis	P_1							1		2							
Polygnathus	P_2		3	66			157	4	2	5		1	1				9
spp.	S_0						22	8		1							
	S_1		1	4		1		4									2
	S_2			12				19									2
	S_{3-4}		3	105			79	44									4
	M		1	40			66	12		1			2				1
H. perplexa	P_1		1										88	7	4	4	
H. homoirregular.	P_1			74	2							2					
Hemilistrona	P_2		1	7			19						26	2			
spp.	S_0			6			3						13				
	S_1						6						10				
	S_2			2	1		4						16				
	S_{3-4}			2			15						41				
	M			2	2								19				
N. communis	P_1	1					4				2					6	2
L. glaber	P_1	20										3					20
L. granulosus	P_1		6										7		2	2	
L. styriacus	P_1				2	1					2						
Lagovignathus	P_2												1				4
spp.	S_0	7															1
	S_{3-4}											3					
	M	1	1														
Lagovignathus?	P_1							83	46	70	3	5					
dissimilis	P_2							11	3	10		1					
	S_0								5	5		1					
	S_1							1	2	3	1						
	S_2								10	5	1	2					
	S_{3-4}								14	11	1	1					
	M							1	2			1					
P. pergyrata	P_1												5				
Ancyrognathus?	P_2									2							

Table 5 – continued		J-23	J-20	J-24	J-26a	J-26b	J-27	J-51	J-52	J-64	J-66	J-r.IVc	Wzd-10	Wzd-7	Wzd-2	Wzd-9	Wzd-13
Palmatolepis	P_1	14	2	1256	4	1	30	22	11	12	6	6	17	42	1	1	22
schindewolfi	P_2			37		1					1						
	S_0			11				1			1						
	S_1			21				1	1			1					
	S_2			14													
	S_{3-4}	1		2													
	M			5					1								
P. trachytera	P_1		10	252													
P. rugosa	P_1						77	9	6	11	6	1					214
Palmatolepis	P_2		1	57			3	1									20
spp.	S_1			2			2										2
	S_2			12			1										
	S_{3-4}			11													5
	M			3			1										3
T. schleizius	P_1	11	11	1443													
Tripodellus	P_1				4	3	882	116	51	83	48	7	59	42		1	111
gracilis	P_2	2	1	192	1		24	45	9	19	7	2	14	10			9
	S_0			67		1	5	6	3	3	2		3				1
	S_1			89		1	10	9	7	6	1	1	4	2			6
	S_2			110	2		17	12	6	9	11	2	6	3			4
	S_{3-4}	1	1	105	1	1	32	32	17	11	6	1	12	11			14
	M	1	1	76	2	1	40	22	8	15	12	6	10	3		1	9
Tripodellus	P_1			87													
donoghuei	P_2			6													
	S_{3-4}			7													
	M			35													
Conditolepis	P_1	78	4	4813								40	52	21			
falcata	P_2	6		256								1	1	3			
	S_0	1		53													
	S_{1-2}	6	1	132								1	1				
	S_{3-4}	8		383								4					
	M	3	1	215									2	2			
C. distorta	P_1												1				
C. inflexoidea	P_1	1															
Conditolepis	P_1	14		1													
marginifera	P_2			1													
D. stabilis	P_1					3	485	20	6	12							
D. micropunctata	P_1						16	1	4	5							1036
D. granulosa	P_1			79										11			
D. brevipennata	P_1					9	69										5
Dasbergina	P_2			16		2	81			2							184
spp.	S_0						14										18
	S_1			1		1	50										25
	S_2					1	42										31
	S_{3-4}			4		5	38										119
	M			2		2	47										121
Pseudopolygnath.	P_1						20	452	173	224	44						
jugosus	P_2						6	92	59	51	6						
	S_0							29	19	10	2						
	S_1							10	4	10							
	S_2							26	7	14							
	S_{3-4}							125	49	50	7						
	M							58	29	18	3						
P. ultimus	P_1										4						
P. ostrovkensis	P_1						26										
A. regularis	P_1													2			
Alternognathus	P_1			91						1	3		82				
beulensis	P_2			20									5	3			
S. velifer	P_1			42									3				

Table 6. Frequencies of conodont elements in samples from the early Famennian of Kadzielnia and Łagów, the Holy Cross Mountains.

KADZIELNIA Łagów Miedzianka		Md-27	Ka-16	Ka-15	Ka-14	Ka-2	Ka-13	Ka-12	Ka-5	Ka-3	Ka-10	Ka-4	Ka-9	Ka-6	Ka-8	Ka-7	Mak-4-5
Icriodus	P_1	2	24		4	11	3	2	15	20	11	13	10	5		2	3
cornutus	P_2-M		2		3	17	6	9	22	8		49	3	18			8
Pelekysgnathus	P_1	18		22	36	145	34	59	36							1	
planus	P_2-M	1		2	2	5	2	2	2								
M. conoidalis	P-M				5			1									
M. circularis	P-M				4					52	10	1	9			1	
Ligonodina	P_1	1			4		1	2	2								
pectinata?	P_2	3	1		4	1		1	3								
albidens	S_0	3			1	9	1		3								
	S_1	3						1									
	S_2	8				3			2								
	S_{3-4}	9			2	11		7	11								
	M	3			4	6		5	7								
Ligonodina	P_1					1				2							
multidens	P_2									3							
	S_0					1				8							
	S_1									1							
	S_2									2							
	S_{3-4}					2				7		5					
	M					3						2					
Lagovidina	P_1	1											1	2		3	
obliqua	P_2									2		2				5	
early form	S_0											2			1	1	
	S_1	1								2		6	2			2	
	S_{3-4}	6								5	2	19	1	3	4	4	
	M	1								6	2	8	2	3	3	5	
Idioprioniodus	S_1															1	
	M															1	
Planadina?	S_{3-4}									2							
A. provarians	S_1	?1														1	
Pandorinellina?	P_1					8	2		21								
vogelgnathoides	P_2					24	3		8								
	S_0					12	1		10								
	S_1					7			6								
	S_2					14	3	2	11								
	S_{3-4}					26	11	4	12								
	M					31	3	2	16								
Vogelgnathus	P_1					42	1	14	1	32	5	99	12	23	4	8	22
unicus	P_2					17		17	1	21		45	3	45	1	4	11
	S_0					8		4	1	2		27	1				1
	S_1					5		5	2	1							
	S_2					9		6	2	5		24	2	6		1	3
	S_{3-4}					10		8	3	11	1	43	2	7		1	2
	M					27		6		15		54	3	10		1	5
Francodina	P_1	2				47		33			3					3	
santacrucensis	P_2	2			1	31		11		3	1	2	1	2	2	3	2
	S_0				1	3		1		1		2				1	
	S_1				1	30					1			2		2	
	S_2	7			1	7	2	11		1	2	7					1
	S_{3-4}	6			4	24	5	16		6	1	19	2	8	5	4	2
	M	5			1	44	9	17		1	5		1		3	6	5

Table 6 – continued		Md-27	Ka-16	Ka-15	Ka-14	Ka-2	Ka-13	Ka-12	Ka-5	Ka-3	Ka-10	Ka-4	Ka-9	Ka-6	Ka-8	Ka-7	Mak-4-5
Francodina	P_1			4		82	23	24	21								
franconica	P_2			2		58	12	35	30								
	S_0			1		23	10	7	11								
	S_1					67	14	29	12								
	S_2			2		34		14	32								
	S_{3-4}		1	2	7	144	14	62	63								
	M					118	12	39	46								
Sweetodina	P										1	5	2	1	2		
mononodosa	S_{3-4}										3	1		1	1		
	M										2	2					
G. dinodontoides	S_2	?1			1												
Mehlina	P_1			4	3	1	2										
kielcensis	M				1												
Mehlina	P_1						7			8							2
aff. *robustidentata*	P_2									2							
M. lunaria	P_1					2											
Polynodosus	P_1									69	27	174	63	106	31	61	17
confluens	P_2									36		48	19	28	7	12	15
	S_0											12	1		1	5	6
	S_1									4		13	4	2			9
	S_2									5		19	2	1		5	7
	S_{3-4}									10		47	1	8	3	4	18
	M									14		32	10	23	3	6	4
Ctenopolygnathus	P_1	1		1?			1		2		1						
brevilamina	S_0						1										
	S_1						1										
	S_2						3										
	S_{3-4}						1										
P. volhynicus	P_1	209															
P. praecursor	P_1		39	1?													
P. semicostatus	P_1									131	23	1		2	6	3	6
P. kadzielniae	P_1			22	148	220	217	19	143								
Polygnathus	P_2	27	7	9	32	132	46	37	75	54	5				2		7
spp.	S_0	8		2	3	20	4	2	3	13					1		
	S_1	4	1		3	12	3	5	4	23							
	S_2	2		1	2	16	7	7	10	10					1		
	S_{3-4}	17	4	14	7	57	33	16	26	54					3		
	M	6	3	4	6	40	25	7	9	43					1	1	4
L. glaber	P_1	4	1		27	5	1		1	64	6	114	38	53	5	23	
L. bilobatus	P_1																3
Lagovignathus	P_2				3	1					5	31	16	24	1	5	5
spp.	S_0				1						1	4	5	7	1		2
	S_1										2	2	3	3		1	
	S_2				1						1	10	1	7		1	
	S_{3-4}				1						11	14	4	19		7	
	M				1							10	8	18		3	
Polylophodonta	P_1	4		1?	1	38	4	13	15								
pergyrata	P_2	2					3	1	9								
	S_0					1			11								
	S_1								7								
	S_2								13								
	S_{3-4}								14								
	M					1			17								
Ancyrognathus	P_1	?2							3								
sp. n.	P_2								4								
	S_{3-4}								8								
	M								4								
Ancyrognathus	P_1			1		1											
sinelamina	P_2			1													
	S_0			1		1											
	S_{3-4}			1													
	M					1											

Table 6 – continued		Md-27	Ka-16	Ka-15	Ka-14	Ka-2	Ka-13	Ka-12	Ka-5	Ka-3	Ka-10	Ka-4	Ka-9	Ka-6	Ka-8	Ka-7	Mak-4-5
K. quadrantinodo-	P_1		7	17	34	650	74	210	78								
solobata	P_2			2	2	68	11	21	11								
	S_0					5											
	S_2					6		2	2								
	S_{3-4}					6			4								
	M				1	14		1	2								
Klapperilepis sp.	P_1										5						
Klapperilepis	P_1	29															
quadrantinodosol.	P_2	8															
K. arcuata?	P_1		6														
K. subrecta	P_1								65								
Klapperilepis	P_1					58	9	13	45								
regularis	P_2								2								
	S_2								2								
Klapperilepis	P_1									2	11	222	44	120	33	17	16
rhomboidea	P_2										1	1	1	1	1		1
	S_2											1	1	1			
	S_{3-4}											2					
	M											1					
Klapperilepis	P_1	21		10	36	58	8	5		49							9
circularis	P_2	1				5	1	1									
	S_1					2											
	S_2					2	1										
	S_{3-4}					2											
	M					2											
K. termini	P_1	33		5	42	380	50	162	63								
K. crepida	P_1					47	5	24	77	78							
Klapperilepis	P_2					14	3	9									
termini	S_0				1			1	2								
crepida	S_1					2											
	S_2					3		1									
	S_{3-4}								2								
	M					9		3									
Palmatolepis	P_1	11	8	14	58	65		5		61	26	53	27	29	36	84	9
perlobata	P_2	2		2	15	1				19	10	28	6	9	6	30	7
	S_0							1		1		3				4	
	S_1				2	1				6	1	3		6		2	2
	S_2	1		2	1	1				2	4	1		4	8	9	
	S_{3-4}			2	2	3		2		6	3	4			4	8	3
	M					1				6	1	1	3	1		3	3
T. variabilis	P_1		4	16	131	641	142	191	177								
T. donoghuei	P_1									16	23	12	10	13		12	
Tripodellus	P_1				2?	17	15	44	92	13	23						92
lobus	P_2				6	62	10	22	17		11						26
	S_0				1	8		2	2								6
	S_1				1	20	1	7	3								8
	S_2					14	1	1	3								15
	S_{3-4}					42	9	13	13								21
	M				6	16	9	11	6		1						14
Tripodellus	P_1	68								189	56	408	69	188	91	135	53
minutus	P_2	1								51	2	107	4	47	5	36	8
	S_0									7	1	17	1	5	1	3	
	S_1									4	4	26	1	20	1	8	
	S_2									27	8	39	2	20	4	10	
	S_{3-4}	1								36	4	75	7	26	7	23	
	M	1								35	3	65	6	35	7	18	4
C. tenuipunctata	P_2	152	3	34	202	913	141	270	315								
C. prima	P_1									148	125	566	208	225	179	131	
C. glabra	P_1																131
Conditolepis	P_2	5			1	105	10	13	32	52	19	100	57	72	17	4	16
tenuipunctata	S_0							2			1		1	1			
prima	S_1					3		2	2		2						
glabra	S_2					4	1	1	2		4		6	4			1
klapperi	S_{3-4}					4		6	3	13	8	66	9	14	2		8
	M	1				9	1	4	1	6		19	10	14		1	3

