

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

JERZY DZIK

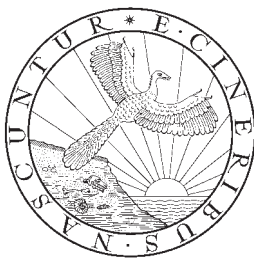
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The stratigraphically complete and extremely fossiliferous geological sections in the Holy Cross Mountains and Sudetes, Poland, cover the whole history of the Famennian tropical high-diversity pelagic ecosystem. Apparatus reconstruction of 142 conodont 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 that 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 wide-spread) 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 successful 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

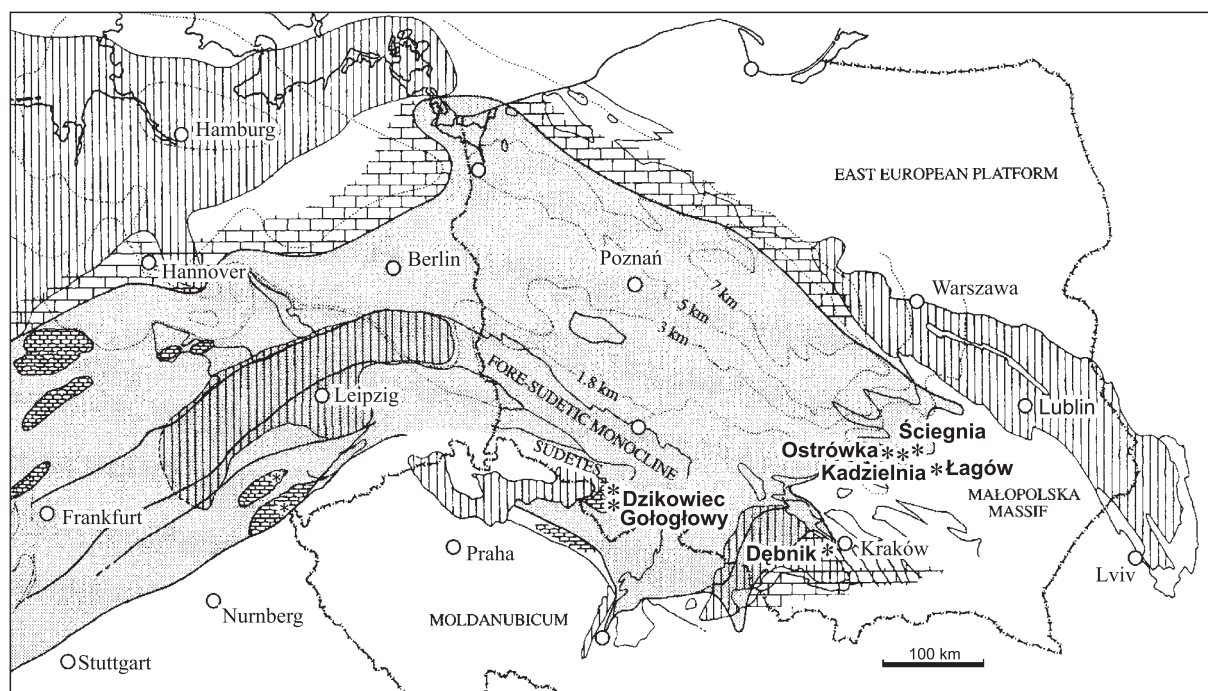


Fig. 1. Non-palinspastic palaeogeographic map of central Europe in the Famennian (for sources see Dzik 1997, fig. 1). Known extent of the latest Devonian to earliest Carboniferous limestone facies shown by brick pattern, cephalopod limestone as fine shallower facies as coarser; areas of intense subsidence, 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; Pajchłowa 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-

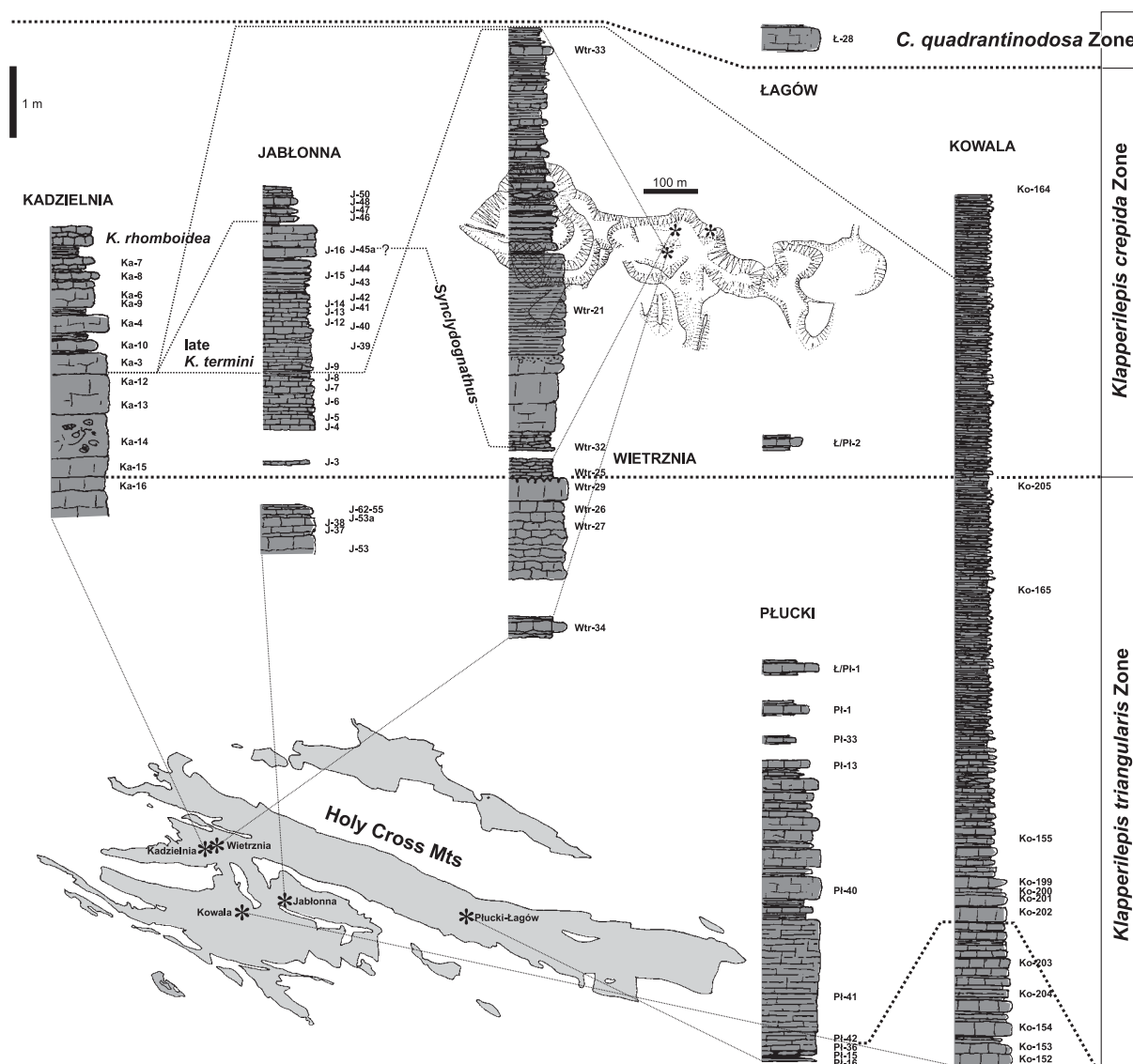


Fig. 2. The sampled sections of the early Famennian in the Holy Cross Mountains, with their relative position shown on a diagrammatic map of the extent of exposures of the Devonian. Position of zonal boundaries and their correlation indicated by broken lines. Composite section of Wietrznia is assembled 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 succession. Most of samples contained rare and strongly tectonically deformed conodonts. They apparently represent a transgressive succession 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.

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 priodiodinid (sample Dz-51) and a few more species (Dz-52), including *Dasbergina micropunctata*, *Mehlina*, *Brammehla*, 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 Famennian 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

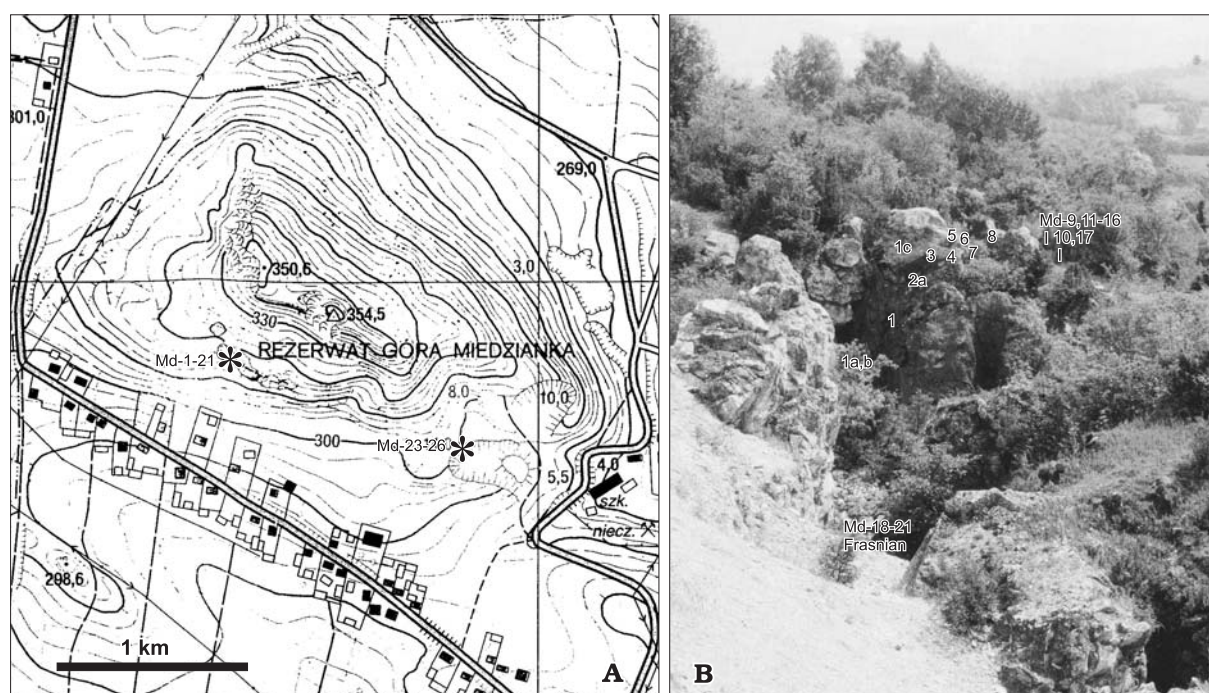


Fig. 4. Location of the Famennian exposures at Miedzianka in the Holy Cross Mountains (A) and places from where samples were taken (B); view from west.

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. Succession 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 verneuli*. 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 succession 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 disloca-

tions 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 Samsowicz 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 Łągów-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 clymenioid 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), *Concavicularis* 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 succession 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 en-

countered 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 successions 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–Famennian 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 (1912a) 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 Wietrzna 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 syndimentary. 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 *Concavicularis* 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). *Syncladognathus 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 re-building 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 Ślupecka 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 Pl-40) contains the first *Klapperilepis delicatula*.

The Ślupecka 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 succession 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 ferruginous 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 Ślupecka 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 1912b), 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 syndimentary 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 sup-

ports 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, offering 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 succession 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 intended 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 population 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 Plucki 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 elsewhere (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. proto-rhomboidea*, 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 P₁ element and widening the platform of P₂ 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 P₂ 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 P₁ 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 P₁ 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*. In 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 upper part of the velifera (or the whole trachytera) Zone.

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

***Lagovignathus styriacus* Zone.** — The change from *Lagovignathus granulatus* 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 P₂ 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

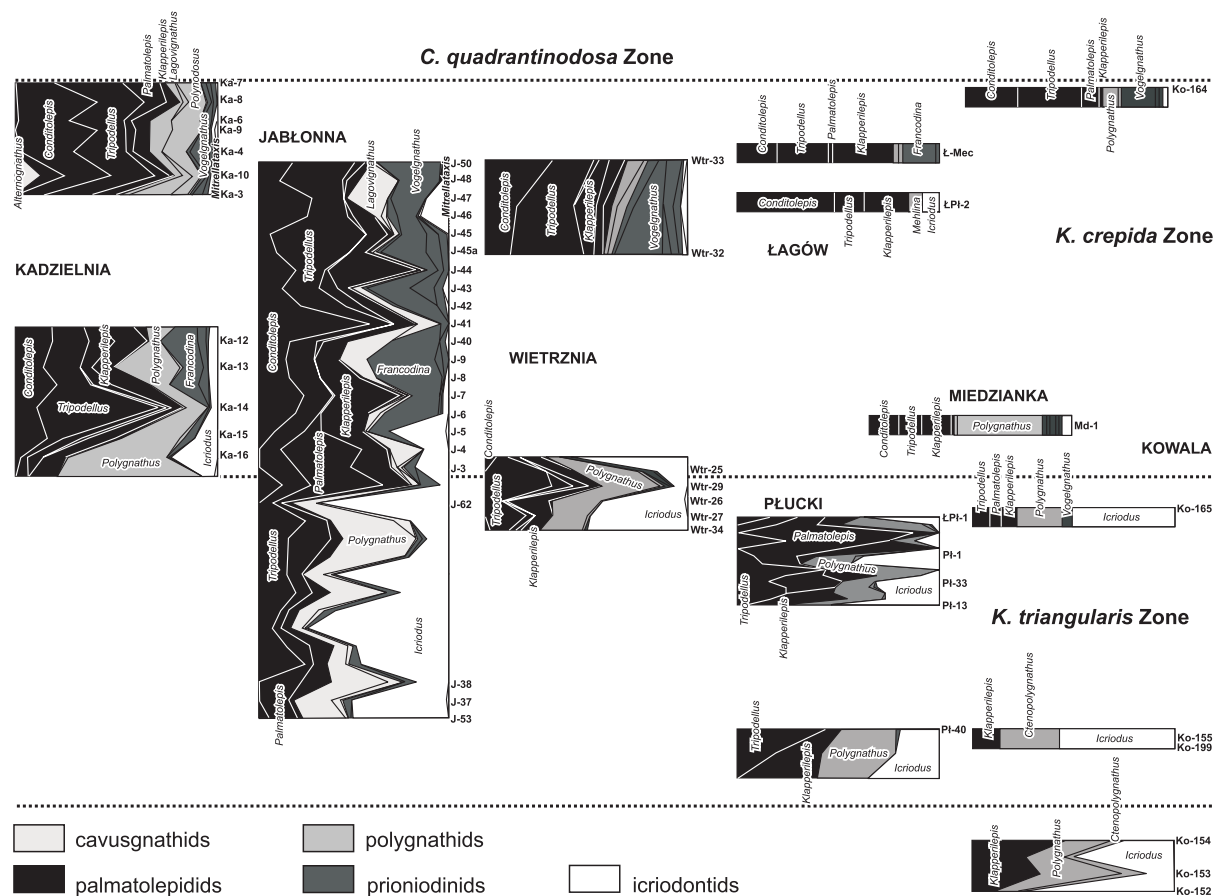


Fig. 5. Logs of percent contribution of conodont elements representative of the main lineages for samples from the early Famennian of the Holy Cross Mountains. Relative position of samples standardized in reference to proposed chronologic subdivisions.

