Genus **Planadina** gen. n.

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

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

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

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

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

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

Material. — 396 specimens.

Diagnosis. — As for the genus.

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

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

Family **Polygnathidae** Bassler, 1925

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

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

Genus **Pandorinellina** Müller *et* Müller, 1957

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

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

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

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

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

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

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

Material. — 350 specimens.

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

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

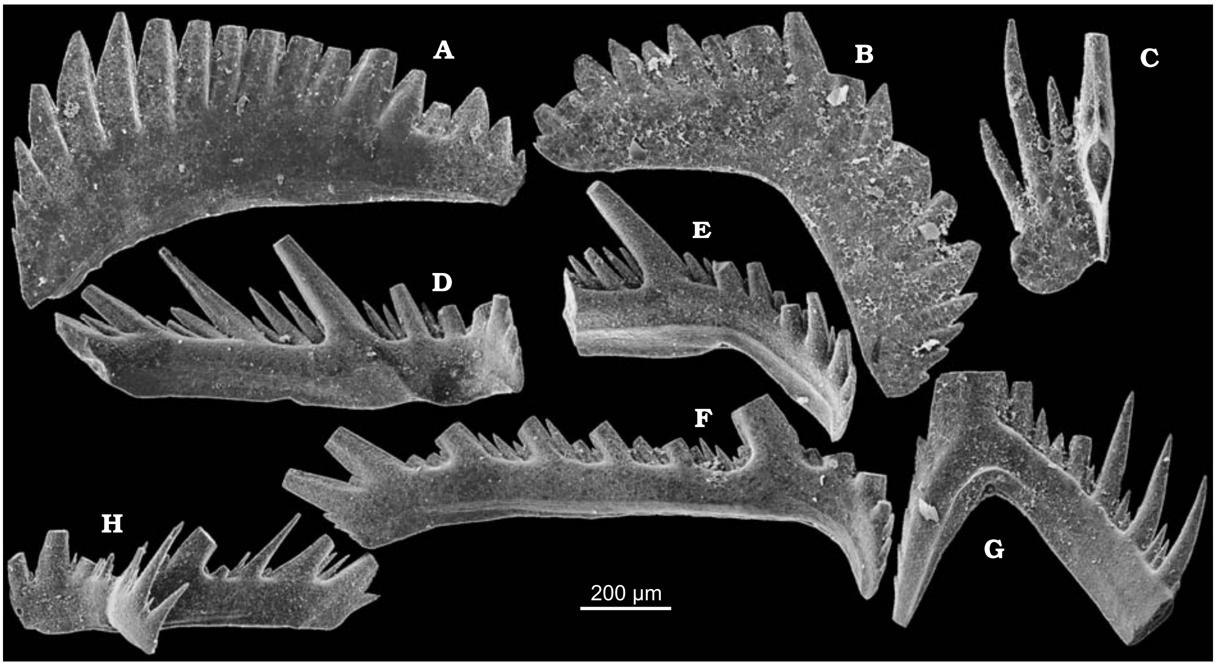


Fig. 44. Enigmathic non-platform polygnathid with possible francodinid affinities *Pandorinellina*? *vogelgnathoides* sp. n. from the *K. crepida* Zone at Kadzielnia (A–G, sample Ka-5; H, sample Ka-3) in the Holy Cross Mountains. P_1 (A), P_2 (B), S_0 (C), S_1 (D and H), S_2 (E), S_{3-4} (F), and M (G)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

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

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

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

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

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

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

Material. — 3,244 specimens.

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

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

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

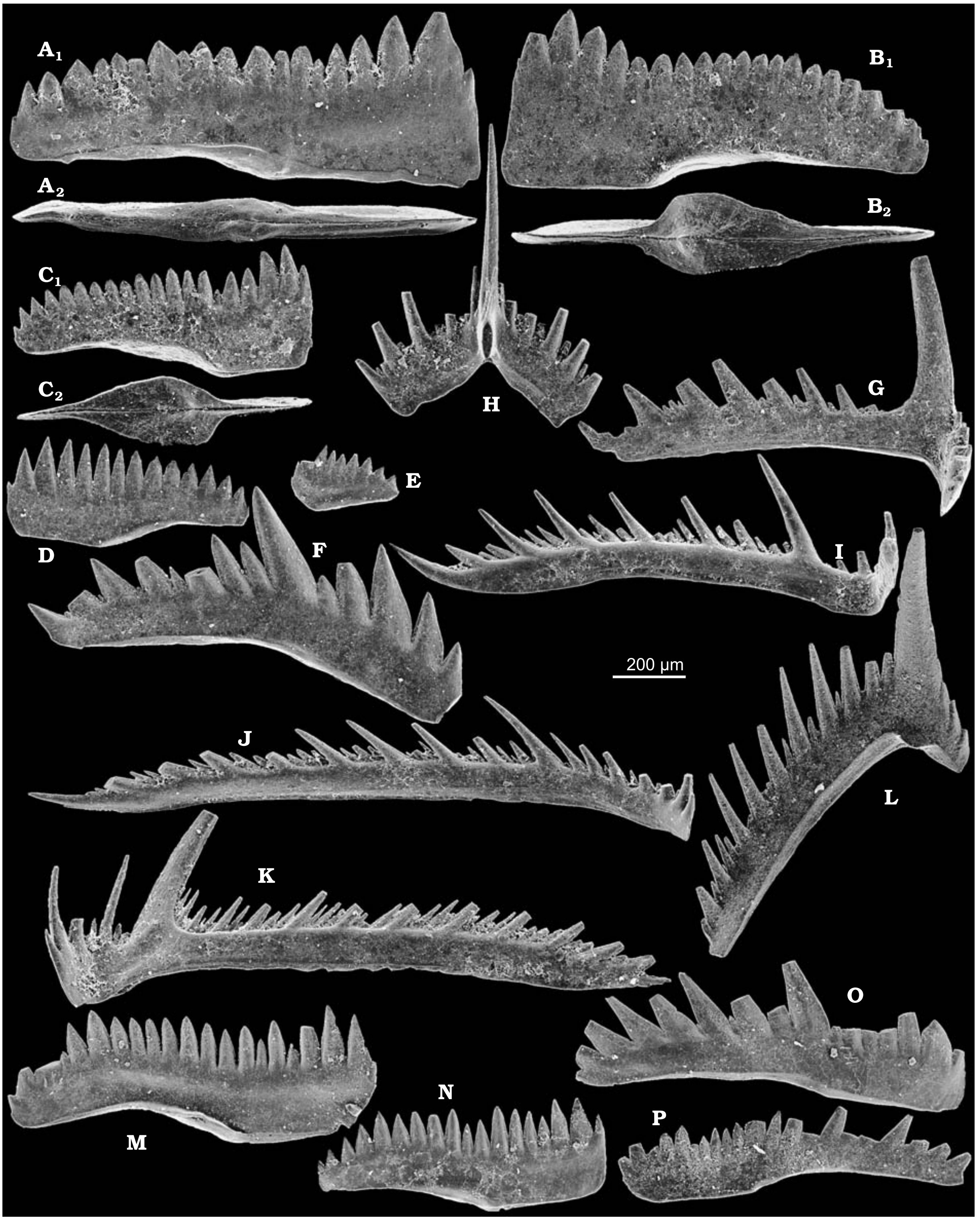


Fig. 45. Underived non-platform polygnathids *Pandorinellina* from the late Famennian of the Holy Cross Mountains. **A**–**L**. *P. vulgaris* sp. n. from the *P. trachytera* Zone at Jabłonna (bed 24). P_1 (A–E), P_2 (F), S_0 (G, H), S_1 (I), S_2 (J), S_{3-4} (K), and M (L) elements; specimens ZPAL cXVI/2180–2191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

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

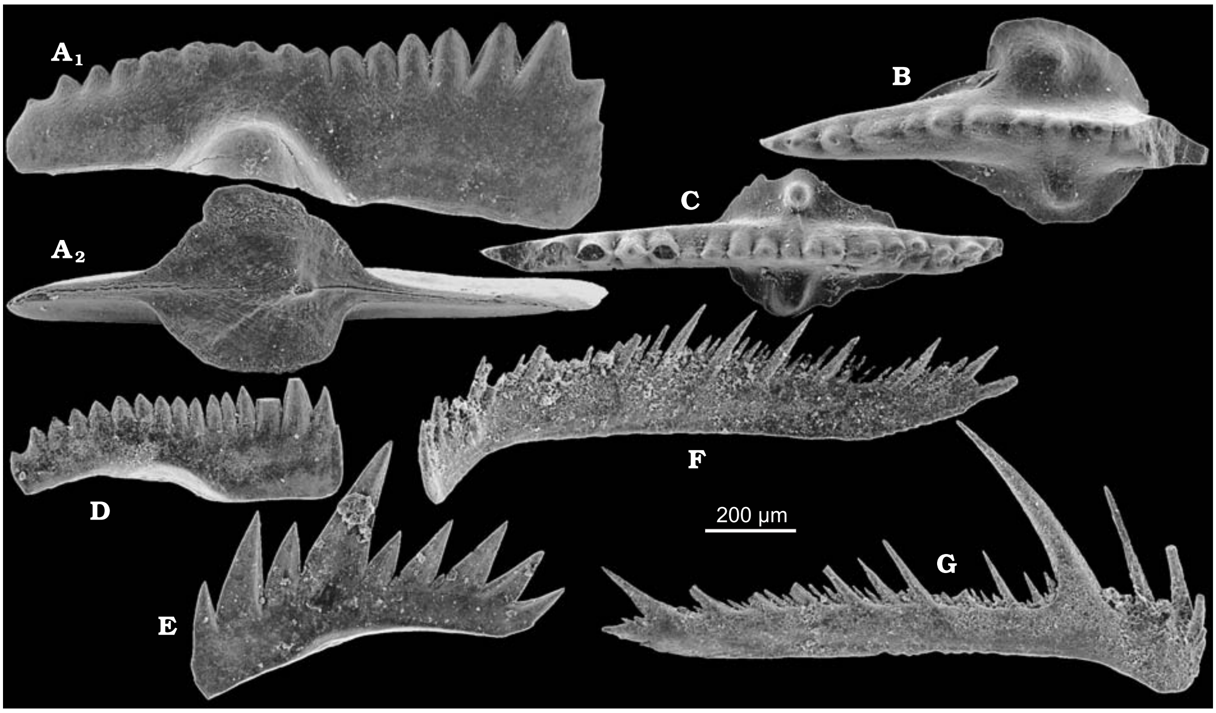


Fig. 46. Non-platform polygnathid *Pandorinellina bituberculata* sp. n. from the *P. jugosus* Zone at Jabłonna (sample J-51) in the Holy Cross Mountains. P_1 (A–D), P_2 (E), S_2 (F), and S_{3-4} (G) elements; specimens ZPAL cXVI/2199–2205 (holotype, A), respectively.

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

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

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

Derivation of name: Referring to fragility of specimens.

Material. — 219 specimens.

Diagnosis. — Extremely flat P_2 elements with irregular denticulation.

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

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

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

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

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

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

Material. — 49 specimens.

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

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

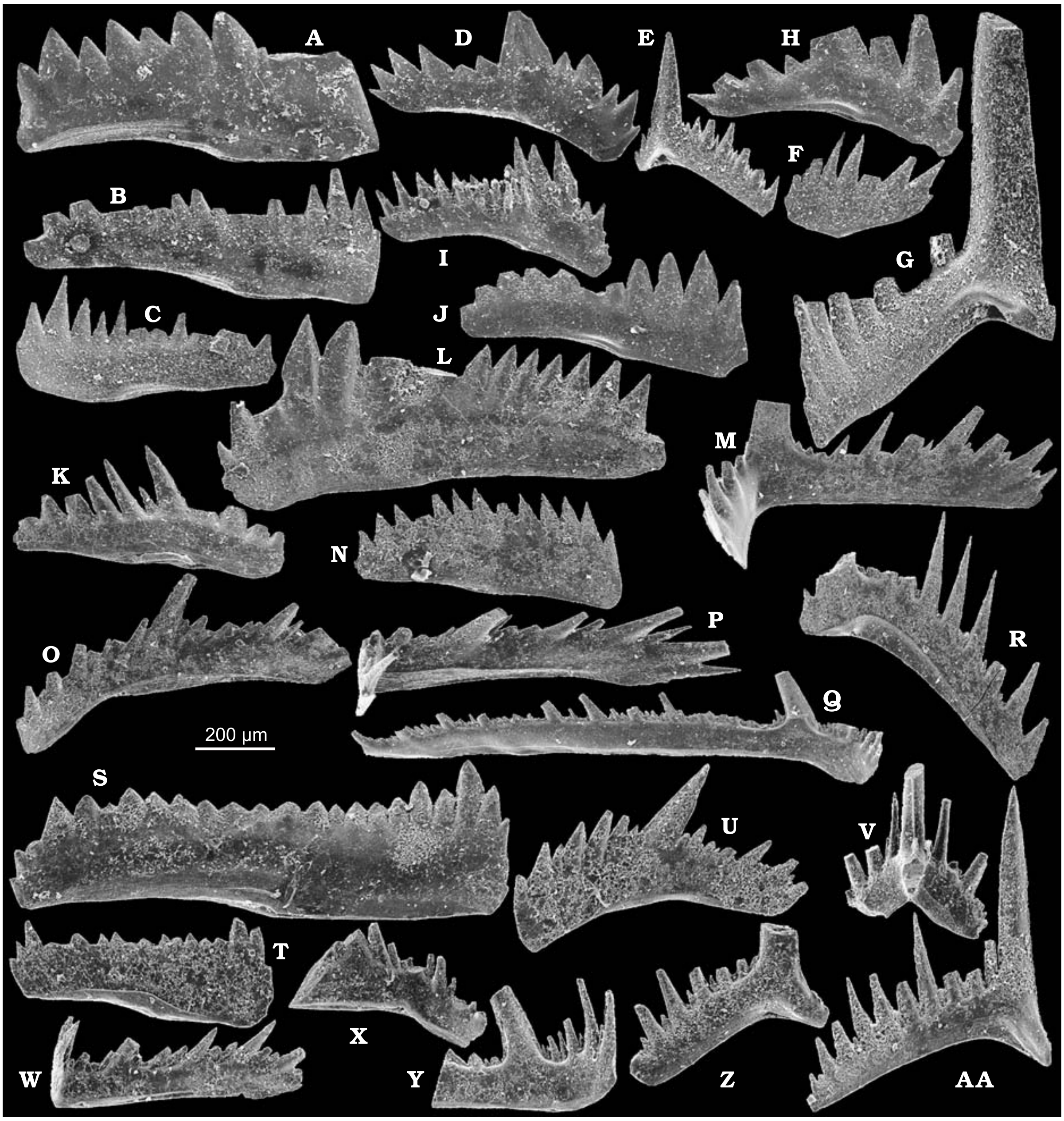


Fig. 47. Non-platform polygnathids *Mehlina*. **A**–**R**. *M. kielcensis* sp. n. from the *K. triangularis* Zone at Płucki (A–G, sample Pł-1) and Jabłonna (H, I, and J, sample J-53a), and the *K. crepida* Zone at Jabłonna (K–R, bed 3) in the Holy Cross Mountains. P_1 A–C, F, J–L, and N), P_2 (D, H,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

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

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

Genus ***Mehlina*** Youngquist, 1945

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

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

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

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

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

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

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

Material. — 527 specimens.

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

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

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

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

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

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

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

Material. — 426 specimens.

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

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

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

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

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

Material. — 2,050 specimens.

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

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

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

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

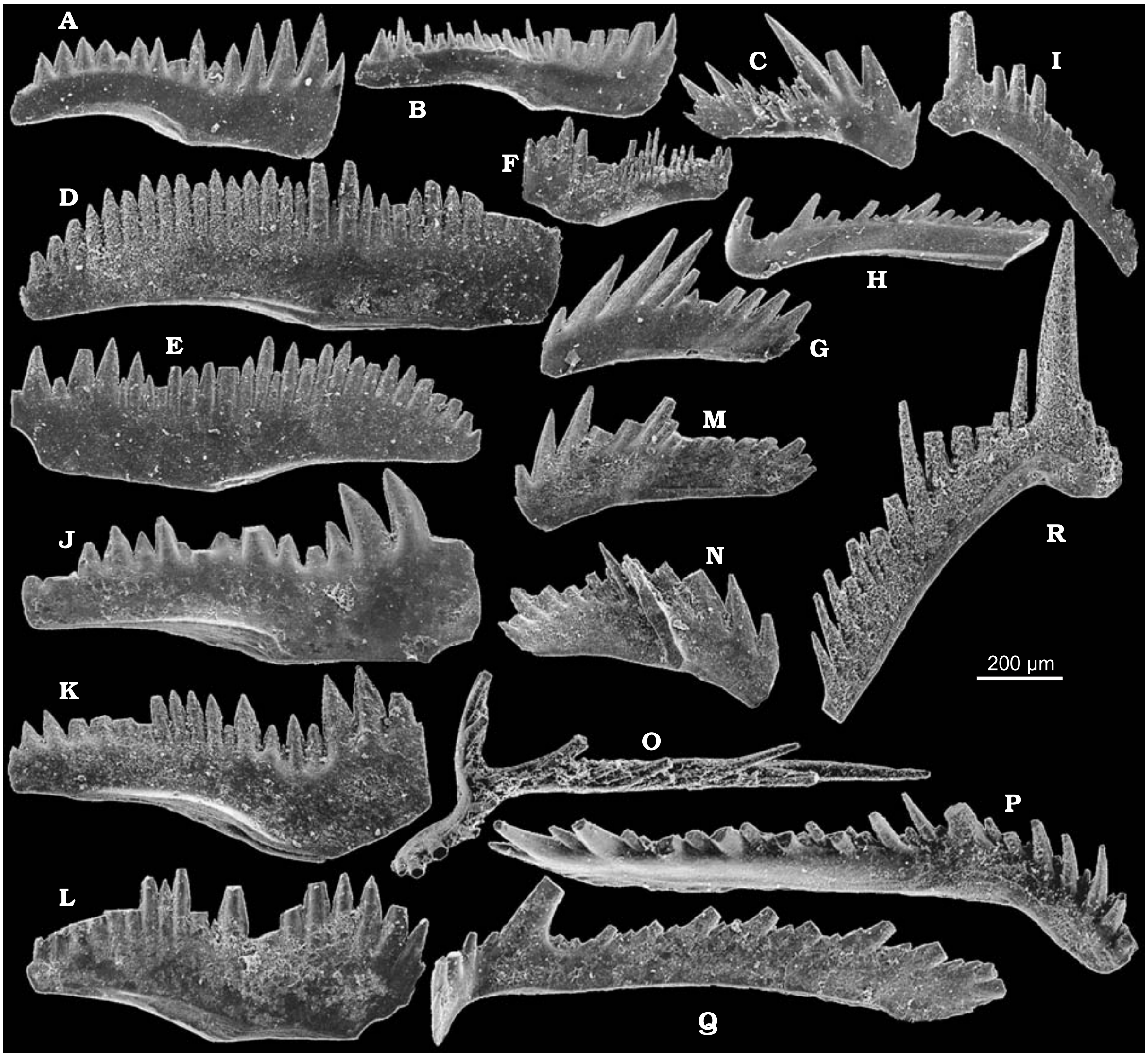


Fig. 48. Non-platform polygnathids *Mehlina strigosa* (Branson *et* Mehl, 1934) from the *P. trachytera* Zone at Kowala (A–C, sample Ko-15) and the *P. jugosus* Zone at Ostrówka (D–I, sample Ost-185) and Jabłonna (J–R, bed 27) in the Holy Cross Mountains. P_1 (A, B, DF, and J–L), P_2 (C, G, M, N), S_0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

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

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

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

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

Material. — Two specimens.

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

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

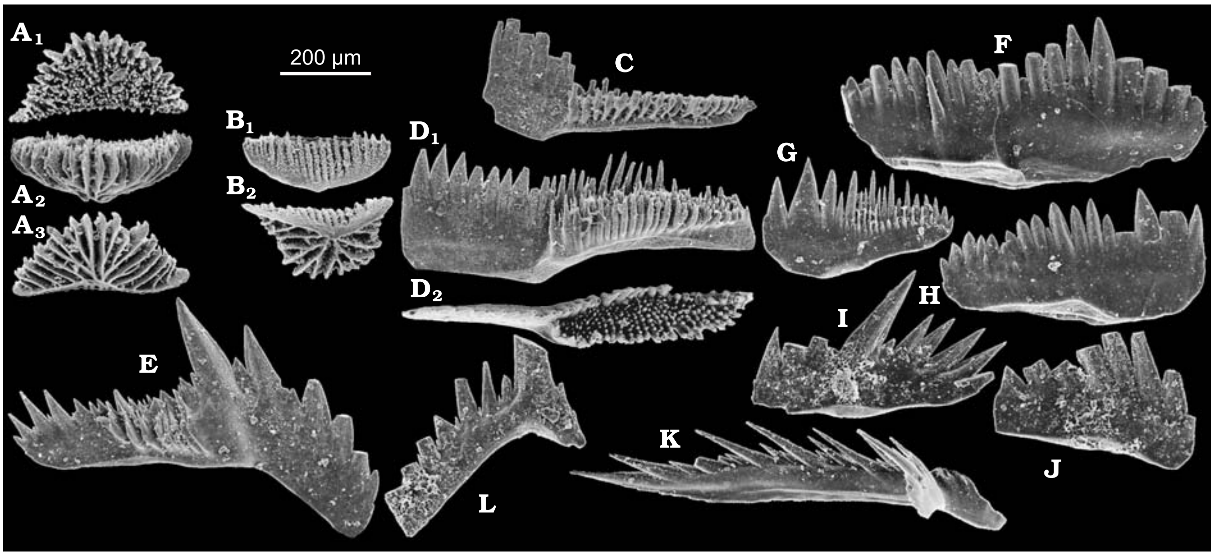


Fig. 49. Species of *Mehlina* bearing peniculus at adult stages and pathological polygnathid elements. **A**, **B**. *Mehlina lunaria* sp. n. from the *K. crepida* Zone at Kadzielnia (sample Ka-2). P_1 elements; specimens ZPAL cXVI/2125, 2126 (holotype, A). **C**–**E**. Extreme icrion-bearing elements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

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

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

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

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

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

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

Material. — 285 specimens.

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

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

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

Genus ***Polynodosus*** Vorontzova, 1993

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

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

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

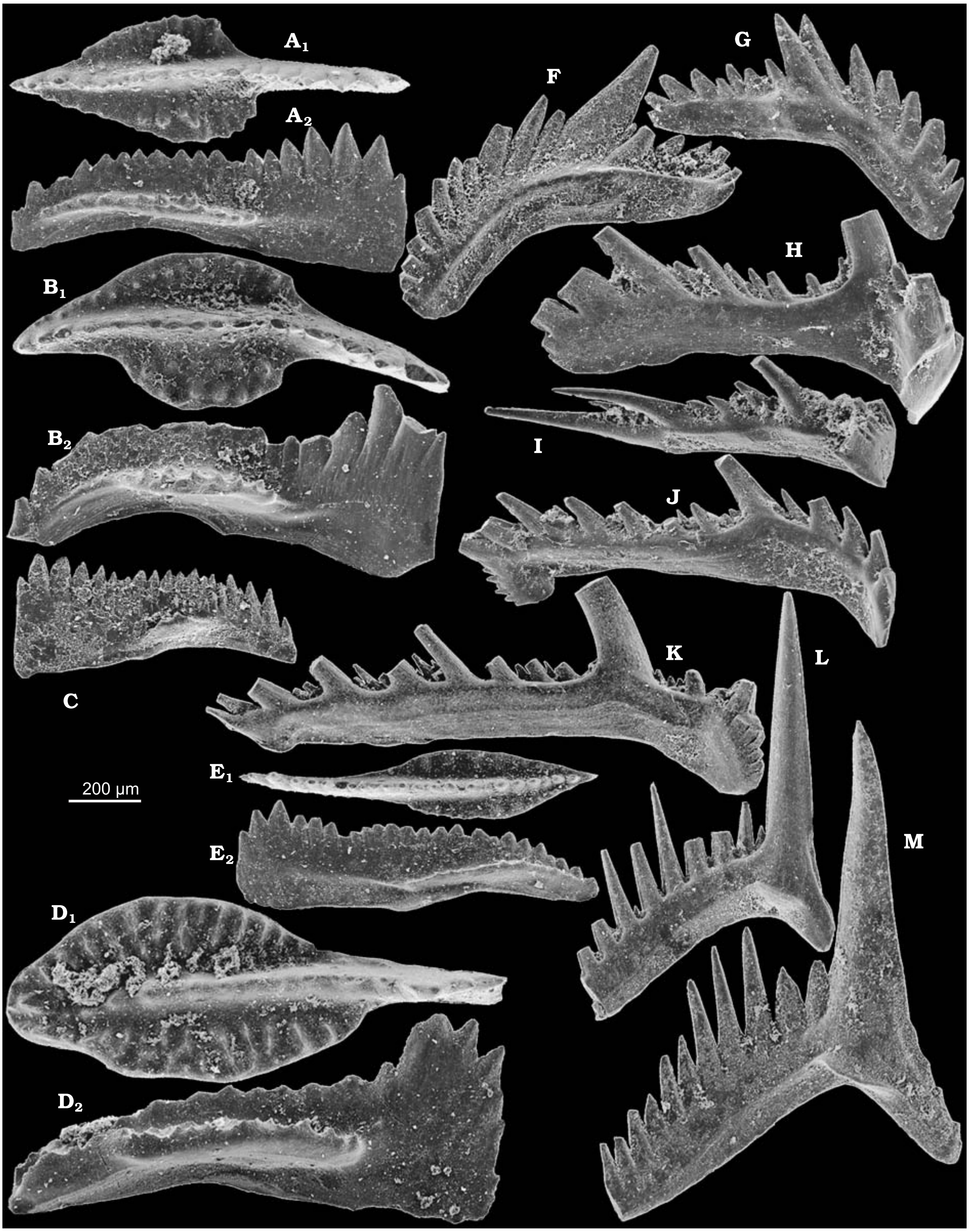


Fig. 50. Platform-bearing derivative of *Mehlina*, a population of robust *Polynodosus transitus* sp. n., including possible *P. lauriformis* (Dreesen *et* Dusar, 1974) (D, E), from the *C. quadrantinodosa* Zone at Łagów (sample Ł-26) in the Holy Cross Mountains. P_1 (A–E), P_2 (F, G), S_0 (H), S_1 (I),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