Table 6 – continued	Md-27	Ka-16	Ka-15	Ka-14	Ka-2	Ka-13	Ka-12	Ka-5	Ka-3	Ka-10	Ka-4	Ka-9	Ka-6	Ka-8	Ka-7	Mak-4-5
Conditolepis P_1									5		69		20	1		
falcata P_2									1		5		1	1		
S_2											1					
M											1			1		
C. klapperi P_1								1?		59		2		1		20
Alternognathus P_1									1	21				1	2	
pseudostrigosus P_2										14						
S_0										5						
S_1										6						
S_2										3						
S_{3-4}										17						
M										14						
reworked elements	24															

Table 7. Frequencies of conodont elements in samples from the early Famennian of Karczówka, Kowala, and Wietrznia, the Holy Cross Mountains.

KOWALA WIETRZNIA	Karczówka	Ko-152	Ko-143	Ko-153	Ko-154	Ko-204	Ko-203	Ko-202	Ko-200/1	Ko-199	Ko-155	Wtr-34	Wtr-26	Wtr-29	Wtr-25	Wtr-19
Icriodus P_1	1	163	31	78	85	151	48	64	11	13	48	101	17			
alternatus P_2-M		26		35	57	201	5	12	2	1	8	95	14			
Pelekysgnathus P_1	84						1	2				2	15	15	29	179
planus P_2-M	15												3			30
Mitrellataxis sp.P-M	34												1			
Ligonodina P_1	1													1		
sp. indet. P_2	2														2	
S_0	1					1	1									
S_1						1										
S_2						1			1	1						
S_{3-4}	4					1						2		1	1	
M						2								1		
Idioprioniodus P_2															4	
uncadinoides S_{3-4}														2	5	
M															2	
G. dinodontoides S_0					1											
Vogelgnathus P_1						1			1							
variabilis P_2						1										
S_2						1										
S_{3-4}						2										
M						1										
Francodina P_1																1
santacrucensis P_2																4
S_{3-4}																5
M																3
Francodina P_1													1	2		
franconica S_1														2		
S_{3-4}														2		
M. robustidentata P_1	2?															
M. kielcensis P_1	12															
C. brevilamina P_1	1		10		7	8		3	1	3	2	3		2	2	2
Ctenopolygnathus P_2	1		7			4		1						2		
Immognathus S_0					4										1	
S_1		2	1	2	5	2						1				1
S_2			2	6	5					1						1
S_{3-4}	2		9	1	13	5	2	1		1						
M			1		8	1						1		2	1	2
P. volhynicus P_1	1351															
P. praecursor P_1		9	30	13	65	31	13	38	10	5	13	18				
P. semicostatus P_1													13	40	38	13

Table 7 – continued	Karczówka	Ko-152	Ko-143	Ko-153	Ko-154	Ko-204	Ko-203	Ko-202	Ko-200/1	Ko-199	Ko-155	Wtr-34	Wtr-26	Wtr-29	Wtr-25	Wtr-19
Polygnathus spp. P_2	156	2	13		24	16	3	7	6		6	8	5	12	8	1
S_0	4	2	1	1	9	2	1	4				7	1		1	1
S_1	10		4	2	3	1	4				1	2	2	2		
S_2	12	1	4	7	9	1	1	5			1	6	2	3	2	1
S_{3-4}	38	6	40	10	29	21	9	12	2	1	5	21	1	7	8	3
M	49	6	11	9	10	9	5	10	3	1	2	10	5	5	2	2
Ancyrognathus P_1	5												1			2
sinelamina P_2	4													1		2
M													1			5
Manticolepis? P_1											5					
K. ultima P_1		26	78	54	266											
K. triangularis P_1	122					73	53	12	13	8	3		9			
Klapperilepis P_2	8		6	2	28	43	14	1	2	5						
ultima lineage S_0					1	2										
S_1						3										
S_2	1			1		3	1									
S_{3-4}		1		1	4	7	1									
M				1	2	2										
K. delicatula P_1							7				1					
K. protorhomb. P_1																1
K. schuelkei P_1	45					60	19	21	6	14	5	15	6			
K. spathula P_1														9		
K. quadr-nodosol. P_1															10	17
Klapperilepis P_2						18		3	1			8	4	1	2	2
spathula lineage S_0													1			
S_1																1
S_2							1					2			1	
S_{3-4}						6	1	1		1		6	1	2	1	
M						9		1				6		1	3	
Klapperilepis P_1	129												5			16
wolskae P_2	8															
S_2	1															
K. circularis P_1														2	5	
K. regularis P_1	11															
K. robusta P_1													2			
Klapperilepis P_1														17	7	
termini P_2														2		
Palmatolepis P_1												14		17		17
sandbergi P_2												3		7		3
S_1														1		
S_2												1				
S_{3-4}												1				
M														1		
T. clarki P_1						253	34	43	20	37	9					
T. variabilis P_1	145											69	4	69	45	18
T. lobus P_1													2			
Tripodellus P_2	1					17	1	2	1			5	1	3	3	
spp. S_0						1							1	2		
S_1															2	
S_2						2						3				
S_{3-4}						5						4		2	3	
M						5						3	2	2	4	2
T.? subtilis P_1															2	
C. lobicornis? P_1											4					
C. tenuipunctata P_1																19

Table 8. Frequencies of conodont elements in samples from the early famennian of Kowala, the Holy Cross Mountains.

KOWALA		Ko-165	Ko-205	Ko-164	Ko-162	Ko(?)-168	Ko-161	Ko-15st	Ko-163	Ko-160	Ko-158	Ko-159	Ko-157a	Ko-157	Ko-20	Ko-19-19a	Ko-14
Icriodus	P_1	161									44	70	38				
alternatus	P_2-M	56									19	24	20				
Pelekysgnathus	P_1		5														
planus	P_2-M		4														
M. circularis	P-M			7	1	2	3	46	6			1	5	3	2	1	2
Ligonodina	P_1											1					
sp. indet.	P_2	1		1			1		1					1			
	S_1							1	1		1						
	S_2	1		1			1		1		1						
	S_{3-4}			1		1	2	1		1							
	M			3	1		2		1	2							
Pluckidina?	P_1		1														
sp.	S_{3-4}											1					
Branmehla	P_1								2								
cf. *bohlenana*	S_1								1								
	M								1								
Apatognathus	P							15				1					
provarians	S										1	1					
Vogelgnathus	P_1	1		20			1	31	23	1	7	35	38	9			
proclinatus	P_2	?		21		3		28	23	1	5	6	4	1			
	S_0								1					1			
	S_1								4			2	1				
	S_2	2					1	5	5		2	1	3	1			
	S_{3-4}	6				1	1	7	14	1	3		2	1			
	M	8				3	3	3	9	1	3	2	1				
Urbanekodina	P_1							6									
undata	S_1							6									
	S_{3-4}	1						15									
Sweetodina	P					8											
monodentata	S_{3-4}					1											
	M					2											
Mehlina	P_1							36									
strigosa	P_2							8									
P. cf. *transitus*	P_1				3		7	11									
P. lauriformis	P_1									9	3	9	5	9	4	7	3
P. triphyllatus	P_1					9	7										
Polynodosus	P_2			1		3	3	15		1	2	3	4	2		5	
spp.	S_0										1		1			1	
	S_1											1	1				
	S_2					1				1		1	1	1		1	
	S_{3-4}					3						2	1			2	
	M					1			1	1			2	1	1	2	
Polynodosus	P_1							4									
confluens	P_2							5									
P. nodoundatus	P_1										3	1			1		6
Ctenopolygnathus	P_1	4		3													
brevilamina	S_{3-4}		1														
Polygnathus	P_1	40	8		1		116	90						31			
praecursor	P_2	16	1	3	3		41	25						1			
	S_0	2		3			3	7						3			
	S_1	4	1	4			14	10						1			
	S_2	5	2		1		5	13						3			
	S_{3-4}	12	5	8	1		20	36						7			
	M	12			3		22	25						3			
L. bilobatus	P_1					11	14	35	6	12	5	7	13	9	3	2	3
L. lagoviensis	P_1									3					17	1	11
L. fallax	P_1							23									

Table 8 – continued		Ko-165	Ko-205	Ko-164	Ko-162	Ko(?)-168	Ko-161	Ko-15st	Ko-163	Ko-160	Ko-158	Ko-159	Ko-157a	Ko-157	Ko-20	Ko-19-19a	Ko-14
Lagovignathus	P_2					2		16	3	3	1		2	4	5	3	2
spp.	S_0							2	1	1	2	1	1	5	1		1
	S_1								3		1	3		2	1		3
	S_2					1			4		2	3		5	1		2
	S_{3-4}					7			4	10	17	3	2	12	5	1	9
	M					1		8	4	5	1	1		4	6		10
P. pergyrata	P_1					1						3					
Klapperilepis	P_1	25	3														
spathula	P_2	6															
	S_2	1															
	M	1															
K. wolskae	P_1		1														
K. circularis	P_1				1												
K. protorhomboid	P_1	2	1														
Klapperilepis	P_1			9	4	18											
rhomboidea	M					2											
P. sandbergi	P_1	12	19	15													
P. perlobata	P_1					4	10	63	6	5	9	4	14	7	9	2	3
P. ampla	P_1											2			8	10	14
Palmatolepis	P_2	7	1	4			1	10			1	1	2	3	1	1	3
spp.	S_0			2				2			1						
	S_1			2				3					2				
	S_2	1						6		1						1	
	S_{3-4}	2	1			1		4			2			1			
	M	1	1					1					1		2		
Tripodellus	P_1	31	23	29	12	41	16	140	25	14	17	32	19	15	5	15	4
minutus	P_2	4		9		3	1	18	1	7	6	6	2	2	1	4	1
	S_0			1		1		2						1		1	
	S_1			1		3		9	3	1	3	2	1		1	1	
	S_2		1	2		1		3	1		3				1		
	S_{3-4}	1		13		4	2	10	7	1	5	3	11	5		3	
	M	1		11		5	5	13	5	2	2	2	6	5	2	4	
T. lobus	P_1			6													
	P_2			6													
T. donoghuei	P_1			8													
C. linguiloba	P_1			15													
Conditolepis	P_1			35	20	37	22										
prima-glabra	P_2			9	2												
	S_0			1		1											
	S_1			2		1											
	S_2			2		1											
	M			7	1												
Conditolepis	P_1							258	21	14	4	3					
glabra-distorta	P_2							1									
C. distorta	P_1											1	40	85	15	54	1
Conditolepis	P_1				11	34	63	144	23	1	11	5	111	67	47	46	28
falcata	P_2				3	3	3	13	1		3		14	7	7	3	1
	S_0							1			1		2	2		1	1
	S_{1-2}						1	2	1		1		9	2	3	1	
	S_{3-4}					1	3	11	2		2		5	5	3	2	6
	M					1		3	5		2		12	11	3	5	1
C. quadrantinod.	P_1				2	7	55										
C. inflexoidea	P_1							48	4	2							
C. marginifera	P_1							128	25	10	6	1	7	4	1	10	6
Conditolepis	P_2				2	2	7	4			1	2		1			
quadrantinodosa	S_0					1											
marginifera	S_2					1				1				1			
	S_{3-4}					1	2	4	1							1	
	M						5	1									

Table 9. Frequencies of conodont elements in samples from the mid Famennian of Kowala and Miedzianka, the Holy Cross Mountains.