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 connection 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 (Łągów) 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 Łągów, 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

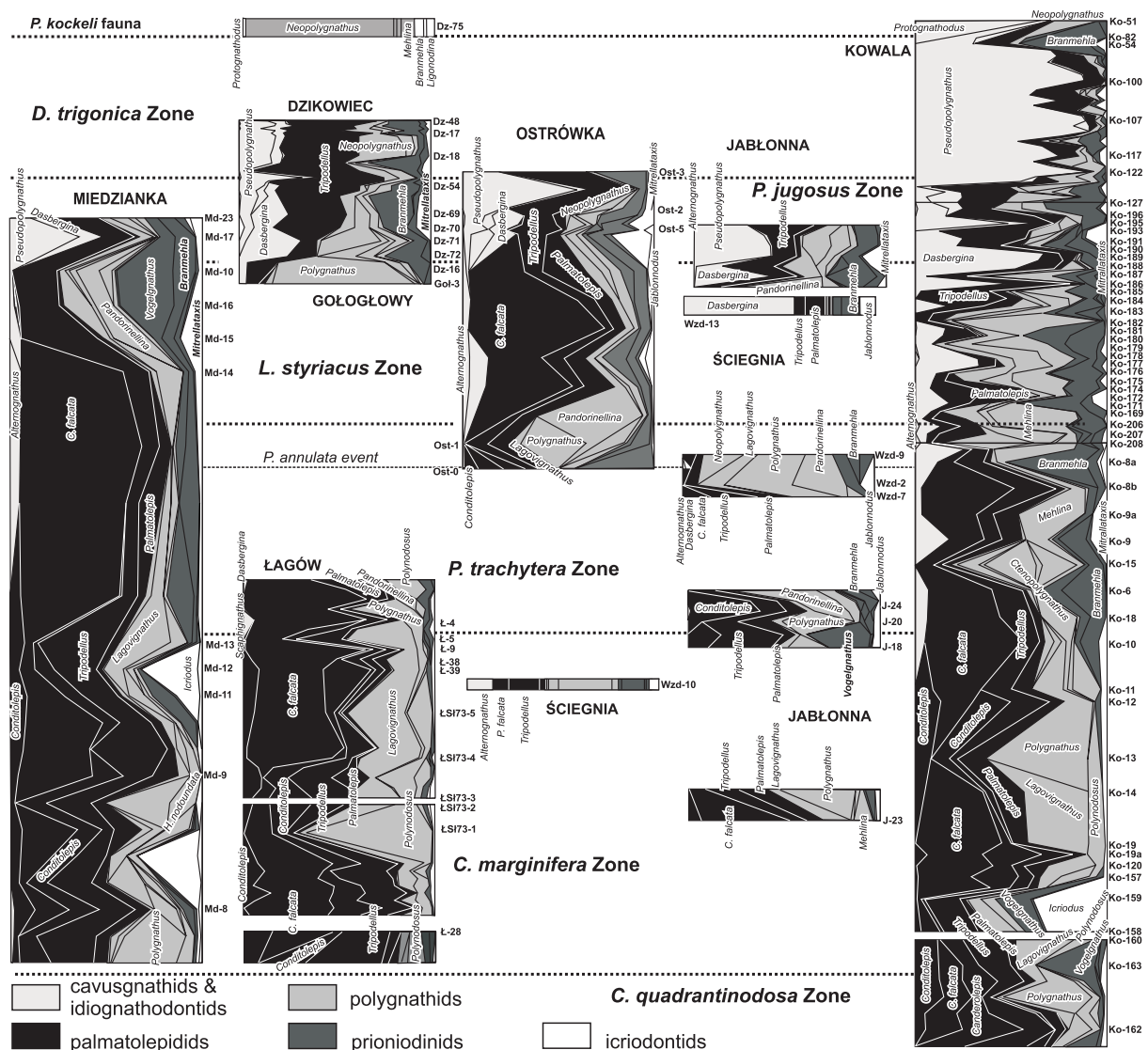


Fig. 6. Logs of percent contribution of conodont elements representative of the main lineages for samples from the early Famennian of the Sudetes and Holy Cross Mountains. Relative position of samples standardized in reference to proposed chronologic subdivisions.

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 rhythmicity 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 successions 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 spe-

cies 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 chronophylogenetics (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 stratophylogenetics 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 chronophylogenetics 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.

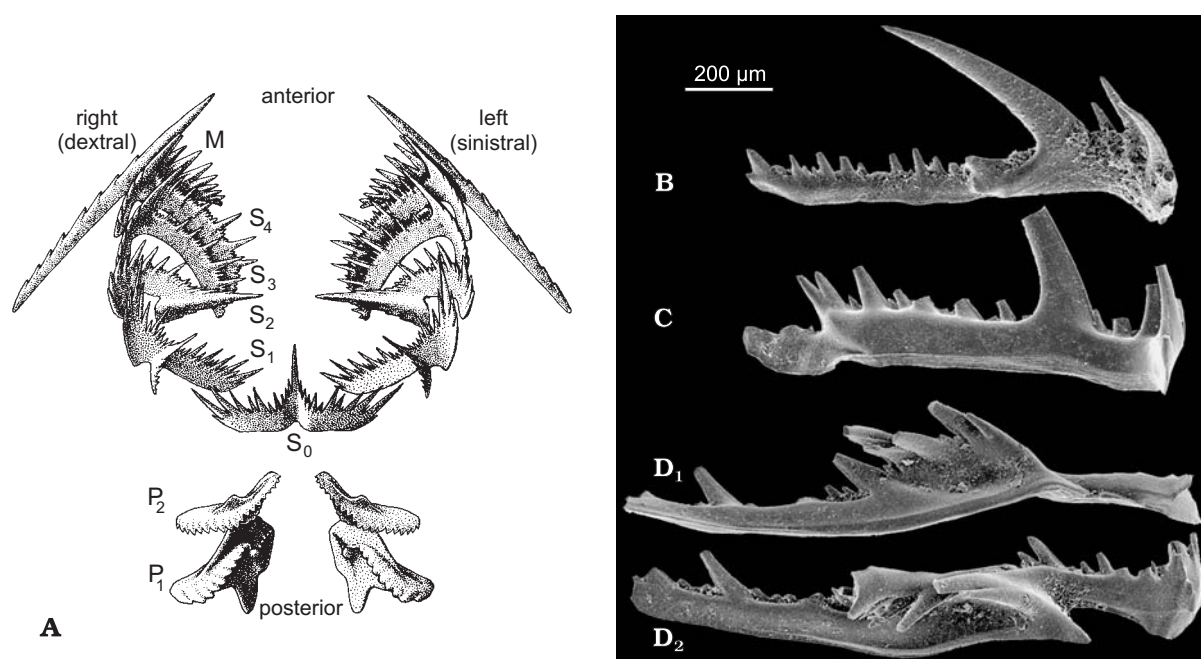


Fig. 7. **A.** Apparatus of the best known palmatolepidid conodont, the latest Frasnian *Lagovignathus bogartensis* (Stauffer, 1938). Reconstruction based on the cluster described by Lange (1968; with orientation of S₀ reversed and S₁ arbitrarily chosen, slightly modified after Dzik 1991), seen from 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 regenerating 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

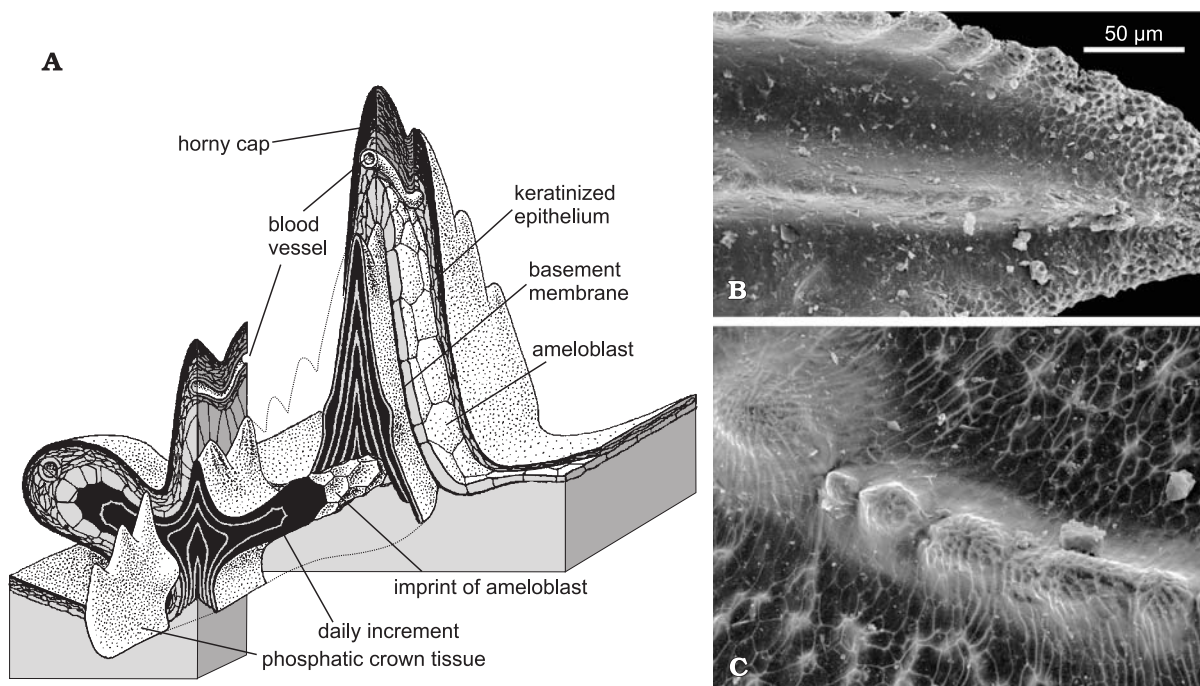


Fig. 8. **A.** Diagrammatic presentation of the model of conodont element growth and morphogenesis with assumption that the phosphatic tissue was an internal skeleton under a keratinous working surface (modified after Dzik 2000). **B.** Imprints of ameloblasts restricted to the most intensely growing 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 Plucki (sample Pl-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 ancyrodelellids, 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. Usually 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 proliferation 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 massive 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.

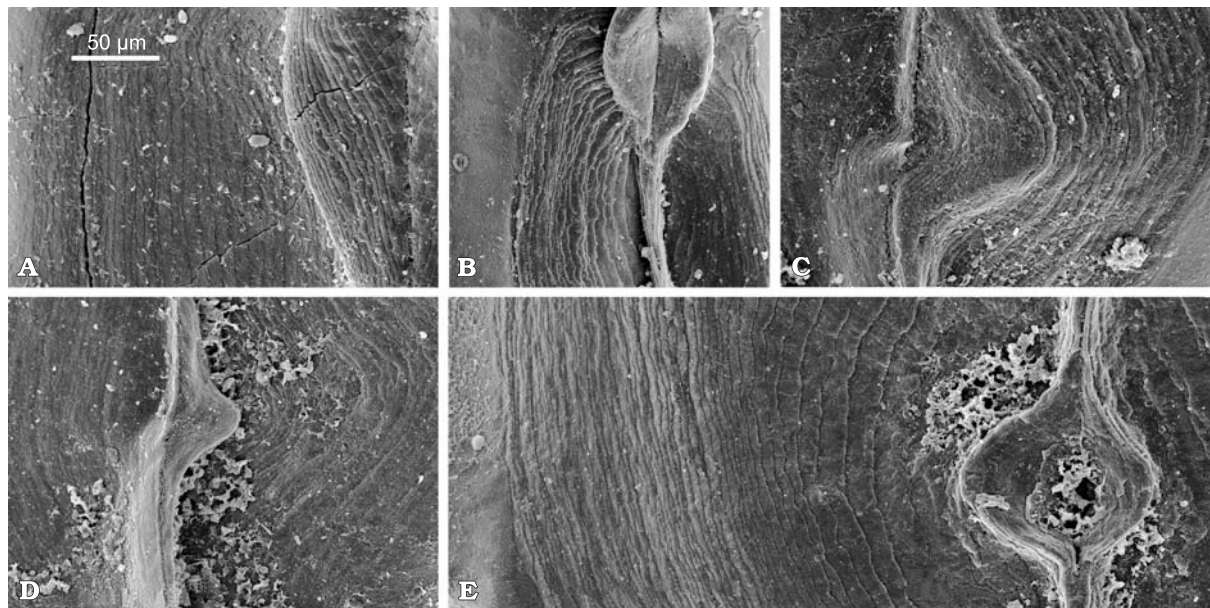


Fig. 9. “Sinuosa” larva of the Famennian conodonts and evolution of timing of its metamorphosis. Bases of P_1 elements with presumably daily increments are shown. **A.** *Alternognathus beulensis* Ziegler *et* Sandberg, 1984 from the *P. trachytera* Zone at Ściegna (Wzdół Plebański, sample Wzd-10; ZPAL 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 morphogenetic 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 is 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 disappearance 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).

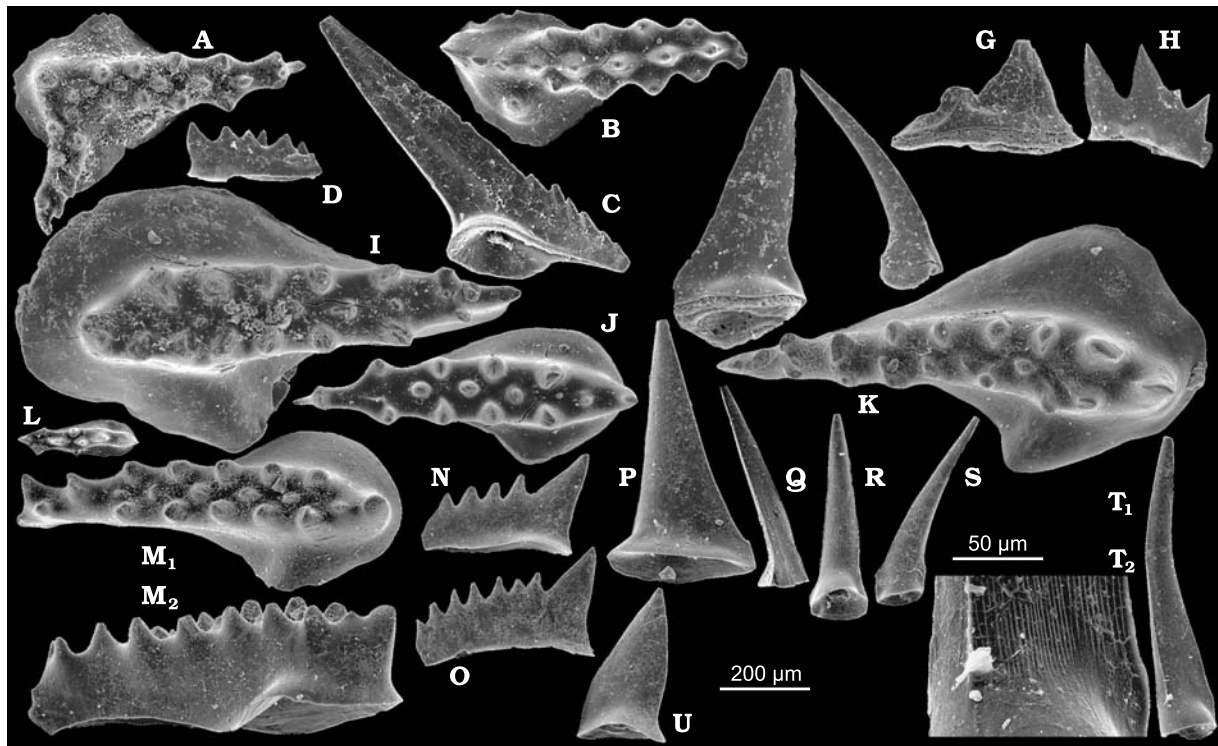


Fig. 10. Primitive Famennian icriodontids from the Holy Cross Mountains in occlusal (A, B), K, I–L₁, and posterior views. **A.** *Latericriodus* sp.: left P₁ element from the *Klapperilepis triangularis* Zone at Jabłonna (sample J-53a); specimen ZPAL cXVI/1705. **B, C.** *Latericriodus* (or *Antognathus*) *rarus* sp. n.: left P₁ (holotype) and P₂ 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 Pl-36) and the *K. triangularis* Zone at Jabłonna (L–U, sample J-53a); P₁ (C, I–K, M–O), P₂ (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 P₁ 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 P₁ 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: P₁ 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 P₁ 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 P₁ 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 P₂ 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 P₁ 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 Pt-36 (Fig. 10D–K) P₁ 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 P₂ 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 P₁ element inclined dorsally, narrow icrion of P₁ 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 *Pelekynathus* 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-