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

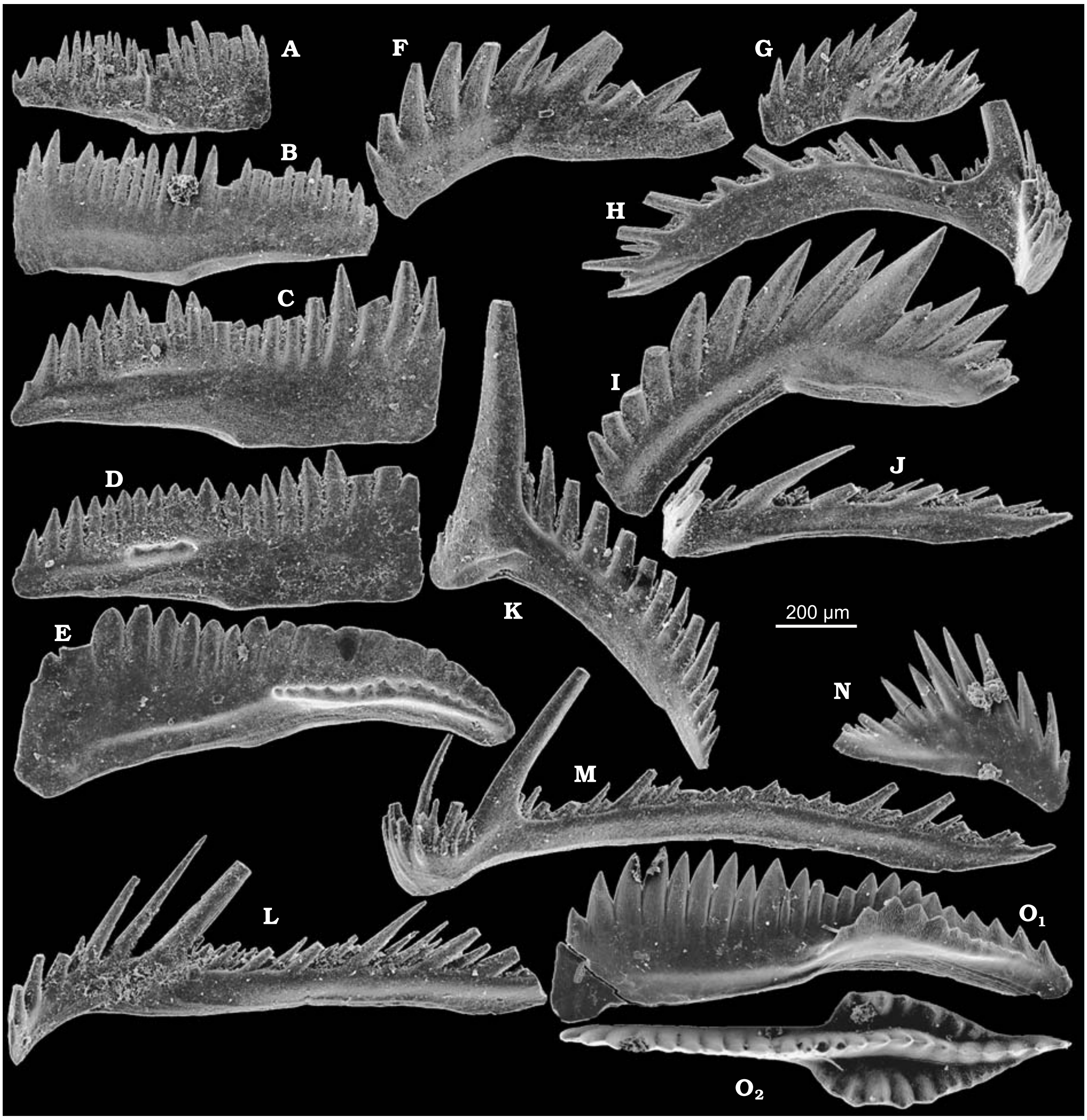


Fig. 51. Platform-bearing derivative of *Mehlina*, *Polynodosus* from the Famennian of the Holy Cross Mountains. **A**–**M**. Late population of gracile *Polynodosus transitus* sp. n. from the *P. trachytera* Zone at Jabłonna (bed 24). P_1 (A–E), P_2 (F, G, and I), S_0 (H), S_1 (J), S_2 (L), $S_{3–4}$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

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

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

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

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

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

Material. — 5,272 specimens.

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

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

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

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

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

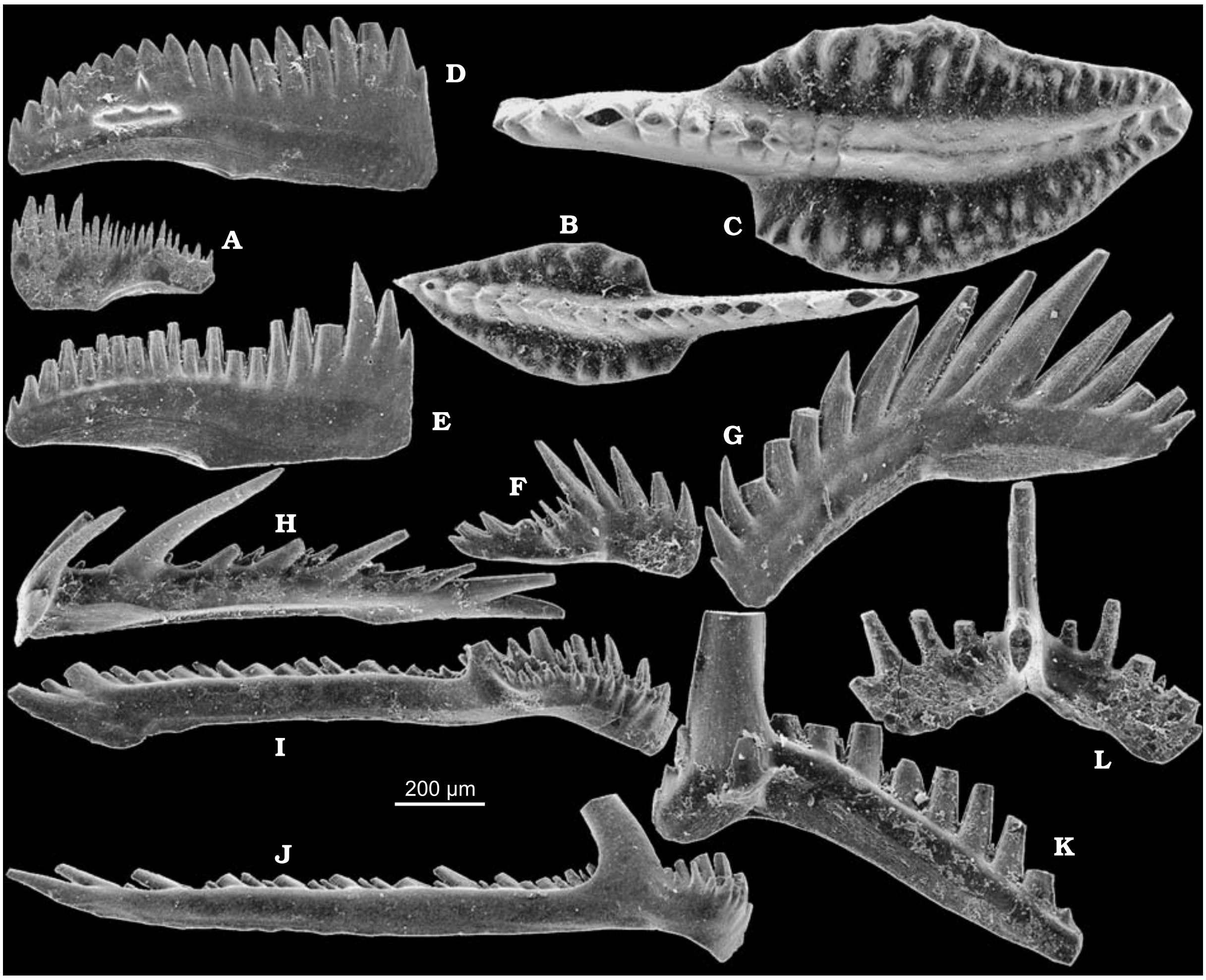


Fig. 52. Platform-bearing derivative of *Mehlina*, *Polynodosus lauriformis* (Dreesen *et* Dusar, 1974) from the *L. styriacus* Zone at Ostrówka (A–E and J, K, sample Ost 12; F–I and L, sample Ost 11) in the Holy Cross Mountains. P_1 (A–E), P_2 (F, G), S_0 (L), S_1 (H), S_2 (I), S_{3-4} (J), and M (K)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

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

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

Material. — 367 specimens.

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

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

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

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

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

Material. — 1,011 specimens.

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

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

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

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

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

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

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

Material. — 1,106 specimens.

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

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

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

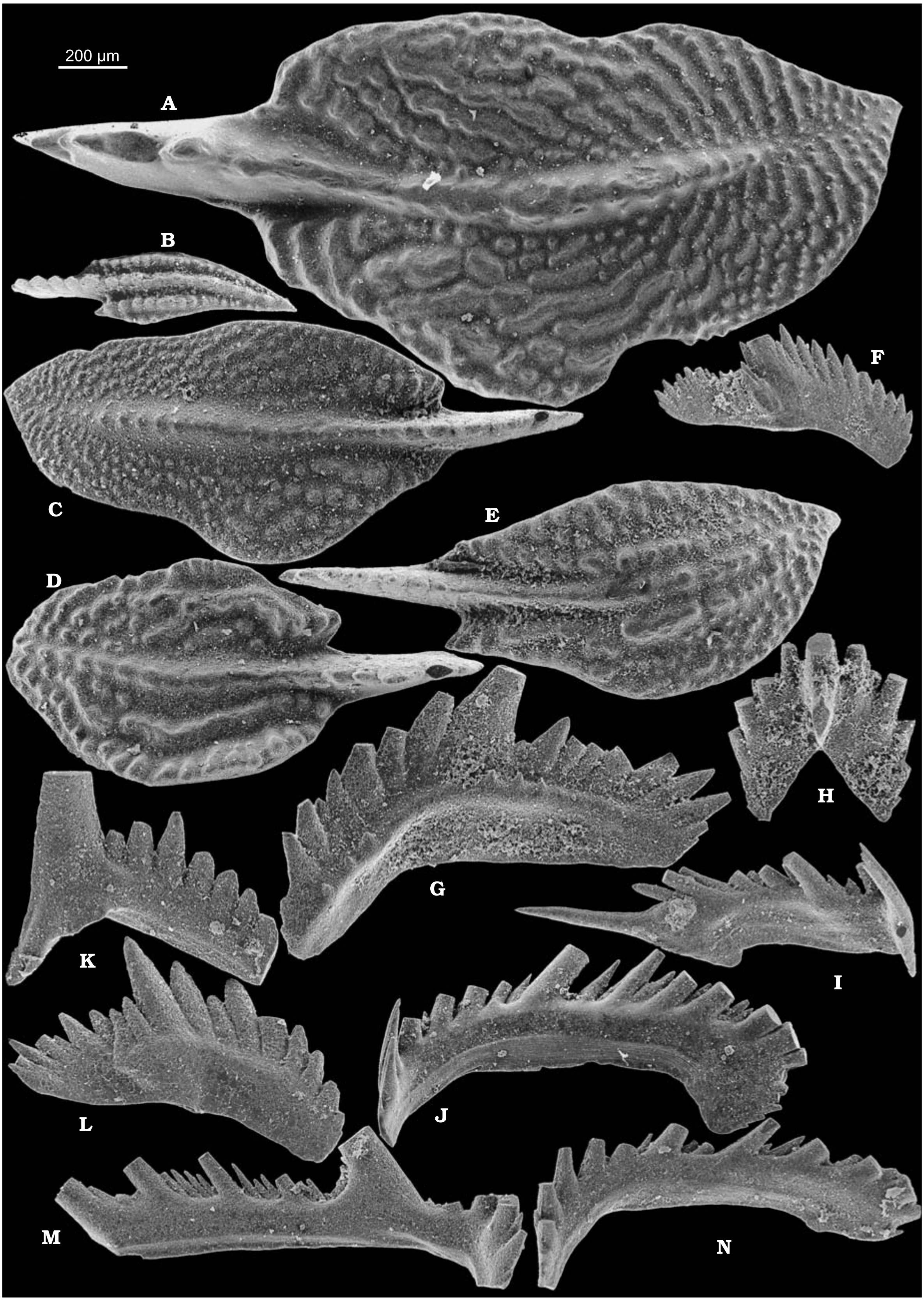


Fig. 53. Elaborate platform-bearing *Polynodosus confluens* (Ulrich *et* Bassler, 1926) from the *K. crepida* Zone at Kadzielnia (A and J, sample Ka-7; B and D, sample Ka-6; C, E–I, K, L, and N, sample Ka-4; M, sample Ka-10) in the Holy Cross Mountains. P_1 (A–E), P_2 (F, G, and L), S_0 (H), S_1 (I),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

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

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

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

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

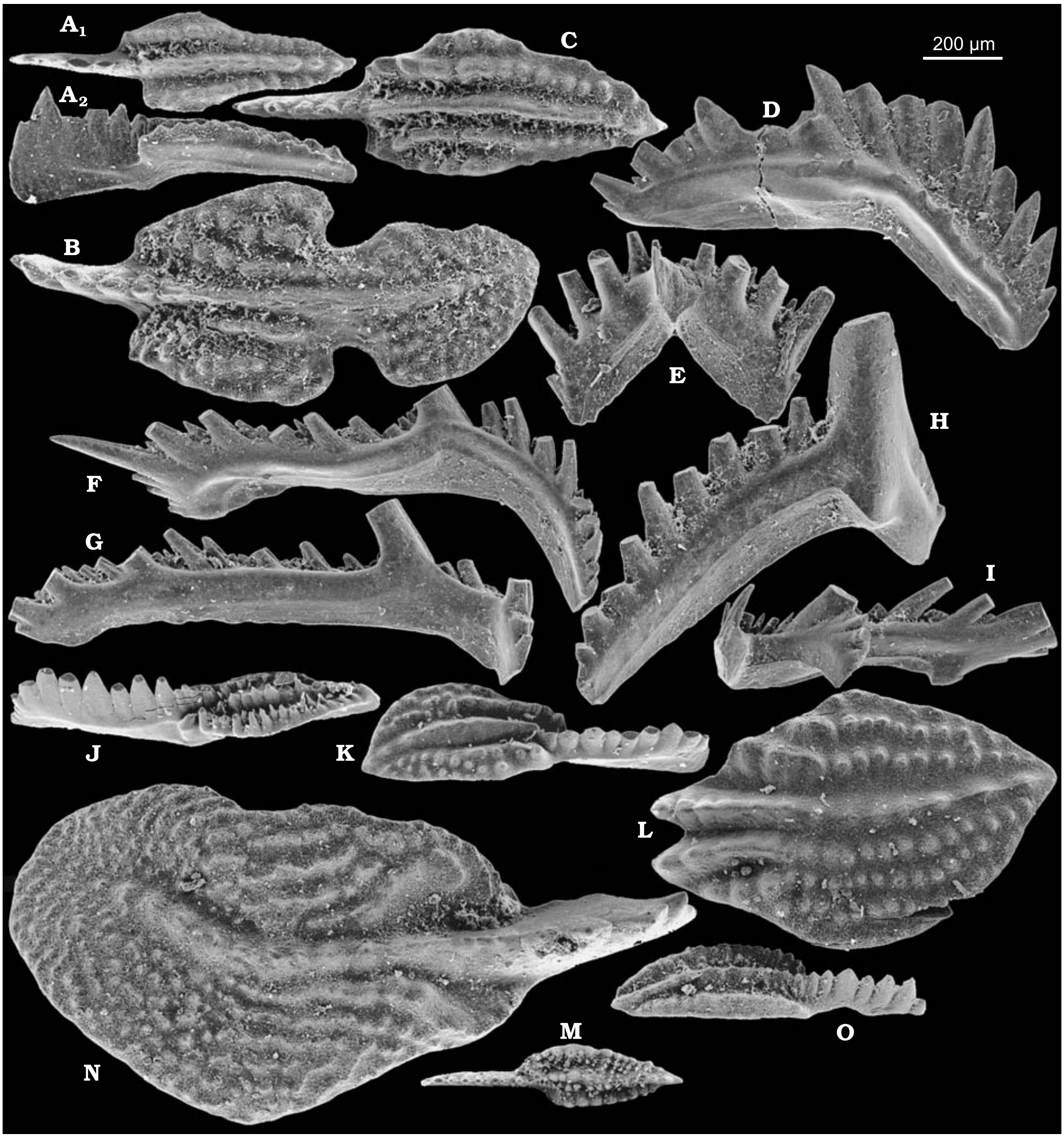


Fig. 54. Advanced species of *Polynodosus*. **A**–**I**. *P. triphyllatus* (Ziegler, 1960) from the *C. quadrantinodosa* Zone at Łagów (A, B, sample Ł-26; C–I, sample Ł-27) in the Holy Cross Mountains. P_1 (A–C), P_2 (D), S_0 (E), S_1 (aberrant with additional process, I), S_2 (F), S_{3-4} (G), and M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

Material. — 276 specimens.

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

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

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

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

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

Material. — 58 specimens.

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

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

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

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

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

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

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

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

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

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

Material. — 933 specimens.

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

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

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

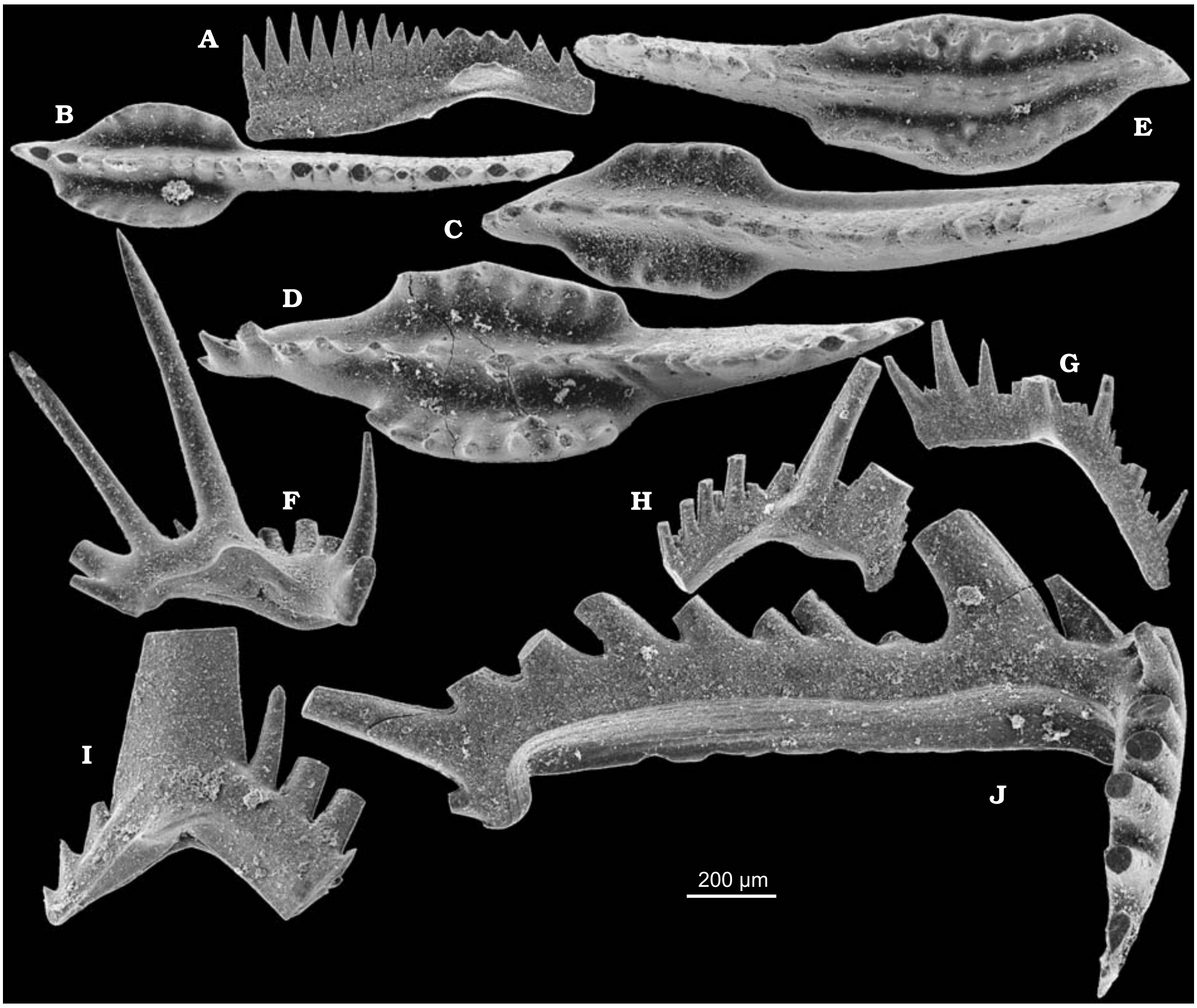


Fig. 55. *Ctenopolygnathus brevilamina* (Branson *et* Mehl, 1934), a polygnathid with probably secondarily reduced platform and paedomorphic appearance of elements, from the *K. triangularis* Zone at Płucki (sample Pł-1) in the Holy Cross Mountains. P_1 (A–E), S_1 (F), S_2 (G, H), S_{3-4} (J), and M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

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

Genus *Immognathus* gen. n.

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

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

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

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

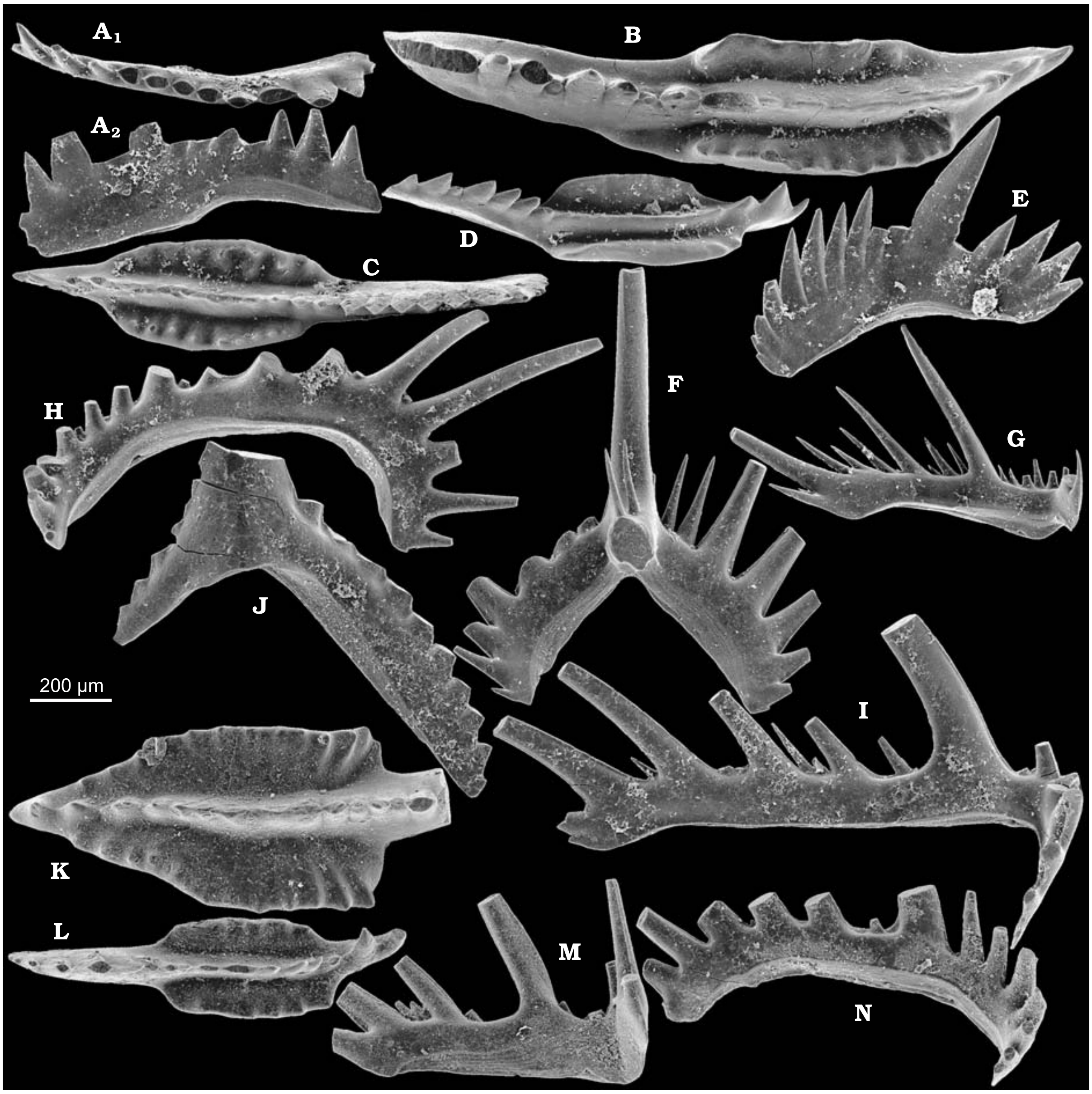


Fig. 56. Simplified polygnathid *Ctenopolygnathus brevilamina* (Branson *et* Mehl, 1934) from the *K. triangularis* Zone at Kowala (A, B, F–J, sample Ko-154; C–E, sample Ko-143) and Jabłonna (K–M, sample J-53a) and the *K. crepida* Zone at Kadzielnia (N, sample Ka-3) in the Holy Cross Mountains. P_1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

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

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

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

Material. — 738 specimens.