KOWALA Miedzianka		Ko-13	Ko-12	Ko-11	Ko-10	Ko-18	Ko-16?	Ko-15	Ko-9	Ko-9a	Ko-8b	Ko-8a	Md-1c	Md-2c	Md-2a	Md-1b	Md-1a
J. oistodiformis	P-M								12	16						4	
J. erectus	P-M														1		
Icriodus cornutus	P_1											21	14	26	5	47	
	P_2-M											2	1	1		16	
M.? asymmetr.	P-M								3	1							
M. circularis	P-M	1	3	2	3					2		10	17	3	6		1
Ligonodina cf. *pectinata*	P_2												1	4			
	S_0													1			
	S_2												2				
	S_{3-4}												3	4			
	M												2	2			
Lagovidina obliqua	P_1												3				
	P_2												2				
	S_0													1			
	S_1													2			
	S_2												1	1			
	S_{3-4}												3	3			
	M												3	3			
Idioprioniodus ruptus?	P_1							1	1			6					
	P_2						1	1	1		1	5					1
	S_0										1	24					
	S_1	1															
	S_2							2	2			5					
	S_{3-4}										3	36			1		
	M											2			1		1
Guizhoudella dinodontoides	P_2							2									
	S_{3-4}					2											
	M								1								
B. bohlenana	P_1		1		4	23	52										2
B. inornata	P_1											193					
B. suprema	P_1							21	21								
Branmehla spp.	P_2				2	2	7	7	7			29					1
	S_0		1				1					21					
	S_1		1		1	2	3	3	3			14		1?			
	S_2					3	3					106					
	S_{3-4}				1	3	8					91					
	M					14	6	2	2	1	1	65					
Apatognathus provarians	P														2		1
	S_{1-2}												1		4		1
Vogelgnathus unicus	P_1				2	20	29	2	2	6	5	8	9	4	2		
	P_2					3	5	3	3	3	1	1	6	1			
	S_0					2				1		1					
	S_1							1	1	3							
	S_2					2	1	1	1	1		2	2	1	3		
	S_{3-4}					1	4					2		1	1		
	M					4			1				3	4	2		
Urbanekodina undata	P_2														1		
	S_1														4		1
	S_2														2		
	S_{3-4}														19	1	1
Planadina plana	S_0								1								2
	S_{1-2}								1		2						
	S_{3-4}								1								
	M								1								
Pandorinellina vulgaris	P_1							12				11			19		
	P_2							2				3			2		
	S_0														2		
	S_1														6		
	S_2														5		
	S_{3-4}														20		
	M														10		

Table 9 – continued		Ko-13	Ko-12	Ko-11	Ko-10	Ko-18	Ko-16?	Ko-15	Ko-9	Ko-9a	Ko-8b	Ko-8a	Md-1c	Md-2c	Md-2a	Md-1b	Md-1a
Mehlina strigosa	P_1			6		6	6	18	24	30	3	35			4	8	
	P_2			4		2	3	2	1	13		9			2	1	
	S_0			1						7							
	S_1									6							
	S_2									10	4						
	S_{3-4}			1						39	1						
	M			1		1				10	1	2					
Polynodosus lauriformis	P_1					1		47									4
	P_2	2						9							2		6
	S_0																1
	S_1							2									
	S_2							4									1
	S_{3-4}							6									3
	M	1						10							2		5
Polynodosus triphyllatus	P_1												62	75			1
	P_2												14	1			
	M												5				
Polynodosus nodoundatus	P_1	2		2	1										6		
	P_2														1		
Polygnathus semicostatus	P_1		1	2?	2	97		76	1			6	317	441	1		
	P_2					4		15					28	43			1
	S_0					1		2					6	10			
	S_1							3					5	10			
	S_2					2		3					3	6			
	S_{3-4}					4		6					6	23			
	M					4		15					18	22			
Hemilistrona perplexa	P_1				4	1	5		2			4	11	51			9
	P_2						5		1			1		8			1
	S_{3-4}								1			1		7			
	M											2					
Neopolygnathus communis	P_1											7	1				
	P_2											3					
L. bilobatus	P_1	1?	5	11	2			9					5	58		10	5
L. fallax	P_1				3?		2	24							13		7
L. granulosus	P_1					1	2										
L. styriacus	P_1										3						
Lagovignathus spp.	P_2	23	3	3				15								3	
	S_0		1														
	S_1	2	1													1	
	S_2	1	1					2								1	
	S_{3-4}	6	2					3								2	
	M	6	2					11								1	
P. pergyrata	P_1							6									1
	P_2							6									
Klapperilepis rhomboidea	P_1												10	7			
	P_2													1			
	S_1													1			
Palmatolepis schindewolfi	P_1	4	8	7	2	20	5	11	16	15	4	30	31	81	35	4	17
	P_2	2		2			1	2	1		1	1	31	42	3		6
	S_0					1				1				1			
	S_1						1	1	1		1		3	5	2		
	S_2					1						1	1	2			1
	S_{3-4}							1	1				5	3	1		2
	M	1				1		1	1				2	5	1		
P. ampla	P_1	4															
Palmatolepis trachytera	P_1					3		2	2	26							
	P_2								1	1							

Table 9 – continued		Ko-13	Ko-12	Ko-11	Ko-10	Ko-18	Ko-16?	Ko-15	Ko-9	Ko-9a	Ko-8b	Ko-8a	Md-1c	Md-2c	Md-2a	Md-1b	Md-1a
T. minutus	P_1		15	12	5	73	20	19									
Tripodellus	P_1												18	32			
lobus	P_2												10	14			
T. schleizius	P_1	2							19	20	17	72	203	390	67	19	8
T. donoghuei	P_1												2?				
Tripodellus	P_2		2		1	7	7	1	1		1	14	14	50	6	2	2
spp.	S_0					1	1					7	2	5	4	1	
	S_1					2				1		8	2	12	3	1	1
	S_2		1	2		7	4			1	1	7		11	2		
	S_{3-4}	1	1			7	17	1		3	6	22	12	32	8	3	
	M		2		1	5	5	1	1	3	1	24	4	25	15	5	1
C. linguiloba	P_1												12	34			
C. glabra	P_1												157	134	71		
C. distorta	P_1	7	20												15	24	23
Conditolepis	P_1		9	18	34	184	83	25	25	71	52		1		77	26	50
falcata	P_2		2	1	1	12	18	1	1	5	3				7	6	2
	S_0					2	3	1	1							3	
	S_{1-2}		2			4	2	3	3	3	1				2		
	S_{3-4}		3	1	3	8	5	5	5	7	1				9		
	M		1	1	2	11	4	5	5	8	1				3		1
C. quadrantinod.	P_1												13	11	54		
C. inflexoidea	P_1																2
Conditolepis	P_1	6	14	8												5	8
marginifera	P_2															2	
	M															1	
Conditolepis	P_2												35	27	4		
quadrantinod.	S_2												2	6	1		
marginifera	S_{3-4}												1	4			
	M												1	2			
D. micropunctata	P_1						3										
Dasbergina	P_1								4	3	3						
granulosa	P_2										1						
A. pseudostrigos.	P_1												3	19	6		
A. regularis	P_1				4	25	4		17	9	4	88					
Alternognathus	P_2					2	8				1	19		2	1		
spp.	S_0					2	1					5					
	S_1					1						4					
	S_2					4	2		1			2					
	S_{3-4}					6	4		9			22					
	M					1	3		9			12			1		

Table 10. Frequencies of conodont elements in samples from the late Famennian of Kowala, the Holy Cross Mountains.

KOWALA		Ko-208	Ko-207	Ko-206	Ko-169	Ko-170	Ko-171	Ko-172	Ko-173	Ko-174	Ko-175	Ko-176	Ko-177	Ko-178	Ko-179	Ko-180	Ko-181
J. erectus	P-M														1		
Latericriodus rarus	P_1							2									
M. circularis	P-M	2	1		1		4			6		2		3	3	2	3
Idioprioniodus	P_1				1						1				1		
ruptus	P_2	1						1					1	1			
	S_0	1													1		1
	S_1									1		1			1		
	S_2		2							1		1					
	S_{3-4}	1							1	1	1	1	1	1	1		1
	M	1											1				
Idioprioniodus	P_1					1											
uncadinoides?	P_2					2											
	S_0					1											
	S_{3-4}					2											

Table 10 – continued		Ko-208	Ko-207	Ko-206	Ko-169	Ko-170	Ko-171	Ko-172	Ko-173	Ko-174	Ko-175	Ko-176	Ko-177	Ko-178	Ko-179	Ko-180	Ko-181
B. bohlenana	P_1	3	1	16	9	2	16	3	2	16	26	7	2	7			
B. inornata	P_1														29	17	20
Branmehla	P_2	1		1			1	1						3		1	4
spp.	S_0								1								
	S_1										2				1		1
	S_2						2				2				1	1	
	S_{3-4}					1					2				1	2	
	M			1		1			2	4	1			1	3	1	6
Vogelgnathus	P_1	1		1						2		2	2		9		
branmehloides	P_2			1				1							2		
	S_2			1													
Vogelgnathus	P_1		2										1	5	6	28	68
werneri	P_2												1	1		3	2
	S_2																2
Sweetodina	P																
monodentata	S_{1-2}		1														
	S_{3-4}		1														
	M				1					1		1			1		
Planadina	S_{1-2}										1						
plana	S_{3-4}										1						
Pandorinellina	P_1	6	2	28	23	11	2	1	1	12	2	4	4	9	43	2	60
vulgaris	P_2	1		2	2	3			1	2	6		1	1	4		11
	S_0									5	4		1		2		6
	S_1			1	1			1		4	1			1	4		8
	S_2					3				9	2				2		5
	S_{3-4}			2	6	6			1	13	4		3		13		18
	M	1		1	4	6		1	2	4	1		1		11		7
Mehlina	P_1	1		3	3	2	1	4	1	20	3	6	4	15	13	6	8
strigosa	P_2	1		1		1	1			6	1	2	3	4	9	4	3
	S_0													2		1	
	S_1											1		2		2	
	S_2											3					
	S_{3-4}											3		3		6	
	M									2			1	1	5	2	1
Immognathus sp.	P_1																2
P. pennatulus	P_1				?		4										
H. perplexa	P_1	5	9	5		11		3		10	31	3	5	3	10	1	2
H. margaritata	P_1				7												
Hemilistrona	P_2		3	1	1	1				3	2	1		2	1	2	1
spp.	S_0													1			
	S_1		1		1									2			
	S_2		1											2			
	S_{3-4}		3														
	M		1											1			
N. communis	P_1	36	3	1												2	
L. granulosus	P_1	3	4	7	2												
L. styriacus	P_1				12		6	13	6	16	1	3			1	2	8
Lagovignathus	P_2										1						
spp.	S_1		1	1													
	S_2		1														
	S_{3-4}		3	1													
	M		1	1													
Palmatolepis	P_1	2	2	10	4	3	6	10	6	6	7	6	4	1	1	20	25
schindewolfi	P_2		1							3							1
	S_{3-4}															2	
	M									1							
P. rugosa	P_1												?1				5
Tripodellus	P_1	2	2	10	2	2	4	3	2	9	10	11	9	12	8	11	29
gracilis	P_2		1			2	3			3		5		2	3	1	6
	S_0									1		1	2				2
	S_1							1					1		1		2
	S_2									1	2		2	2			
	S_{3-4}			1			1			1	1	3	3	1	3	5	1
	M				1	1	2	2				2		1	1	1	3

Table 10 – continued		Ko-208	Ko-207	Ko-206	Ko-169	Ko-170	Ko-171	Ko-172	Ko-173	Ko-174	Ko-175	Ko-176	Ko-177	Ko-178	Ko-179	Ko-180	Ko-181
T. mancus	P_1													1			9
C. falcata	P_1																1
D. granulosa	P_1													1			
A. regularis	P_1	2		2									1				1

Table 11. Frequencies of conodont elements in samples from the late Famennian of Kowala, the Holy Cross Mountains.