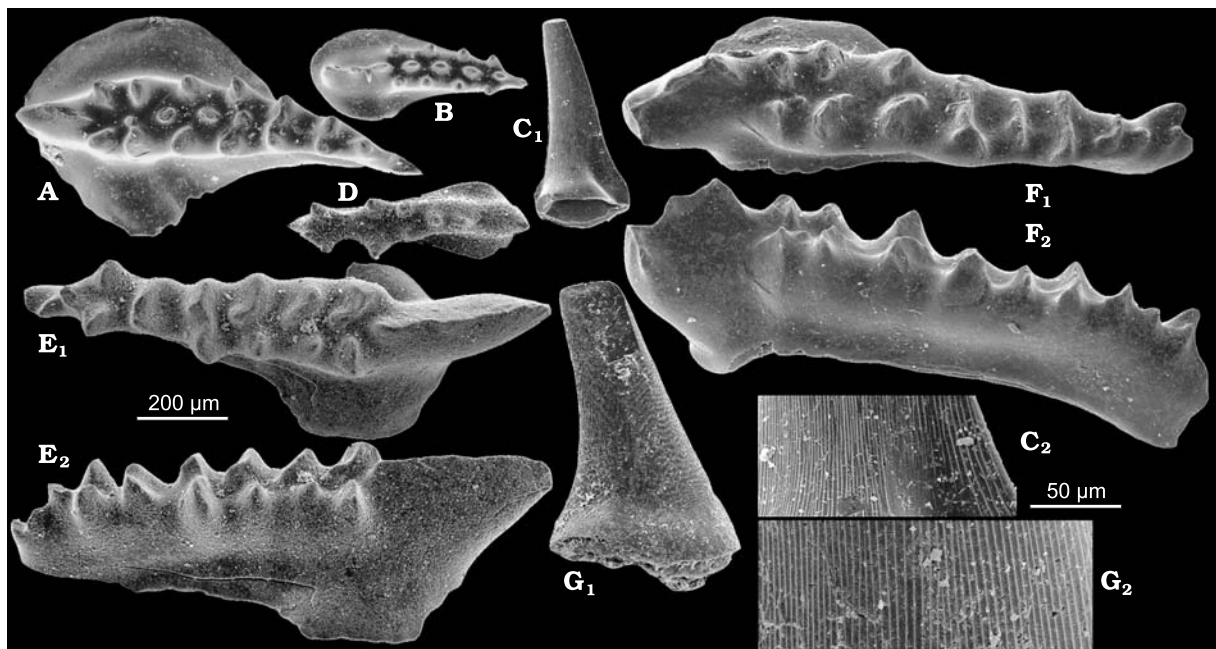


Fig. 11. Mid Famennian icriodontid *Icriodus cornutus* Sannemann, 1955 from Kadzielnia in the Holy Cross Mountains. **A–C.** Ancestral population from the late *K. triangularis* (sample Ka-16) with almost vertical cusp, transitional from *I. alternatus*; P_1 (A, B) and P_2 (C) elements ZPAL cXVI /1646, 1648, and 1647. **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 Washington 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)

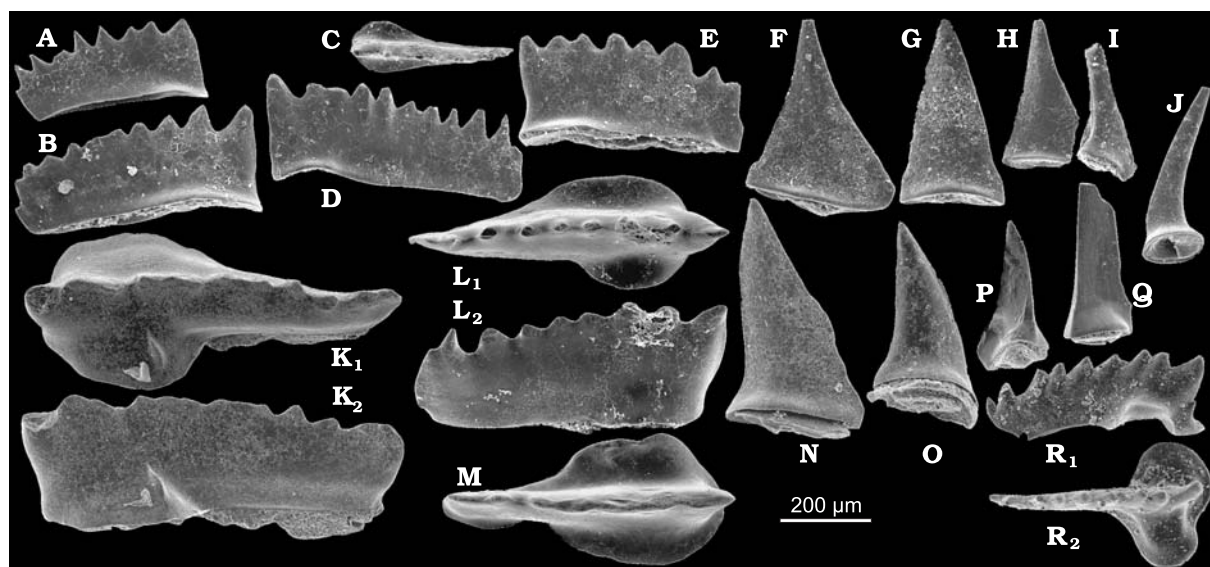


Fig. 12. Icriodontids without icrion from the Famennian of the Holy Cross Mountains and Sudetes. **A–Q.** *Pelekysgnathus planus* Sannemann, 1955 from the early Famennian at Jablonna (A, H, sample J-53a; B–G, I, J, sample J-5,) and Karczówka (K–Q); P_1 (A–E, K–M) and P_2 (F, N) and S (G–J, O–Q) elements 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 single 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, transversely 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 taxonomic 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 panderoodontid 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 protopanderoodontids 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 protopanderoodontid conodonts. Although not all element types represent truly discrete classes and morphological transitions are more common than in undoubted protopanderoodontids, 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 protopanderoodontids (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 protopanderoodontids, 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.

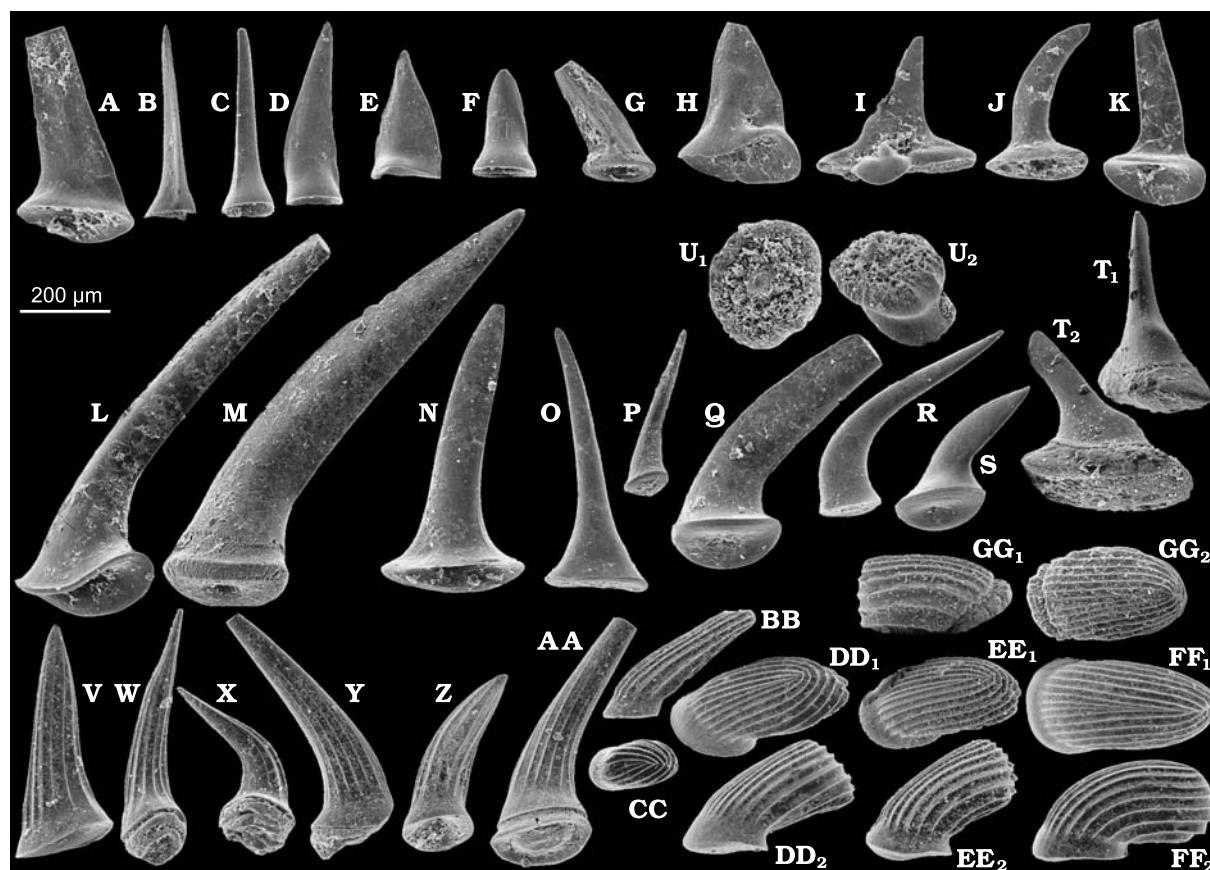


Fig. 13. Possible Famennian icriodontids with completely reduced platform series in the apparatus. A–K. *Mitrellataxis? asymmetrica* sp. n. from the *L. styriacus* Zone at Ostrówka (sample Ost-12); specimens ZPAL cXVI/1575, 1567, 1576, 1573 (holotype, D), 1574, 1572, 1571, 1569, 1568, 1570, 1566, respectively. 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 Dębik 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 Wietrzna.

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-mineralized 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 base, 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 Ściegna 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.

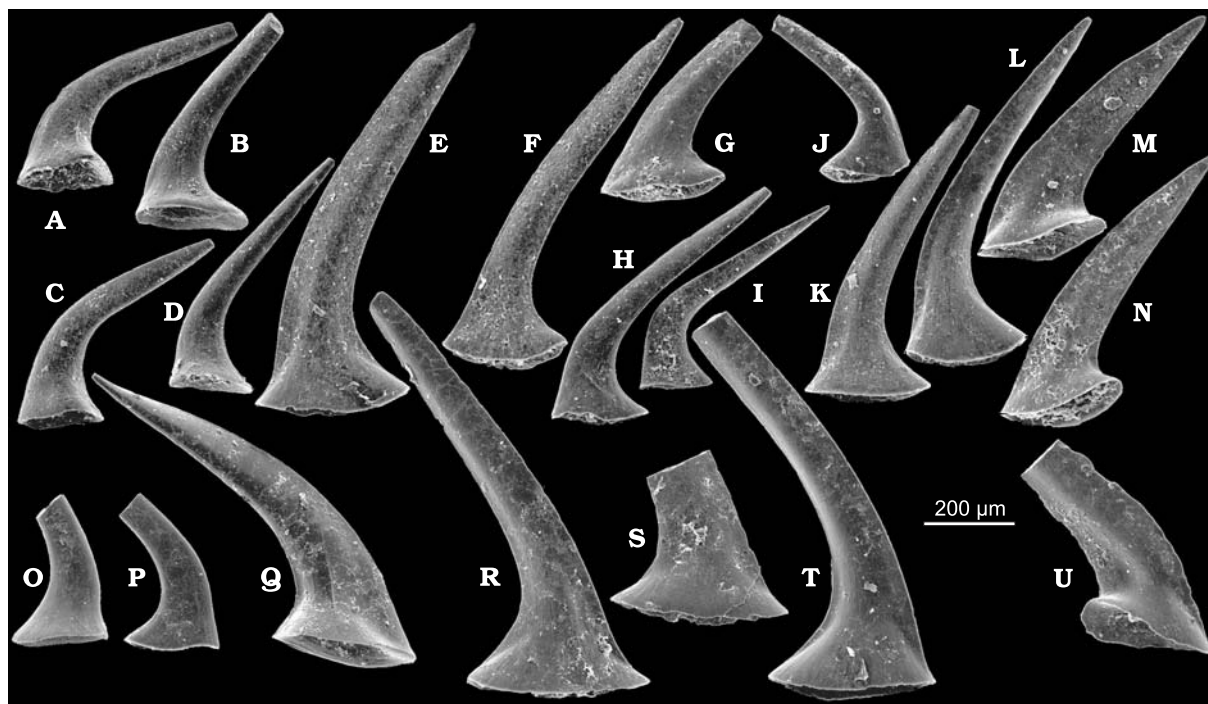


Fig. 14. Simple-cone *Jablonnodus oistodiformis* sp. n. from the early *P. trachytera* Zone at Jabłonna (bed 24; A–N) and the *L. styriacus* Zone at Ostrówka (O–U, sample Ost-12) in the Holy Cross Mountains; all in posterior view. A, B, O, P. Right and left P_1 ? elements; specimens ZPAL cXVI/1545, 1546, 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 P₁ elements, base outline of possible P₂ elements is circular. Elements with a rather erect cusp show the symmetry transition series from the strictly symmetrical probable S₀ elements through those with the base flattened from one side (S₁₋₂) to those having flattening on both sides (S₃₋₄). 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: P₁ 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 (I₁) and medial (L₂ and M₂) views. A, B. Left P₁? elements; specimens ZPAL cXVI/1586–1587, respectively. C, D. Right P₂ (?) elements 1588, 1589. E, F, H–L. Right and left S₂₋₄? elements 1591, 1593, 1596, 1600, 1590, 1592, and 1597. G, M. S₀? elements 1602 and 1601. N–O. Right S₁? 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.

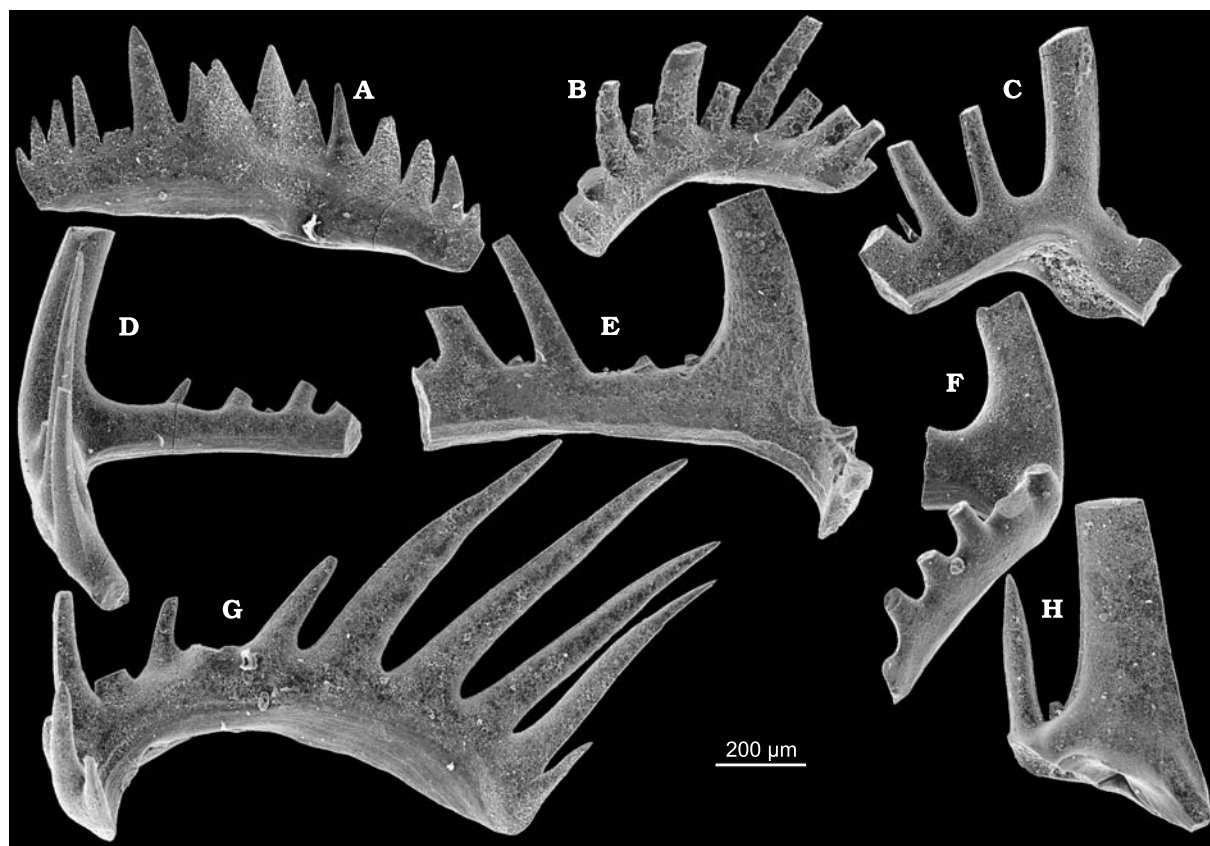


Fig. 16. Specifically undetermined early Famennian prioniodinid *Ligonodina* sp. from the *K. triangularis* Zone at Jabłonna (sample J-58) in the Holy Cross Mountains. P_1 (A), P_2 (B), S_0 (D), S_1 (C), S_2 (G?), S_{3-4} (E, F), and M (H) elements; specimens ZPAL cXVI/11728, 1729, 1731, 1730, 1733,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