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

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

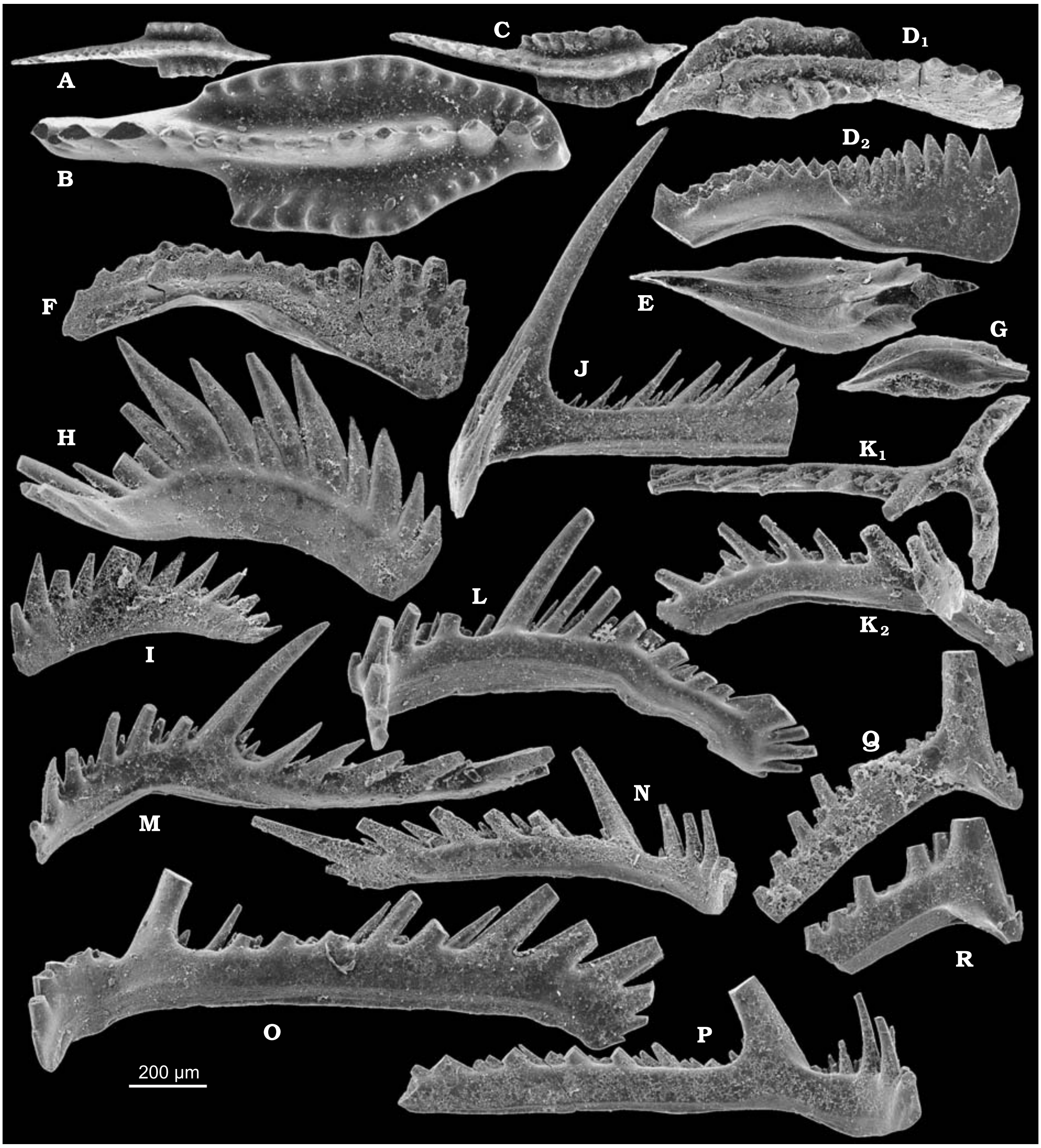


Fig. 57. Polygnathid with *Siphonodella*-like basal cavity, *Immognathus streeli* (Dreesen, Dusar *et* Groessens, 1976) from the *K. crepida* Zone at Wietrznia (A–E, H, J, L, M, Q and O, sample Wtr-21) and Jabłonna (G, I, K, N, P, and R, sample J-45a) in the Holy Cross Mountains. P_1 (A–G), P_2 (H, I),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

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

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

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

Material. — 47 specimens.

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

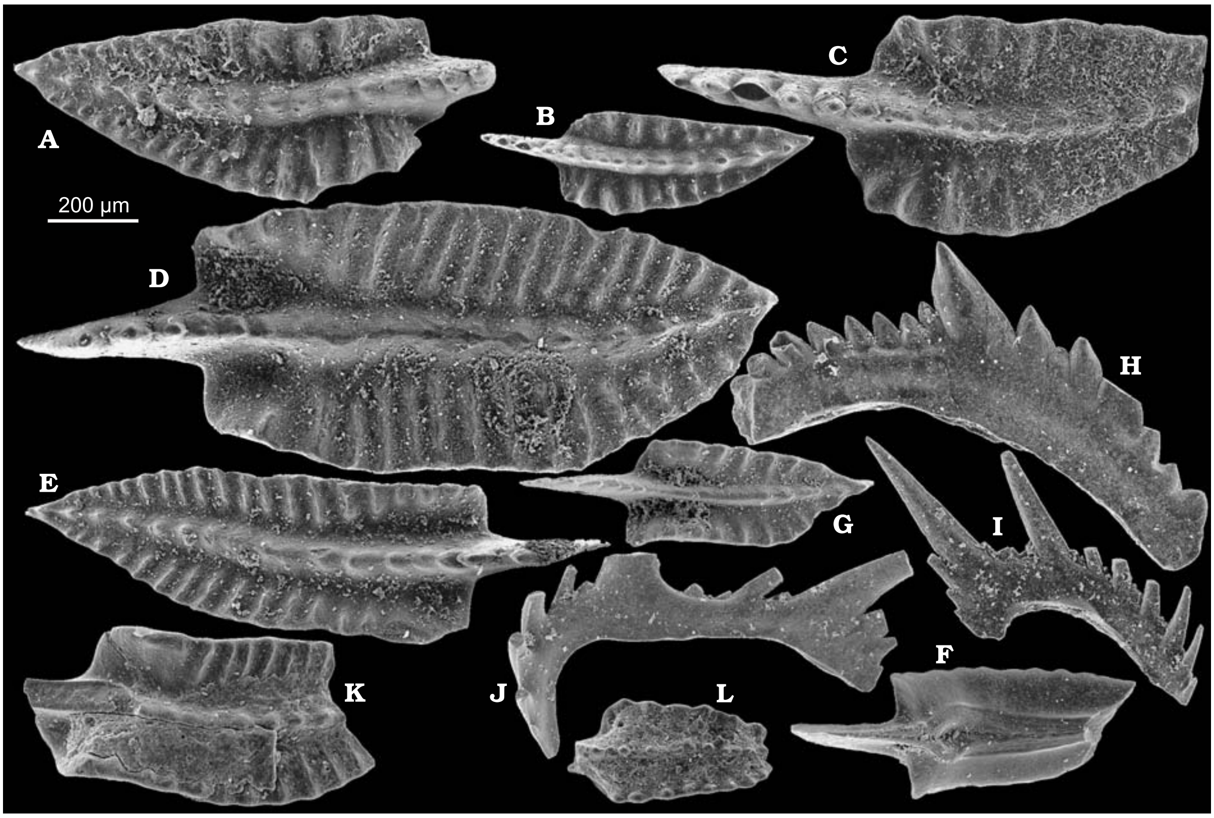


Fig. 58. Late Famennian *Siphonodella*-like polygnathids. **A**, **C**. *Polygnathus pennatulus* Ulrich *et* Bassler, 1926 from the *L. styriacus* Zone at Ostrówka (sample Ost-12) in the Holy Cross Mountains, possibly end members of population variability of *Hemilistrona perplexa*. P_1 elements; specimens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

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

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

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

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

Genus ***Polygnathus*** Hinde, 1879

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

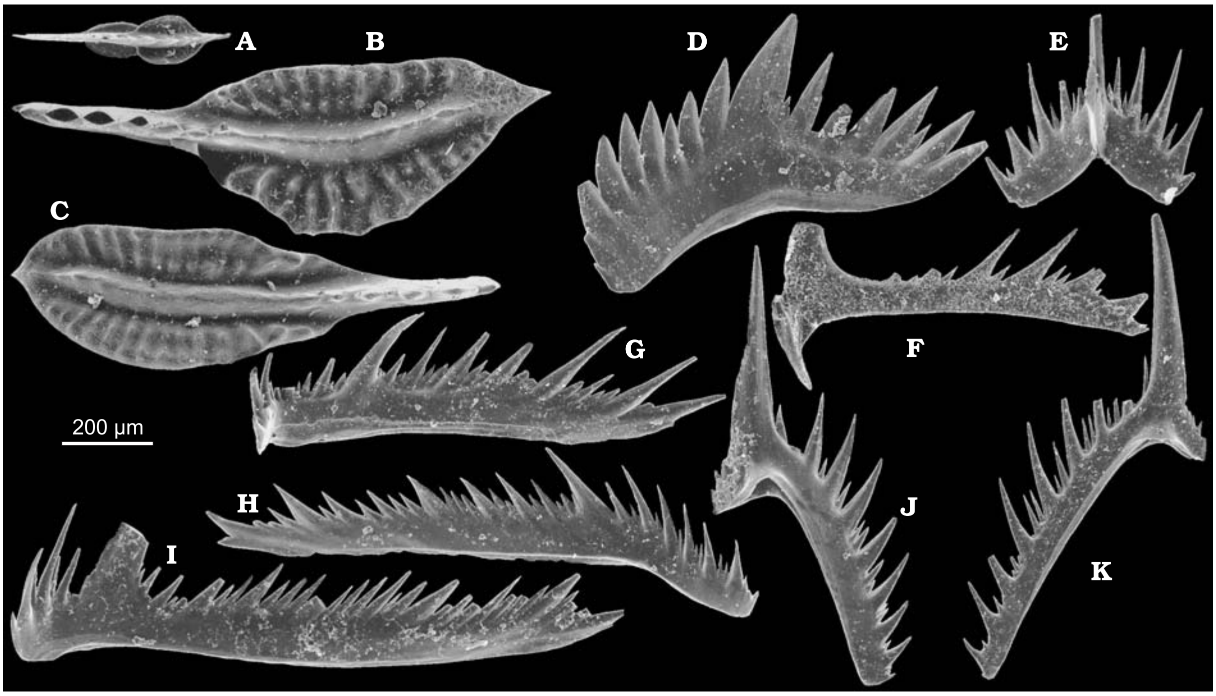


Fig. 59. Direct successor of the Frasnian lineage of asymmetric platform-bearing polygnathids, *Polygnathus praecursor* Matyja, 1993 from the earliest pre-*K. triangularis* Zone of the Famennian at Płucki (sample Pł-36) in the Holy Cross Mountains. P_1 (A–C, juvenile and probable adults; note that sinistral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

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

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

Material. — 5,369 specimens.

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

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

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

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

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

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

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

Material. — 1,896 specimens.

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

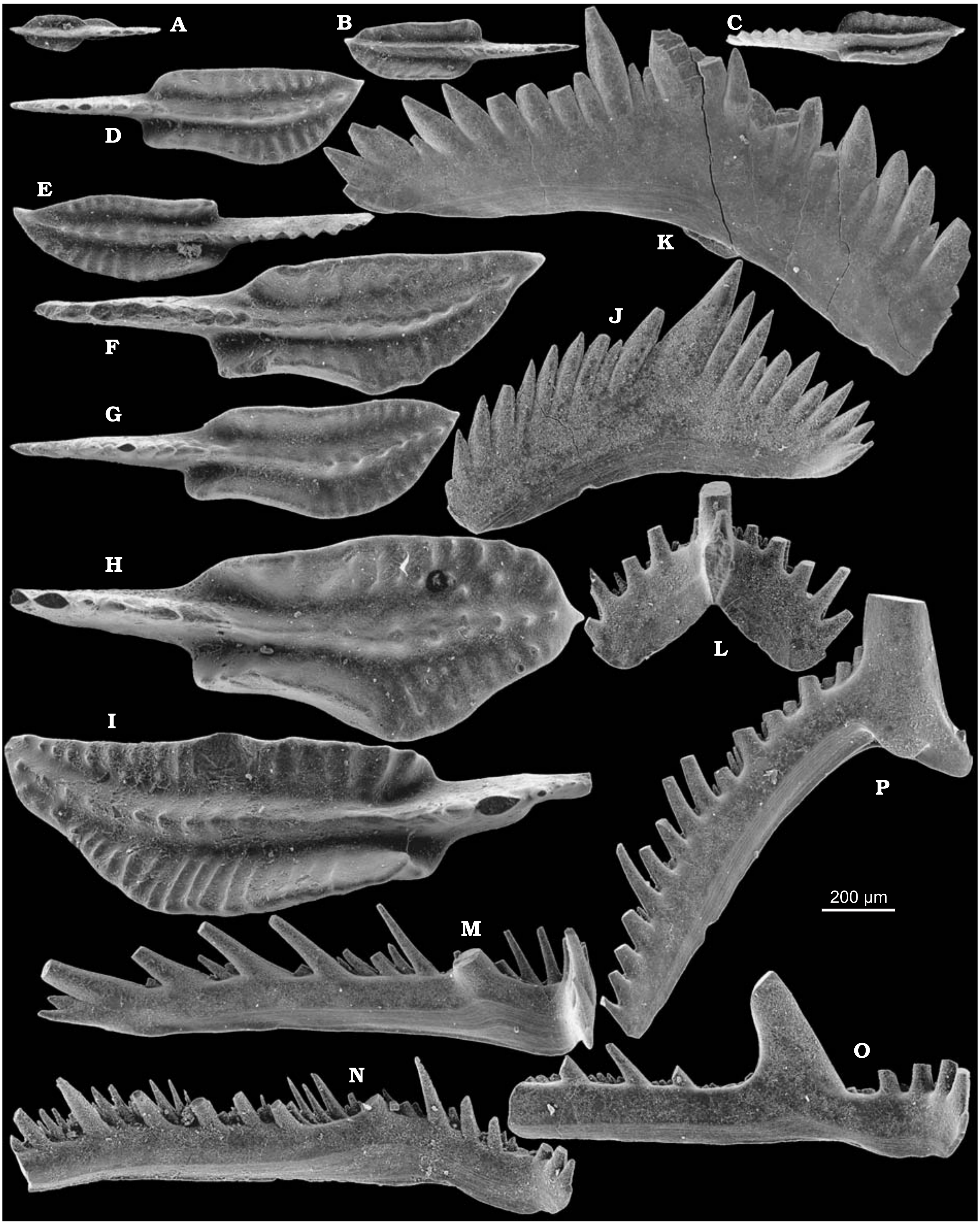


Fig. 60. Typical platform-bearing polygnathid *Polygnathus praecursor* Matyja, 1993 from the *K. triangularis* Zone at Jabłonna (A–H, sample J-53a; I, K–P, sample J-58; J, sample J-59) in the Holy Cross Mountains. P_1 (A–I, ontogenetic series of element pairs), P_2 (J, K), S_0 (L), S_1 (M), S_2 (N),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

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

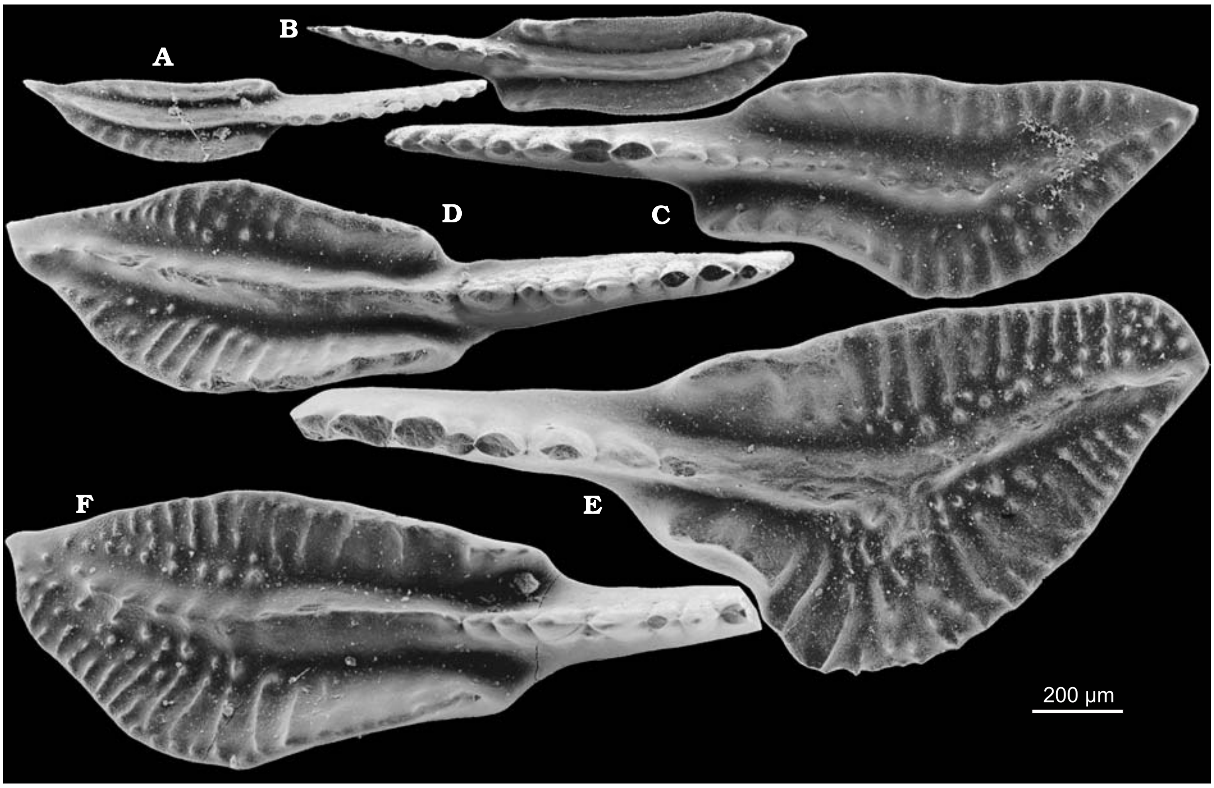


Fig. 61. Late population of *Polygnathus praecursor* Matyja, 1993 from the late *K. triangularis* Zone at Kadzielnia (sample Ka-16) in the Holy Cross Mountains. P_1 elements; specimens ZPAL cXVI/2487, 2486, 2488, 2490, 2489, and 2491, respectively.

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

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

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

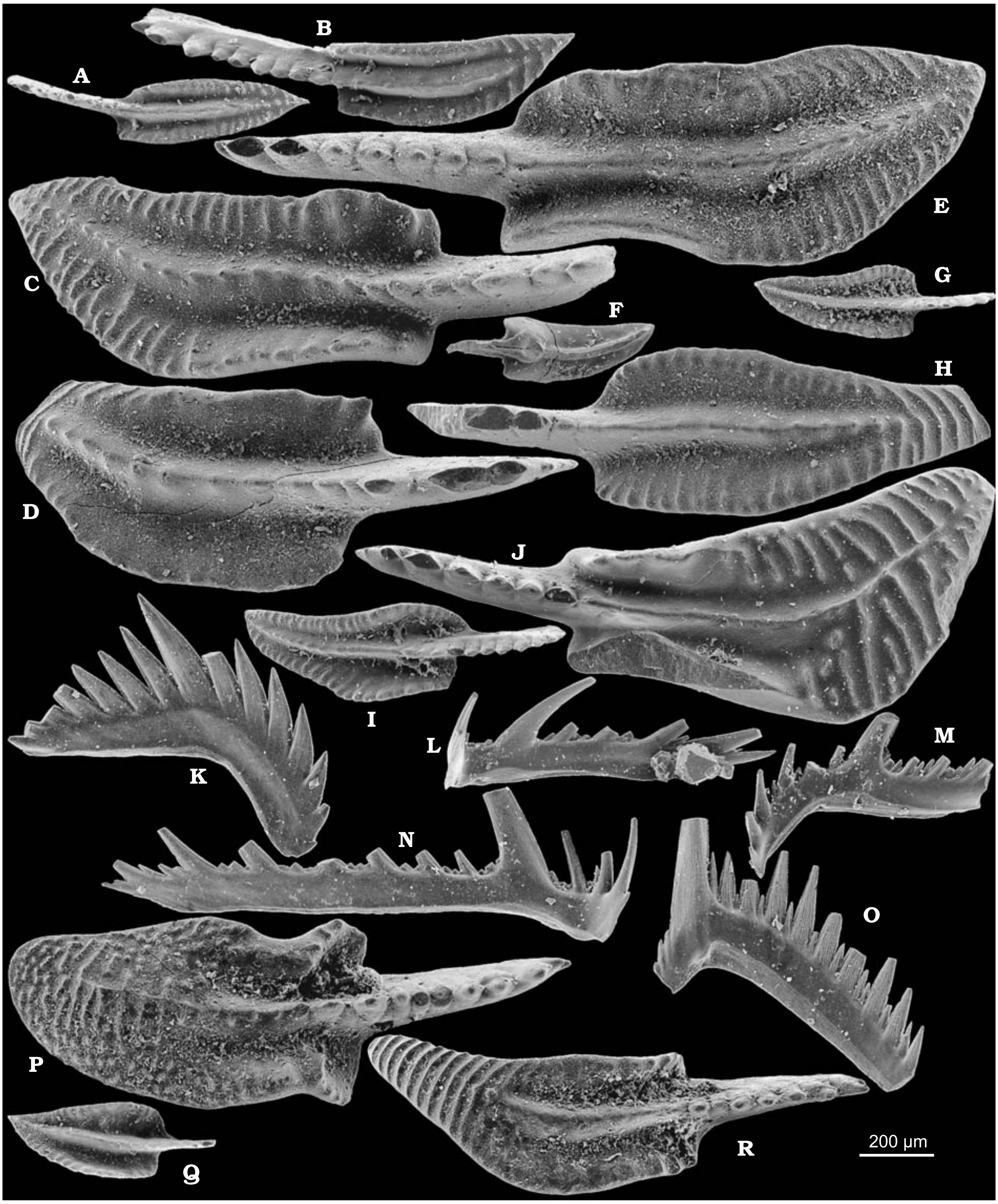


Fig. 62. *Polygnathus semicostatus* Branson *et* Mehl, 1934 from the *P. trachytera* Zone at Kowala (A, B, F, G, I–O, sample Ko-15), *K. crepida* Zone at Kadzielnia (C–E, H, sample Ka-3), and the *C. quadrantinodosa* Zone at Łagów (T, X, sample Ł-32; Q, sample Ł-27) in the Holy Cross Mountains. P$_1$ (A–J, P–R), P$_2$ (K), S$_1$ (L), S$_2$ (M), S$_{3–4}$ (N), and M (O) elements; specimens ZPAL cXVI/2517, 2516, 2493, 2495, 2492, 2514, 2515, 2494, 2495, 2519–2509, 2520–2524, 2526, 2570, and 2525, respectively.

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

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

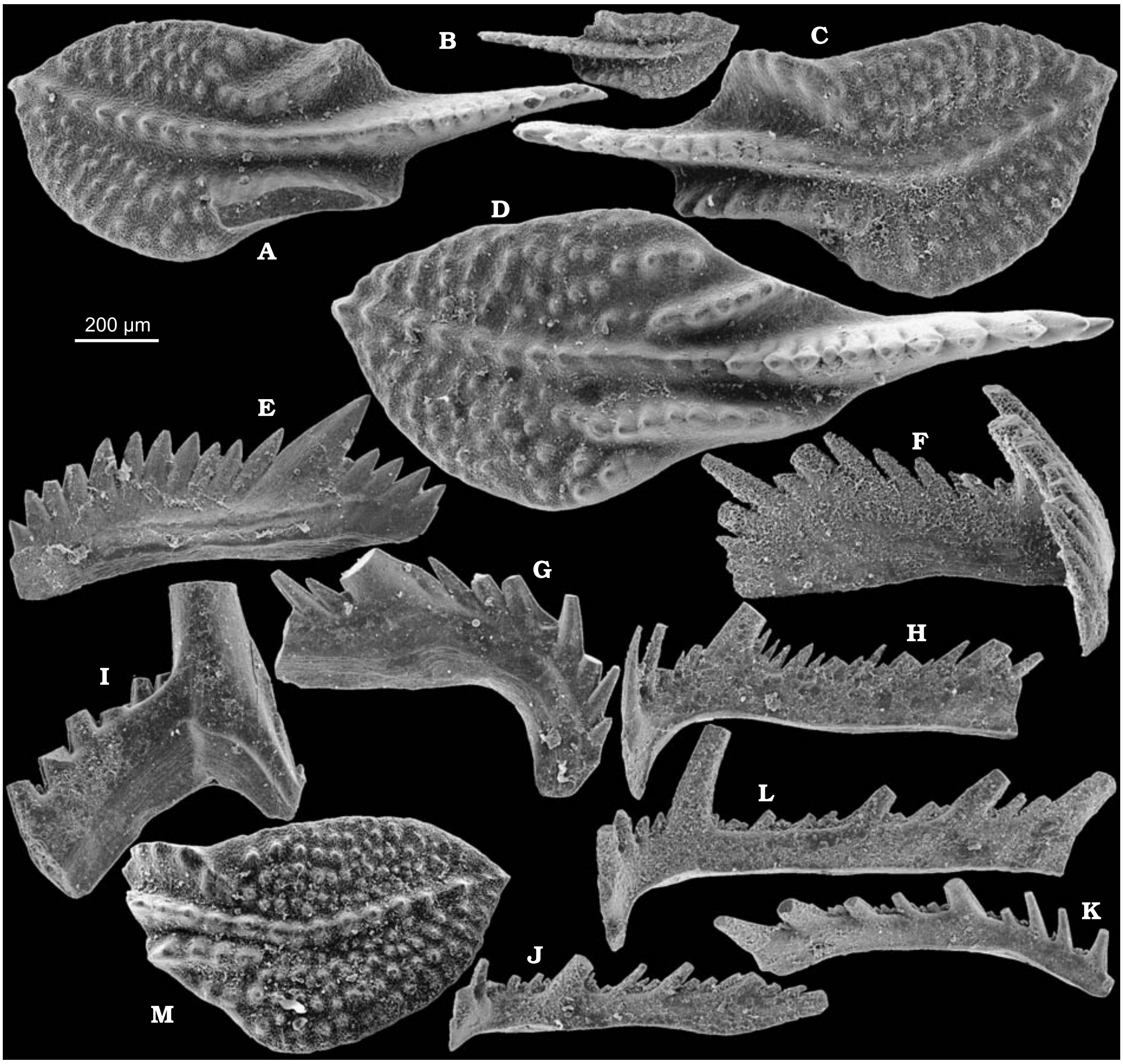


Fig. 63. Problematic *Polygnathus*? *experplexus* (Sandberg *et* Ziegler, 1979) from the *L.styriacus* Zone at Ostrówka (A, D–F, sample Ost-12; B, C, I–K, sample Ost-293) in the Holy Cross Mountains and Dzikowiec (L, sample Dz-71) in the Sudetes. P_1 (A–D, L), P_2 (E), S_0 (F), S_1 (J?), S_2 (G, K?),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

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

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

Material. — 554 specimens.