KOWALA		Ko-182	Ko-183	Ko-184	Ko-185	Ko-186	Ko-6	Ko-187	Ko-188	Ko-189	Ko-190	Ko-4	Ko-191	Ko-192	Ko-193	Ko-3	Ko-167
J. erectus	P-M															?2	14
M. circularis	P-M	1	3	1	1	3	3	1	4	1	21	5	21	15	98	8	3
Idioprioniodus	P_1						1			1					1		
ruptus	P_2		3		2				4					1	2	1	1
	S_0							4	2				2	3			3
	S_1		3					1	1				1	2		1	1
	S_2		1												1	1	1
	S_{3-4}	1	1					3					2	2	11	3	2
	M							2					2		1		2
G. trigonica	S												1				
B. bohlenana	P_1		16					15	11	5	14		57		21		
B. inornata	P_1						2					4		48		3	58
Branmehla	P_2		2		2			2					11				2
spp.	S_1								1				2	1			1
	S_2							1	2			1	1				1
	S_{3-4}								1				2	1			5
	M		4						1	3							3
A. varians	S				1										1	1	
Vogelgnathus	P_1	1		12	3	12	7		16	5	47		29	27	32	5	2
branmehloides	P_2		3			5	2			1	4		1	5	13	8	
	S_0										1		1	2	5	1	
	S_1												1				
	S_2					1	1		1		1		1	2	10	1	
	S_{3-4}					1	1		2	1	3		2	2	2	4	
	M					2	1		4	3				4	7	1	
Vogelgnathus	P_1		14					2	8		8						
werneri	P_2		5						2								
Sweetodina	P		4	1									1		9		
monodentata	S_{1-2}		1														
	S_{3-4}		4		1												
	M		2												1		
Planadina	P_1										1						
plana	P_2										1						
	S_0										2					1	
	S_{1-2}									1	1	1				1	1
	S_{3-4}						2				8	1	2		1	3	
	M										4						
Pandorinellina	P_1	58	1		3	15									12		10
vulgaris	P_2	4	1			3											
	S_0	4															
	S_1	2			1	1											
	S_2	5			2	1											
	S_{3-4}	4				6											
	M	8			1	2											
Mehlina	P_1		16	6	12	1	5	5	29	6	11	1	3	18	32	14	37
strigosa	P_2		2	1	1		2	1	11		3		1	5	3		8
	S_0																
	S_1		2		1				1		1					2	
	S_2		2						2								
	S_{3-4}		4				2		12								
	M		8				2		3	1	2			7	1	4	

Table 11 – continued		Ko-182	Ko-183	Ko-184	Ko-185	Ko-186	Ko-6	Ko-187	Ko-188	Ko-189	Ko-190	Ko-4	Ko-191	Ko-192	Ko-193	Ko-3	Ko-167
Polygnathus	P_1						?8				10	3	15	1	59	4	10
experplexus	P_2														3		1
	S_0																3
	S_2																1
	S_{3-4}																5
	M														7		1
H. perplexa	P_1	4	23	2	6	3		1	2	4							
H. homoirregul.	P_1										10		1	1			
H. pulchra?	P_1														4	5	1
Hemilistrona	P_2		1	1							3				1		
spp.	S_1														1		
Neopolygnathus	P_1	1				1		8	2	37			2				8
communis	P_2							1	1								
N. vogesi juv.?	P_1										1		2	1			
Lagovignathus	P_1		26	12		3	2	2		2	2		2	1	2		
styriacus	P_2		3														
Lagovignathus?	P_1																26
dissimilis	P_2																4
Palmatolepis	P_1	8	15	5	5	2	2	3	3	6	10	2	14	7	6	4	5
schindewolfi	P_2		1		1						3	1	3	3			3
	S_1										1			1			
	S_2								1						1		
	M				1				1				4				
Palmatolepis	P_1		7	5		6	5		11	3	24		85	22	10	3	
rugosa	P_2		1								2		7				
Tripodellus	P_1	5	9	8	20	24	12	52	24	44	67	5	62	56	212	44	93
gracilis	P_2	1	2	2	6	5	8	10	3	5	15	2	7	4	19	3	14
	S_0		1		4	1	1	5	1	1	7	1		2	5	2	5
	S_1	1	1	1	1	3	1			1	6		4	7	5	2	2
	S_2					1	3	5	2		5	1	2	1	12	3	7
	S_{3-4}		2	2	7	3	4	7	6	5	14		7	3	7	3	17
	M		3	1	2	2	5	10	2	3	8	1	3	3	12	5	8
D. stabilis	P_1							102	7	122	379		60	28	139	20	21
D. micropunctata	P_1					3	1										2
D. brevipennata	P_1										50	7	548				
D. kovalensis	P_1																10
D. aff. *kayseri*	P_1													2			
Dasbergina	P_2							4	1	8	62		47	8	32	9	
spp.	S_0							3		4	7		3	3	5	4	
	S_1							1		3	3		8	4	3	1	
	S_2							6		5	12		9	3	7	3	
	S_{3-4}							10		5	34		35	12	15	10	
	M							7	1	4	40		21	3	6	5	
P. ostrovkensis	P_1			3												1	
P. jugosus	P_1						3					36					36
Pseudopolygnath.	P_2			2								2					19
spp.	S_0			1													5
	S_1			2													7
	S_2			1													13
	S_{3-4}			2								4					16
	M			1								2					10
A. regularis	P_1				?1												

Table 12. Frequencies of conodont elements in samples from the late Famennian of Kowala, the Holy Cross Mountains.

KOWALA		Ko-131	Ko-194	Ko-130	Ko-2	Ko-195	Ko-196	Ko-1	Ko-128	Ko-197	Ko-127	Ko-198	Ko-126	Ko-124	Ko-166	Ko-122	Ko-121
J. erectus	P-M				7	2		1									
M. circularis	P-M	2	13			3				34	1	3		2	13		
Ligonodina	P_1										1						
sudetica?	P_2				1					2	1				2		1
	S_0		1							2		1					
	S_1		1		1		1			2		2					
	S_2				1	1											
	S_{3-4}		1			1				7		2		1	2		
	M				1	3				4		1			1		
Guizhoudella	S									1		1					
triangularis	M											1					
Branmehla	P_1	37			29	75	12	21		191	61	188	2	25	57	2	2
inornata	P_2					5	2			15	4	12			2		1
	S_0									1							
	S_1				2		1			2	1	3			1		
	S_2					1	1			6	1	11					
	S_{3-4}					2	1			8		7					
	M				1	2	1			5	1	9					
Apatognathus	S		2														
varians	M		1														
Vogelgnathus	P_1		4												1		
branmehloides	P_2							1									
	M		1														
Planadina	S_0																
plana	S_{1-2}		1		1										2		
	S_{3-4}														1		
	M		2														
Pandorinellina	P_1						1								40		
vulgaris	P_2														16		
	S_0														8		
	S_1														4		
	S_2														9		
	S_{3-4}														29		
	M														16		
P. bituberculata	P_1	?21															
Mehlina	P_1	7	2	1	4	8	13	2	1	92	14	55		14			
strigosa	P_2		1							6	2						
	S_0									5	1						
	S_2									4	3	3					
	S_{3-4}									9	3	5					
	M					2					1						
P. pennatulus	P_1														1	3	5
P. experplexus	P_1	1			19	40									21		
	P_2	1				4											
	S_0				1												
	S_1				1												
	S_2							1									
P. znepolensis	P_1	2			1	14		1						7	2		
Hemilistrona	P_1	1			1	1											
pulchra	P_2					1											
Neopolygnathus	P_1		19	2					5	136	17	39	1	1	4	10	10
communis	S_0									5		1	1				
	S_{3-4}												4				
	M									1							
Lagovignathus?	P_1	46			6	15		11						15	23		
dissimilis	P_2	11			3	8		3						2	2		
P. schindewolfi	P_1		1		4		7	2							1		
Palmatolepis	P_1	7	1		1		16	2						1	4		
rugosa	P_2						1										
	M						1										

Table 12 – continued		Ko-131	Ko-194	Ko-130	Ko-2	Ko-195	Ko-196	Ko-1	Ko-128	Ko-197	Ko-127	Ko-198	Ko-126	Ko-124	Ko-166	Ko-122	Ko-121
Tripodellus	P_1	29	51	8	15	35	31	19	5	85	29	77	4	27	105	9	1
gracilis	P_2	3	3	1	2	5	6	4	1	15	7	17		8	25		
	S_0				2	1	3			5	1	2		1	4		
	S_1		1		1	2	5			5	2			1	6		
	S_2	1			2	2	6			8	4	5		2	12		
	S_{3-4}				2	5	14	3		17	7	9		3	25		
	M	2	4		1	7	7	2		5	2	4		2	15		
T. gonioclymeniae	P_1														2		
Dasbergina	.P_1		15			75				23	24	19	3	11	37	2	1
stabilis	P_2		3			30				6	3						
	S_0		2			6				4							
	S_1		2							6							
	S_2		2			3				2							
	S_{3-4}		3			15				13							
	M		2			5				14							
D. micropunctata	P_1													1			
D. ziegleri	P_1							4									
D. kovalensis	P_1							20	4								
Dasbergina	P_1									1		1					
marburgensis	P_2									2							
D. trigonica	P_1														1	2	
D. aff. *kayseri*	P_1							1		3							
D. kayseri	P_1											7					
Dasbergina?	P_2									1		2					
Pseudopolygnath.	P_1	187		3	172	254	12	110	1	11		8					
jugosus	P_2	10			31	7	2	32	1		1	8		1		2	
	S_0	1			2	3	1	4			1	2		1			
	S_1	4			11			3				2		1			
	S_2	3			5	1	2	1			2	3		2			
	S_{3-4}	5			32	9	7	22			3	7		2			
	M	2			6	3		11			2	4		1			
P. ostrovkensis	P_1								17		13	6					
P. aculeatus	P_1									4		2	1	15		31	36
Alternognathus	P_1									5							
regularis	P_2									1							
	S_0									1							
	M									1							

Table 13. Frequencies of conodont elements in samples from the latest Famennian of Kowala, the Holy Cross Mountains.