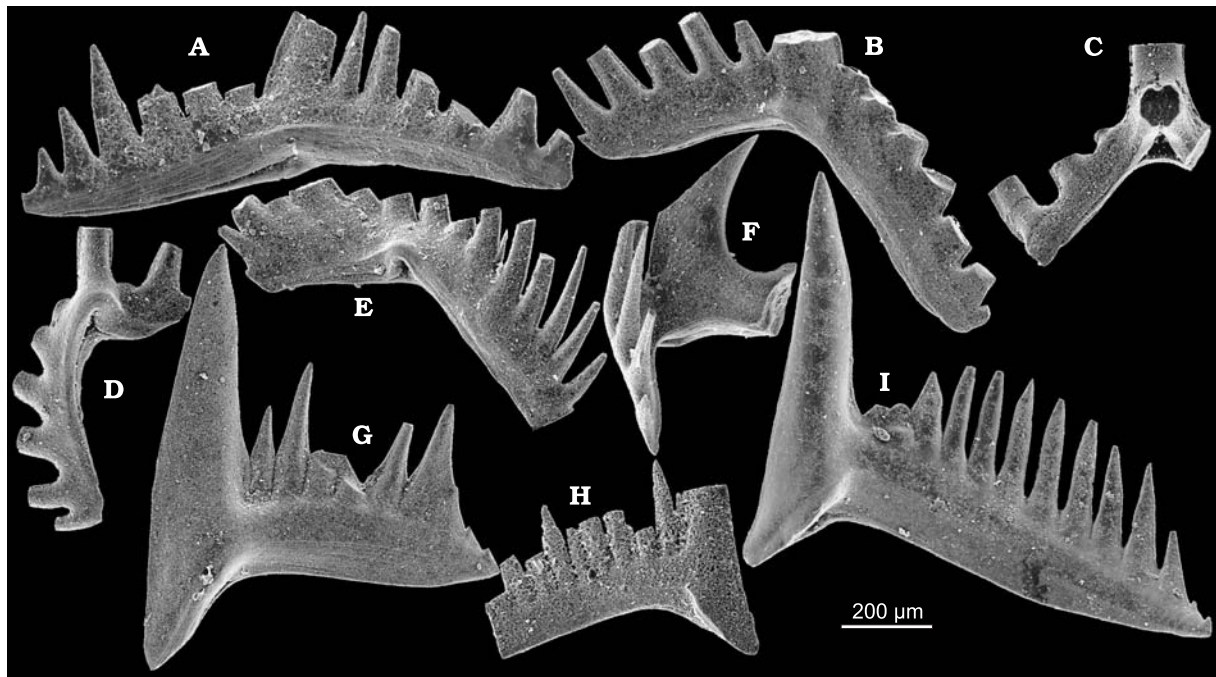


Fig. 17. Early Famennian successors of the main prioniodinid lineage of *Ligonodina* from the Holy Cross Mountains. **A, B.** *Ligonodina pectinata* Bassler, 1925 from the earliest Famennian at Plucki (sample Pl-40); S_4 (A) and M (B) elements ZPAL cXVI/1712, 1713. **C–T.** *Ligonodina albidens* sp. n. from the late *K. triangularis* and *K. crepida* zones at Jabłonna (bed 7, C; J-6, D–G; J-45a, H–N) and Wietrzna (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 Pl-40 (Fig. 17B), which may be an extreme variety of *Ctenopolygnathus* and a robust but teratologically deformed specimen from sample Pl-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.

Occurrence. — Only the earliest Famennian at Plucki, 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 Wietrzna located above the Frasnian mudmound.

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

Ligonodina multidentis 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.

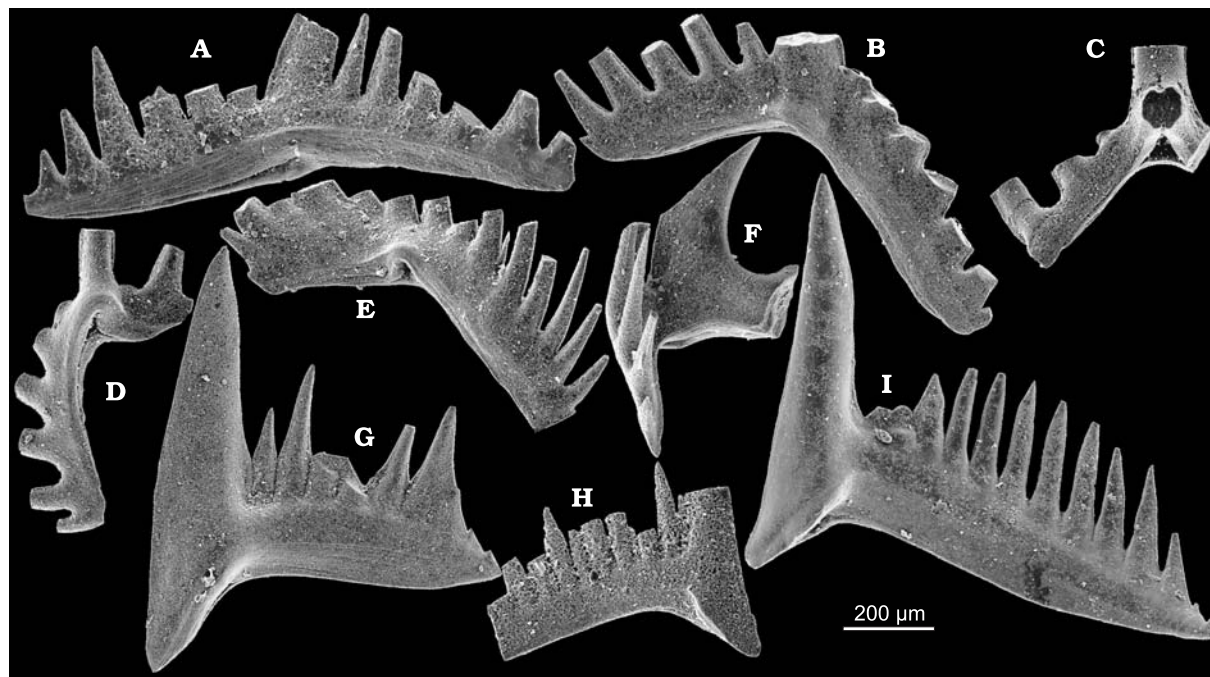


Fig. 18. Generalized early Famennian prioniodinid *Ligonodina multidentis* sp. n. from Kadzielnia (A, F, and H, sample Ka-2; B–E, and G, sample Ka-3) and Miedzianka (I, sample Md-1) in the Holy Cross Mountains. P_1 (A), P_2 (B), S_0 (C), S_1 (D), S_2 (E), S_{3-4} (F), and M (G–I) elements; specimens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

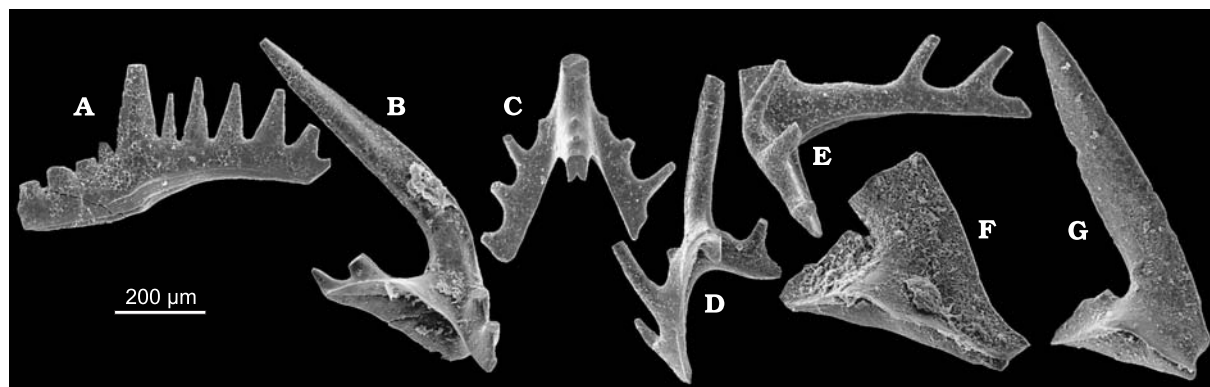


Fig. 19. Simplified early Famennian prioniodinid *Ligonodina latibasalis* sp. n. from Jabłonna (A–F, sample J-45a) and Wietrznia (G, sample Wtr-32) in the Holy Cross Mountains. P₁ (A), P₂ (B), S₀ (C), S_{1–2} (D), S_{3–4} (E), and M (F, G) elements; specimens ZPAL cXVI/1744–1749 (holotype, F), and 1755, 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 P₂ 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.

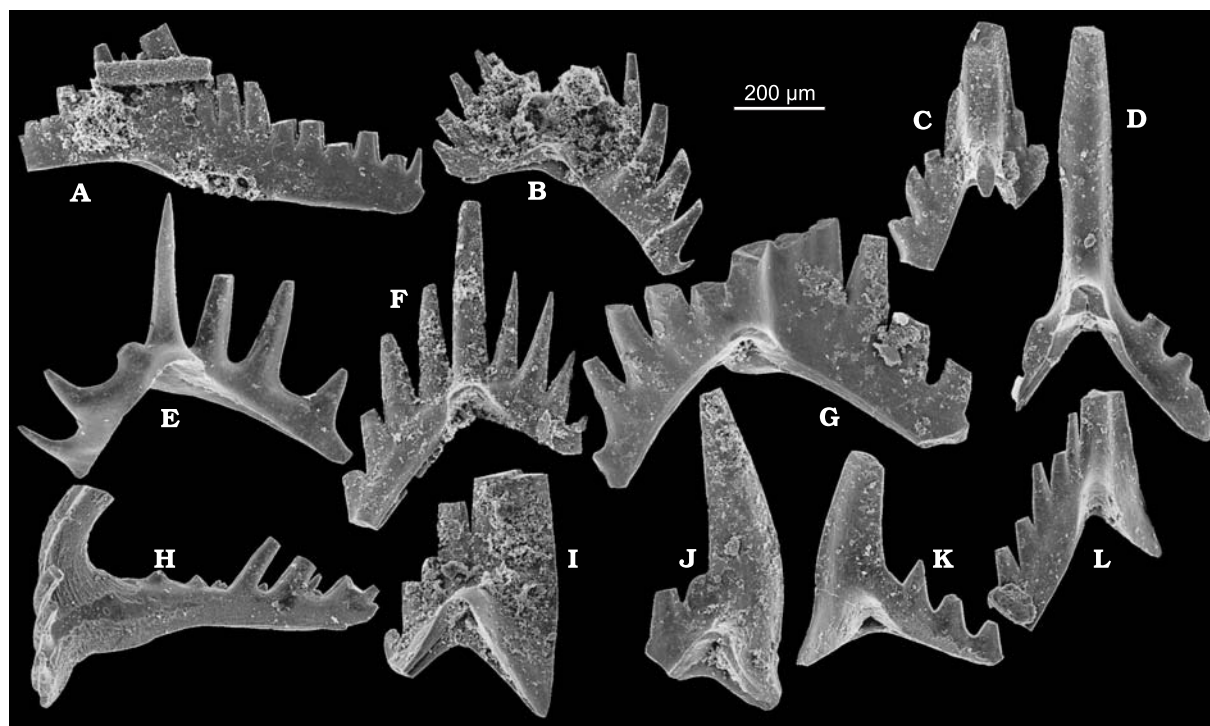


Fig. 20. Problematic late Famennian prioniodinid *Ligonodina sudetica* sp. n. from Dzikowiec, the Sudetes (A, D, H, and L, sample Dz-9; B, C, F, and I, sample Dz-8; E, G, J, and K, sample Dz-10). P₁ (A), P₂ (B), S₀ (C, D), S₁ (E), S₂ (F, G), S₃₋₄ (H), and M (I–L) elements; specimens ZPAL cXVI/1877, 1886, 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, S₃ and S₄ 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 S₁ elements (also M elements) and generally more delicate denticulation of S elements. The angular appearance of S₁ 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.

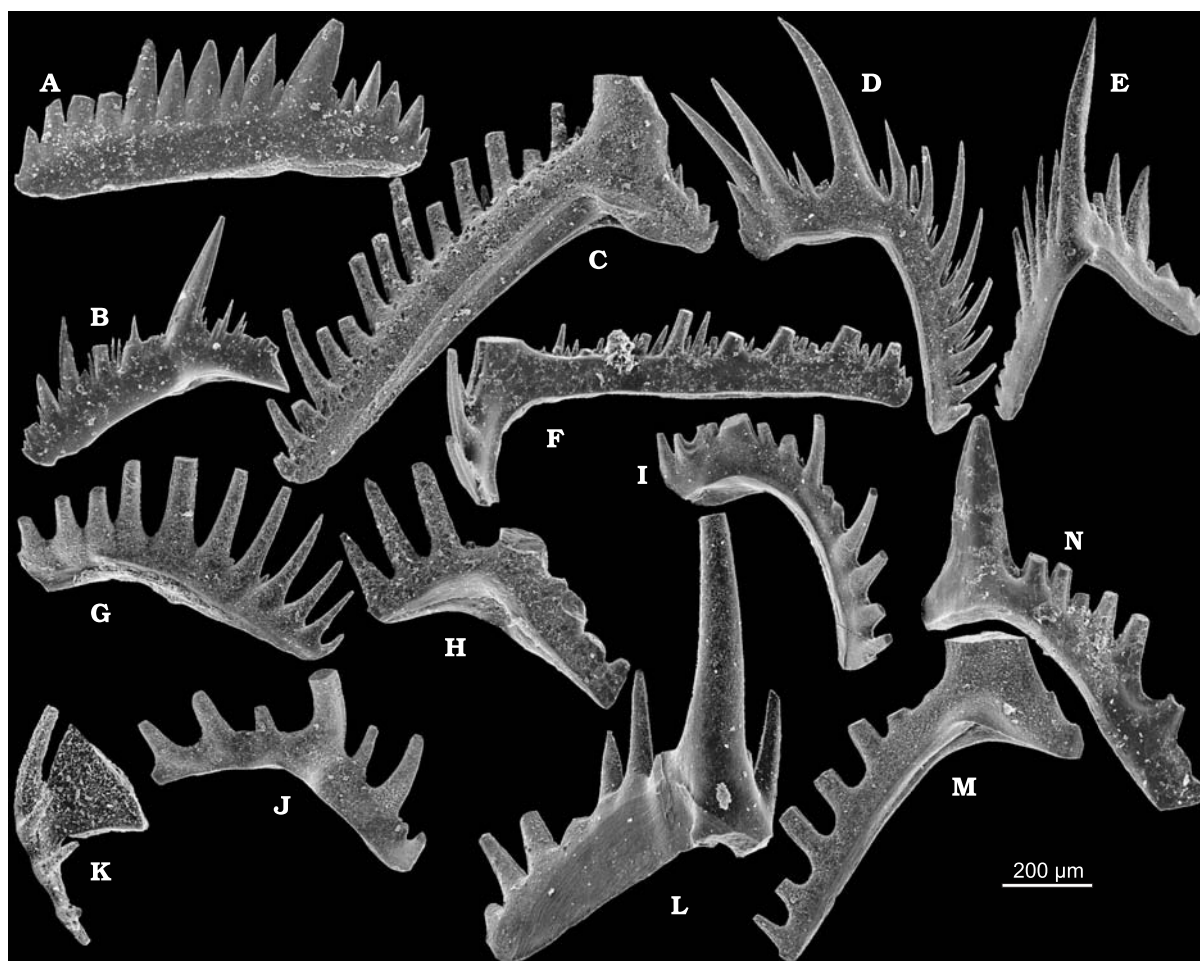


Fig. 21. Early Famennian successors of the prioniodinid lineage of *Pluckidina lipperti* (Bischoff, 1956) from the beginning of the *K. triangularis* Zone at Plucki (samples Pl-36, A, B, and F) somewhat younger strata at the same locality (sample Pl-1, D, E) and transition from the *K. triangularis* 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. P₁ (A, G), P₂ (B, H and J), S₀ (F), S₁ (E and L), S₂ (D and I), S₃₋₄ (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 S₃₋₄ 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 P₂ with the dorsal process angularly bent close to the base and a tendency to develop an additional process near the bending.