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

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

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

Polygnathus extralobatus Schäfer, 1976
(Figs 64A–K and 130)

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

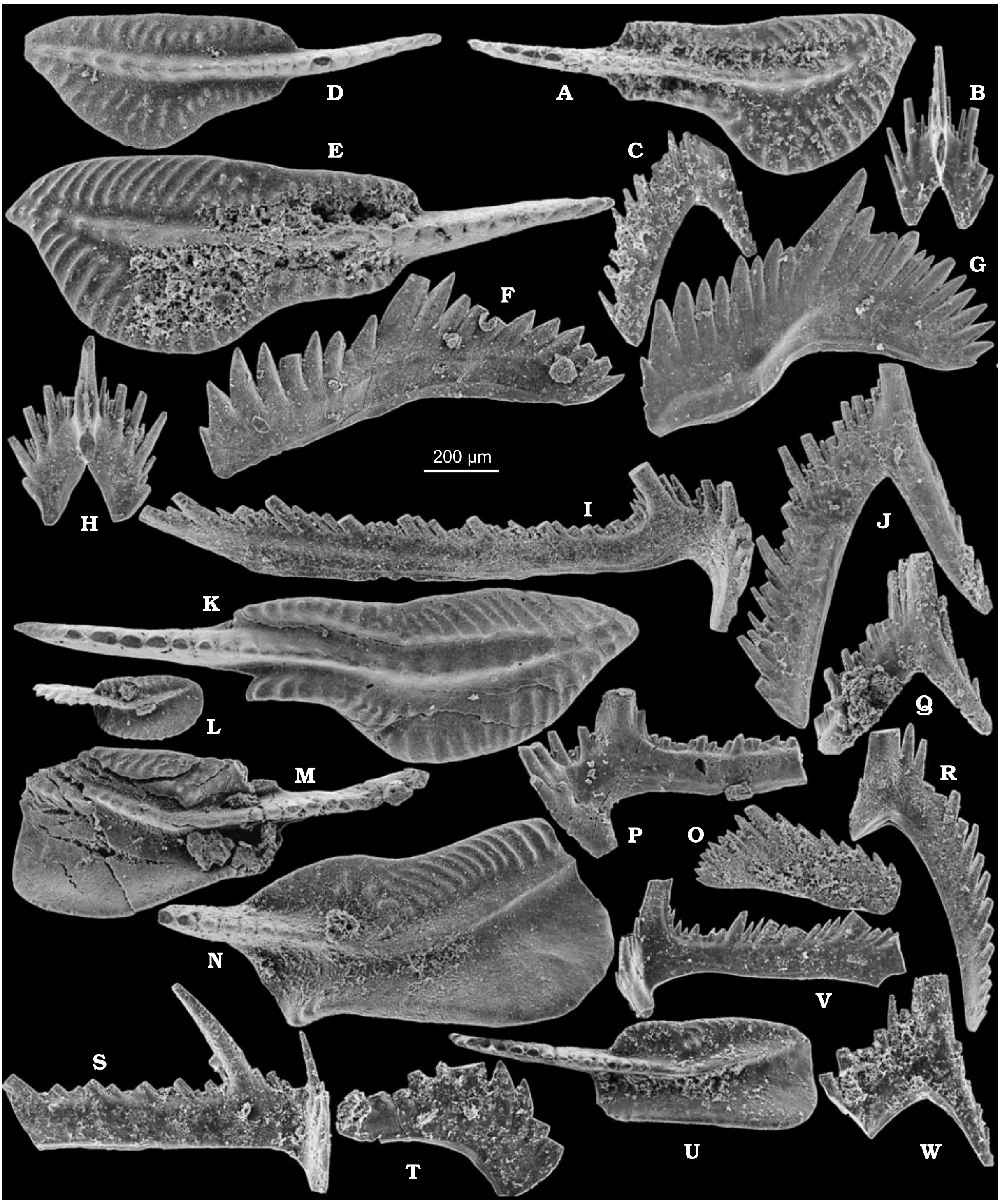


Fig. 64. Late Famennian polygnathids from the *P. jugosus* Zone at Ostrówka (D, N, O–R, sample Ost-265) and Jabłonna (E–J, bed 27) in the Holy Cross Mountains, Gołogłowy (K–M, Q, sample Goł-3) and Dzikowiec (A–C, sample Dz-53) in the Sudetes. **A**–**K**. *Polygnathus extralobatus* Schäfer, 1976. P_1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

Material. — 1,014 specimens.

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

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

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

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

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

Material. — 445 specimens.

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

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

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

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

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

Material. — 832 specimens.

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

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

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

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

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

Material. — 1,893 specimens.

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

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

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

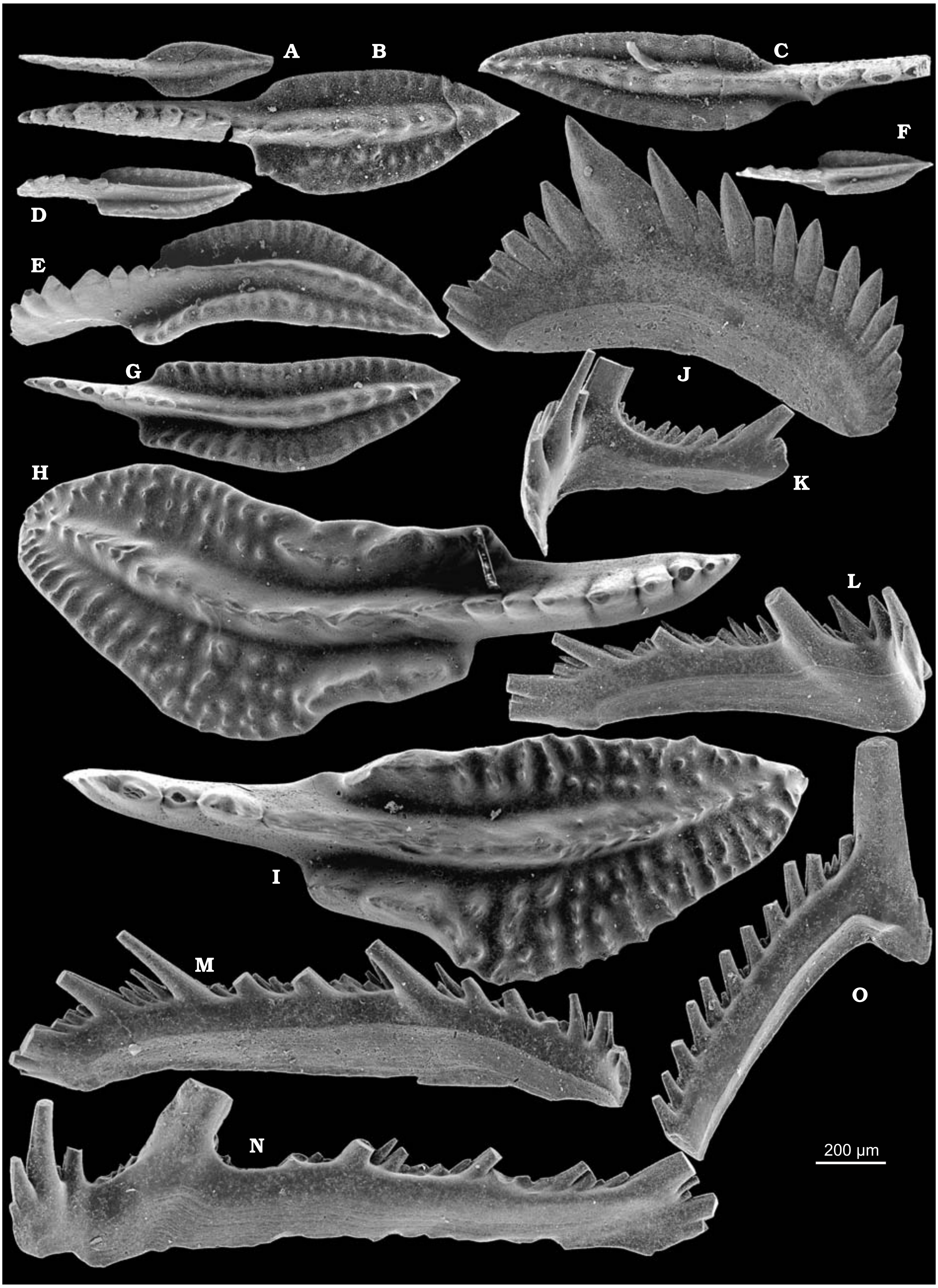


Fig. 65. Early Famennian narrow-platform polygnathids from *K. triangularis* Zone of the Holy Cross Mountains. **A**–**C**. *Polygnathus procerus* Sannemann, 1955 from Jabłonna (A, B, sample J-58; C, sample J-59). P_1 elements; specimens ZPAL cXVI/2450–2452. **D**–**O**. *Polygnathus volhynicus* Drygant,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

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

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

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

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

Material. — 1,458 specimens.

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

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

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

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

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

Material. — 77 specimens.

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

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

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

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

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

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

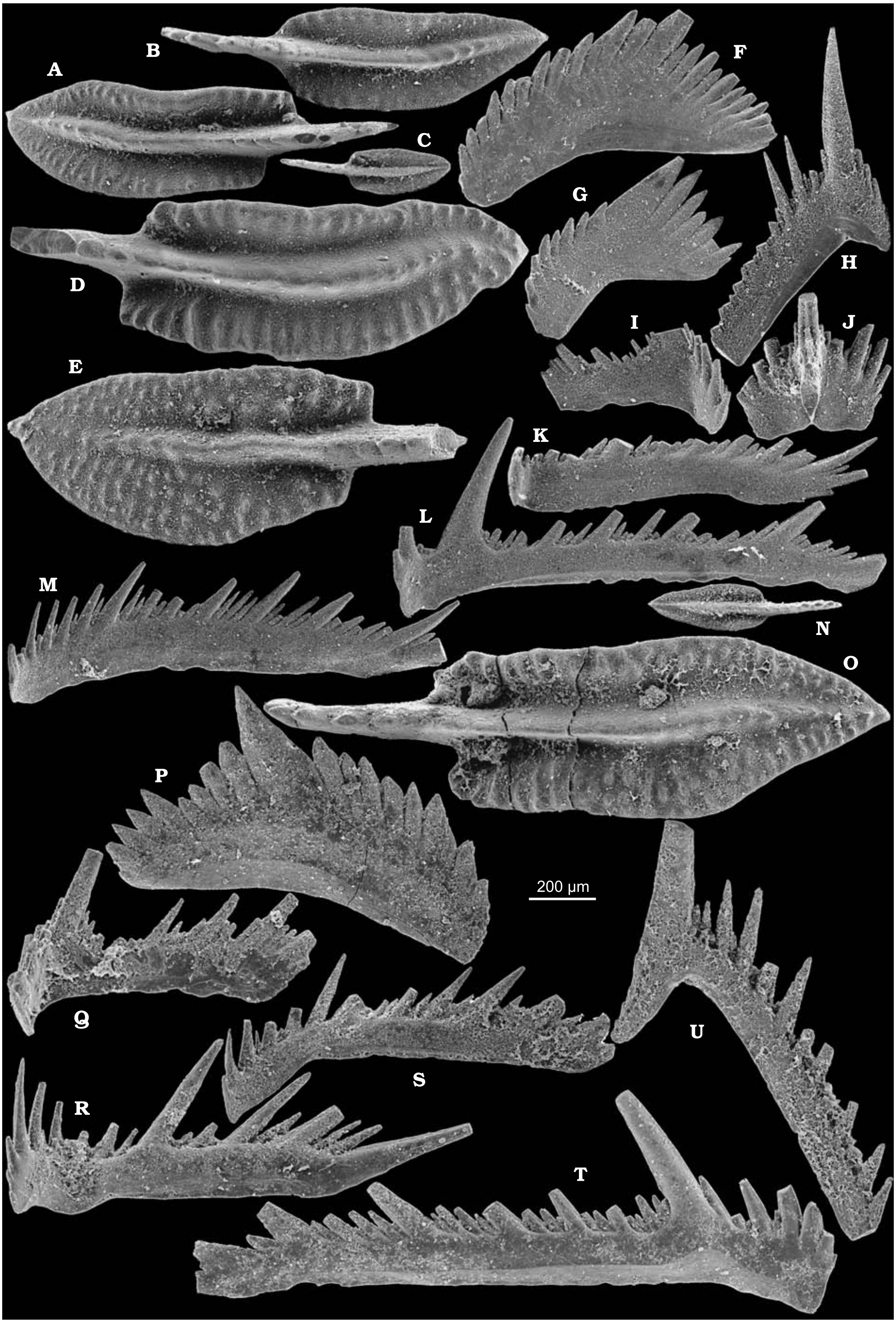
Diagnosis. — Polygnathids with elaborate platform developed also in P_2 elements; platform of P_1 elements with ridges parallel to blade in rostral ventral part and with tuberculated convex and strongly asymmetric dorsal part; remaining elements of the apparatus similar to *Polynodosus*.

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

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

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

Material. — 787 specimens.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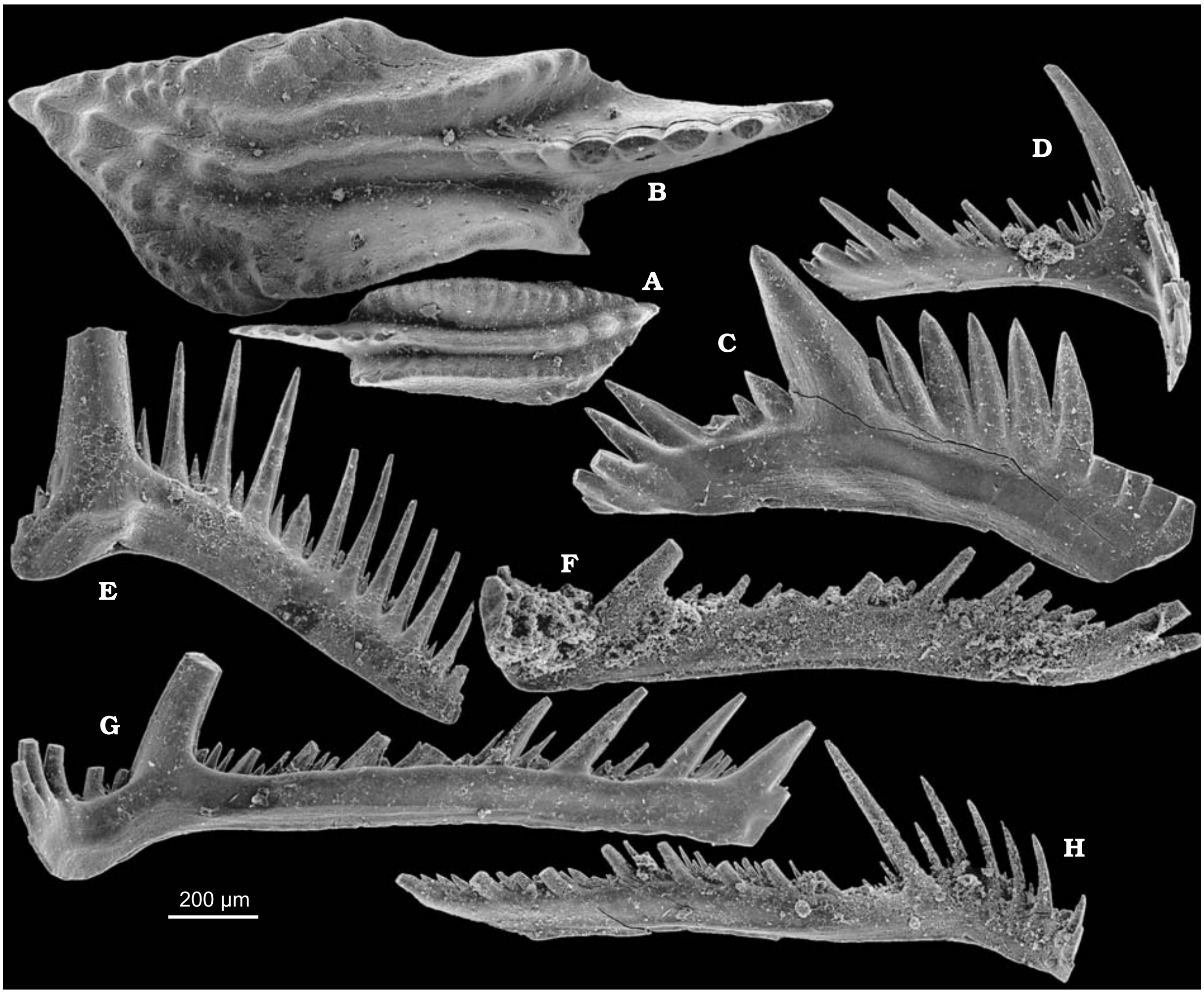

Fig. 67. *Hemilistrona perplexa* (Thomas, 1949), a ridged platform-bearing polygnathid, from the *C. marginifera* Zone at Ściegnia (Wzdół Plebański; sample Wzd-10) in the Holy Cross Mountains. P_1 (A, B), P_2 (C), S_0 (D), S_1 (E), S_2 (F), S_{3-4} (G), and M (H) elements; specimens ZPAL cXVI/2641–2644,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

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

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

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

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

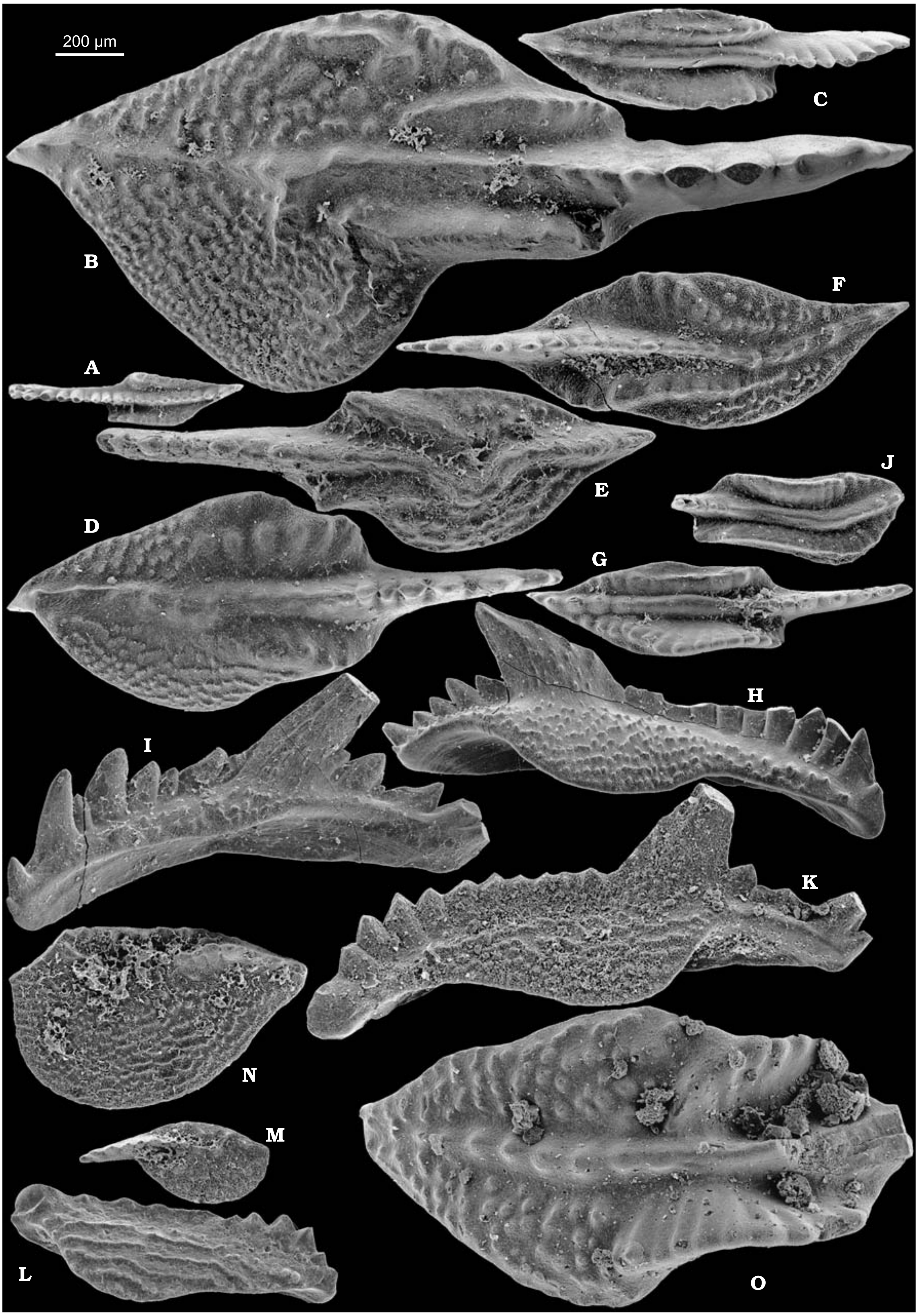


Fig. 68. Polygnathids with platform-bearing P_2 element. **A–K**, **O**. *Hemilistrona homoirregularis* (Ziegler, 1971) from the *L.styriacus* Zone at Ostrówka (A–K, sample Ost-12) in the Holy Cross Mountains and Gołogłowy (O, sample Goł-3) in the Sudetes. P_1 (A–G, J, O), P_2 (H, I, K), elements; specimens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

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

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

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

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

Material. — 810 specimens.

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

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

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

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

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

Material. — 14 specimens.

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

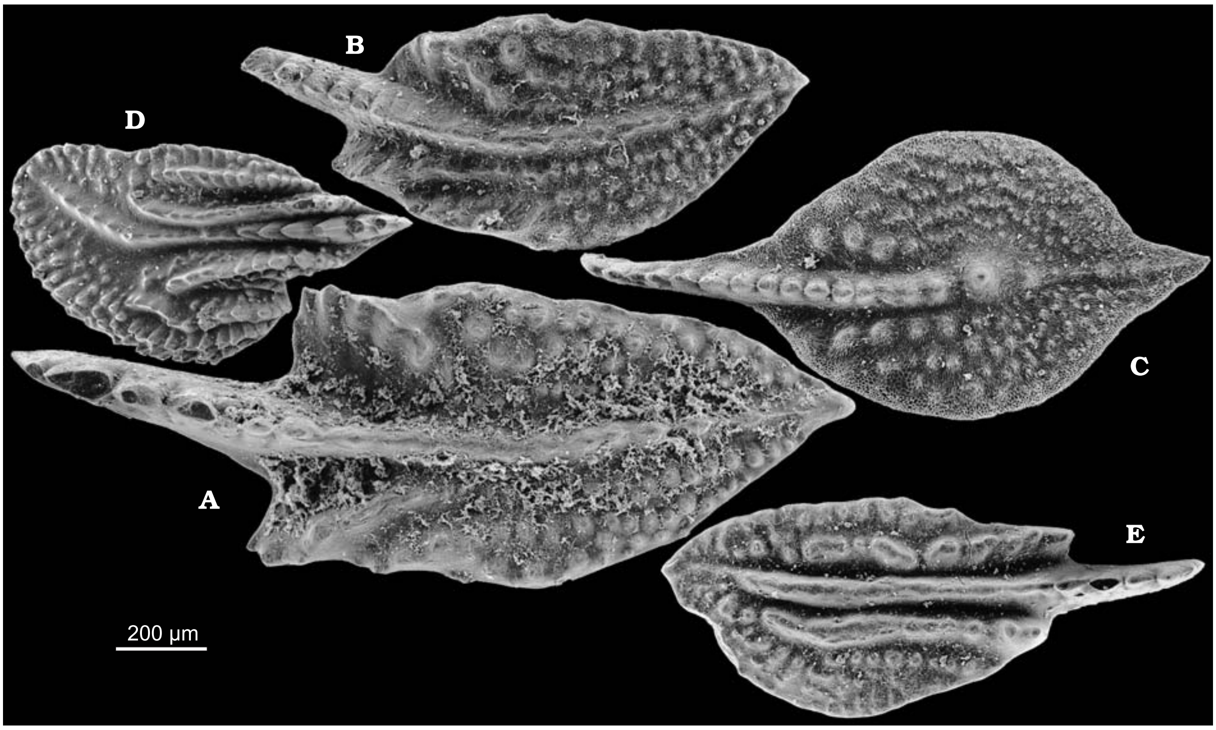


Fig. 69. *Hemilistrona margaritata* (Schäfer, 1976), a polygnathid with ornate platform, from the *L. styriacus* Zone at Ostrówka (A–C, sample Ost-12; D, E, sample Ost-293) in the Holy Cross Mountains; specimens ZPAL cXVI/2651, 2655, 2661, 2669, and 2674, respectively.

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

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

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

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

Material. — 14 specimens.

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

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

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

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

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

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

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

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

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

Material. — 1,447 specimens.

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

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

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

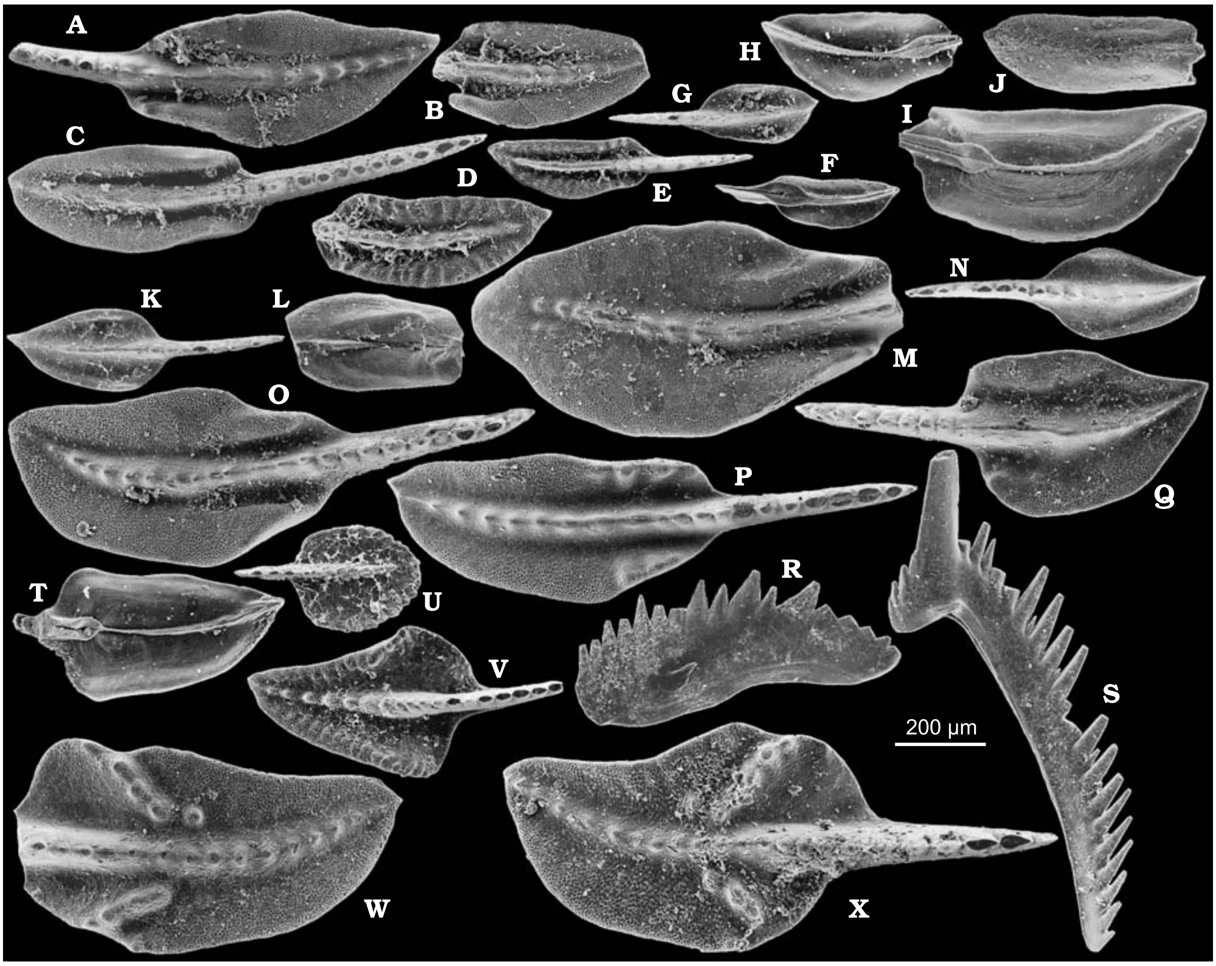


Fig. 70. Famennian populations of *Neopolygnathus*. **A–S**. *N. communis* (Branson *et* Mehl, 1934) from the *C. quadrantinodosa* Zone at Łagów (A, B, samples Ł-27), the early *L. styriacus* Zone (C–F, sample Ost-12) at Ostrówka, the *P. trachytera* Zone at Kowala (G–J, sample Ko-15), the late *L. styriacus*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

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

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

Material. — 595 specimens.