KOWALA		Ko-120	Ko-119	Ko-118	Ko-117	Ko-116	Ko-114-115	Ko-113	Ko-110	Ko-109	Ko-108	Ko-107	Ko-105	Ko-103	Ko-80	Ko-79	Ko-137
Dollymae?	P_1															1	
M. circularis	P-M			2	1	15		2					1		3		3
M. coronella	P-M					1											
Idioprioniodus	P_1								2								
ruptus?	P_2			1		3										1	
	S_0															1	
	S_1								1								
	S_2					1				1		2					
	S_{3-4}				1	1			1						1		
	M																
Branmehla	P_1	1				21	4	7	17					11	1	1	3
inornata	S_1					1											
	S_{3-4}					1											
	M					1											
M. strigosa	P_1			1		4		7									2
P. pennatulus	P_1	1	2	2	1	16		3			1	3	1			3	
N. communis	P_1			14	1	13	1	4		1	1		2	1			
N. vogesi	P_1								6								

Table 13 – continued		Ko-120	Ko-119	Ko-118	Ko-117	Ko-116	Ko-114-115	Ko-113	Ko-110	Ko-109	Ko-108	Ko-107	Ko-105	Ko-103	Ko-80	Ko-79	Ko-137
Tripodellus	P_1	1	1	7	2	41	8	5	8		2	3	5	6	11	18	11
gracilis	P_2					1									1		2
	S_2																1
	S_{3-4}					1									1	1	1
	M								1						1	1	
T. gonioclymeniae	P_1			7	1	12		1	1								
D. stabilis	P_1					2					4						
D. trigonica	P_1	1							2				1			1	
P. aculeatus	P_1	31	5	34	15	263	19	25	90	11	26	53	65	40	24	11	
Pseudopolygnath.	P_1		1	5	3	34	7								2	63	28
ziegleri	P_2	1	1		4	15		3	6	1		1	2		1	5	2
	S_0					3											
	S_1					1											
	S_2					6											
	S_{3-4}		1			7		2	1						3	4	1
	M					1										3	4
P. ultimus	P_1							3	30	6	13	19	2	18			
P. praesulcatus	P_1					14			1								

Table 14. Frequencies of conodont elements in samples from the latest Famennian of Kowala and late Famennian of Miedzianka, the Holy Cross Mountains.

KOWALA MIEDZIANKA		Ko-102	Ko-101	Ko-100	Ko-98	Ko-97	Ko-93	Ko-92	Ko-55	Ko-54	Ko-82	Md-14	Md-15	Md-16	Md-10a	Md-17	Md-23-6
Jablonnodus	P_{1-2}											7					
erectus	S_0											4					
	S_{1-2}											8					
	S_{3-4}											7				1	1
	M											5					
I. cornutus	P_1											1		2			
Dollymae?	P_1	1															1
guizhouensis	S-M																3
M. circularis	P-M	3							1	47		97	20	21	4	16	6
Idioprioniodus	P_1											1					
ruptus?	P_2				1				1	7		3		1			3
	S_0								1	3		4	1		3		
	S_1								1	5		3	1	1			1
	S_2									3		3			1		
	S_{3-4}	3			2		1		2	5		7	1		1		2
	M								1	4		4	2	2	1		
B. bohlenana	P_1											60	4	11	6	13	5
B. inornata	P_1	5							9	21							3
B. suprema	P_1							1	22	215	3						
Branmehla	P_2									18		7	2	2	7	9	1
spp.	S_0									1		2	1	1	4	2	
	S_1									2		5		1	6	2	
	S_2									9		7		1	10	5	
	S_{3-4}									5		6	2	2	4	12	
	M									8		13	2	4	2	15	1
Synclydognathus?	S_1									1							
A. varians	S	4								1			1				
Vogelgnathus	P_1											67	1	37	39	12	6
branmehloides	P_2											13	7	15	15	9	1
	S_0											3				3	
	S_1											2				2	
	S_2											2		1		2	
	S_{3-4}											5	1	7		5	
	M											11		6		11	

Table 14 – continued		Ko-102	Ko-101	Ko-100	Ko-98	Ko-97	Ko-93	Ko-92	Ko-55	Ko-54	Ko-82	Md-14	Md-15	Md-16	Md-10a	Md-17	Md-23-6
Vogelgnathus	P_1											4		22	19	2	
werneri	P_2											2		8	7		
	S_0														4		
	S_1														5		
	S_2														7		
	M											1		2	14		
Sweetodina	P_2						1	1							1		
monodentata	S_{3-4}										1						
	M										1						
Planadina	S_0										4						
plana	S_2									2	2				1		
	S_{3-4}										2		1	3	1		
	M										1						
Pandorinellina	P_1									4			10	31	17		2
vulgaris	P_2												6	1	5		1
	S_0												3		3		
	S_2												4		3		
	S_{3-4}												7		12		1
	M												2	1	6		
Mehlina	P_1	1					1		1	33			2	5	2	6	5
strigosa	P_2									8			1	2	2		1
	M									2					1		
Polynodosus	P_1											31			10		
lauriformis	P_2											8			4		
	S_1											2			3		
	S_2											1			1		
	S_{3-4}											4			4		
	M											26			2		
P. diversus	P_1											20					
P. semicostatus	P_1											294		8	3		1
P. extralobatus	P_1							1		1							
P.? experplexus	P_1												4	1	8	4	8
P. pennatulus	P_1	2			2	3	2	3		3							
Polygnathus	P_2											33			2	1	
spp.	S_1											20		2			
	S_2											24					
	S_{3-4}											71					
	M											42					
Hemilistrona	P_1											70					
perplexa	P_2											27					
	S_0											26					
	S_1											2					
	S_2											4					
	S_{3-4}											19					
	M											14					
Neopolygnathus	P_1	6	1										3	26	12	44	3
communis	P_2												1	2			1
	S_0												2	3			2
	S_1													1			
	S_2													7			
	S_{3-4}													9			
	M													2			
Lagovignathus	P_1											1			7	5	
styriacus	P_2											1				1	
P. pergyrata	P_1											1					
Palmatolepis	P_1												5		3	10	
schindewolfi	S_{3-4}													1			
	M												1				
P. rugosa	P_1													5	1		

Table 14 – continued		Ko-102	Ko-101	Ko-100	Ko-98	Ko-97	Ko-93	Ko-92	Ko-55	Ko-54	Ko-82	Md-14	Md-15	Md-16	Md-10a	Md-17	Md-23-6
Tripodellus	P_1	25	8	7	14	9	10	7		89	8	388	39	44	44	61	15
gracilis	P_2	2			1					19		50	10	11	12	6	3
	S_0									1		10	3	2	1	1	2
	S_1									5		17	1	3	6	1	5
	S_2									1		18	2	4	3	3	1
	$S_{3\text{-}4}$									8		41	9	4	9	9	2
	M	1			1					7		38	7	6	11	13	
C. distorta	P_1											6		4		1	
Conditolepis	P_1											1462		3		2	
falcata	P_2											244					
	S_0											30					
	$S_{1\text{-}2}$											34				1	
	$S_{3\text{-}4}$											196					
	M											146					
D. stabilis	P_1				1	2										64	13
D. micropunctata	P_1														1		
D. ziegleri	P_1									1							
D. trigonica	P_1	1					1			4	1						
P. jugosus	P_1												9	6	1	94	2
P. aculeatus	P_1	3	27	49				31		37							
P. ultimus	P_1	89	5	5	152	45	37	7	81	149	7						
Pseudopolygnath.	P_2	2			8	4			7	14	1					18	
spp.	S_0	1							1	2						4	
	S_1								1	5						8	1
	S_2								4	10						7	2
	$S_{3\text{-}4}$	1				2			2	12						47	3
	M								2	12						16	2
P. praesulcatus	P_1										3						
Alternognathus	P_1											241					
beulensis	P_2											9					
	M											3					
S. leptus	P_1											19					

Table 15. Frequencies of conodont elements in samples from the mid Famennian of Łagów, the Holy Cross Mountains.

ŁAGÓW		Ł-28	Ł-12	Ł-21	Ł-24	Ł-23	Ł-26	Ł-27	Ł-11	Ł-32	Sł73-1	Sł73-2	Sł73-3	Ł-22	Sł73-11	Sł73-4	Sł73-12
J. erectus	P-M															16	
Icriodus	P_1			1	5		1	2		2		1	14				18
cornutus	P_2-M	5	1	1				48	2	17		2	3			1	1
M. circularis	P-M	28			31		12	3			2	68	45	5		39	
Ligonodina	P_1						2	4		2		1		1		1	
pectinata	P_2	4	1		3	1	1	2		7			1	1	1	5	
	S_0				5		4	5		2				1			
	S_1	1			1		1	2					1	1		14	
	S_2				1		3	1		1						7	
	$S_{3\text{-}4}$	5		1	10	3	11	13		11		4	3			9	1
	M	2			11		9	5		2						1	
Lagovidina	.P_1	14		2	7		4	3		11							
obliqua	P_2	24		1	6		3	5	1	4							
	S_0	12			6		6	4	1	9							
	S_1							3	1				1				
	S_2				7	2	4			2			1				
	$S_{3\text{-}4}$	51		7	54	16	53	20	5	31					1		
	M	26			23	1	28	11		19							

Table 15 – continued		Ł-28	Ł-12	Ł-21	Ł-24	Ł-23	Ł-26	Ł-27	Ł-11	Ł-32	Sł73-1	Sł73--2	Sł73--3	Ł-22	Sł73--11	Sł73-4	Sł73-12
Branmehla	P_1	3			13		2	14		3		9	8			14	1
bohlenana	P_2	3			2			5		2		5	5				
	S_0											1					
	S_1											1					
	S_2				1			5				8					
	M	2			3			6		6		4					
G. dinodontoides	S						2						1				
Apatognathus	P							1				22	26			1	
provarians	$S_{1\text{-}2}$ M				1			4				33	21			23	
	$S_{3\text{-}4}$	4						1				18	9			5	
Vogelgnathus	P_1	88		2	48	2	38	51	3	46		17	14			58	3
unicus	P_2	28			6		11	15		12		2	2			5	
	S_0	4			1			4		1							
	S_1	1								5							
	S_2	4			5		5	6		5			1				
	$S_{3\text{-}4}$	5			6			8	1	3		1	1			1	1
	M	27			11			15		11		2					
Sweetodina	P	75	2	4	48	9	37	23	7	18		1	2		13		1
lagoviensis	S_0	11					1										
	S_1	3				5		4		1		2			1		
	S_2	11			1		2	4		3			1				
	$S_{3\text{-}4}$	34			6	2	7	2		3		2	4		5		
	M	41			?1		?1	7	1	4		2			1		
Planadina plana	S_2															13	1
Mehlina	P_1	7		1	23		13	9	2	15		58	56	21	27	8	4
robustidentata	P_2	2			11		6	5	4	7		9	17	8	11	2	
	S_0								3						2		
	S_1								1	1							
	S_2								4								
	$S_{3\text{-}4}$								7			12					
	M				1		2		3					3	6	2	
Polynodosus	P_1	48	7	9	120	7	85	61	5	100	1	97	76		27	20	1
transitus	P_2	39		6	40		28	15		42		32	38		8	13	11
	S_0	40			21		28	13				12	1				
	S_1	21			37		26	2				5					
	S_2	27			43	3	41	7				1	15			10	2
	$S_{3\text{-}4}$	85	2		92		102	11				7	29			23	5
	M	22	4		100		59	14				4			1	14	7
P. lauriformis	P_1				29		19	7				3?					
Polynodosus	P_1	12	3	14	105	6	63	28	1	70	51		43	30	35		
triphyllatus	P_2	3	1	6	52		25	23		33	28		23	13	6		
	S_0							7		1	9		4	1			
	S_1						1	15		2			1	2			
	S_2						4	12		3				10	3		
	$S_{3\text{-}4}$			8	10		10	8		5			5	17	12		
	M			3	6	3	4	18		27	9			3	1		
P. nodoundatus	P_1											21	37				
Polygnathus	P_1	3?		4	28	1	11	9		24	4	5	12			21	2
semicostatus	P_2			1	3						1		4			9	
	S_0										1						
	S_1				1												
	S_2				2											2	4
	$S_{3\text{-}4}$				2												7
	M										2	2				11	
Lagovignathus	P_1	114	12		456		317	236	6	352		30	17		8	47	4
bilobatus	P_2	58	9		178		129	83	2	132	2	37	15		3		11
	S_0		1		6		5	12	2	21		5				4	
	S_1		1					7	3	21						5	
	S_2		2		5			28	2	80						5	
	$S_{3\text{-}4}$		2		88		10	82	5	121						17	18
	M	28	6		7		3	61	3	63		25				15	9
L. lagoviensis	P_1															255	41
L. fallax	P_1											287	243	5	90		