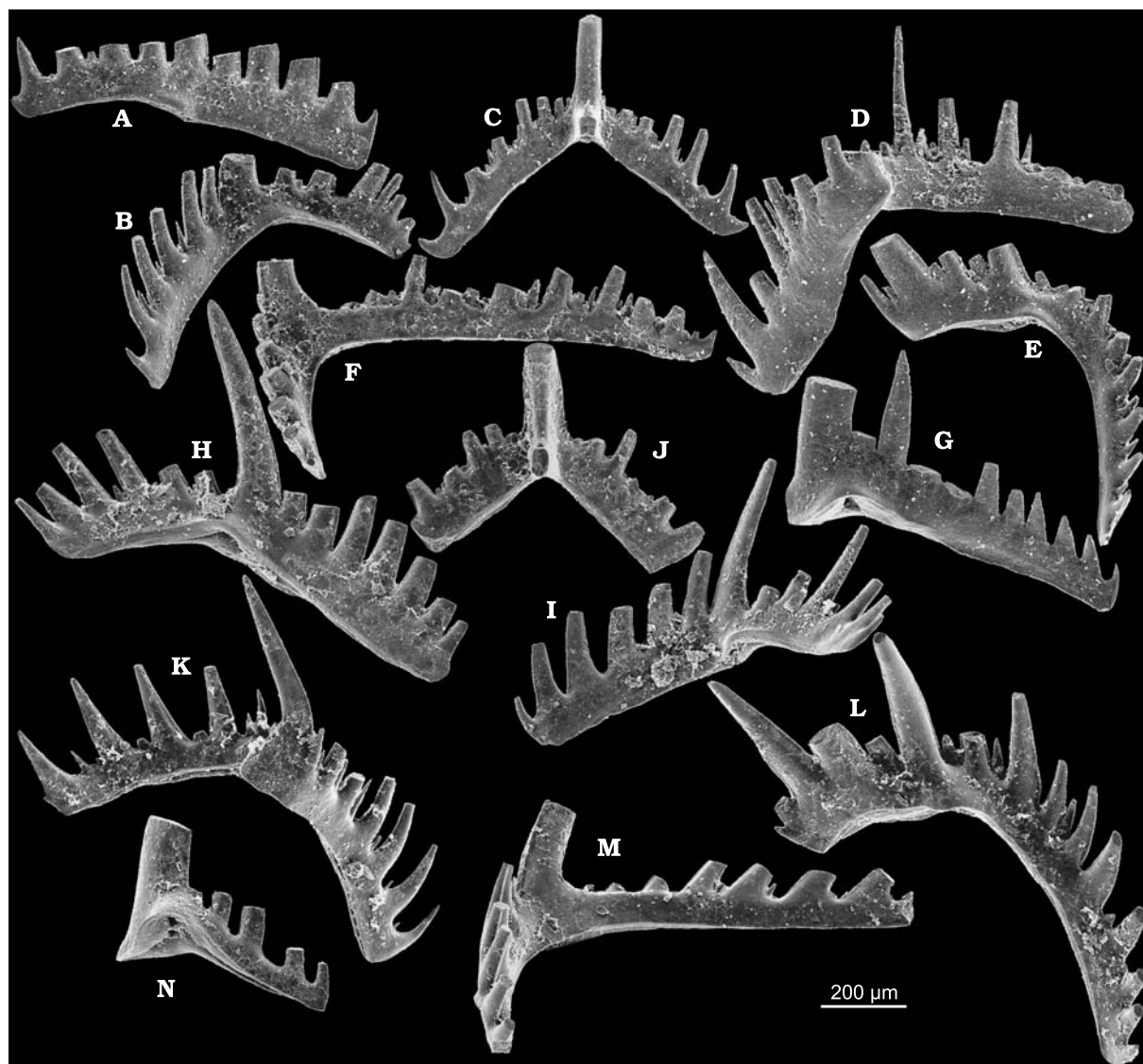


Fig. 22. Late Famennian prioniodinid *Pluckidina purnelli* sp. n. from the *P. trachytera* Zone at Jabłonna (A–G, bed 24) and the *L. styriacus* Zone at Ostrówka (H–N, sample Ost-12) in the Holy Cross Mountains. P_1 (A and H), P_2 (B and I), S_0 (C and J), S_1 (D and K), S_2 (E and L), S_{3-4} (F and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

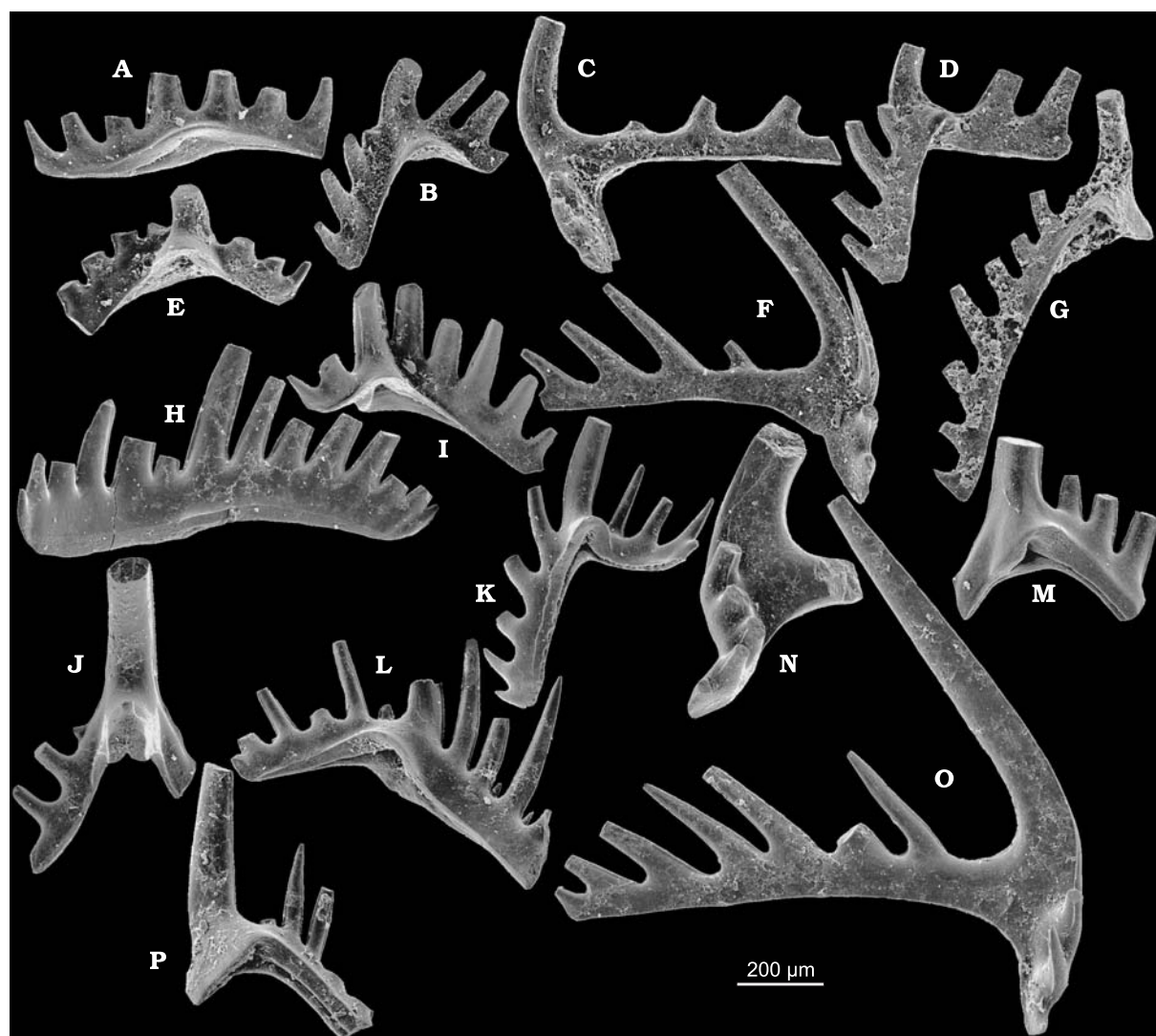


Fig. 24. Possible ancestor of Carboniferous prioniodinids, *Idioprioniodus ruptus* sp. n. from the *P. trachytera* Zone at Jabłonna (A–G, bed 24) and the *L. styriacus* Zone at Miedzianka (M, N, sample Md-14), and Ostrówka (H–L, O, P, sample Ost-12). P_1 (A and H), P_2 (B and I), S_0 (C and J), S_1 (D 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 *Idioproniodus* 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.

Idioproniodus 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 Wietrzna, are associated with the set of other elements of *Idioproniodus*. 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*.

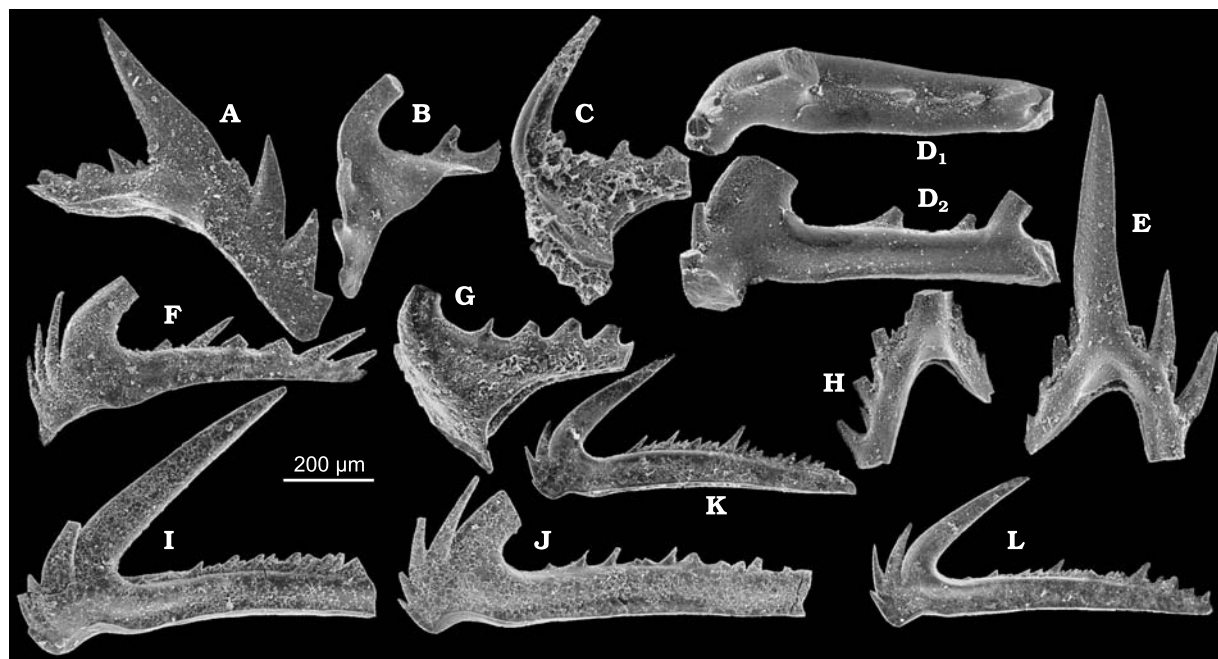


Fig. 25. Aberrant prioniodinid *Uncadina* and its poorly known possible less derived relative. A–H. *Idioproniodus uncadinoides* sp. n. from the *K. triangularis* Zone at Wietrzna (uncertain taxonomic identity; A, D, E, and H, sample Wtr-25) and Jabłonna (G, sample J-45a), and the *P. jugosus* Zone of 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 Wietrzna 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 Wietrzna.

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

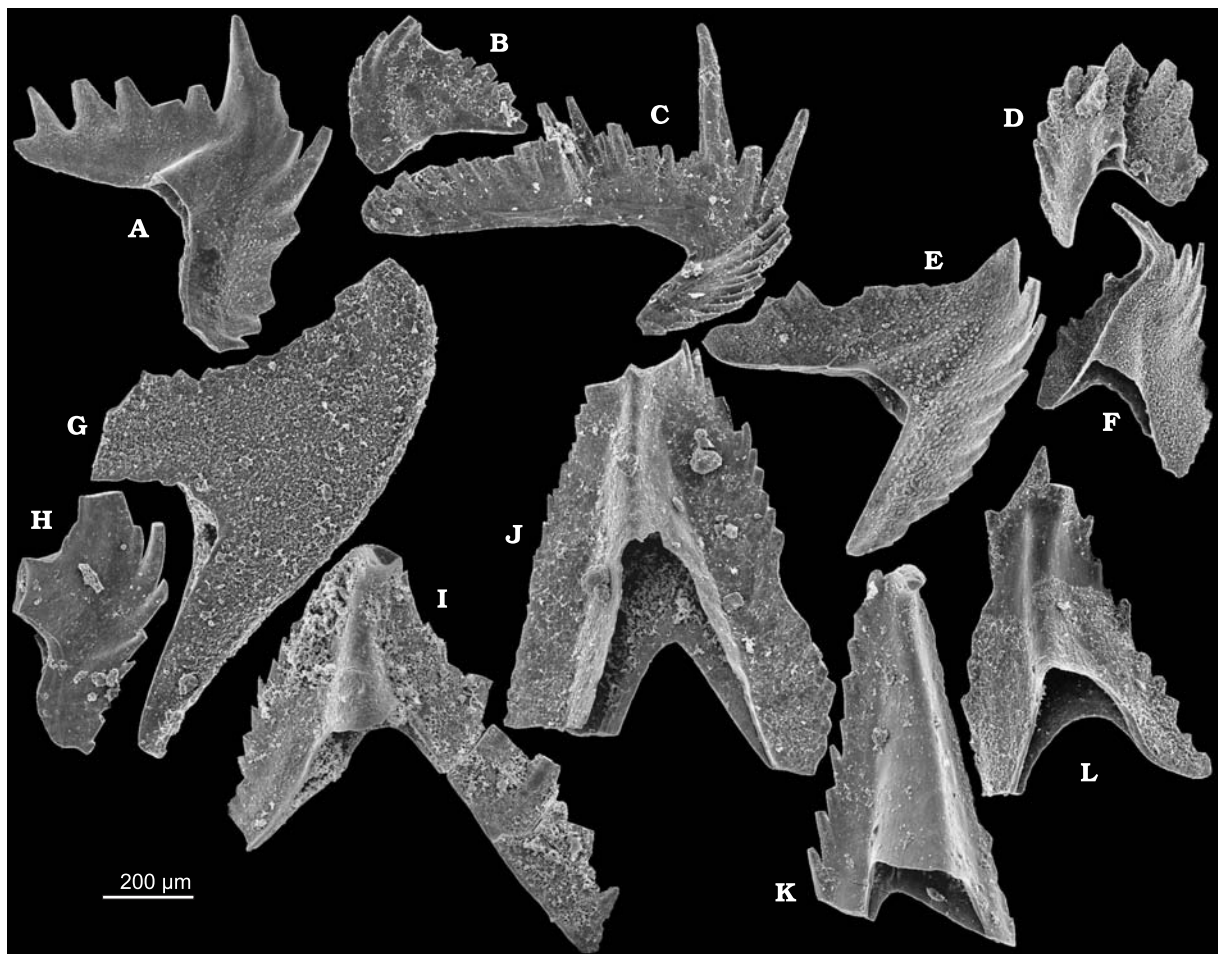


Fig. 26. Bizarre probable prioniodinid *Guizhoudella triangularis* Wang et Wang, 1978 from the *P. jugosus* Zone at Ostrówka (sample Ost 185, A, B, D–F and Ost-265, G), the *K. crepida* Zone at Jabłonna (C, sample J-46; L, bed 27; J, sample J-66), the late *K. triangularis* Zone at Wietrzna (I, sample 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-