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

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

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

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

Genus ***Lagovignathus*** gen. n.

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

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

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

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

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

Material. — 749 specimens.

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

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

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

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

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

Material. — 3,891 specimens.

Diagnosis. — Slight constriction in the middle of the heart-shaped outline of the flat, smooth platform.

Remarks. — This is clearly a successor of *L. glaber* and whether to distinguish them at the chronospecies or chronosubspecies rank is a matter of convenience. Differences are minor and ranges of population variability clearly overlap.

Occurrence. — The late *K. crepida* to *L. styriacus* zones at Kadzielnia, Jabłonna, Kowala, Miedzianka, and Ostrówka.

Lagovignathus fallax (Helms *et* Wolska, 1967)
(Figs 72J–Q and 131)

Type horizon and locality: Grey, bedded limestone of lower marginifera Zone from the old Geipelsch quarry in Schleiz, Thuringia (Helms and Wolska 1967).

Material. — 1,273 specimens.

Diagnosis. — Willow leaf-shaped platform ornamented with minute tubercles.

Remarks. — Rare specimens from the *C. quadrantinodosa* Zone at Łagów (samples Ł-27 and Ł-26), associated with *Polynodosus transitus* and probably belonging to that species (Fig. 50D), resemble *L. fallax* in the minute tuberculation of the platform. The regular denticulation and short dorsal process of P_2 elements make any relationships of this species to *Polynodosus* unlikely.

Basal cone of the platform-lacking larva is significantly larger in this species than in other coeval species of *Lagovignathus*, but in subsequent growth the boundary between conical and inverted basal cavity smoothened.

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

Lagovignathus? *dissimilis* (Helms *et* Wolska 1967)
(Figs 73 and 131)

Type horizon and locality: Grey-purple, thin bedded limestone of the *Clymenia* Zone from Alte Heerstrasse near Oettersdorf, Thuringia (Helms and Wolska 1967).

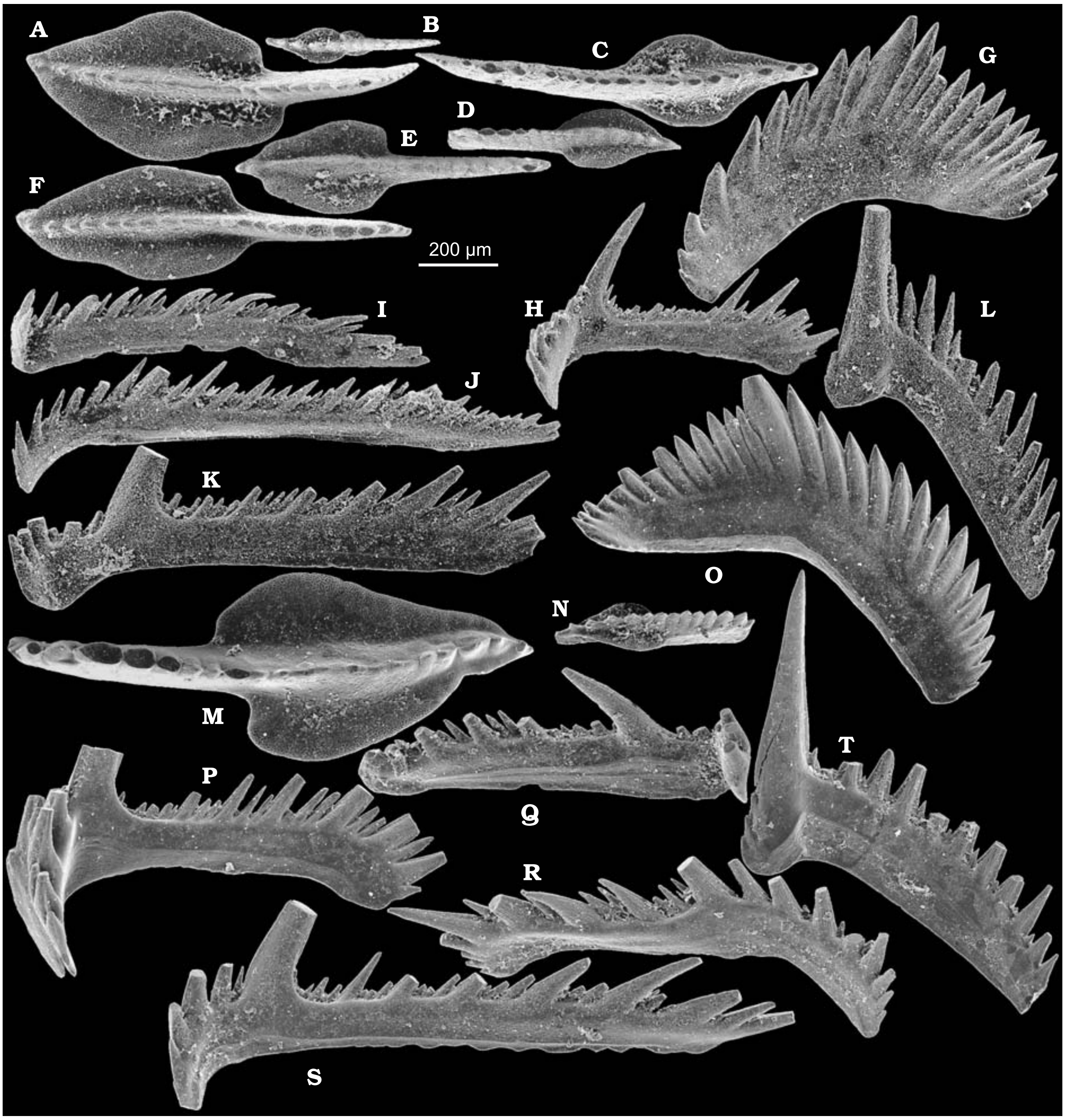


Fig. 71. Species of *Lagovignathus* with smooth platform from the Holy Cross Mountains. **A**–**L**. *Lagovignathus glaber* (Ulrich *et* Bassler, 1926) from the *K. crepida* Zone at Kadzielnia (A–C, E, sample Ka-14; D, F–L, sample Ka-4). P_1 (A–F), P_2 (G), S_0 (H), S_1 (I), S_2 (J), $S_{3–4}$ (K), and M (L) elements; specimens ZPAL cXVI/2529, 2532, 2530, 2533, 2531, and 2534–2540, respectively. **M**–**T**. *Lagovignathus bilobatus* (Ziegler, 1962) from the *C. quadrantinodosa* Zone at Łagów (sample Ł-32). P_1 (M, N), P_2 (O), S_0 (P), S_1 (Q), S_2 (R), $S_{3–4}$ (S), and M (T) elements; specimens ZPAL cXVI/2542, 2541, 2543, 2547, and 2549, respectively.

Material. — 513 specimens.

Diagnosis. — P_2 elements of robust appearance, with incipient platform, P_1 elements with usually narrow but robust platform and with extensive asymmetric basal cone.

Remarks. — Dense denticulation of juvenile P_1 elements somewhat resembles peniculus and together with the shape of the platform in P_1 elements may suggest affinities with *Polynodosus* (especially *P. lauriformis*). No transitional forms have been found, however. The basal cone, which corresponds to an expanded sinuosa larva, points to *Lagovignathus fallax* as the alternative ancestor. The shape of the platform and outline of mature P_1 elements fits this possibility even better. Probable M element is also unlike that of *Polynodosus*.

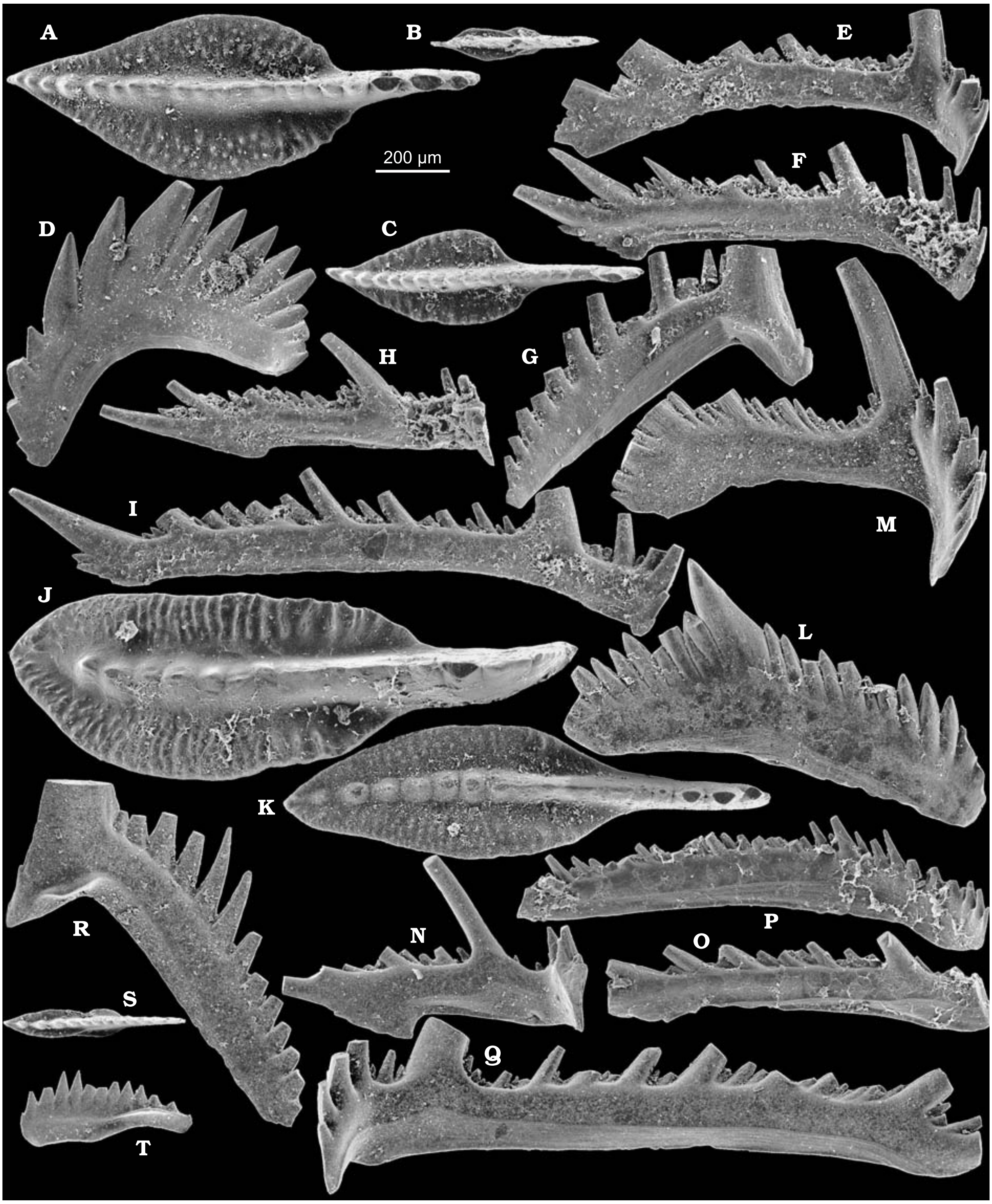


Fig. 72. Early species of *Lagovignathus* with tuberculated platform from the Holy Cross Mountains. **A–I**. *Lagovignathus lagowiensis* (Helms *et* Wolska, 1967) from the *C. quadrantinodosa* Zone at Łagów (sample ŁSł73-5). P_1 (A–C), P_2 (D), S_0 (E), S_1 (H), S_2 (F), $S_{3–4}$ (I), and M (G) elements; specimens ZPAL cXVI/2552, 2550, 2551, 2553, 2554, 2556, 2558, 2555, and 2557, respectively. **J–Q**. *Lagovignathus fallax* (Helms *et* Wolska, 1967) from slightly older part of the same zone at the same locality (sample ŁSł73-2). P_1 (J, K, S, T), P_2 (L), S_0 (M), S_1 (N, O), S_2 (P), $S_{3–4}$ (Q), and M (R) elements; specimens ZPAL cXVI/2562, 2561, 2563, 2564, 2566, 2565, 2568, 2569, 2560, and 2559, respectively.

The evolutionary change with respect to *L. fallax* was the probable further extension of the sinuosa larva stage and development of strong asymmetry of the basal cone in its P_1 element. As a result, a situation developed closely similar to that in advanced species of the palmatolepidid *Tripodellus* lineage.

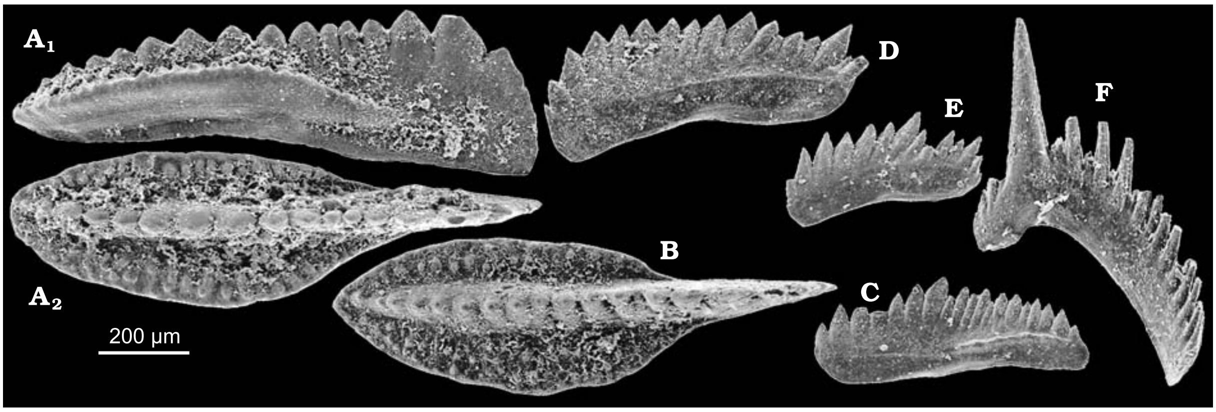


Fig. 73. *Lagovignathus? dissimilis* (Helms *et* Wolska 1967) from the *P. jugosus* Zone at Jabłonna (sample J-51) in the Holy Cross Mountains. P_1 (A–C), P_2 (D, E), and M (F) elements; specimens ZPAL cXVI/2172–2177, respectively.

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

Lagovignathus lagowiensis (Helms *et* Wolska, 1967)
(Figs 72A–I and 131)

Type horizon and locality: Sacculus bank with *Cheiloceras lagowiense* and *Dimeroceras lentiforme*, mixed uppermost rhomboidea and upper marginifera zones according to Helms and Wolska (1967).

Material. — 3,379 specimens.

Diagnosis. — Leaf-like, relatively wide platform of P_1 elements ornamented with small tubercles.

Remarks. — The species is preceded in the Łagów section by the somewhat similar *L. fallax* but transition between these species has not been demonstrated. A much more probable origin from *L. glaber* would require only development of tuberculation of the platform. This is actually the only apparent difference between these species.

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

Lagovignathus granulosus (Branson *et* Mehl, 1934)
(Figs 74A–C and 131)

Type horizon and locality: Famennian shale at Noel, Missouri (G. Klapper personal communication 2005).

Material. — 39 specimens.

Diagnosis. — Leaf-like, relatively wide platform of P_1 elements densely ornamented with relatively large tubercles.

Remarks. — The species is so similar to the significantly older *L. lagowiensis* that, despite the discontinuous fossil record at Łagów, the ancestor-descendant relationship seems almost certain. Specimens with smooth concave areas near the ventral end of the platform are transitional to *L. styriacus*, the successor of *L. granulosus* in the same lineage.

Occurrence. — The *P. trachytera* Zone at Łagów, Miedzianka, Jabłonna, Kowala, and Wzdół.

Lagovignathus styriacus (Ziegler, 1957)
(Figs 74D–F and 131)

Type horizon and locality: Sample 73 from a nodular goniatite limestone collected in a quarry between Steinberg and Hitzendorf near Graz, Austria.

Material. — 287 specimens.

Diagnosis. — Wide and asymmetric platform of P_1 element with densely tuberculated dorsal part separated from smooth ventral areas by a transverse row of larger tubercles.

Remarks. — Early populations of *L. styriacus* show great variability in their platform outline, some specimens being narrower even than in the ancestral *L. granulosus*. The transition apparently took a significant time span, the zonal boundary is thus hardly clear-cut. It is possible that some populations from Ostrówka

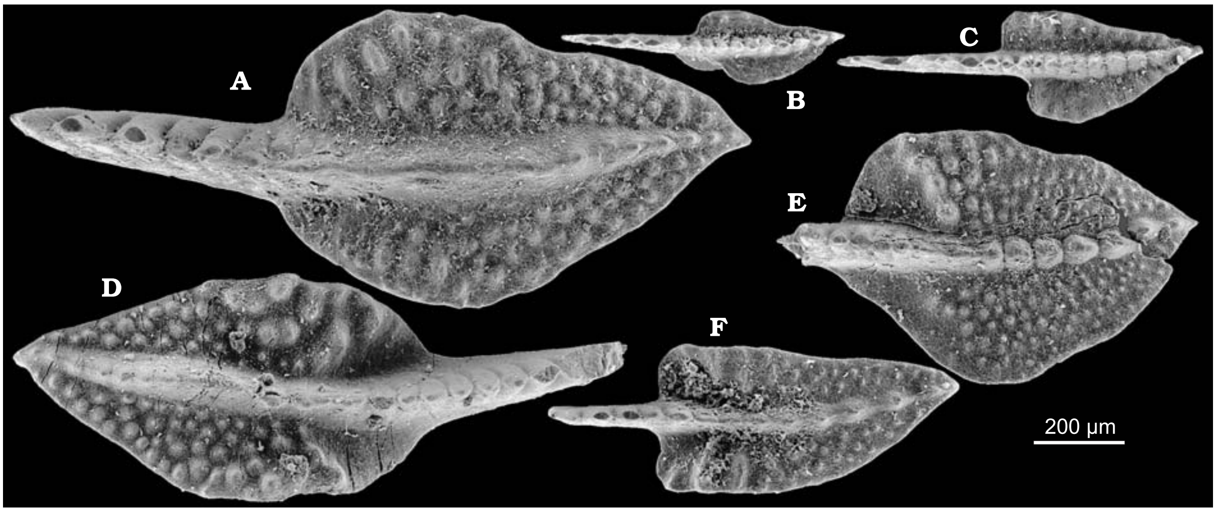


Fig. 74. Late species of *Lagovignathus* with tuberculated platform from the Holy Cross Mountains. **A–C**. *Lagovignathus granulosus* (Branson *et* Mehl, 1934) from the *P. trachytera* Zone at Jabłonna (bed 24). P_1 elements; specimens ZPAL cXVI/2709, 2711, and 2710, respectively. **D–F**. *Lagovignathus styriacus* (Ziegler, 1957) from its nominal Zone at Miedzianka (D, sample Md-6) and Ostrówka (E, F, sample Ost-265). P_1 elements; specimens ZPAL cXVI/2714, and 2712, 2713, respectively.

co-occurring with *P. trachytera* actually represent *L. granulosus*, not *L. styriacus* as suggested by their variable morphology.

Occurrence. — The nominal zone at Jabłonna, Ostrówka, Kowala, and Miedzianka.

Family **Ancyrognathidae** fam. n.

Diagnosis. — Robust and sharply denticulated elements with clearly terminal growth, P_1 element with reduced free blade in adult specimens, S_{1-2} elements bear short processes, M element with prominent and well denticulated external process.

Remarks. — The morphology of the ancyrognathid apparatus elements is in many respects transitional between that of the Polygnathidae and Palmatolepididae. Like the palmatolepidids, processes of elements of *Ancyrognathus* are relatively short and with the clearly terminal growth. *Mesotaxis* is apparently the ancestor of the palmatolepidids although, except for the M element, it has not developed all their diagnostic characters (symmetrical element lacking medial process, lobate platform of P_1 elements).

Genera included. — *Mesotaxis* Klapper and Philip, 1972; *Ancyrognathus* Branson *et* Mehl, 1934; *Ancyrolepis* Ziegler, 1959; *Polylophodonta* Branson *et* Mehl, 1934.

Genus ***Ancyrognathus*** Branson *et* Mehl, 1934

Type species: *Ancyrognathus symmetricus* Branson *et* Mehl, 1934 from the Famennian Saverton Shale at Sees Creek in Monroe County, Missouri (Ziegler 1975).

Diagnosis. —Elongated platform in P_1 elements, tending to develop a prominently tuberculation; triramous in early species; other elements of the apparatus tend to develop a rudimentary platform but still of a generalized polygnathid morphology.

Ancyrognathus sinelamina (Branson *et* Mehl, 1934)
(Figs 75A–H and 132)

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

Material. — 22 specimens.

Diagnosis. — Slender P_1 elements virtually without free blade and any flank lobe of the platform; minute basal cone (pit).

Remarks. — The transition from the biramous latest Frasnian ancyrognathids to this species has been documented by Schülke (1996); probably the early Famennian type species of the genus derived at the transi-

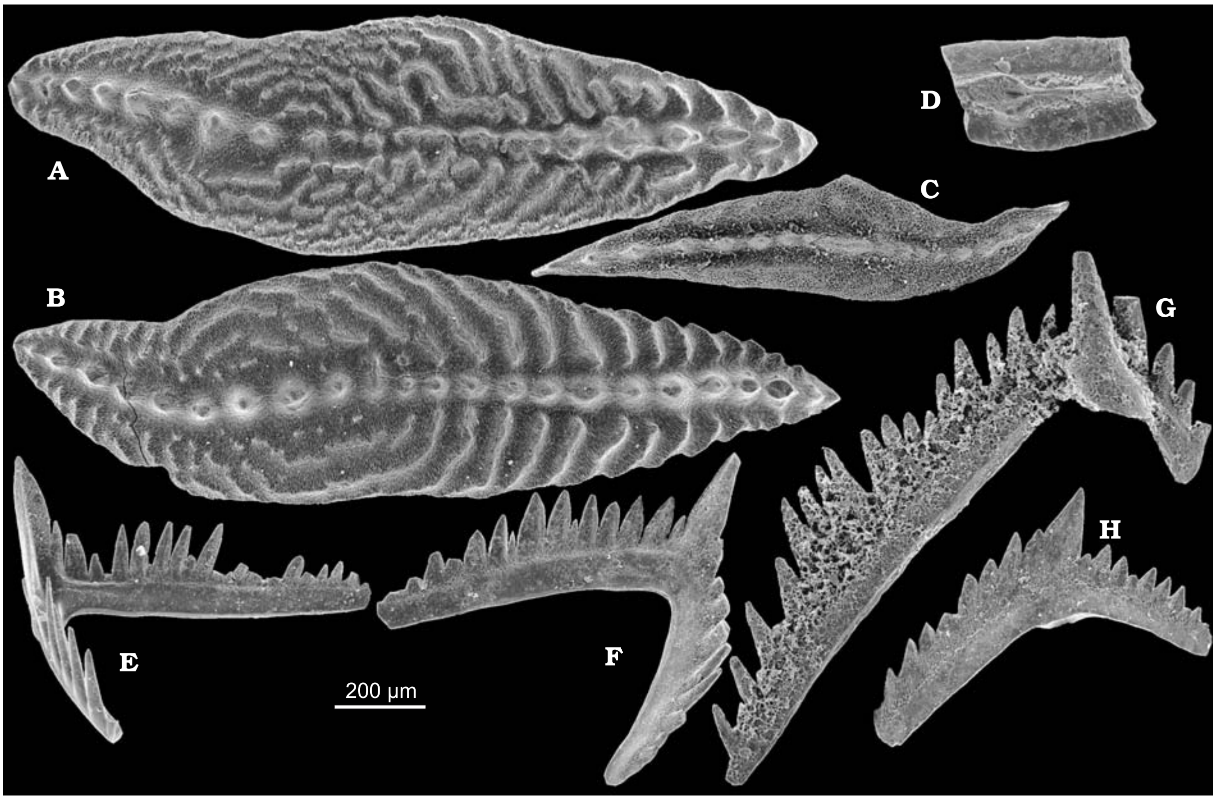


Fig. 75. Typical ancyrognathids from the Holy Cross Mountains, *Ancyrognathus sinelamina* (Branson *et* Mehl, 1934) from the late *K. triangularis* Zone at Karczówka (A, B), the *K. crepida* Zone at Jabłonna (C–F, H, I, bed 3) and Kadzielnia (G, sample Ka-2). P_1 (A–D), P_2 (H), S_0 (E), S_{3-4} (F), and M (G, I) elements; specimens ZPAL cXVI/2604–2607, 2609, 2610, 2612, 2608, and 2611, respectively.

tion. Schülke (1999) attempted restoration of the apparatus but only identification of P_1 elements is supported here. Ramiform elements similar to those associated with Frasnian species of *Ancyrognathus* (Dzik 2002) co-occur with platform elements of *A. sinelamina* in the Holy Cross Mountains.