Table 15 – continued		Ł-28	Ł-12	Ł-21	Ł-24	Ł-23	Ł-26	Ł-27	Ł-11	Ł-32	Sł73 -1	Sł73 -2	Sł73 -3	Ł-22	Sł73 -11	Sł73 -4	Sł73 -12
Lagovignathus	P_2											36	36	1	28	113	31
lagoviensis	S_0											2	21		10	54	9
fallax	S_1											16	34		5	52	6
	S_2											20	18		11	63	17
	S_{3-4}											76	77	3	19	245	37
	M											26	71	2	15	100	25
Polylophodonta	P_1	3			52		17	31					4			27	7
pergyrata	P_2	1			?		?	5					1			39	
	S_0				7		5	1					1				
	S_1	2			4		1										
	S_2				4		1										
	S_{3-4}	1			4		1						3				
	M				2												
Klapperilepis	P_1	6	4		52		27	88		65							
rhomboidea	P_2	5						1		1							
	S_2	2						1		1							
	M	4						1		2							
Palmatolepis	P_1	186	16	29	115	17	79	66	13	169	3	60	70	61	28	52	6
perlobata	P_2	26	4	9	54	5	22	33	4	36		15	14	11	5	7	
	S_0	2			1			1		2		1	1			1	
	S_1	3			6		5	1	1	8		2	1	3	2	3	
	S_2	10			2		2	1		1		3	5				
	S_{3-4}	6			7	2	1	3	1	3		2	1		3		
	M	11			8	2	6	2	1	8		3				2	
Palmatolepis	P_1	7														168	11
ampla	P_2	7															
	S_2	2															
	M	7															
Tripodellus	P_1	844	29	138	1444	90	846	1066	75	1174	5	333	378	59	132	48	84
minutus	P_2	81	4	7	139	7	77	97	8	110	1	36	45	2	22	16	19
	S_0	32	1	1	15		5	22	3	13	1	5	13	3	2	4	3
	S_1	33		1	7		8	28	4	37		10	18		9	7	1
	S_2	49	1	1	30	1	22	24	3	27		16	24	4	9	3	4
	S_{3-4}	69	1	1	75	3	54	85	6	69		25	49	6	14	18	15
	M	108	2	4	103	11	79	57	7	98	1	39	51	10	11	15	27
C. linguiloba	P_1				1												
C. glabra	P_1	243	47	238	1344	85	859	569	13	1141	10	536	288	48	134	228	
	P_2	12															
Conditolepis	P_1	1140	107	430	3204	156	2389	1233	89	2628	18	185	151	2	55	902	270
falcata	P_2	140	3	11	197	5	121	159	8	173		10	10	1	5	138	66
	S_0	17	1		10		17	15		15					1	13	3
	S_{1-2}	51	1	1	2	1	9	29	5	61	1	2	1			35	19
	S_{3-4}	73	2	1	74	3	55	22	6	59	2	6	3		2	239	112
	M	40	1		80	1	55	91	1	76	2	7	4		2	86	28
C. distorta	P_1																6
C. quadrantinod	P_1	607	9		579	61	311	313	32	475							
C. inflexoidea	P_1											6	47	7	11		
C. marginifera	P_1											97	149	27	54	53	9
Conditolepis	P_2	45				9		63	3	74		7	8			1	5
quadrantinod.	S_0	1						1				1					
inflexoidea	S_1	6										3	1	1			
marginifera	S_2	18				1			1	2		3	2				4
	S_{3-4}	12				1		4	2	7		1	2			2	
	M	8				1		4	2	7							
S. velifer	P_1					1										2	

Table 16. Frequencies of conodont elements in samples from the mid Famennian of Łagów and Miedzianka, Holy Cross Mountains.

ŁAGÓW MIEDZIANKA		Sł73 -5	Ł-13	Ł-39	Ł-38	Ł-9	Ł-5	Ł-4	Ł-10	Ł-25	Mak -2	Ł-40	Md- 4	Md- 8	Md- 3c	Md- 4c	Md- 5c
Jablonnodus	S_0																1
oistodiformis	S_{1-2}																8
	S_{3-4}				1			1	1			5					9
	M														1		5
J. erectus	P-M									5							
Icriodus	P_1				8	4	29	1	1				3	23			
cornutus	P_2-M				2	2											
Pelekysgnathus	P_1		1														
M. circularis	P-M	53	2	2	20	15	8				2	7			3	1	71
Ligonodina	P_1	4			1		1					1					
cf. *pectinata*	P_2	8					4			1		1					
	S_0				1		1			1							
	S_1						1					1					
	S_2	2					1										
	S_{3-4}	3			3	2	13										
	M				1		1										
Lagovidina	P_1				1										1		
obliqua	P_2				1										1		
	S_0														2		
	S_1														2		
	S_{3-4}														1		
Idioprioniodus	P_1													1			1?
ruptus?	P_2																1
	S_1																1
	S_2																1
	S_{3-4}													1			3
	M																1
Branmehla	P_1	5	5		1				2	4	18	26					28
bohlenana	P_2										6	5					9
	S_0											1					5
	S_1											1					8
	S_{3-4}											5					3
	M											2					13
Guizhoudella	S_{1-2}																3
dinodontoides	S_{3-4}																2
	M																7
Apatognathus	S_{1-2}													1			
provarians	S_{3-4}				1		3							1			
Vogelgnathus	P_1	54		3	18		3			2		2			4	8	74
unicus	P_2			1	13	1	2					2			3		35
	S_0			1													3
	S_1				1												1
	S_2				5												4
	S_{3-4}	14			2									1			4
	M				3					1					2	5	19
Vogelgnathus	P_1																5
werneri	P_2																7
	S_2																2
	S_{3-4}																1
	M																2
Urbanekodina	P_1														10		4
undata	P_2														1		1
	S_0														2	2	
	S_1														6	1	1
	S_2																1
	S_{3-4}														10		
	M														3		
Sweetodina	P	3					3					1			1?		2
lagoviensis	S_1	3										2					
	S_{3-4}	3				1											1

Table 16 – continued		Sł73-5	Ł-13	Ł-39	Ł-38	Ł-9	Ł-5	Ł-4	Ł-10	Ł-25	Mak-2	Ł-40	Md-4	Md-8	Md-3c	Md-4c	Md-5c
Planadina	S_0	2					1										
plana	S_{1-2}				1	3	1	2		1		1					
	S_{3-4}	2		1	1	2	3							1			
	M	1		1		3											
Pandorinellina	P_1	52	5							2	7	33			3	3	
vulgaris	P_2	2	2									11			1	2	
	S_1															2	
	S_{3-4}															5	
	M		2									6				1	
Mehlina	P_1															2	2
strigosa	P_2															2	1
	M															1	
Polynodosus	P_1	105								2	11	10		3	6		5
transitus	P_2	82								2	6	7					
	S_0	60									6	15					
	S_1	46									10	16					
	S_2	57									6	10					
	S_{3-4}	223									31	58					
	M	115								1	8	3					
P. triphyllatus	P_1														6		
P. diversus	P_1																38
P. nodoundatus	P_1	14			3	11				5			16	6			
Polynodosus	P_2	3				6				1				1	2		11
spp.	S_0														1		
	S_1														1		3
	S_2																2
	S_{3-4}																2
	M																9
Immognathus	P_1			1										1		4	
streeli	P_2														1		
	S_1														1		
	S_2														4		
Polygnathus	P_1		1	2	48	8	30	2	3	39	5	2	40	20	13		95
semicostatus	P_2				7		12		2	7		3	1	3			4
	S_0									3							5
	S_1					1	1			4							1
	S_2					1	2			4				1			7
	S_{3-4}				6	11	1		1	12							33
	M					5			1	3	2	4		1			3
Neopolygnathus?	P_1																1
Hemilistrona	P_1			1		5			1							1	23
perplexa	P_2															1	
	S_1																2
	S_2																1
	S_{3-4}															1	
	M																6
Lagovignathus	P_1	9		4	22	6	33				2				11	5	
bilobatus	P_2	3		1	26	2	59								5		
	S_0				12										1		
	S_1				11										1		
	S_2				10										6		
	S_{3-4}					5	22	2							1		
	M				14	3	13	1									
Lagovignathus	P_1	538		4	44	21	95	2									
lagoviensis	P_2	253		1	5	10	34										
	S_0	73		1	2		12										
	S_1	54			1		9										
	S_2	102					27										
	S_{3-4}	430		1	66	5	45										
	M	185				2	20										
L. granulosus	P_1							4									

Table 16 – continued		Sł73-5	Ł-13	Ł-39	Ł-38	Ł-9	Ł-5	Ł-4	Ł-10	Ł-25	Mak-2	Ł-40	Md-4	Md-8	Md-3c	Md-4c	Md-5c
Polylophodonta	P_1	105		1	49	9	7										
pergyrata	P_2	60			15					1							
	S_0	2															
	S_{3-4}						2										
Klapperilepis	P_1			1	16									1	2		
rhomboidea	P_2																
	S_1				1												
	S_2				1												
	M				3												
Palmatolepis	P_1	49	3	4	55	50	17	1	3	7	15	25	6	5	10	4	170
schindewolfi	P_2				7	11				1	1	3	2	4	3	1	24
	S_0				1												
	S_1				3				1							3	2
	S_2				2										1		8
	S_{3-4}	3			4						2			1			8
	M	1			7						1						
Palmatolepis	P_1	65		1			68										
ampla	P_2	7					44										
	S_0	1					1										
	S_1	3					13										
	S_{3-4}						2										
	M	2					4										
P. trachytera	P_1							1			1	9					
Tripodellus	P_1												4	6			
lobus	P_2													1			
Tripodellus	P_1	114	4	2	86	27	153	2	2	11	39	26	24	9	64	26	229
minutus	P_2	5	1		8	12	54		2		13	26		1	7	5	27
	S_0		1		2	2	10				3	16		1	2		8
	S_1	2			2	3	6		1		9	19			1	1	10
	S_2	1			3		5		2		11	23			5		9
	S_{3-4}	5	3		21	9	14			2	23	40			7	6	42
	M	6			5	2	13				4	13		3	7	5	18
T. donoghuei	P_1																6
C. linguiloba	P_1				2								1	1			
C. glabra	P_1			16									18	13	28		
C. distorta	P_1	223		6	27	32	75	5			4				32	29	6
Conditolepis	P_1	1715	47	25	327	384	141	10	33	74	255	182		5	81	56	640
falcata	P_2	129	2	1	56	38	32			3	3	4			7	18	95
	S_0	10			2	8	3					1				2	15
	S_{1-2}	23	1		16	11	12		1	1	3				3	4	35
	S_{3-4}	97	2	1	32	57	9		2	9	4	2			4	8	92
	M	52	2	2	31	23	6		2	3	3	5			6	4	43
C. quadrantinod.	P_1												1	5			
C. inflexoidea	P_1				6						2				27		
C. marginifera	P_1	229		2	21	6	5								6	5	3
Conditolepis	P_2	65			10								1		1		
inflexoidea	S_0			2	4										1		
marginifera	S_2				1										1		
	S_{3-4}	4		1	3										4		
	M			2	3		1								1		
D. stabilis	P_1										2	2					
Alternognathus	P_1									2	2	6					96
regularis	P_2											2					10
	S_0																10
	S_1																6
	S_2																9
	S_{3-4}																28
	M											5					6
S. velifer	P_1						2	1	4								

Table 17. Frequencies of conodont elements in samples from the late Famennian of Ostrówka, the Holy Cross Mountains, and Gołogłowy, the Sudetes.