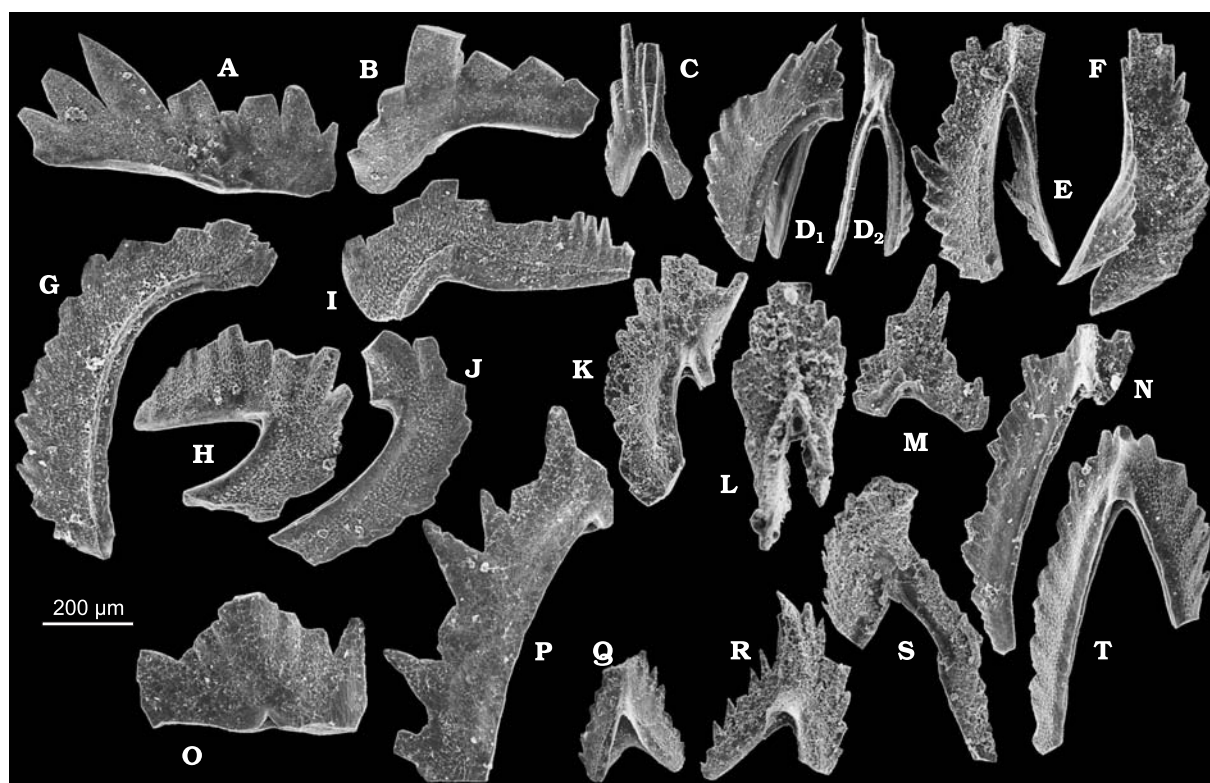


Fig. 27. Bizarre probable prioniodinid *Guizhoudella dinodontoides* sp. n. from the *L. styriacus* Zone at Miedzianka (sample Md-14, A, B, H, J, T), Jablonna (C–F, K, M, O–S, sample J-45a; L, bed 12), and Kowala (G, I, sample Ko-18; N, sample Ko-154) in the Holy Cross Mountains. P_1 (A?), P_2 (B?), S_0 (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 Jablonna, 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 Famennian 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.

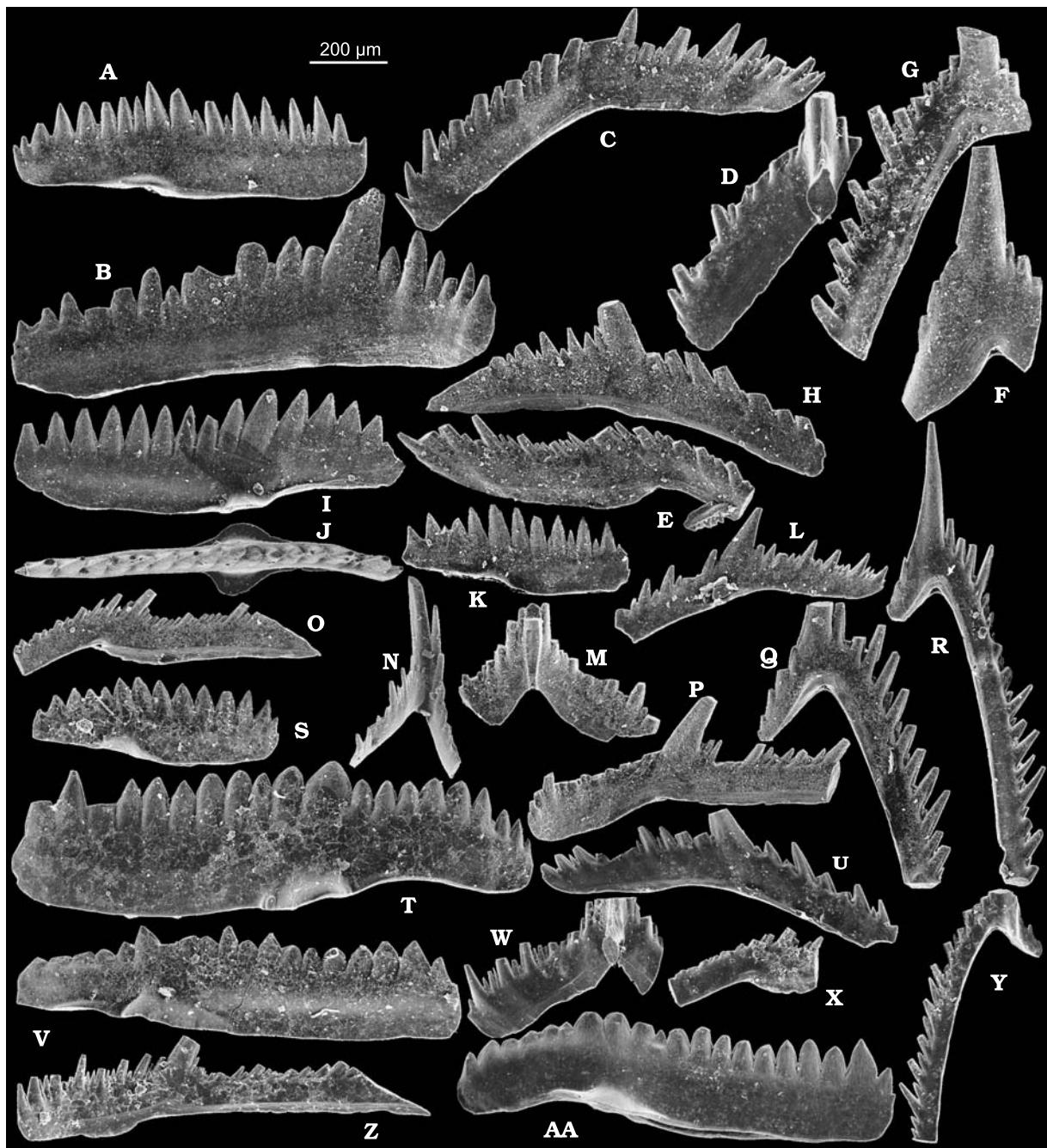


Fig. 28. Early gondolellid *Branmehla bohlenana* (Helms, 1959) from the *C. quadrantinodosa* Zone at Łagów (A–F, sample ŁS173-2) and the *K. crepida* zones at Wietrznia (G, sample Wtr-21) and the *L. styriacus* Zone at Miedzianka (H–R, sample Md-14) and Ostrówka (S, T, sample Ost-5; W–AA, sample Ost-15,) in the Holy Cross Mountains. P₁ (A, B, I–K, T–V, and AA), P₂ (E, H, L, and U), S₀ (D, M, and W), S₁ (N), S₂ (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 P₁ element with relatively low cusp.

Remarks. — The geologically oldest populations of *Branmehla* from Łagów (sample ŁS173-2; 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 highly arched in *B. bohlenana* (note that the geologically later *Pluckidina lipperti* from the *K. crepida* Zone exhibits the same tendency; Fig. 21N).

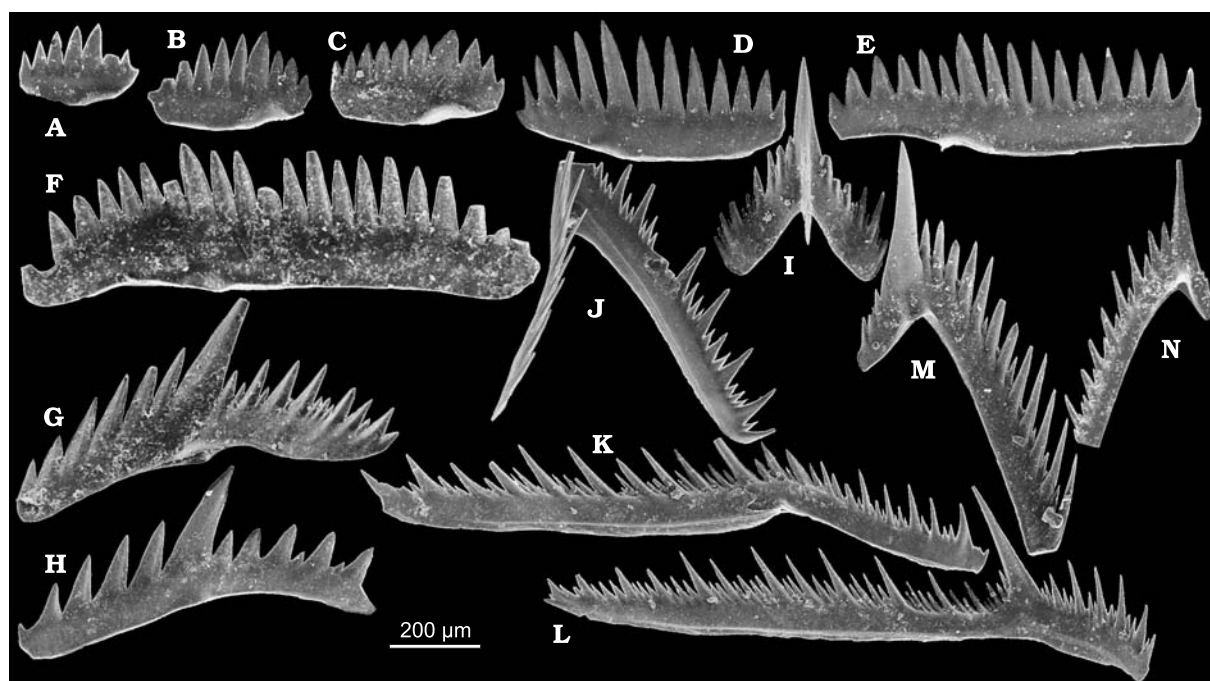


Fig. 29. Juvenile specimens of early gondolellid *Branmehla bohlenana* (Helms, 1959) from the *P. trachytera* Zone at Kowala (sample Ko-8a) in the Holy Cross Mountains. P₁ (A–F), P₂ (G, H), S₀ (I), S₁ (J), S₂ (K), S_{3–4} (L), and M (M and N) elements; specimens ZPAL cXVI/2339, 2338, 530, 2337, 2336, 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 representative 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 domination 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 P₁ 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. — P₁ elements with high, sharp denticles, which decrease linearly in size with distance from the cusp, to give the element a polygonal profile.

Remarks. — Mature P₁ 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.

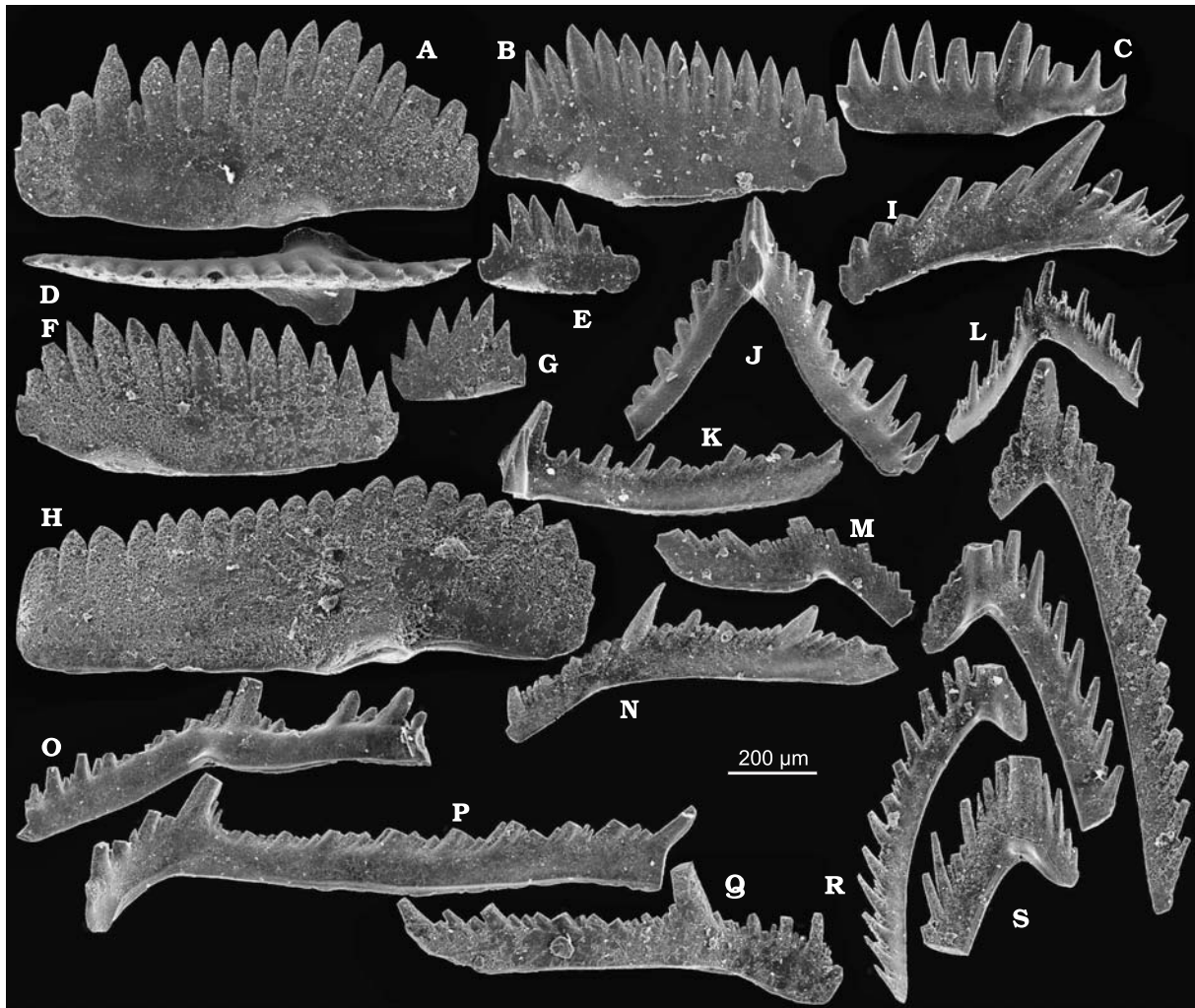


Fig. 30. Paedomorphic early gondolellid *Branmehla inornata* (Branson *et* Mehl, 1934) from the *P. jugosus* Zone at Jabłonna (A, F, G, and S, bed 27) and Ostrówka (B–E, I–R, and T, U, sample Ost-185; H, sample Ost-5) in the Holy Cross Mountains. P₁ (A–H), P₂ (I, J, K), S₀ (J, K), S₁ (L), S₂ (M–O), S_{3–4} (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 P₁ element laterally bent, widely gaping basal cone.

Remarks. — P₂ 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.

P₁ 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).