Occurrence. — The late *K. triangularis* and early *K. crepida* zones at Jabłonna, Wietrznia, Kadzielnia, and Miedzianka. The species occurs also in the Dębnik area (Baliński 1995).

Ancyrognathus sp. n.
(Figs 9E, 76, and 132)

Material. — 28 specimens.

Remarks. — In the early Famennian of the Holy Cross Mountains rare platform elements similar to those of *Dasbergina kayseri* occur, different from those from their late Famennian type horizon in a less regular outline and coarser tuberculation of the platform. However, rare associated ramiform elements probably belonging to the species support its affinities with *Polylophodonta* and *Ancyrognathus*. Perhaps this is a successor of *A. sinelamina*.

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

Genus ***Polylophodonta*** Branson *et* Mehl, 1934

Type species: *Polygnathus gyratilineatus* Holmes, 1928 from the Gassaway Member of the Chattanooga Shale, Alabama.

Diagnosis. — Wide oval platform in P_1 elements; M element preserves generalized polygnathid morphology.

Remarks. — There are some difficulties with delineating the boundary between early species of the ancyrognathid *Polylophodonta* and homeomorphic advanced platform-bering members of the *Mehlina* lineage (*Polynodosus*) if only platform elements are considered.

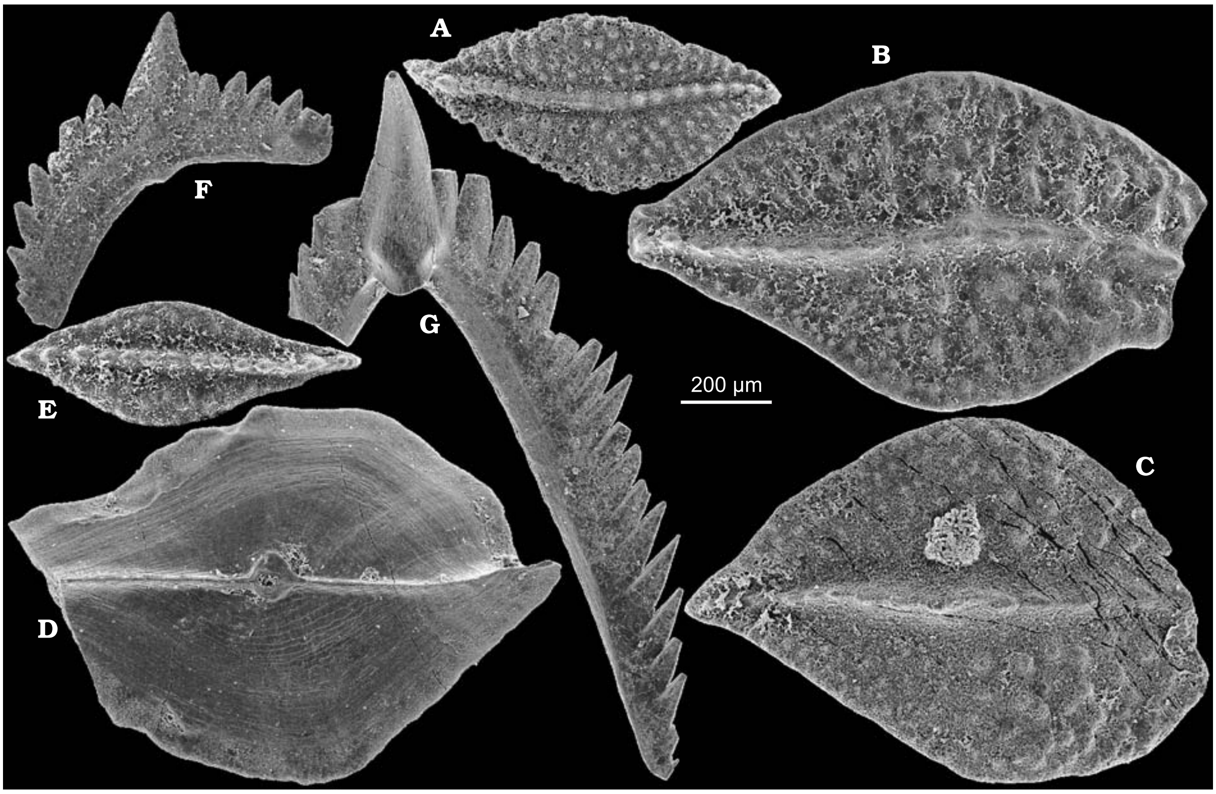


Fig. 76. *Ancyrognathus* sp. n. a relict ancyrognathid from the *K. crepida* Zone at Jabłonna (A–D, sample J-65) and Kadzielnia (E–G, sample Ka-5) in the Holy Cross Mountains.

Polylophodonta ovata (Helms, 1961)
(Figs 77 and 132)

Type horizon and locality: Lower bed of red limestone, lower *Cheiloceras* Zone, in western quarry on Kahlleithe near Rödersdorf, Thuringia (Helms 1961).

Material. — 289 specimens.

Diagnosis. — Row of denticles of the blade of recognizable to the dorsal end of the platform in P_1 elements even in mature specimens.

Remarks. — The oldest occurrence of the species is in bed 4 at Jabłonna, where it occurs together with *Klapperilepis crepida* prior to the entrance of *Conditolepis tenuipunctata*. Elements from there are of a rather robust and irregular appearance. The typical form occurs in the somewhat younger samples J-45a and Wtr-32.

Occurrence. — The late *K. triangularis* and early *K. crepida* Zone at Jabłonna, Wietrznia, and Miedzianka. The species occurs also in the Dębnik area, identified there as *P. confluens* by Baliński (1995).

Polylophodonta pergyrata (Holmes *in* Butts, 1926)
(Figs 78 and 132)

Type horizon and locality: Gassaway Member of the Chattanooga Shale at Quicks Mill, Alabama (Huddle 1968).

Material. — 559 specimens.

Diagnosis. — Concentric ridges forming a fingerprint-like appearance of the mature platform of P_1 elements.

Remarks. — Many species names are available for advanced *Polylophodonta*. Although it cannot be excluded that several biological species are represented in the studied material, I am not able to find any discontinuity in the observed population variability.

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

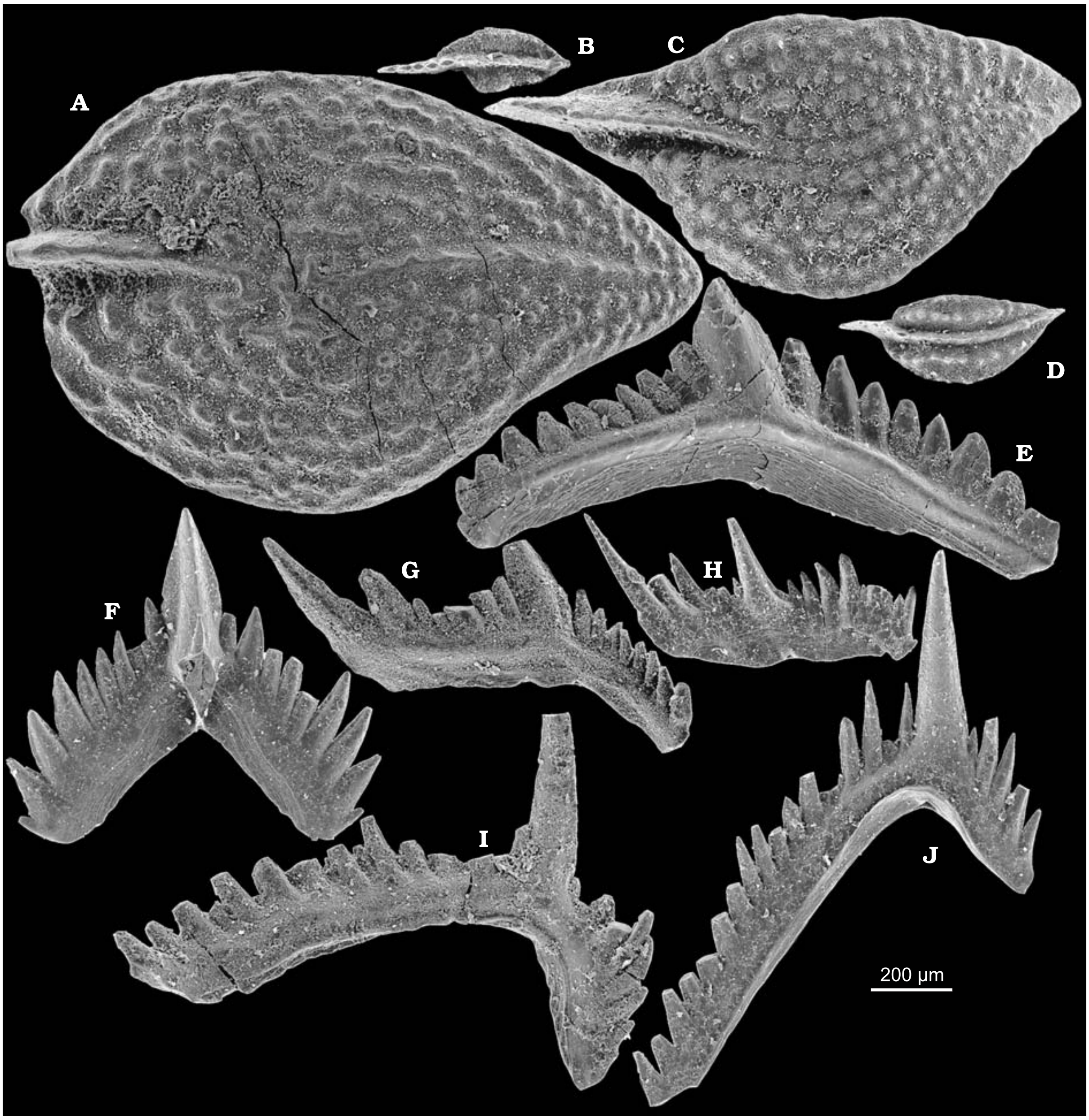


Fig. 77. Derived ancyrognathid *Polylophodonta ovata* (Helms, 1961) from the early *K. crepida* Zone at Wietrznia (A, D, sample Wtr-32) and the *K. triangularis* Zone at Jabłonna (B, E, H, I, J, sample J-45a; F, G, sample J-44) in the Holy Cross Mountains. P_1 (A–D), P_2 (E), S_0 (F), S_1 (H), S_2 (G), S_{3-4} (I), and M (J) elements; specimens ZPAL cXVI/2579, 2582, 2580, 2581, 2583, 2584–2588, respectively.

Family **Palmatolepididae** Sweet, 1988

Diagnosis. — Apparatus with M element having straight processes and S_0 element with more or less reduced medial process; usually lobate platform-bearing P_1 and P_2 elements.

Genus ***Klapperilepis*** Dzik, 2002

Type species: *Palmatolepis triangularis* Sannemann, 1955 from the early Famennian of Frankenwald.

Diagnosis. — P_1 elements with raised tip of the dorsal process and underived appearance of the remaining elements of the apparatus.

Remarks. — Discrimination of early sympatric species of *Klapperilepis* is a difficult task and while discussing their taxonomy in the context of the end-Frasnian events I failed to find a satisfactory solution (Dzik

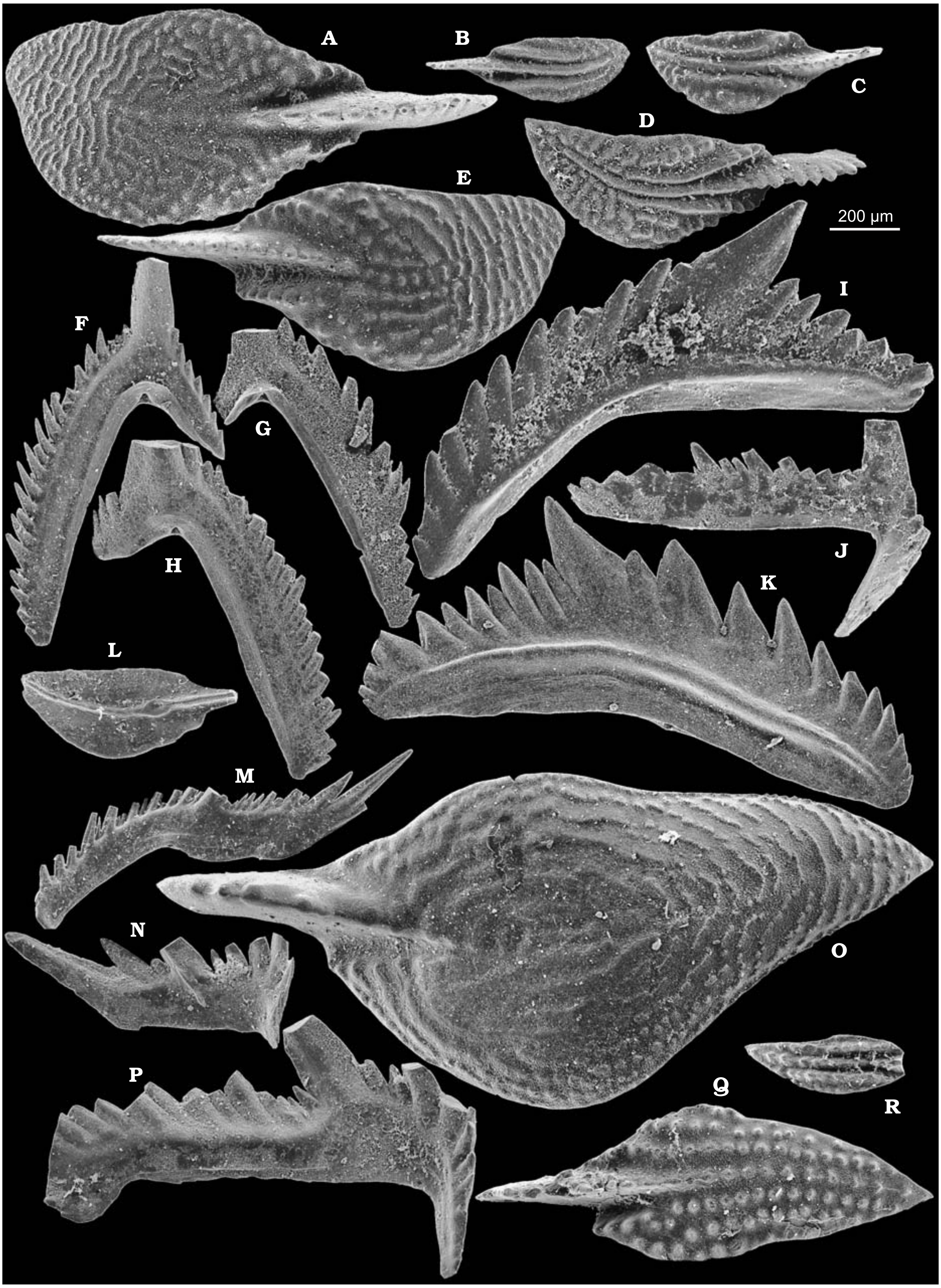


Fig. 78. Derived ancyrognathid *Polylophodonta pergyrata* (Holmes *in* Butts, 1926) from the *K. crepida* Zone at Kadzielnia (A, H, sample Ka-12; B, D, K, sample Ka-5; G, J, and M–R, sample Ka-2) and Jabłonna (C, E, F, and L, bed 7), and the *C. quadrantinodosa* Zone at Łagów (I, sample Ł-26) in the Holy Cross Mountains. P_1 (A–E, L, O, Q, R), P_2 (I, K), S_1 (N), S_2 (M), $S_{3–4}$ (P), and M (F–H) elements; specimens ZPAL cXVI/2596, 2594, 2573, 2595, 2574, 2575, 2613, 2597, 2159, 2617, 2591, 2572, 2619, 2614, 2618, 2620, and 2615, 2616, respectively.

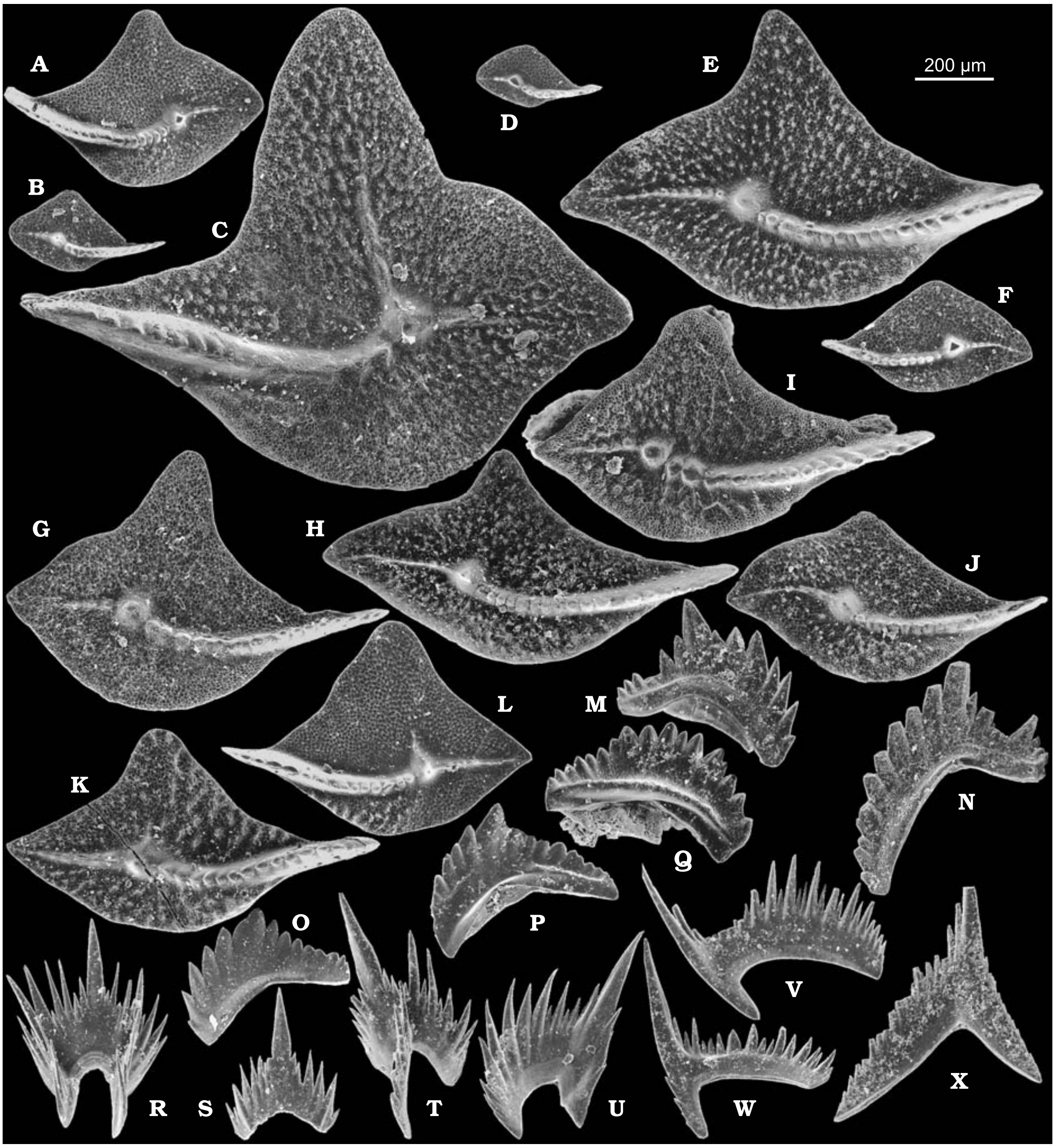


Fig. 79. Ancestor of Famennian palmatolepidids, *Klapperilepis ultima* (Ziegler, 1958) from the pre-*K. triangularis* Zone strata at Płucki (sample Pł-36) in the Holy Cross Mountains. P_1 (A–L), P_2 (M–Q), S_0 (R, S), S_1 (T), S_2 (U), $S_{3–4}$ (V, W), and M (X) elements; specimens ZPAL cXVI/1512, 1503, 1506, 1513, 1509, 1505, 1502, 1510, 1508, 1511, 1507, 1504, 1514, 1518, 1516, 1517, 1515, and 1519–1525, respectively.

2002). No doubt that several new lineages emerged soon after the taxonomic diversity of the palmatolepidids was reduced to the single species, *K. ultima*.

This is proven by the occurrence of two distinct types of M elements in sample Pł-42: one of the primitive latest Frasnian morphology, the other of an appearance similar to that of *K. quadrantinodosolobata*. Other ramiform elements of the *Klapperilepis* apparatus do not form any discrete classes and are probably indistinguishable at the species level. It seems reasonable to assume that the P_1 elements morphologically closest to *K. ultima* belong to the same apparatus as the associated primitive M elements. Platform elements of this kind show a relatively sinuous course of the blade. Juveniles may resemble *Conditolepis tenuipunctata* or *Klapperilepis circularis* (in Dzik 2002, table 2 they were provisionally listed under these names). Somewhat arbitrarily this population is here considered to be the oldest *K. triangularis*.

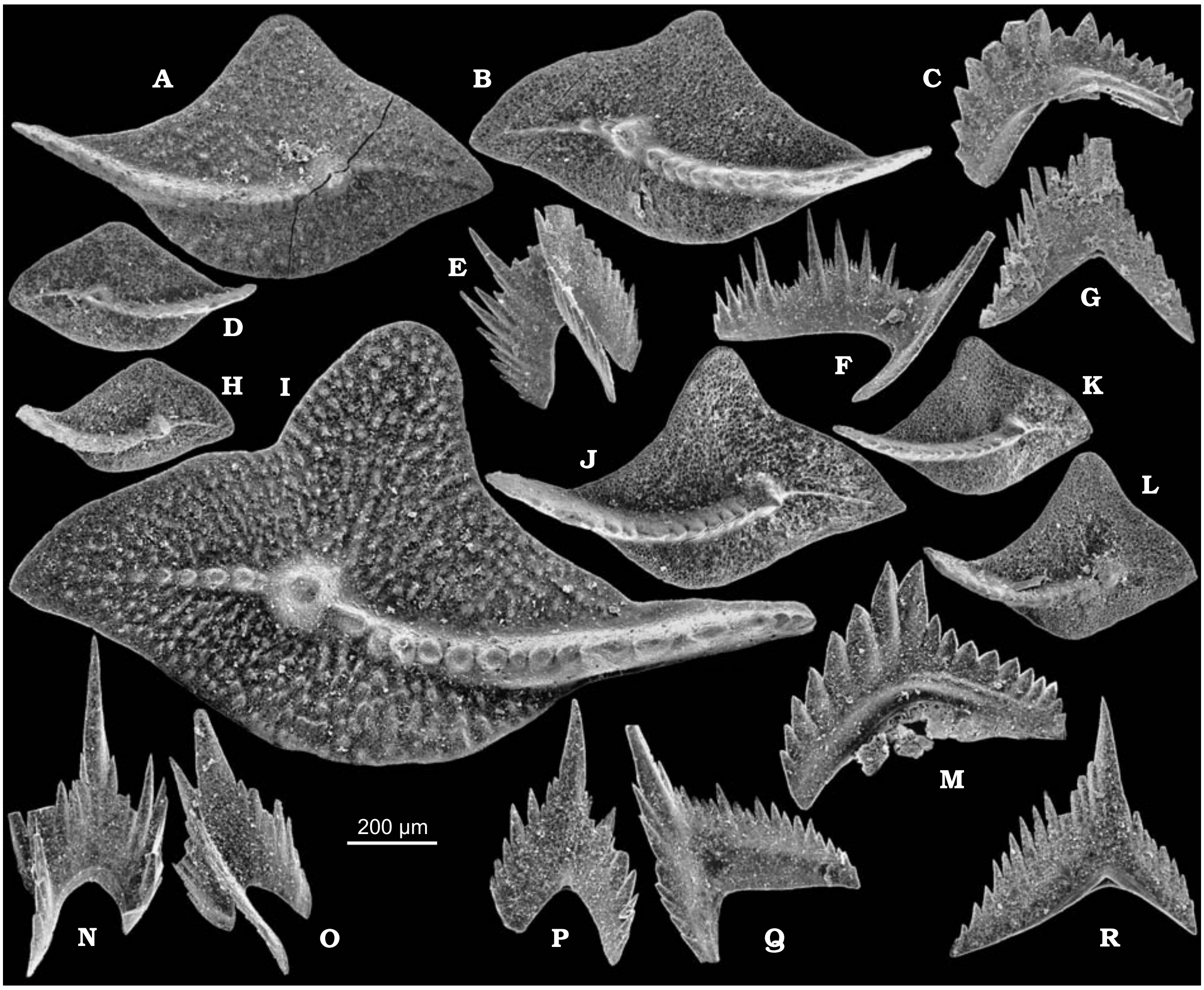


Fig. 80. Palmatolepidids of the *Klapperilepis triangularis* (Sannemann, 1955) lineage from its nominal zone strata at Płucki in the Holy Cross Mountains. **A–G**. *K. triangularis* from sample Pł-42. **H–R**. Probable ancestral population of *Palmatolepis initialis* sp. n. (sample Pł-1). P_1 (A, B, D, H–L), P_2 (C and M), S_0 (N), S_1 (E and O), S_2 (P), $S_{3–4}$ (F and Q), and M (G and R) elements; specimens ZPAL cXVI/1232, 1233, 1235, 1234, 1237–1239, 1344, 1339, 1340, 1341, 1343, 1345, 1346–1348, and 1350, 11351, respectively.

Using the same line of reasoning one would expect that P_1 elements resembling those of *K. spathula* in sample Pł-42 are conspecific with the advanced M elements. Although there is no apparent gap between the range of its morphologic variability and that of associated *K. triangularis*, such an interpretation is consistent with the apparatus reconstruction proposed by Schülke (1999) for the species here named *K. schuelkei* sp. n.

The remaining morphotype of platform elements in sample Pł-42 is much more clearly delimited. In having a rhomboidal outline of the smooth platform with raised margins and a straight blade it closely resembles *Tripodellus clarki* and probably represents its early population. There is a gradual transition towards morphologies with a wide platform resembling *K. delicatula*.

Klapperilepis ultima (Ziegler, 1958)
(Figs 8C, 79, and 135)

Type horizon and locality: Latest Frasnian sample 27 from Sessacker II trench (Ziegler 1958).

Material. — 2,084 specimens (1,207 from the Famennian).

Diagnosis. — Relatively wide and short platform of P_1 elements, underived appearance of A-shaped M elements.