OSTRÓWKA Gołogłowy		Ost-0	Ost-1	Ost-1a	Ost-10	Ost-12	Ost-11	Ost-15	Ost -16	Ost -7	Ost - 265	Ost-293	Ost -5	Ost -2-2a	Ost - 185	Ost-3	Goł-3
Jablonnodus	P_1			1	1	19		1	1								
oistodiformis	P_2			1	1	16	6	4									
	S_0					64	4	4									
	S_{1-2}				1	102	5	3									
	S_{3-4}			8	2	210	16	16	2								
	M			2	1	76	2	4									
Jablonnodus	P_1										99	3?	1				
erectus	P_2									2	32	2?					
	S_0									1	103						
	S_{1-2}									2	74						
	S_{3-4}									3	178						
	M										18						
Latericriodus	P_1												1				
rarus	P_2-M												2				
Icriodus	P_1	135															
cornutus	P_2-M	6															
Pelekysgnathus	P_1											1					
M. asymmetr.	P_1-M					68		8			40						
M. circularis	P_1-M		3	16	5	395	15	59		203	259	120	146	43	197	38	
Pluckidina	P_1														1		
purnelli	P_2			1		10	1	1	1		1			1	5		
	S_0				1	2											
	S_1				1	10	2	1						1	3		
	S_2			1		5									2		
	S_{3-4}			2		16	3								4		
	M					2									5		
Idioprioniodus	P_1					12		2			2	1	3			2	
ruptus?	P_2	1	1	2	1	17		2		3	8	7	5		5	7	2
	S_0		1	1		15	1	2		2	10	2	3	1	2	2	1
	S_1			1		4	1			3	4	2	7	3	2	4	5
	S_2	1		3		20		1		2	8	1	11		3	3	1
	S_{3-4}		4	10	2	23		2		10	37	17	20	5	14	19	3
	M				1	11	1	2		2	8	1	4	1	3	5	
B. bohlenana	P_1									53	27	47	187				
B. inornata	P_1		40	63	28	462	167	202	3	12	977	41	79	76	304	31	
B. suprema	P_1														1	359	
B. disparilis	P_1															1	
Branmehla	P_2		2	3	6	43	22	25	2	7	110	1	24	1	8	21	
spp.	S_0					3	2	1			32		3	2	16	5	
	S_1				2	1	2	4			40		2	1	9	2	
	S_2					19	7	9		2	127		15	7	16	13	
	S_{3-4}		1		3	35	9	8	1		210		14	5	27	26	
	M		2		1	49	15	22	1	12	241	2	18	6	8	8	
Guizhoudella	P_1														1		
triangularis	P_2														1		
	S_{1-2}														1		
	S_{3-4}						1				1				3	1	
	M							1							2	1	
Apatognathus	S_{1-4}									2	4				5	2	5
varians	M										1				1		
Vogelgnathus	P_1	5		2	2	33	21	48	1	8	1	3					
branmehloides	P_2				2	28	1			2	4	1					
	S_0			1	1	3				1	6					1	
	S_1					5				1	2	1				1	
	S_2					4		1	2		2	1					
	S_{3-4}			4		12	1	2	2		2	1		?		1	
	M			2		31	2	1			7						
Vogelgnathus	P_1		1		7	251	1		2	2		1	5				
werneri	P_2					10			1								
	M					22											

Table 17 – continued		Ost-0	Ost-1	Ost-1a	Ost-10	Ost-12	Ost-11	Ost-15	Ost -16	Ost -7	Ost - 265	Ost-293	Ost -5	Ost -2-2a	Ost - 185	Ost-3	Goł-3
Urbanekodina	S_1					1							1				
undata	S_2					2											
	S_{3-4}					1											
Sweetodina	P						1			2	20	3		3	5		
monodentata	S_0										2				1		
	S_1										1						
	S_2						1								1		
	S_{3-4}										4			1	4	1	
	M										5			1			
Planadina	S_0		1			5				2	7	1	2				
plana	S_{1-2}			1		3					11	1	6				
	S_{3-4}	2	6		1	13	2	3		7	19	2	46				
	M	1	1	2		4		1		8	10	7	23		1		
P. vulgaris	P_1		49	100	33	332	69	54	2	11	161	12		31			
P. fragilis	P_1														64	37	
P. bituberculata	P_1									2		5	14				
Pandorinellina	P_2		8	46	14	130	36	16	1		42	4		14	74	4	
spp.	S_0			18			4	3	1		35	1		3			
	S_1			19			6	9						2		1	
	S_2						7	6	1		12			12			
	S_{3-4}			59		48	57	34	2		47	4		33		8	
	M			31		3	14	10	2		20	2		16		2	
Mehlina	P_1		8							14	354	1	50	50	252		
strigosa	P_2		2							2	20		2	1	15	1	
	S_0										3						
	S_1														3		
	S_2													1			
	S_{3-4}																
	M										27		1		3		
P. transitus	P_1	18		67				58									
P. lauriformis	P_1				20	154	29				319	4	5				
Polynodosus	P_2	5		30	9	93	19	35			111	3					
spp.	S_0			13	1	8	7	9									
	S_1				4	13	8	24	1								
	S_2			4	1	49	8	11	1								
	S_{3-4}			5	10	76	33	58	2								
	M			10	2	78	26	32	2			1					
Polynodosus	P_1	9															
nodoundatus	P_2	1															
	S_2	1															
	S_{3-4}	2															
H. perplexa	P_1																10
H. margaritata	P_1		6	2		4					2						
H. homoirregular.	P_1		24	9	11	57	7	13	1	51	30	7	275	1	2	1	
Hemilistrona	P_2		2	4		4		6	1	2	59	9	37				3
spp.	S_0										2		1				
	S_1					2					14						
	S_2										17		2			1	
	S_{3-4}					1			3	1	25	1	9			1	
	M					2											
Ctenopolygnathus	P_1		5							13	2	8	17				1
sp.	P_2																4
	S_{3-4}																2
	M																2
Immognathus?	P_1										3	4?	4	1		20	
rhabdotus	P_2															2	
Polygnathus	P_1		16														
pennatulus	P_2		5														
P. procerus?	P_1					21											
P. semicostatus	P_1	2	1		2	20	26	10				7	4	1			12
P.? experplexus	P_1		106			1					155	74					
P. obliquicostatus	P_1		5								52		11		2		
P. znepolensis	P_1										192		3				119

Table 17 – continued		Ost-0	Ost-1	Ost-1a	Ost-10	Ost-12	Ost-11	Ost-15	Ost-16	Ost-7	Ost-265	Ost-293	Ost-5	Ost-2-2a	Ost-185	Ost-3	Goł-3
P. extralobatus	P_1																67
Polygnathus spp.	P_2		1			1	8	5			11				3		15
	S_0					2											2
	S_1		1			3											2
	S_2		1			3											1
	S_{3-4}		12		4	7		1									14
	M		7	1	2	3		1			14		16				14
Neopolygnathus communis	P_1					25		2		3	4	3	3	90	514		
	P_2												1	2	34		
	M														18		
L. bilobatus	P_1	11				4	1						5	19	2	3	
L. granulosus?	P_1		23			1	?	1									
L. styriacus	P_1									11	16	5	31				
Lagovignathus spp.	P_2	6	4										1	8		1	
	S_0												2			1	
	S_1												1				
	S_2												1				
	S_{3-4}	1											3			3	
	M	2											3				
L.? dissimilis	P_1												39				
P. pergyrata	P_1	2				3							1				
Synclydognathus sp.	P_2					2											
	M					2											
Palmatolepis schindewolfi	P_1	8	51	278	90	785	187	209	22	10	99	15	97				
	P_2	6	2	17	2	90	7	18		3	25	4	8				
	S_0			2		6		1			3						
	S_1			2	2	37	3	3	1		11	1	1				
	S_2			3	1	10	2	6		1			1				
	S_{3-4}				1	16	1	1		1	12		1				
	M	1				25		3		3	26		2				
Palmatolepis trachytera	P_1		1	84	45	196	64	80	1								
	P_2					24	2	2									
	S_1					3											
	S_2			1		4											
	S_{3-4}			1		4			1								
	M					1	1										
Palmatolepis rugosa	P_1									22	77	29	71				11
	P_2									2	3	3	3				
T. schleizius	P_1	21	48	131	39	1173	163	264	7								
T. gracilis	P_1									106	1647	146	260	209	922	562	19
T. donoghuei	P_1		3	12	4	94											
T. mancus	P_1												2				
T. gonioclymeniae	P_1														4		
Tripodellus spp.	P_2	1	2	15	5	42	16	20		7	350	3	27	37	175	109	
	S_0			4	2	7		9		1	66	1	7	2	45	11	
	S_1			4	1	8	7	4		2	62		3	12	56	8	
	S_2		1	8		16	3	13		3	152	2	5	16	67	14	1
	S_{3-4}	1	2	34		31	20	35		9	315	2	23	23	177	29	
	M	3		6	5	25	6	16	4	15	243	10	23	24	152	56	
C. distorta	P_1	43															
Conditolepis falcata	P_1	37	1	748	347	2019	2685	1669	26	1	11	4	4				
	P_2	5	1	79	23	328	119	143				1					
	S_0			4	5	88	9	29									
	S_{1-2}	3		20	3	84	35	27									
	S_{3-4}	2		50	18	356	412	135	3								
	M	4		23	10	403	66	128	3	1		4					
Conditolepis marginifera	P_1	27									1						
	S_{3-4}	1															
Dasbergina stabilis	.P_1	1			3	32	1	11		53	921	87	326	55	286	23	11
	P_2	1								6			30	13		5	
	S_0									4			1		41		
	S_1									1	11?		5		26		
	S_2									1			22		64		
	S_{3-4}									8			31		185		
	M	2													91		
Dasbergina micropunctata	P_1									18	18	28	12				
	P_2									16	13						
D. granulosa	P_1		2	99	22	186			1	1	14	3	13	9			
D. marburgensis	P_1														30		
D. trigonica	P_1															16	
Dasbergina kayseri	P_1												2	9	27		
	P_2														5		
	S_0														1		
	S_{3-4}														1		
D. ziegleri	P_1									83	37	69	78	6	1		
Dasbergina spp.	P_2			18		71				10			9	1	4		
	S_0				8	117				1							
	S_1			13	6	130				2							
	S_2			16	9	122				3							
	S_{3-4}			85	17	330				10							
	M			15	17	199				5							
P. jugosus	P_1											6		6	48		
Pseudopolygnath. ostrovkensis	P_1					2				34	435	59	146	123	383		
	P_2										164	8	58	28	55	22	
	S_0										64	1	9	8	14	5	
	S_1										54	1	11	5	13		
	S_2										94		14	4	12	10	
	S_{3-4}										341	5	29	14	23	22	
	M										148	6	22	20	25	2	
P. ziegleri	P_1															264	
Alternognathus beulensis	P_1			50	24	377	111	114	2	4	3	4	10	1	4	5	
	P_2			5	2	39	2	24				1	4			5	
Scaphignathus leptus	P_1		1	11	4	15		17					2				
	P_2			2		2		3									
	M							1									

Table 18. Frequencies of conodont elements in samples from the late Famennian of Miedzianka, the Holy Cross Mountains, and Dzikowiec, the Sudetes.