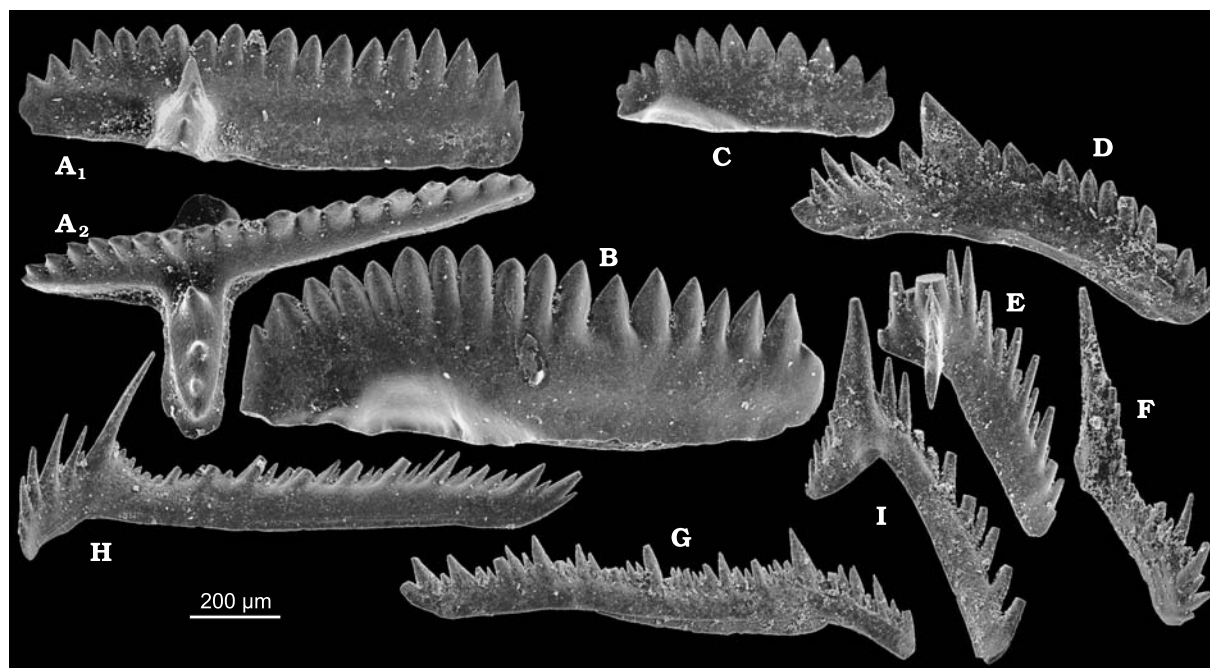


Fig. 31. Advanced late Famennian species of *Brannmehla* from the *D. trigonica* Zone at Ostrówka (sample Ost-3) in the Holy Cross Mountains. A. *Brannmehla disparilis* (Branson *et* Mehl, 1934). P₁ element; specimen ZPAL cXVI/2016. B–I. *Brannmehla suprema* (Ziegler, 1962). P₁ (B, C), P₂ (D), S₀ (E), S₁ (F), S₂ (G), S_{3–4} (H), and M (I) elements; specimens ZPAL cXVI/2017–2024, respectively.

Material. — Four specimens.

Diagnosis. — Base of P₁ elements laterally expanded to form denticulated transverse processes.

Remarks. — Even more prominent lateral process may develop in P₁ 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 S₀ 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 *Syncladognathus*) and similar Silurian *Ozarkodina*, it was proposed by myself that they represent the same clade (Dzik 1991). The occurrence of *Syncladognathus* 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 *Syncladognathus* 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.

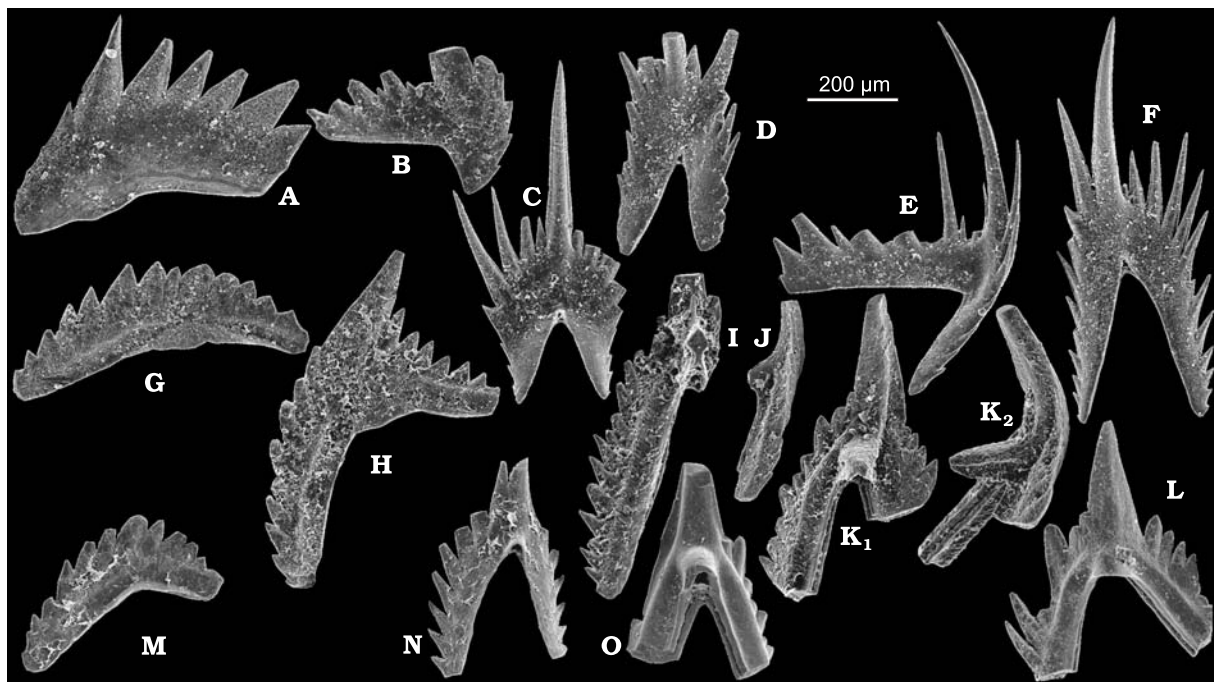


Fig. 32. Famennian ozarkodinids *Synclydognathus* from the Holy Cross Mountains. A–F. *Synclydognathus ancestralis* sp. n. from the *K. crepida* Zone at Wietrzna (sample Wtr-32). P₁ (A), P₂ (B), S₀ (C), S_{1–2} (D), S_{3–4} (E), and M (F) elements; specimens ZPAL cXVI/1819–1824 (holotype, F), respectively. G–K. *Synclydognathus triramosus* sp. n. from the *P. trachytera* Zone at Jabłonna (bed 24). P₁ (G), P₂ (H), S₀ (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). P₂ (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 Wietrzna, 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 Wietrzna 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; S₀ element with a short denticulated medial process.

Remarks. — From the morphologically closest Carboniferous type species (Rexroad and Varker 1992), differs in arched profile of P₁ and incipiently triramous S₀ and M elements.

Occurrence. — Only the type horizon and locality.

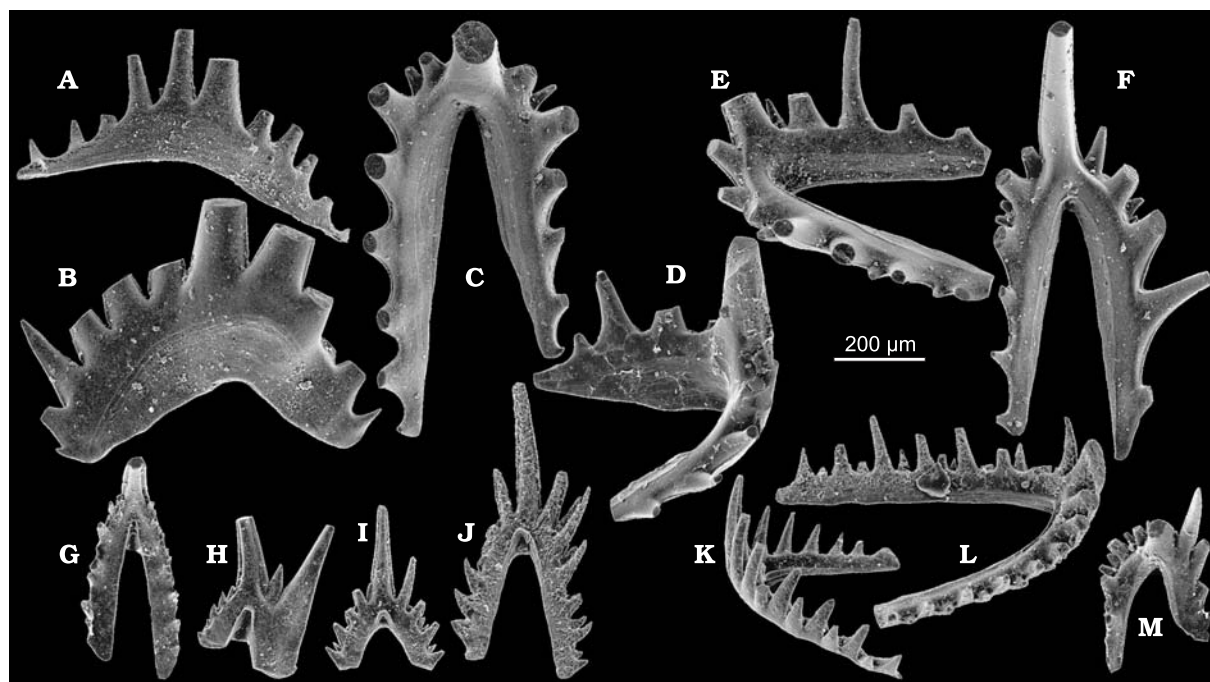


Fig. 33. Famennian ozarkodinids *Apatognathus* from the Holy Cross Mountains. **A–F, I–M.** *Apatognathus provarians* Nicoll, 1980 from the late *K. crepida* Zone at Łagów (A–F, sample ŁSI73-2; M, sample Ł-27) and the *K. triangularis* Zone at Jabłonna (I–L, sample J-45a). P (A, B), S_0 (I), S_{1-2} (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.

Syncladognathus sp.
(Fig. 32I–M)

Material. — Five specimens.

Remarks. — Rare specimens from sample Ost-12 may represent a new species of *Syncladognathus* representing another link between the early Famennian and Carboniferous 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 Canning 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, Wietrzna, 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 pedomorphic 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-pedomorphic. 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 Plucki 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 Wietrzna, Holy Cross Mountains.



Fig. 35. Pedomorphic 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 Wietrzna (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.

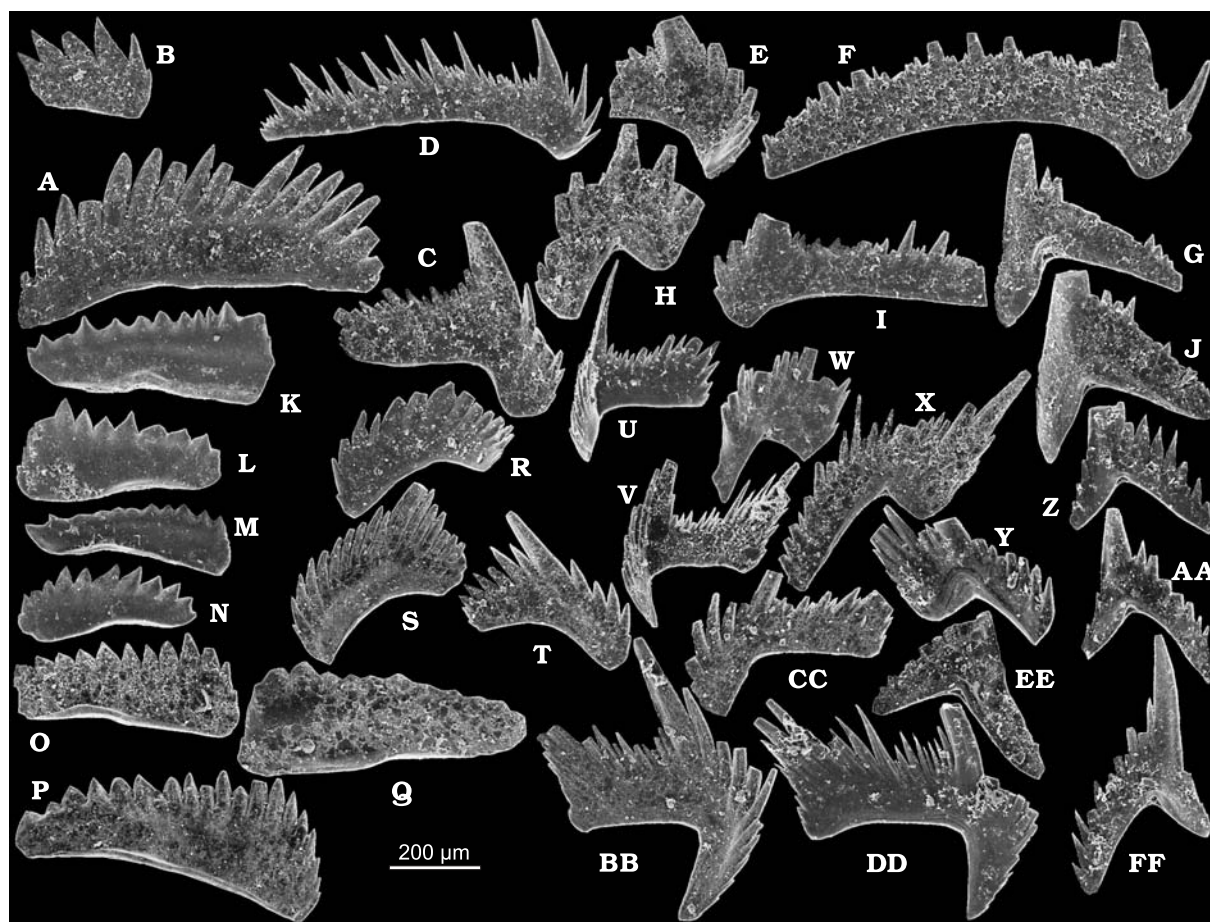


Fig. 36. Derived species of the francodinid *Vogelgnathus* from the early Famennian of the Holy Cross Mountains. **A–J.** *V. arcuatus* sp. n. from the *K. crepida* Zone at Wietrznia (A, H–J, sample Wtr-21; B–G, sample Wtr-32). P_1 (A, B), P_2 (C), S_0 (D, E), S_2 (H), S_{3-4} (F and I), and M (G and 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 pedomorphic 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 Łągów, 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.

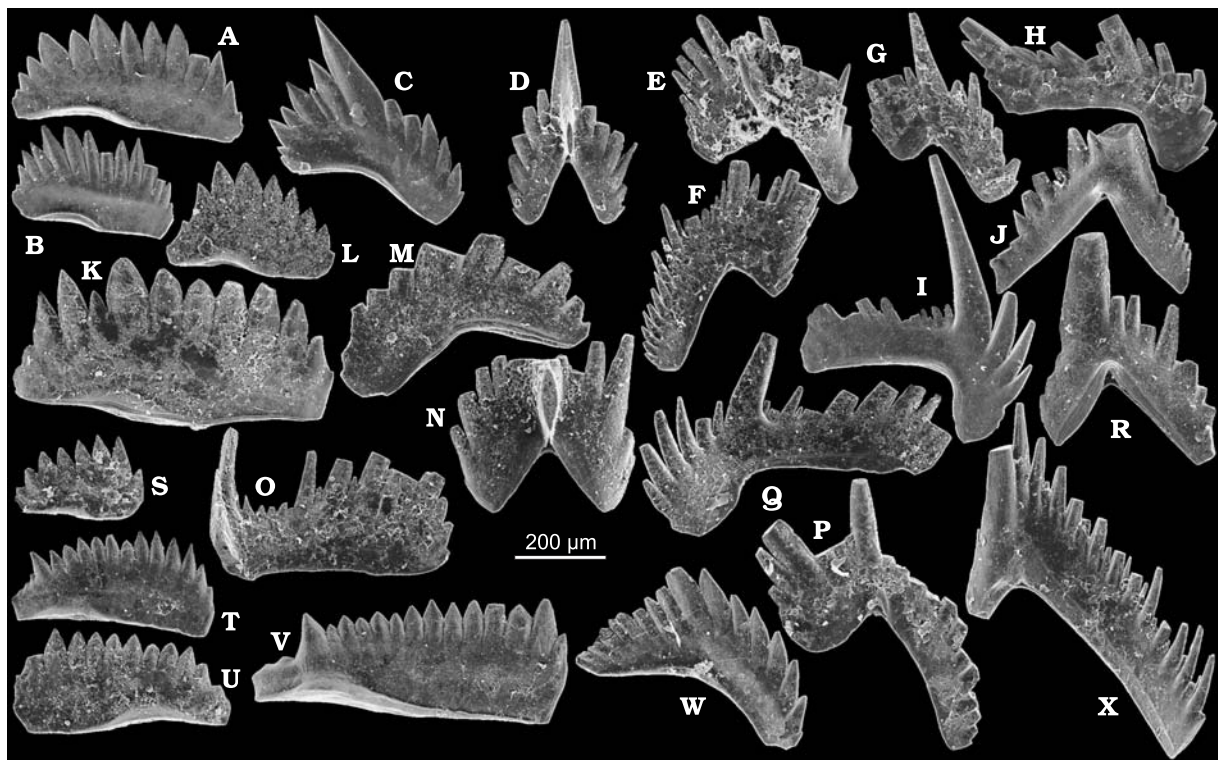


Fig. 37. Late species of the francodinid *Vogelgnathus* from the mid Famennian of the Holy Cross Mountains. **A–R.** *V. branmehloides* sp. n. from the *L. styriacus* Zone at Ostrówka (A–J, sample Ost-12) and the *P. jugosus* Zone at Jabłonna (K–R, bed 27). P_1 (A, B and K, L), P_2 (C and M), S_0 (D 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. wernerii* (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 P₁ elements to Carboniferous elements at that time classified in *Pinacognathus*, which later appeared to represent P₂ 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 P₁ 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 weneri (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 P₁ 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 weneri* Ziegler, 1962 to *Vogelgnathus campbelli*. Apparatus composition of the species is poorly known and non-P₁ 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-