Remarks. — There is a gradual evolutionary change in the morphology of P_1 elements obscured by a wide population variability (Dzik 2002). This variability makes the lineage to be of little correlative value. The apparatus of the species is documented with clusters of elements from the earliest Famennian at Płucki (samples Pł-20 and Pł-16), some representing significant portions of the apparatus (Dzik 2002). *Palmatolepis praetriangularis* Ziegler and Sandberg, 1988 has been pointed out by Klapper *et al.* (2004) to be a junior subjective synonym of *P. ultima*.

Occurrence. — The origin of the lineage remains cryptic. Populations from the latest Frasnian do not seem to differ from those from the beginning of the Famennian. At Płucki specimens with somewhat elongated platform classified within the succeeding *K. triangularis* appear in a greater number in sample Pł-42 (note, however that this character is size-dependent), at Kowala in sample Ko-155.

Klapperilepis triangularis (Sannemann, 1955)
(Figs 80A–G, 81A–J, and 135)

Type horizon and locality: Nodular limestone at Schübelebene in Frankenwald (Sannemann 1955b; Ziegler 1975).

Material. — 422 specimens.

Diagnosis. — P_1 elements relatively elongated and M elements usually with relatively wide angle between processes.

Remarks. — P_2 elements of the apparatus were identified by van den Boogaard and Kuhry (1979); the complete apparatus was restored by Schülke (1999).

This is a variable species, both in respect to the outline of platform in P_1 elements, which ranges from that typical to *K. ultima* to that of early species of *Palmatolepis*, but also in the prominence of the cusp and curvature of P_2 elements. The mean value of elongation index of the P_1 elements is, however, distinctly higher than in *K. ultima* (Dzik 2002, 2004), remaining elements of the apparatus being hardly distinguishable. In fact, to distinguish these chronospecies a large sample is needed and singler elements are of little taxonomic value.

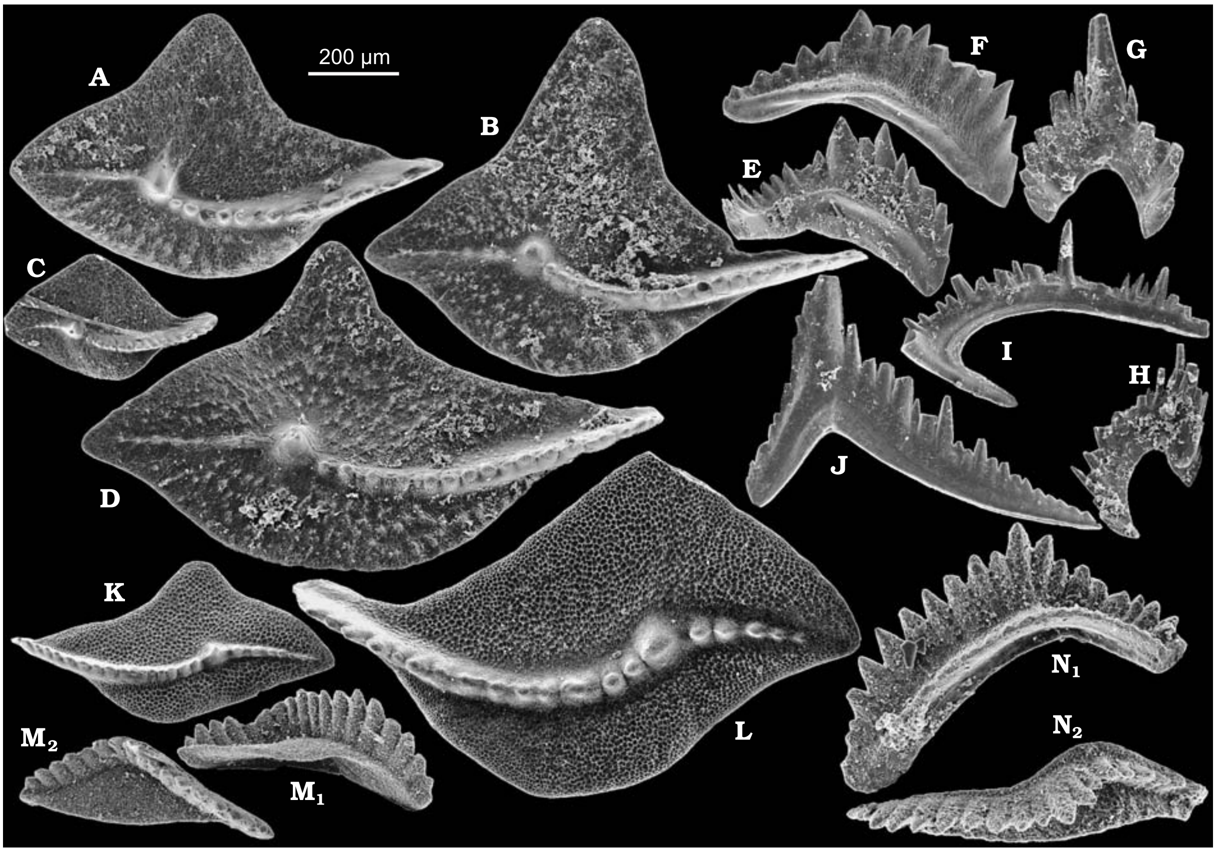


Fig. 81. Species of the palmatolepidid *Klapperilepis* from the early Famennian of the Holy Cross Mountains. **A**–**J**. *K. triangularis* (Sannemann, 1955) from its nominal Zone strata at Kowala (A, B, H–J, sample Ko-153; C–G, sample Ko-154). P_1 (A–D), P_2 (E, F), S_0 (G), S_1 (H), S_{3-4} (I), and M (J) elements; specimens ZPAL cXVI/2732, 2733, 2727, 2728, 2729–2731, and 2734–2736, respectively. **K**–**N**. *Klapperilepis regularis* (Cooper, 1931) from the late *K. triangularis* Zone at Karczówka (K, L) and the *K. crepida* Zone at Kadzielnia (M, Ka-12) and Miedzianka (N, sample Md-1). P_1 (K, L) and P_2 (M, N) elements; specimens ZPAL cXVI/2919, 2820, 2818, and 2955.

Some late populations (e.g., Pł-1; Fig. 80H–R) show robust denticulation of ramiform elements and widely angular processes of the M element typical of *Palmatolepis initialis* sp. n.

Occurrence. — Zone of its own at Płucki, Karczówka, Kowala, and Wietrznia.

Klapperilepis regularis (Cooper, 1931)
(Figs 81K–N and 134)

Type horizon and locality: Woodford Shale of the Arbuckle Mountains, Oklahoma (Cooper 1931).

Material. — 222 specimens.

Diagnosis. — Sinuously curved P_1 elements with subparallel margins of wide platform; angularly bent P_2 elements with low denticles and posteriorly wide platform.

Remarks. — Apparatus was partially restored by Schülke (1999) with the M element indicating a relationship to *Klapperilepis triangularis*. P_2 elements of the same morphology as those from the Montagne Noire occur in the Holy Cross Mountains.

Occurrence. — The late *K. triangularis* and *K. crepida* zones at Jabłonna, Karczówka, Kadzielnia and Kowala.

Klapperilepis protorhomboidea (Sandberg *et* Ziegler, 1973)
(Figs 82A–C and 134)

Type horizon and locality: 7.5–8.5 m above the base of the West Range Limestone at Bactrian Mountain, Nevada.

Material. — 32 specimens.

Diagnosis. — Platform in minute P_1 element of variable, more or less rhomboidal outline and with irregularly distributed tubercles, mostly on the ventral anterior quadrant.

Remarks. — Apparatus was restored by Schülke (1995). The species changes into *K. rhomboidea* but the transition is rather unclear because of the great population variability and generally low number of elements in studied samples.

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

Klapperilepis rhomboidea (Sannemann, 1955)
(Figs 82D–H and 134)

Type horizon and locality: Nodular limestone of upper *Cheiloceras* Stufe at Kirchgattendorf in Frankenwald (Sannemann 1955b; Ziegler 1975).

Material. — 557 specimens.

Diagnosis. — Platform in minute P_1 element of angularly oval outline, without posterior lobe, smooth.

Remarks. — Metzger (1994) proposed a P_2 element identification that seems unlikely to be correct. The species is well represented in some samples by P_1 elements but other elements of the apparatus are difficult to collect because of their small size. They are identified as belonging to this species mostly on the basis of their unusually primitive morphology compared with the age of the sample.

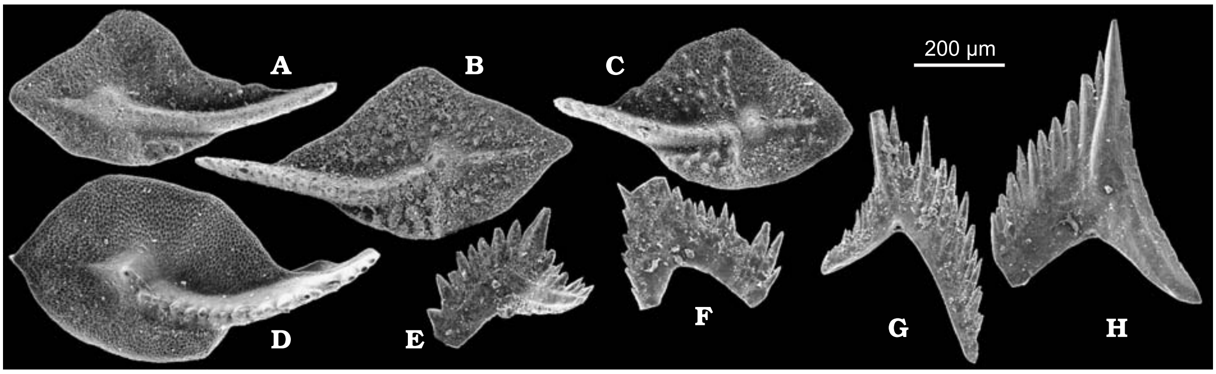


Fig. 82. Palmatolepidids of the *K. rhomboidea* lineage from the Holy Cross Mountains. **A**–**C**. *Klapperilepis protorhomboidea* (Sandberg *et* Ziegler, 1973) from the mid *K. triangularis* Zone at Jabłonna (sample J-54). P_1 elements; specimens ZPAL cXVI/2737–2739. **D**–**H**. *Klapperilepis rhomboidea* (Sannemann, 1955) from the *C. quadrantinodosa* Zone at Łagów (sample Ł-32). P_1 (D), P_2 (E), S_2 (F), and M (G, H) elements; specimens ZPAL cXVI/1370–1375, respectively.

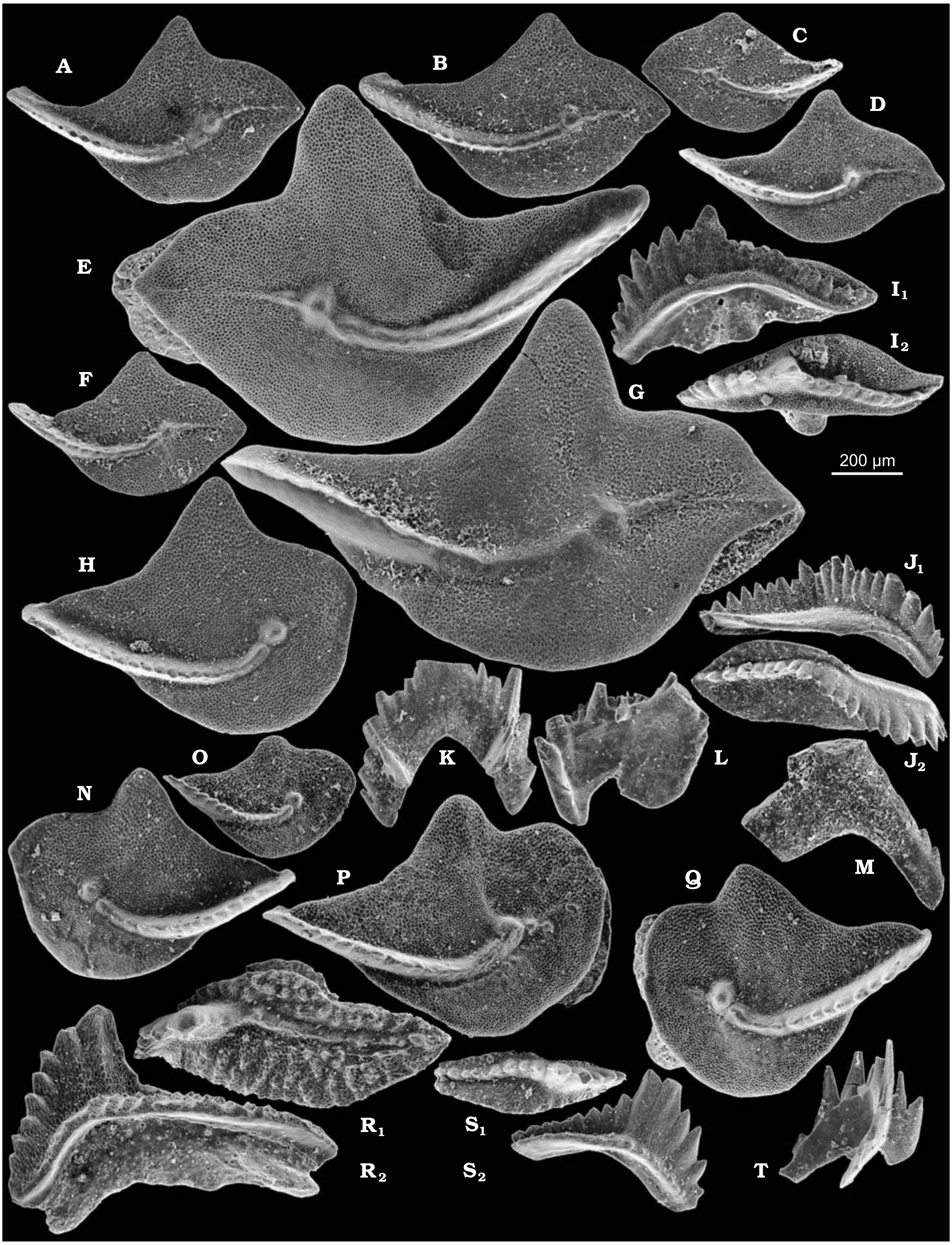


Fig. 83. Palmatolepidids of the *K. circularis* lineage. **A**–**M**. *Klapperilepis wolskae* (Ovnatanova, 1969) from the late *K. triangularis* Zone at Wietrznia (A–D, F–H, J, K, and M, sample Wtr-27) and Karczówka (E, I, and L) in the Holy Cross Mountains. P_1 (A–H), P_2 (I, J), S_2 (K), and M (M) elements; specimens ZPAL cXVI/1449, 2795, 1450, 2949, 1451, 2948, 2806, 2796, 2950, 1452, 1453, 2951, 1454, and respectively. **N**–**T**. *Klapperilepis circularis* (Szulczewski, 1971) from the *K. crepida* Zone at Miedzianka (N, S, T, sample Md-1), Jabłonna (O, P, bed 7), and Łagów? (S, T, sample Ł-Mec). P_1 (N–Q), P_2 (R, S), and S_1 (T) elements; specimens ZPAL cXVI/2952, 2958, 2959, 2956, 2957, and 2953, 2954, respectively.

Occurrence. — The late *K. crepida* Zone (with *C. klapperi*) at Kadzielnia and the *C. quadrantinodosa* Zone at Kowala, Łagów, and Miedzianka. The species occurs also in the Dębnik area (Baliński 1995).

Klapperilepis wolskae (Ovnatanova, 1969)
(Figs 83A–M and 133)

Type horizon and locality: Sandonsk stage at depth 375.4–377.8 m of borehole Ilmen in Woronezh region, Russia; crepida Zone (Ziegler 1975).

Material. — 236 specimens.

Diagnosis. — Oval platform of P_1 elements with prominent narrow extension of the posterior lobe.

Remarks. — Elements of the kind attributed to the apparatus of this species by Metzger (1994) do not occur in the Holy Cross Mountains (perhaps this is a partial apparatus of a new species of *Syncladognathus*) and a different composition is suggested here, although the evidence remains very weak. P_1 elements are extremely variable in Wietrznia (Wtr-27), ranging from an outline resembling that of *K. triangularis* to that of *K. circularis* (Fig. 83D, H).

Occurrence. — The late *K. triangularis* and the early *K. crepida* zones at Płucki, Wietrznia, Karczówka, and Jabłonna.

Klapperilepis circularis (Szulczewski, 1971)
(Figs 83N–T and 133)

Type horizon and locality: Sample X.4 from a bed of cephalopod limestone at the Kadzielnia quarry with early *K. termini*, the *K. crepida* Zone, Holy Cross Mountains.

Material. — 312 specimens.

Diagnosis. — Subcircular outline of platform of P_1 elements with short and wide extension of the posterior lobe and blunt dorsal tip.

Remarks. — Elements of the species are generally much smaller than those of the ancestral *K. wolskae*, even at a stage of apparent maturity. The main distinguishing character is the rounded dorsal tip of the platform and strongly curved blade. No other apparatus elements have been identified with reasonable confidence.

Occurrence. — The *K. crepida* Zone at Kadzielnia, Jabłonna, Wietrznia, Miedzianka, and Kowala. The species occurs also in the Dębnik area (Baliński 1995).

Klapperilepis schuelkei sp. n.
(Figs 84A–H and 133)

Holotype: Specimen ZPAL cXVI/1240 (Fig. 84A).

Type horizon and locality: Sample Pł-42, early Famennian earliest *K. triangularis* Zone at Płucki, Holy Cross Mountains.

Derivation of name: To honour the contribution of Immo Schülke to understanding this species.

Material. — 25 specimens.

Diagnosis. — Smooth platform of P_1 elements with pointed lobe, M element with fan-like arrangement of denticles, P_2 elements with weakly developed platform and regular denticulation.

Remarks. — The apparatus of this species was restored by Schülke (1999) as *Palmatolepis arcuata*, but as I already pointed out elsewhere (Dzik 2002, p. 624), the type horizon of the holotype of *Palmatolepis arcuata* of Schülke (1995) is of significantly younger age and cannot serve as the name-bearer for it. Instead, I suggested *Palmatolepis marginata clarki* Ziegler, 1962 as possibly conspecific with this early member of the *Klapperilepis* lineage, although the latter species has been synonimized with *Tripodellus variabilis* by Schülke (1999). Without additional topotype material large enough to enable apparatus reconstruction it is hard to decide on such subjects and the only basis for this decision was that the type specimen of *K. clarki* shows a more rounded appearance of the lobe and its more transverse direction that is typical for *T. variabilis*. Admittedly, the three specimens from the type horizon illustrated by Ziegler (1962, pl. 2: 20–25) show a robust platform margin typical of early *Tripodellus*. Moreover, the co-occurrence of the type material with the rather advanced member of the *Klapperilepis* lineage, *K. quadrantinodosolobata*, supports the Schülke's (1999) idea that *P. clarki* is a member of another lineage, thus belonging rather to *Tripodellus*. To clarify these nomenclatorial uncertainties, I propose a new name for this species, based on the material from the earliest Famennian and accept Schülke's (1999) interpretation of *T. clarki*.

Occurrence. — The earliest *K. triangularis* Zone at Płucki.

Klapperilepis spathula (Schülke, 1995)
(Figs 84I–L and 133)

Type horizon and locality: Bed 14 at the Upper Coumiac quarry near Cessenon, Montagne Noire (Schülke, 1995).

Material. — 49 specimens.

Diagnosis. — P_1 element with long and narrow extension of the posterior lobe, its surface ornamented with irregular tuberculation, P_2 elements flat, without platform, regularly denticulated and with posteriorly bent dorsal process.

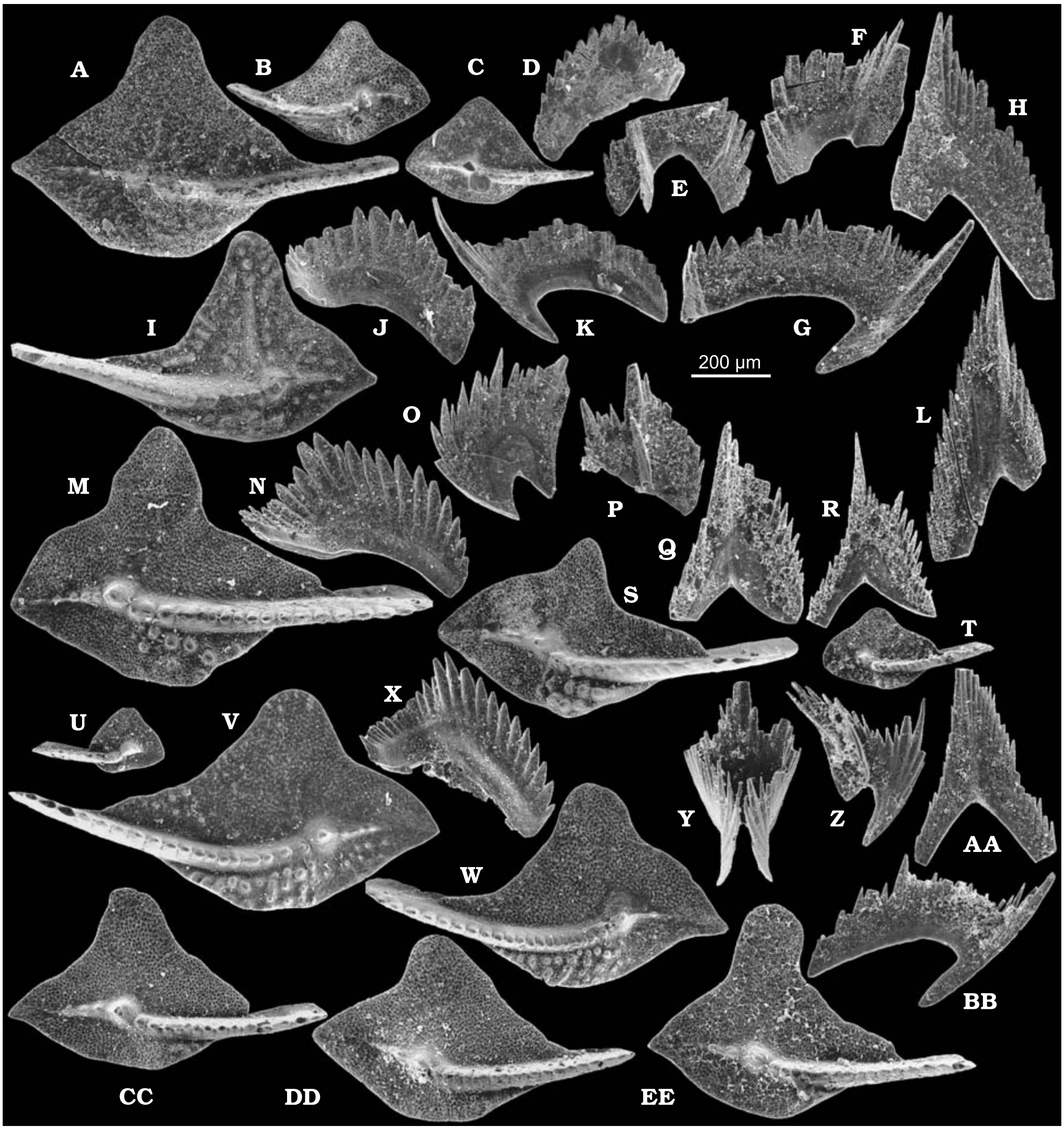


Fig. 84. Early Famennian lobate palmatolepidids from the Holy Cross Mountains. **A–H**. *Klapperilepis schuelkei* sp. n. from the *K. triangularis* Zone strata at Płucki (sample Pł-42; for location and details see Dzik 2002). P_1 (A–C), P_2 (D), S_0 (E), S_1 (F), S_2 (P), S_{3-4} (G), and M (H) elements; specimens ZPAL cXVI/1240 (holotype, A), 1242, 1241, and 1243–1247, respectively. **I–L**. *Klapperilepis spathula* (Schülke, 1995) from the mid *K. triangularis* Zone at Jabłonna (samples J-53, I, J, L and J-53a, K). P_1 (I), P_2 (J), S_{3-4} (K), and M (L) elements; specimens ZPAL cXVI/1262, 1263, 1227 and 1264, respectively. **M–BB**, **CC–EE**?. *Klapperilepis quadrantinodosolobata* (Sannemann, 1955) from the late *K. triangularis* Zone at Jabłonna (M, N, sample J-42; O–S, sample J-45a) and Wietrznia (T–DD, sample Wtr-27). P_1 (M, S–W, possibly CC–EE), P_2 (N and X), S_0 (Y), S_1 (P and Z), S_2 (O), S_{3-4} (BB), and M (Q, R, AA) elements; specimens ZPAL cXVI/1412, 1413, 1330, 1329, 1332, 1331, 1327, 1328, 1433, 1441, 1431, 1434, 1435, 1436, 1439, 1438, 1429, 1432, and 1430, respectively.

Remarks. — Apparatus restoration of Schülke (1995) is confirmed by data from the Holy Cross Mountains. Apart from the platform shape, the most characteristic aspect of this and successive species of the lineage is the stepping arrangement of alternating denticles of S_0 to S_2 elements giving them a highly ordered appearance unknown in any other Famennian conodonts. Also P_2 elements, lacking platform and strongly bent, are of much diagnostic value in this lineage.

Occurrence. — The late *K. triangularis* Zone at Płucki, Wietrznia, Karczówka, Jabłonna, and Kowala.

Klapperilepis quadrantinodosolobata (Sannemann, 1955)
(Figs 84M–BB, CC–EE?, and 133)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955a; Ziegler 1975).

Material. — 4,256 specimens.

Diagnosis. — P_1 element with prominently tuberculated anterior lobe and a tongue-like extension of the smooth posterior lobe, flat P_2 elements with strongly bent dorsal process.

Remarks. — Apparatus composition was restored by Metzger (1994) and confirmed by Schülke (1995). This is the end-member of its lineage sharing with its older relatives the highly regular appearance of ramiform elements.

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

Klapperilepis delicatula (Branson *et* Mehl, 1934)
(Figs 85 and 133)

Type horizon and locality: Base of the Saverton Shale at Sees Creek in Monroe County, Missouri (Ziegler 1975).

Material. — 208 specimens.

Diagnosis. — P_1 element with triangular outline of the platform extending into an extremely wide posterior lobe.

Remarks. — This is the first, and probably only up to the present Famennian conodont with the apparatus confirmed by a natural assemblage (Puchkov *et al.* 1981). Its preservation is not good enough to offer details on morphology of individual elements but the relatively wide angle between processes of the M element resembles early species of *Klapperilepis*. In sample Pł-1 relatively numerous P_1 elements are associated with those of *Palmatolepis sandbergi* and *Tripodellus clarki* and M elements of *K. quadrantinodosolobata* type. This leaves little choice and most probably *K. delicatula* belongs to an advanced lineage of *Klapperilepis*. Perhaps the Russian apparatus represents an early stage in its evolution with characters of the ancestral *K. ultima* still preserved.