MIEDZIANKA Dzikowiec		Md-5	Md-7c	Md-9	Md-6	Md-11	Md-12	Md-13	Md-7	Md-6c	Dz-16	Dz-72	Dz-71	Dz-70	Dz-69	Dz-10	Dz-1
Jablonnodus oistodiformis	S_0									1							
	S_{1-2}									1							
	S_{3-4}									7							1
	M							1		1							
J. erectus	S_{3-4}		2					5		1							
Icriodus cornutus	P_1			1		188	742	2									
	S-M		1	5		26	20	2									
M. circularis	P-M		9			7	47	2		3			1	3	5	53	1
Ligonodina sudetica	P_1															4	
	P_2															6	1
	S_0															4	
	S_1													1		4	
	S_2											1				4	
	S_{3-4}												1?	1	1	2	
	M															5	
Idioprioniodus ruptus?	P_1									1							
	P_2				1				1								
	S_1					1	1			2							
Lagovidina obliqua	P_1		1?														
	S_{3-4}		2														

Table 18 – continued		Md-5	Md-7c	Md-9	Md-6	Md-11	Md-12	Md-13	Md-7	Md-6c	Dz-16	Dz-72	Dz-71	Dz-70	Dz-69	Dz-10	Dz-1
Guizhoudella	S_{1-2}															1	
triangularis	S_{3-4}															2	
	M															1	
B. bohlenana	P_1				1	1		5	18	11							
B. inornata	P_1										3	3	5	5	9		
B. suprema	P_1															139	6
Branmehla	P_2					2			2	8		1			1	12	
spp.	S_0															5	
	S_1					1		1								5	
	S_2							1		4			1		1	14	
	S_{3-4}					1				7			2		1	14	1
	M							1		3			4		1	8	
Apatognathus	P					7	3	1								4	
provarians	S		1			9	2			1		1	3				
Vogelgnathus	P_1		13			121	30	16		20							
unicus	P_2		1			6	3	2		4							
	S_0		3			4											
	S_1		1					1									
	S_2		1			2		1									
	S_{3-4}		3			5		1		1							
	M		2			7	1	2		6							
Urbanekodina	P_1		12			4	1	8									
undata	P_2		2			5	3	11									
	S_0		2			3	2	6									
	S_1		2				1	7									
	S_2		1			2	1	4									
	S_{3-4}		7		1	30	1	21									
	M		1			3		3									
Sweetodina	P		1				1							1		19	2
monodentata	S_{1-2}		1			1		1								1	
	S_{3-4}															6	1
	M					1										1	1
Planadina	S_0						1										
plana	S_{1-2}			2													
	S_{3-4}					1	1						1				
	M						1										
P. vulgaris	P_1					1			7			4					
P. bituberculata	P_1												7				
M. strigosa	P_1			8		23	23	8		5							
M. sudetica	P_1										1		9	2	1	19	1
Mehlina	P_2			1		4	8			3			1		1	5	
spp.	S_1															2	1
	S_2															1	
	M					5				3					1	7	
P. transitus	P_1					14	8										
P. lauriformis	P_1							1?									
P. triphyllatus	P_1		6			10											
P. nodoundatus	P_1	7		9			65										
Polynodosus	P_2		4	3		5	5				1						
spp.	S_1		2														
	S_2					2											
	S_{3-4}		1			3											
	M		3			2											
Immognathus?	P_1										1						
P. semicostatus	P_1		5	13	4	121	45	1	1	3					3		
P. znepolensis	P_1										12		33				
P.? experplexus	P_1												3	3			
P. pennatulus	P_1												3		3		
Polygnathus	P_2			1		10	3								1		
spp.	S_0					3					1		2				
	S_1					1							1				
	S_2			3		2											
	S_{3-4}			3		6		1					3				
	M					3		1			1		3				

Table 18 – continued		Md-5	Md-7c	Md-9	Md-6	Md-11	Md-12	Md-13	Md-7	Md-6c	Dz-16	Dz-72	Dz-71	Dz-70	Dz-69	Dz-10	Dz-1
H. perplexa	P_1					34		11									
H. homoirregular.	P_1								1								
Hemilistrona	P_2					3		1	1								
spp.	S_0							1									
	S_1					1											
	S_2					1		2									
	S_{3-4}					4		7									
	M					4		1									
Neopolygnathus	P_1													1	3	68	2
communis	P_2													1			
	S_{3-4}													1			
N. vogesi	P_1															7	
L. bilobatus	P_1	4	12			12	57	24									
L. fallax	P_1		19	6													
L. lagoviensis	P_1	2					120										
L. granulosus	P_1				5												
L. styriacus	P_1							1	3								
Lagovignathus	P_2	1	3			1	43	1	2								
	S_0		1		1		6	1									
	S_1		2				7	1									
	S_2		2		2		12		1								
	S_{3-4}	1	4		2		14	6	3								
	M		1		2	2	23	1									
L.? dissimilis	P_1										1	2	5				
P. pergyrata	P_1						11										
K. rhomboidea	S_0					1											
Palmatolepis	P_1	5	27	12	2	25	62	16	11	25			2				
schindewolfi	P_2	1	2	1		16	22	2		5							
	S_0			1			1			1							
	S_1		1			2	1			1							
	S_2		1			2				1							
	S_{3-4}					2	4			1							
	M		1				1			2							
P. ampla	P_1	11				4		2									
P. trachytera	P_1								7	8							
P. rugosa	P_1												1				
T. clarki	P_1				1												
Tripodellus	P_1	18	73	147	6	236	478	32	8	36	4	2	11	13	15	182	8
variabilis	P_2		7	6	5	10	28	3	2	3		1			1	19	5
minutus	S_0		2		1	1	3		1	3						4	2
schleizius	S_1		3			3	7	1		1					1	4	2
	S_2		3		2	4	9			1					1	9	1
	S_{3-4}		4	3	1	19	15	4	2	9					1	13	1
	M	1	10	3	2	20	21	9		7			2	1	2	13	2
T. donoghuei	P_1		22				20										
T. gonioclymeniae	P_1															34	
Conditolepis	P_1	20	50		1	169	282	6									
distorta	P_2		5				1										
Conditolepis	P_1	47	172	115	2	219	181	194	84	312							
falcata	P_2	2	38	11		48	21	43	7	26							
	S_0		4	1		8	1	5	1	4							
	S_{1-2}		4	1		11	3	16	2	6							
	S_{3-4}		17	5		29	9	30	3	42							
	M		22	3		29	13	20	4	21							
C. inflexoidea	P_1		6	6			8										
Conditolepis	P_1	4	30	17	1	114	91	23									
marginifera	P_2		3			15	17	1									
	S_0		1		1	2											
	S_1					1											
	S_2		1			3											
	S_{3-4}		1		1	2	2										
	M		2			3											
D. stabilis	P_1							1			1	1		4	14	47	
D. micropunctata	P_1											3	29				

Table 18 – continued		Md-5	Md-7c	Md-9	Md-6	Md-11	Md-12	Md-13	Md-7	Md-6c	Dz-16	Dz-72	Dz-71	Dz-70	Dz-69	Dz-10	Dz-1
D. granulosa	P_1			1					5							1	
D. marburgensis	P_1															33	2
D. kayseri	P_1											1?					
Dasbergina	P_2												6			11	
spp.	S_2												1				
	$S_{3\text{-}4}$											1	5				
	M												3				
Protognathodus	P_1																4
P. jugosus	P_1												5			2	
P. ostrovkensis	P_1															35	3
P. aculeatus	P_1													2	4		
Pseudopolygnath.	P_2															27	
	S_0															2	
	S_1															1	
	S_2															1	
	$S_{3\text{-}4}$															4	
	M															12	1
Alternognathus? sp.	P_1													1		2	
Alternognathus	P_1								3	12							
regularis	P_2									4							
	S_0									4							
	S_1									3							
	S_2									3							
	$S_{3\text{-}4}$									10							
	M									4							

Table 19. Frequencies of conodont elements in samples from the late Famennian of Dzikowiec, the Sudetes.

DZIKOWIEC		Dz-54	Dz-9	Dz-8	Dz-68	Dz-18	Dz-4	Dz-17	Dz-20b	Dz-47	Dz-49	Dz-20a	Dz-74	Dz-7	Dz-19	Dz-48	Dz-75
Jablonnodus	P-M			2				1									
D.? guizhouensis	P_1				1								1			2	
M. circularis	P-M	11	38	21	2	16	3	9	6	6	7	5	2	7	8	29	
Ligonodina	P_1	1	3	1		1					1						1
sudetica	P_2		4	1	1			2	2	1		1			2	1	
	S_0	1	7	1					2		1	1		1		5	1
	S_1	1	4	8				7	1	1	1			2		6	
	S_2		4	1		1		1	2			5		1	2		1
	$S_{3\text{-}4}$	3	10	8	1	3		26	1	2	3	4	3	3	7	4	1
	M		2	3		2	1						1		3	2	
Guizhoudella	S_0																1
triangularis	S_1															1	
	$S_{3\text{-}4}$				1			1									
	M			1													
B. bohlenana	P_1		2	4						2		1					
B. suprema	P_1	38	25	14	2	21	19	18	11	7	40	15	21	44	65	108	1
B. disparilis	P_1											1				2	
Branmehla	P_2	2	5	2		1	1				4	1	8			10	
spp.	S_0	3											1				
	S_1	1	3			2	2								1	1	
	S_2	3	4			1	2	2						1		2	1
	$S_{3\text{-}4}$	1	12	3		1				1				1		2	
	M	3	3	1	1	1				1	6	1	3		2	1	2
A. varians	S-M	2	1	3		1		2	1							1	
Sweetodina	P	7	23	19	1	1	3	5	6	4	5	6	2	6	8	4	
monodentata	S_0		1	1								1				1	
	S_1	1					1			1							
	S_2		1	1				6			1		2	1	1	1	
	$S_{3\text{-}4}$	6	4	12		1	1	2		4	1	3	2	1	5	2	
	M	4	2	1					1		1	1		2	2	2	
P. vulgaris	P_1	1															

Table 19 – continued		Dz-54	Dz-9	Dz-8	Dz-68	Dz-18	Dz-4	Dz-17	Dz-20b	Dz-47	Dz-49	Dz-20a	Dz-74	Dz-7	Dz-19	Dz-48	Dz-75
Mehlina	P_1	16	25	26	13	24	3	13	16	16	1	15	19		7	12	7
sudetica	P_2	2	5	5		2		4	1	5		2	2				
	S_0			2		1											
	S_1		3	1					1			1					
	S_2		3	6													
	$S_{3\text{-}4}$		5	9		1											
	M	1	4	4		1		1		1					1		
P. disparilis	P_1																1
Polygnathus	P_1							3	2						2	5	
semicostatus	P_2															1	
P. pennatulus	P_1	8	1														
P. znepolensis	P_1																1
N. communis	P_1											2		2	1	7	48
N. vogesi	P_1	4	18	7	5	29	2	138	95	52	8	49	14	21	17		
Neopolygnathus	P_2	2	1	1	4	4		45		3	1	5		1	7	2	15
spp.	S_0				1	2						1				1	
	S_1		2													1	
	S_2		1			3			1								
	$S_{3\text{-}4}$				2	7		1		3							3
	M					1		13	1	1		2			4	1	3
Tripodellus	P_1	86	228	231	41	133	15	240	128	87	86	44	62	46	123	337	
gracilis	P_2	8	48	39	2	8	3	19	5	3	10	7	4	5	9	15	
	S_0		9	7		1		3	3	1			1		1	1	
	S_1	5	24	11		1		1	1						1	3	
	S_2	5	36	20		6		6	4	1	3			3	1	3	
	$S_{3\text{-}4}$	12	56	35	3	12		8	5	4	3			2	5	10	
	M	8	40	38	2	9	2	12	4	5	7	3	2	6	5	14	
T. gonioclymeniae	P_1	13	17	14		20	7	18	14	12	20	12	15	9	10		
D. stabilis	P_1	22		1	10			14	2	2		2			7	8	3
D. marburgensis	P_1	5	10	9	3	12	4	46	13								
D. trigonica	P_1									12	15	9	20	24	17	68	
Dasbergina	P_2		1	3				3			1				2	3	
spp.	S_0					1											
	S_2									1						1	
	M					1		2									
P. jugosus	P_1												1				
P. ostrovkensis	P_1		59	48												92	
P. aculeatus	P_1				32												
P. ziegleri	P_1	25															
P. ultimus	P_1					6	10	96	46	47	39	45	17	38	59		
Pseudopolygnath.	P_2	12	24	29	6		1	12	9	5	3	5	1	4	14	15	
	S_0	1	3	1				1	1				2			1	
	S_1	1	2	3	1			2			1						
	S_2		8		1			4	2	3		2	1		3		
	$S_{3\text{-}4}$	3	6	24	6		2	7	5		1	2	1		9	4	
	M		7	9		1	1	6	6	1	1	1			1	4	
Alternognathus? sp.	P_1	2															
P. praesulcatus	P_1				1								1				

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Explanation to index: * — text-fig., bold — description