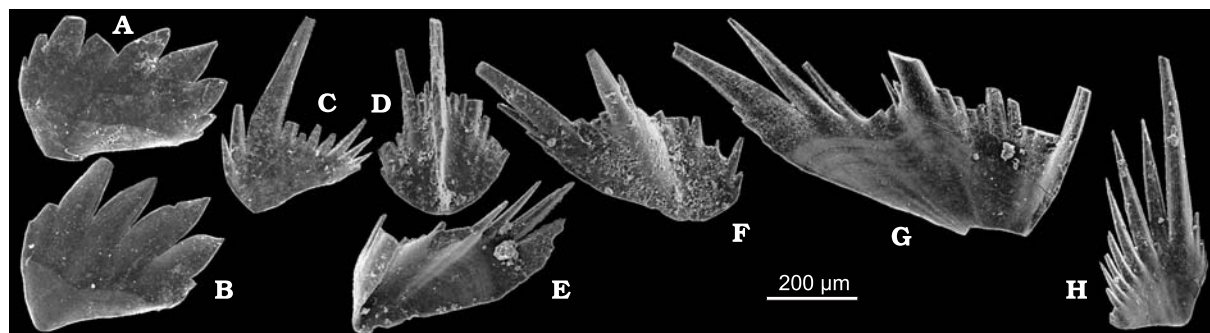


Fig. 38. Extremely paedomorphic francodinid *Urbanekodina undata* sp. n. from the *P. trachytera* Zone at Miedzianka (sample Md-8/9) in the Holy Cross Mountains. P₁ (A, B), P₂ (C), S₀ (D), S₁ (E), S₂ (F), S_{3–4} (G), and M (H) elements; specimens ZPAL cXVI/2025, 2026 (holotype, B), and 2027–2032, respectively.

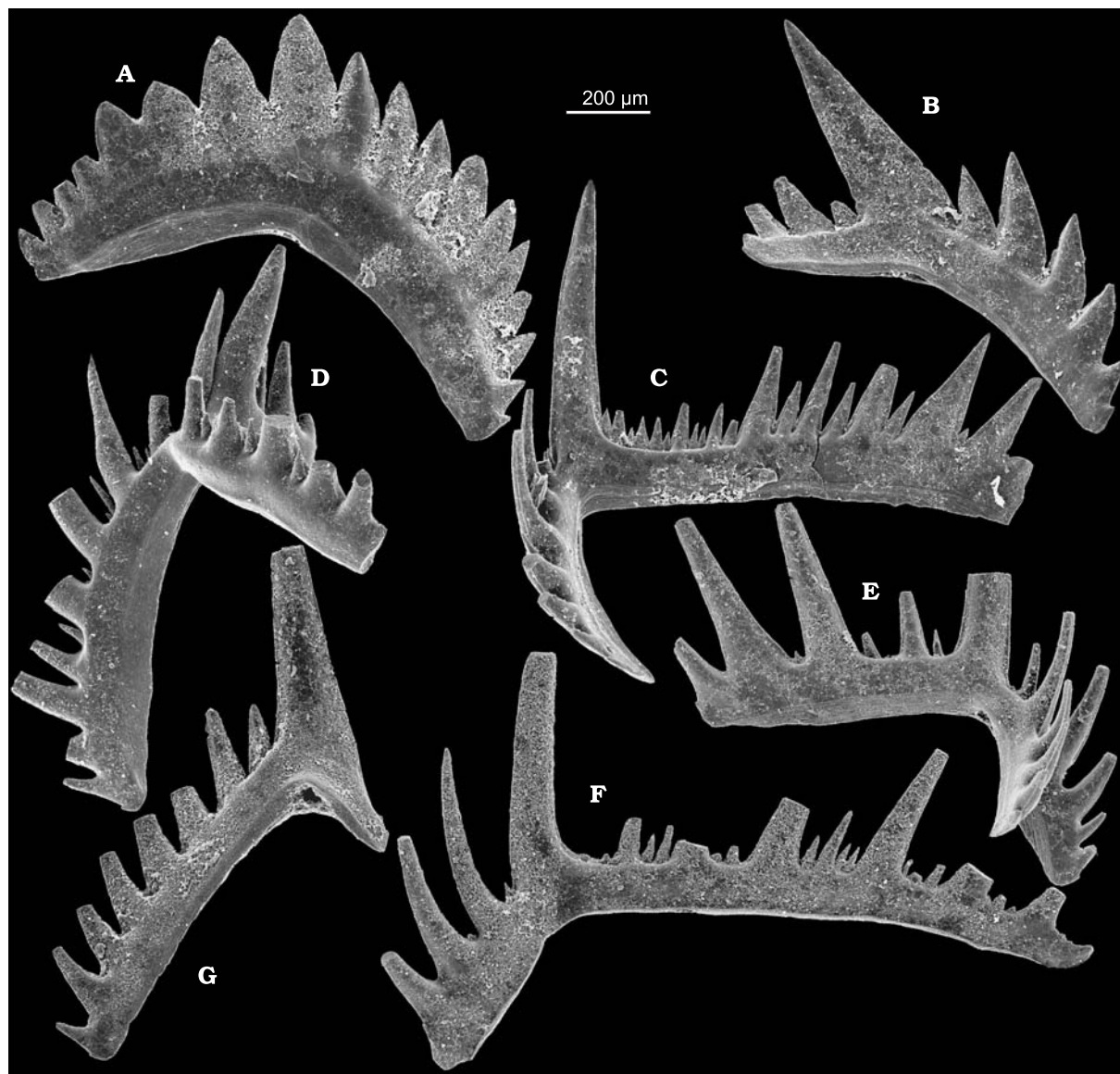


Fig. 39. Large-size francodinid *Francodina santacrucensis* sp. n. from the *K. crepida* Zone at Jablonna (bed 8) in the Holy Cross Mountains. P_1 (A), P_2 (B), S_0 (C), S_1 (D), S_2 (E), S_{3-4} (F), and M (G) elements; specimens ZPAL cXVI/1756–1761 (holotype, E).

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 pedomorphic 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 Sannemann (1955a).

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). P₁ (A), P₂ (B), S₁ (C), S_{3–4} (D), and M (E) elements; specimens ZPAL cXVI/1770–1774. F–L. *F. franconica* (Sannemann, 1955) (bed 8). P₁ (F), P₂ (G), S₀ (H), S₁ (I), S₂ (J), S_{3–4} (K), and M (L) elements; specimens ZPAL cXVI/1763–1769.

F. santacrucensis sp. n. occur at Wietrzna 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 S₁ elements and arched contour of P₁ 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, Wietrzna, 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: P₁ elements are twisted whereas P₂ are laterally bent. S₁ 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 Wietrzna; the *K. crepida* Zone at Jabłonna, Wietrzna 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.

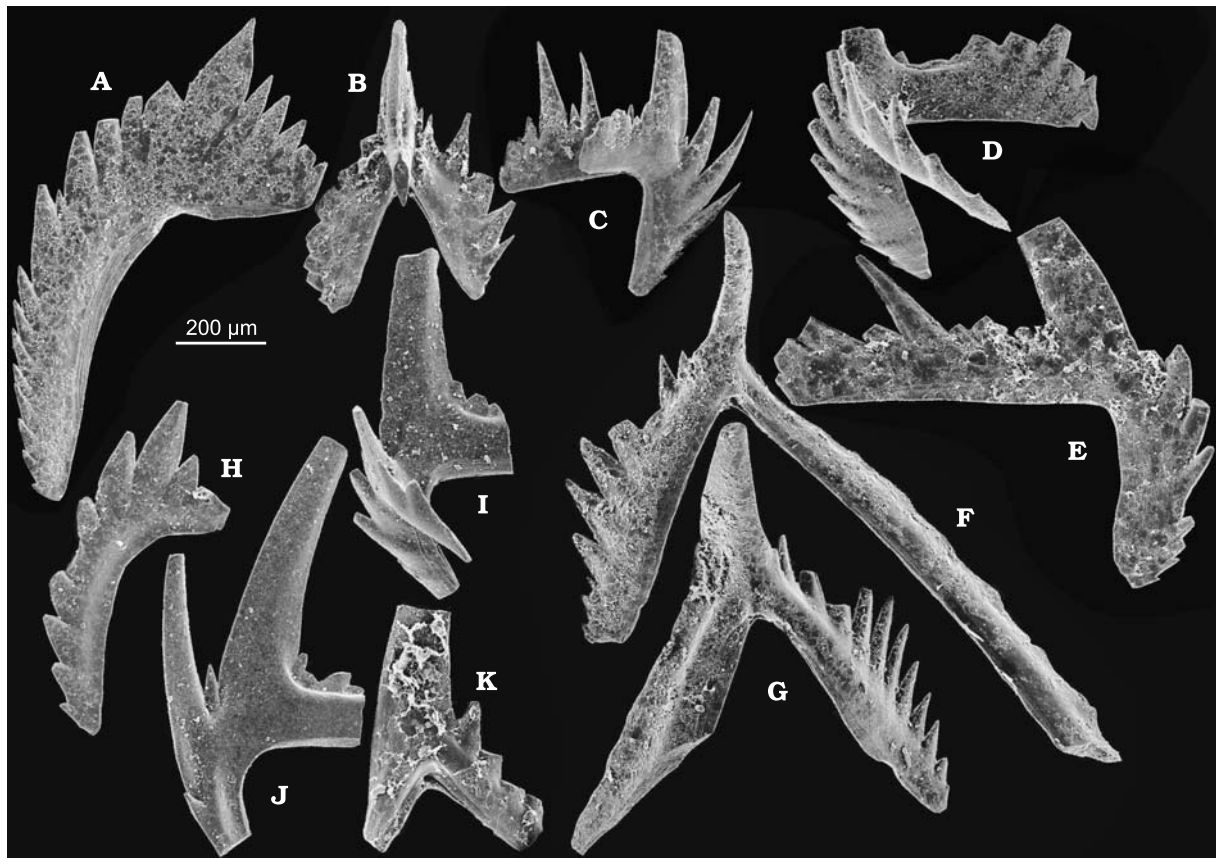


Fig. 41. Advanced francodinid *Sweetodina* from the late *K. crepida* Zone at Łagów in the Holy Cross Mountains. **A–G.** *S. lago-viensis* sp. n. (sample Ł-28). P₁₋₂ (A), S₀ (B), S₁ (C), S₂ (D), S₃₋₄ (E), and M (F, G) elements; specimens ZPAL cXVI/1787–1792 (holotype, F). **H–K.** Early population of *S. monodentata* (Bischoff and Ziegler, 1956) (sample ŁSI73-2). P₁₋₂ (H), S₂ (I), S₃₋₄ (J), and M (K) elements; specimens ZPAL cXVI/1793–1796.

Remarks. — Distinctions between element types of *Sweetodina* are obliterated by the unusually 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 Ściegna (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.

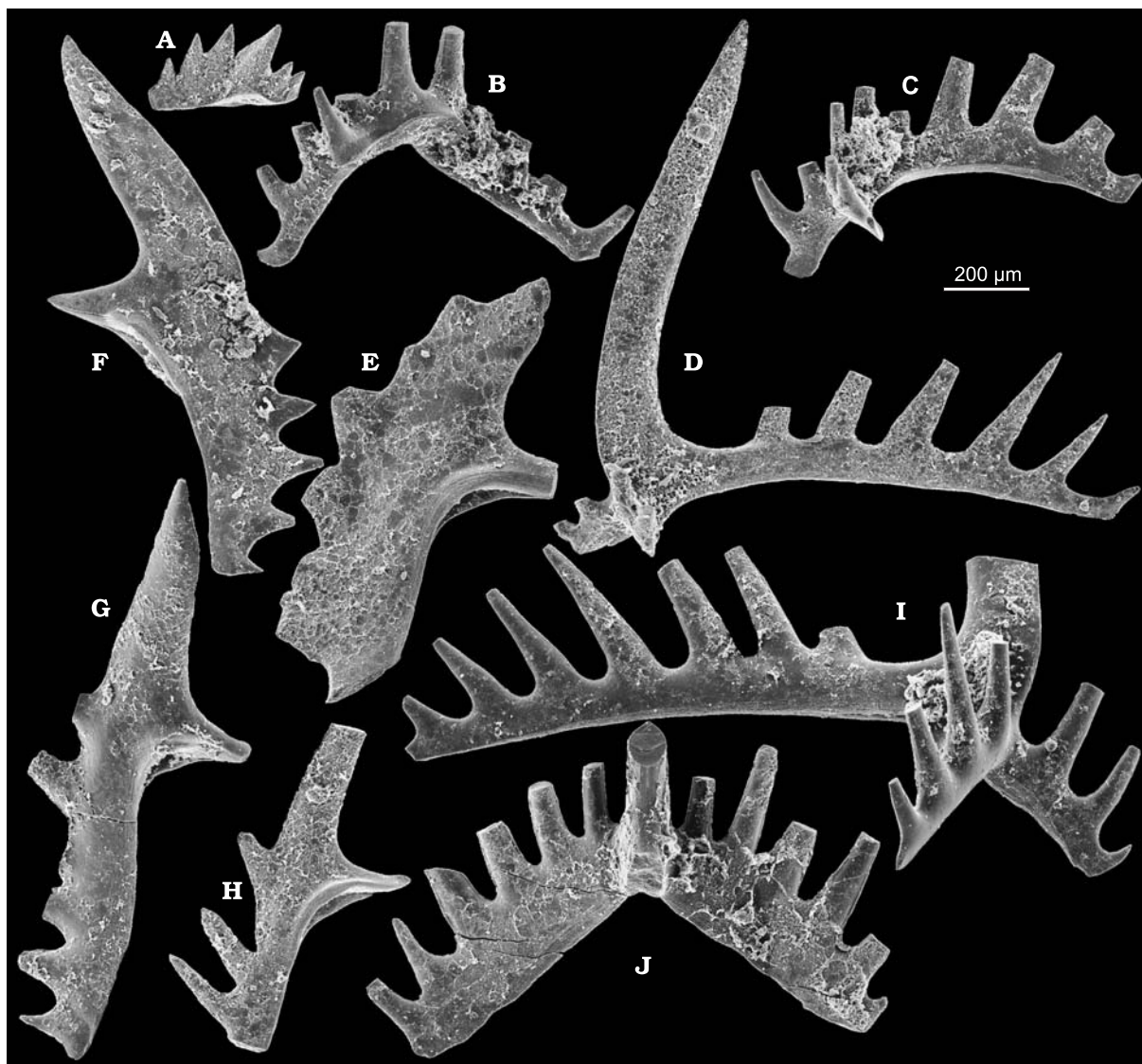


Fig. 43. The advanced francodinid *Planadina plana* (Helms, 1959) from the early *P. jugosus* Zone at Jabłonna (A, D, and F, bed 27), the *C. quadrantinodosa* Zone at Łagów (B, C, sample ŁS173-5), and the *L. styriacus* Zone at Ostrówka (E, H, and J, sample Ost-5; G and I, sample Ost-12) in the Holy Cross Mountains. P₁ (A?), S₀ (J?), S₁ (B?), S₂ (C, I), S₃₋₄ (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 sharply pointed, inner one with a few denticles; outer process of S₃₋₄ 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 S₃ 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.