Occurrence. — The *K. triangularis* Zone at Płucki, Wietrznia, Miedzianka, Jabłonna, and Kowala.

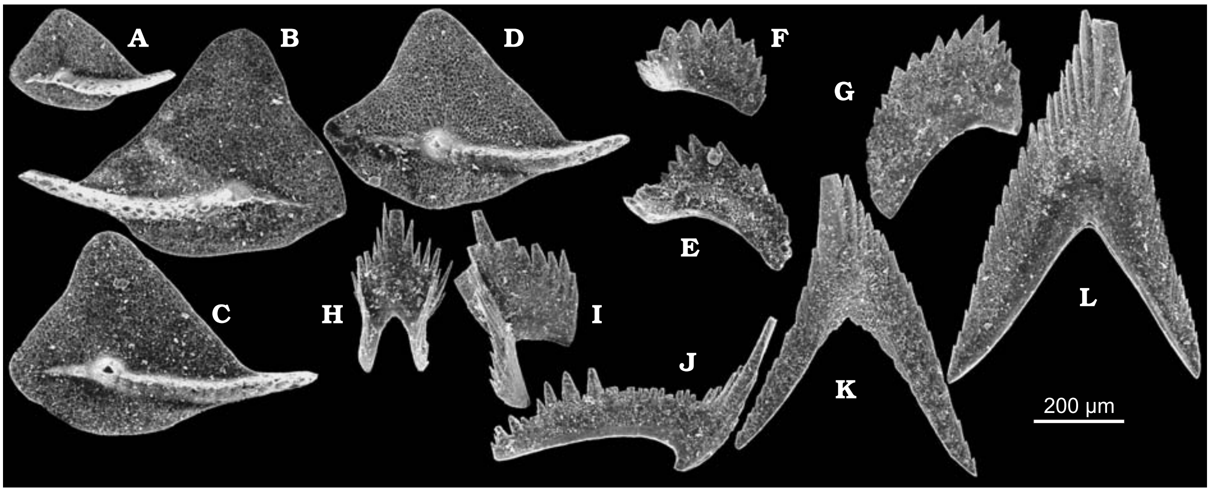


Fig. 85. Palmatolepidid *Klapperilepis delicatula* (Branson *et* Mehl, 1934) from the *K. triangularis* Zone at Płucki (A–G, sample Pł-1) in the Holy Cross Mountains. P_1 (A–D), P_2 (E–G), S_0 (H), S_1 (I), S_2 (O), S_{3-4} (J), and M (K, L) elements; specimens ZPAL cXVI/1359, 1361, 1342, 1360, 1367, 1368, 1362–1366, and 1369, respectively.

Klapperilepis robusta (Schülke, 1995)
(Figs 86A–D and 133)

Type horizon and locality: Bed 72 in Schmidt's quarry in the Kellerwald in the Rhenish Slate Mountains, together with *K. regularis* (Schülke 1995).

Material. — 59 specimens.

Diagnosis. — Platform of P_1 element with small but distinct posterior lobe and pointed dorsal end; juveniles obliquely rhomboidal in outline.

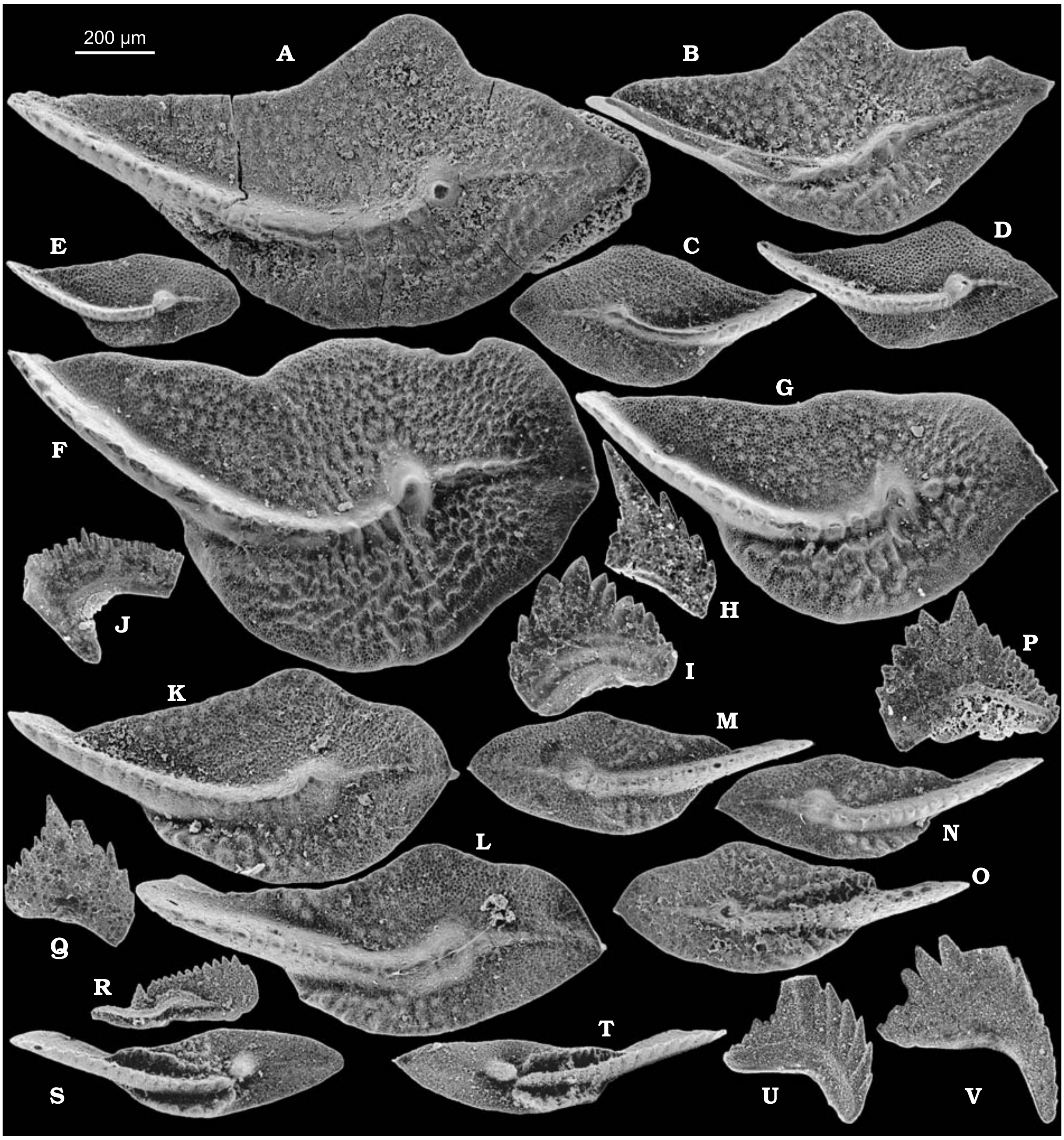


Fig. 86. Robust palmatolepidids of the *K. crepida* group from the Holy Cross Mountains. **A**–**D**. *Klapperilepis robusta* (Schülke, 1995) from the late *K. triangularis* Zone at Wietrznia (A, sample Wtr-26; B–D, sample Wtr-27). P_1 elements; specimens ZPAL cXVI/2797–2800. **E**–**J**. Typical *Klapperilepis crepida* (Sannemann, 1955) from its nominal zone at Wietrznia (sample Wtr-21). P_1 (F, G), P_2 (H, I), and S_{3-4} (J) elements; specimens ZPAL cXVI/2808, 2809, 1962, 2812, and 2811, respectively. **K**–**Q**. Transition series encompassing *K. crepida* and early *K. termini* (Sannemann, 1955) morphologies from Kadzielnia (K–O, Q, sample Ka-14) and Jabłonna (P, sample J-65). P_1 (K–O) and P_2 (P, Q) elements; specimens ZPAL cXVI/2923–2927, 2876, and 2928, respectively. **R**–**V**. Late *K. termini* (Sannemann, 1955) from the *K. crepida* Zone at Kadzielnia (sample Ka-12). P_1 (R–T), P_2 (U), and M (V) elements; specimens ZPAL cXVI/2815, 2813, 2814, and 2816, 2817, respectively.

Remarks. — P_2 elements were identified by van den Boogaard and Kuhry (1979, fig. 18), the complete apparatus by Schülke (1999). The primitive appearance of the M elements indicates a relationship to *Klapperilepis triangularis*. Platform of P_1 element extending almost to the end of the free blade is shared by this species with its successor, *K. crepida*.

Occurrence. — The latest *K. triangularis* Zone at Płucki and Wietrznia.

Klapperilepis crepida (Sannemann, 1955)
(Figs 86E–L and 133)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955*a*; Ziegler 1975).

Material. — 840 specimens.

Diagnosis. — Platform of P_1 element almost lacking the posterior lobe and with blunt dorsal apex, ornamented with irregularly distributed tubercles.

Remarks. — P_2 elements of the apparatus were identified by Schülke (1999). This is a highly characteristic species owing to the robust and somewhat irregular appearance of the platform. The transition from *K. robusta* to *K. crepida* seems to be gradual and identification of some samples may be difficult because of the great variability of both species.

Occurrence. — Zone of its own at Jabłonna, Kadzielnia, Wietrznia, Kowala, and Miedzianka.

Klapperilepis termini (Sannemann, 1955)
(Figs 86M–V and 133)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955a; Ziegler 1975).

Material. — 931 specimens.

Diagnosis. — Platform of P_1 element with rows of high tubercles on both sides of the ventral blade and prominent, isolated cusp.

Remarks. — The P_2 element of the apparatus was identified by Schülke (1999) and such elements also occur in the Holy Cross Mountains.

As already shown by Schülke (1995), early populations of the species (in my material samples J-65, Ka-14, Wtr-25, and Md-27) are morphologically transitional to *K. crepida* and *K. robusta*, with some elements having only one row of relatively low denticles posterior to the blade, others lacking them completely and differing from associsted *K. crepida* only in a narrower platform. There is an apparent change within the lineage towards a more and more narrower platform with a stronger separation of its smooth and flat dorsal area and extremely high ridges on both sides of the blade. The ridges do not reach the cusp, which forms an isolated high conical structure in the middle of the element. This change seems to be of much correlative value.

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

Genus ***Tripodellus*** Sannemann, 1955

Type species: *Tripodellus flexuosus* Sannemann 1955a (P_2 element of *T. minutus*) from the Famennian of Frankenwald.

Diagnosis. — Apparatus with triramous or at least angularly bent P_2 elements, lacking platform in underived species.

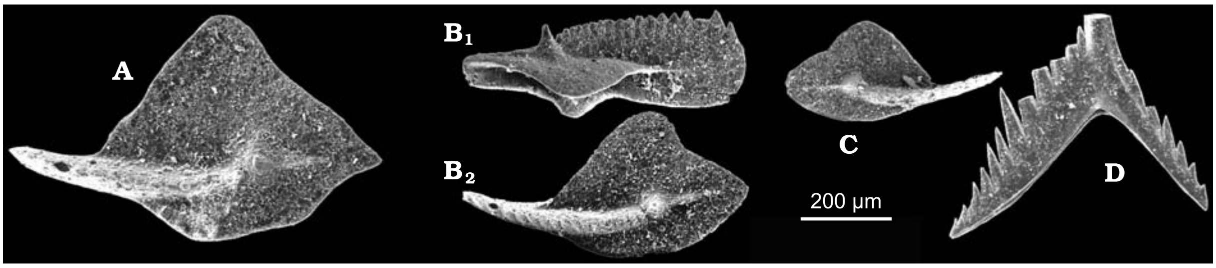


Fig. 87. Earliest species of the palmatolepidid *Tripodellus*, *T. clarki* (Ziegler, 1962) with biramous P_2 elements from *K. triangularis* Zone strata at Płucki (sample Pł-42) in the Holy Cross Mountains. P_1 (A–C) and M (D) elements; specimens ZPAL cXVI/1250, 1249, 1248, and 1251, respectively.

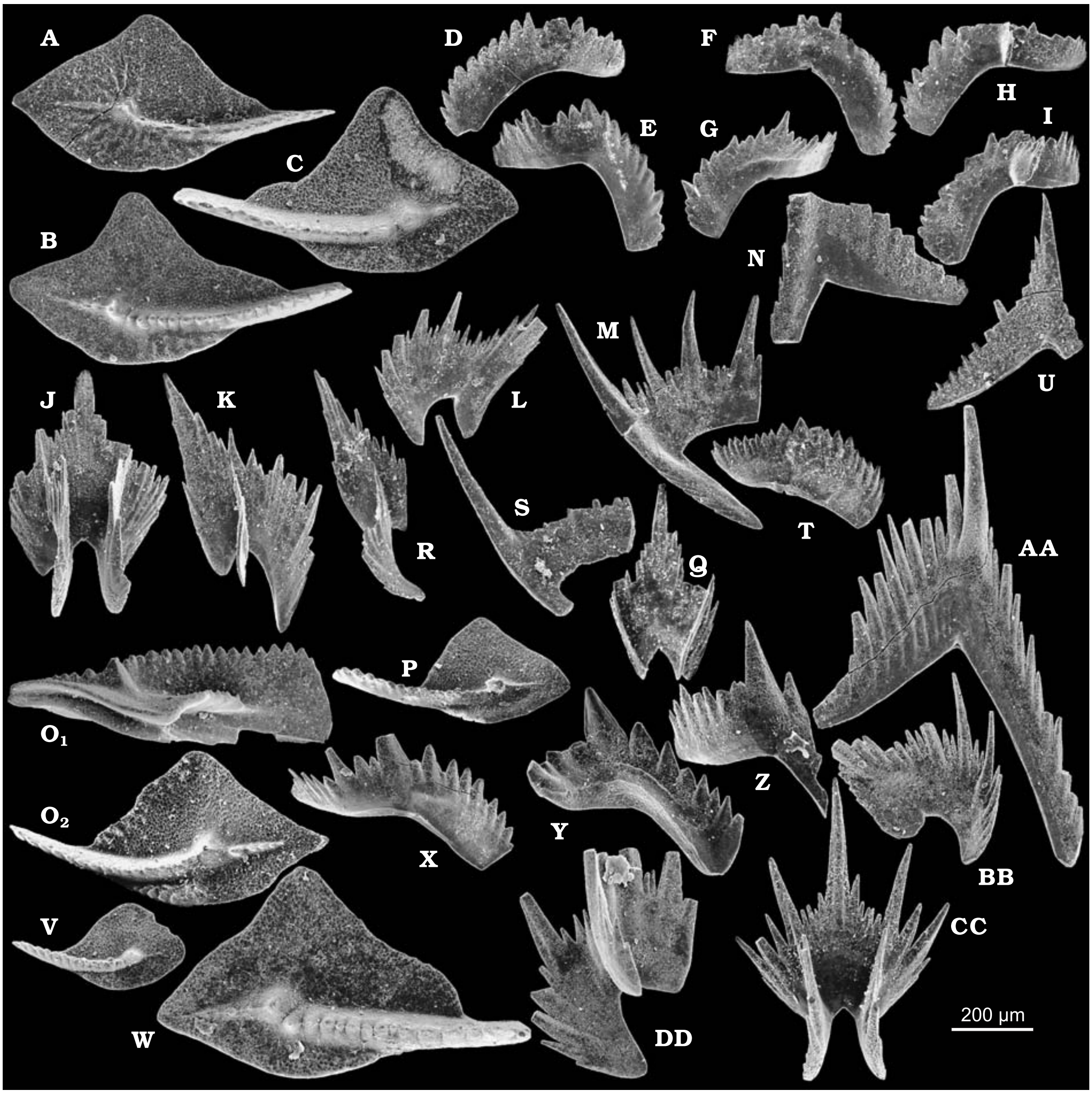


Fig. 88. Typical *Tripodellus clarki* (Ziegler, 1962) from *K. triangularis* Zone strata at Jabłonna (A, C, D, F–H, sample J-53; B, C, E, G, J–N, sample J-53a; V–CC, sample J-58) and Płucki (O–U, sample Pł-1) in the Holy Cross Mountains. P_1 (A–C, O, P, V, W), P_2 (D–I, T, X–Z), S_0 (J, Q, and CC), S_1 (K, R, DD), S_2 (L, BB), S_{3-4} (M, S), and M (N, U, and AA) elements; specimens ZPAL cXVI/1250, 1249, 1248, and 1251, respectively.

Tripodellus clarki (Ziegler, 1962)
(Figs 87, 88, and 134)

Type horizon and locality: Bed 23 in trench II at Seßacker near Oberscheld, Rhenish Slate Mountains (Ziegler 1975).

Material. — 623 specimens.

Diagnosis. — Gently bent P_2 element without platform, rhomboidal outline of relatively wide platform in P_1 element, short processes of M element.

Remarks. — The apparatus was restored by Schülke (1995) as *Palmatolepis variabilis* and *P. delicatula postdelicatula*. I failed to distinguish between these morphologies in my highly variable material from the earliest Famennian. Populations from the late *K. triangularis* Zone are much more advanced towards the morphologies typical of *Tripodellus* and they deserve taxonomic separation as *T. variabilis*.

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

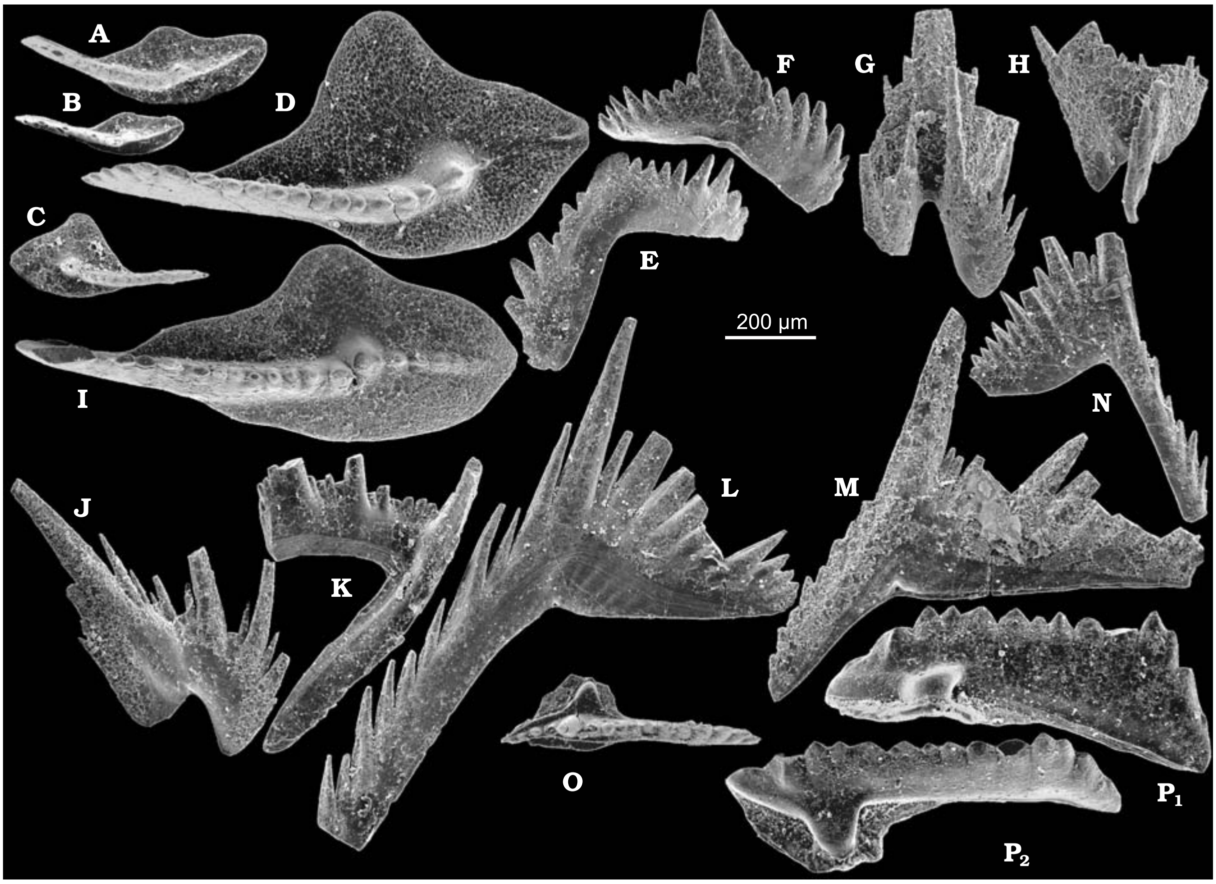


Fig. 89. Species of the palmatolepidid *Tripodellus* with biramous P_2 elements from the *K. crepida* Zone at Jabłonna (A–O, sample J-45a) and Wietrznia (P, sample Wtr-21) in the Holy Cross Mountains. **A**–**N**. *T. variabilis* (Sannemann, 1955). P_1 (A–D, I), P_2 (E, F), S_0 (G), S_1 (H), S_2 (J), S_{3-4} (K), and M (L–N) elements; specimens ZPAL cXVI/1315–1322, 2757, 1338, 1323, 1325, 1326, and 1324, respectively. **O**–**P**. *T. subgracilis* (Bischoff, 1956). P_1 elements; specimens ZPAL cXVI/2834 and 1967.

Tripodellus variabilis (Sannemann, 1955)
(Figs 89A–N and 134)

Type horizon and locality: Black limestone with *Nehdenites verneuili* at Breitengrund, Frankenwald (Sannemann 1955a; Ziegler 1975).

Material. — 22,931 specimens.

Diagnosis. — Angularly bent P_2 element, elongated platform in P_1 element with short, rounded posterior lobe, elongate external process of M element.

Remarks. — It is convenient to separate the early part of the *Tripodellus* lineage into at least three chronospecies (*T. clarki*, *T. variabilis*, and *T. minutus*). *T. variabilis* has been chosen by Schülke (1999) as the name for the first species of the lineage, but there is hardly any evidence that the material of Sannemenn (1955a) truly represents this species as long as advanced *K. termini* and *K. crepida* co-occur in the same bed. The P_2 elements of the palmatolepidids are highly variable and at this stage of the evolution they are hardly of much diagnostic value.

P. variabilis is a senior synonym of *Palmatolepis minuta wolskae* of Szulczewski (1971), on the evidence of material from a bed at Kadzielnia with early *P. termini*.

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

Tripodellus subtilis (Khalymbadzha *et* Chernysheva, 1978)
(Figs 90 and 134)

Type horizon and locality: Famennian of the Urals.

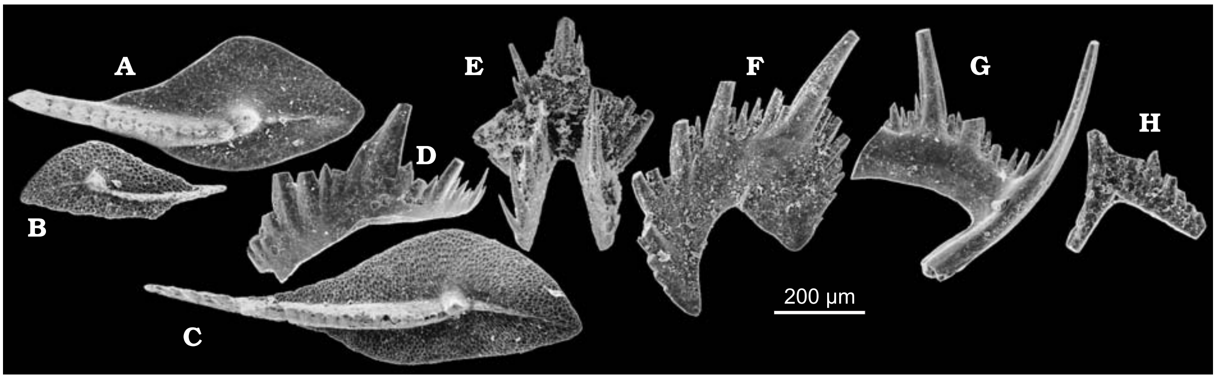


Fig. 90. Palmatolepidid *Tripodellus subtilis* (Khalymbadzha *et* Chernysheva, 1978) with biramous P_2 elements from the late *K. triangularis* Zone at Wietrznia (A, D–H, sample Wtr-27) and the *K. crepida* Zone at Jabłonna (B, C, sample J-45a) in the Holy Cross Mountains. P_1 (A–C), P_2 (D), S_0 (E), S_2 (F), $S_{3–4}$ (G), and M (H) elements; specimens ZPAL cXVI/1422, 1314, 1313, and 1424–1428, respectively.

Material. — 24 specimens.

Diagnosis. — P_1 element with narrow, convex platform of asymmetric lanceolate outline, extending ventrally to half length of the blade.

Remarks. — Taxonomic identification of the species is based on Metzger (1994). Rare elements associated with P_1 elements of the species include biramous P_2 elements, which suggests its origin from *T. variabilis*. If true, this would then be a relict lineage evolving towards reduction of the platform in P_1 elements.

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

Tripodellus lobus (Helms, 1963)
(Figs 91 and 134)

Type horizon and locality: A block of *Cheiloceras* Stufe limestone from a Carboniferous breccia at Langenaubach, Rhenish Slate Mountains (Ziegler 1975).

Material. — 653 specimens.

Diagnosis. — Platform in P_1 element with prominent, narrow posterior lobe, in juvenile specimens oriented somewhat ventrally; angularly bent biramous P_2 element.

Remarks. — Apparatus of the species was reconstructed by Metzger (1994).

Specimens of juvenile morphology typical of this species co-occur with late populations of *T. minutus* and there seems to be no transition between them. This is apparently a successor of *T. variabilis* that became separated from the main lineage represented by *T. minutus* as a result of an allopatric speciation process and subsequent merging of their populations.

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

Tripodellus subgracilis (Bischoff, 1956)
(Figs 89O, P and 134)

Type horizon and locality: *K. crepida* Zone at Bicken quarry (Bischoff 1956).

Material. — Three specimens.

Diagnosis. — P_1 element with very narrow platform bearing sharply triangular small posterior lobe.

Remarks. — Apparatus was restored by Metzger (1994) for a more advanced population with well denticulated posterior process. Biramous P_2 element indicates a close relationship to *T. lobus* and the Polish specimens, lacking denticulation of the posterior process, are transitional to those illustrated by Metzger (1994). *Palmatolepis parva* Klapper *et al*., 2004 may be ancestral to this species.

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

Tripodellus minutus (Branson *et* Mehl, 1934)
(Figs 9D, 92A–J, and 134)

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

Material. — 2,504 specimens.

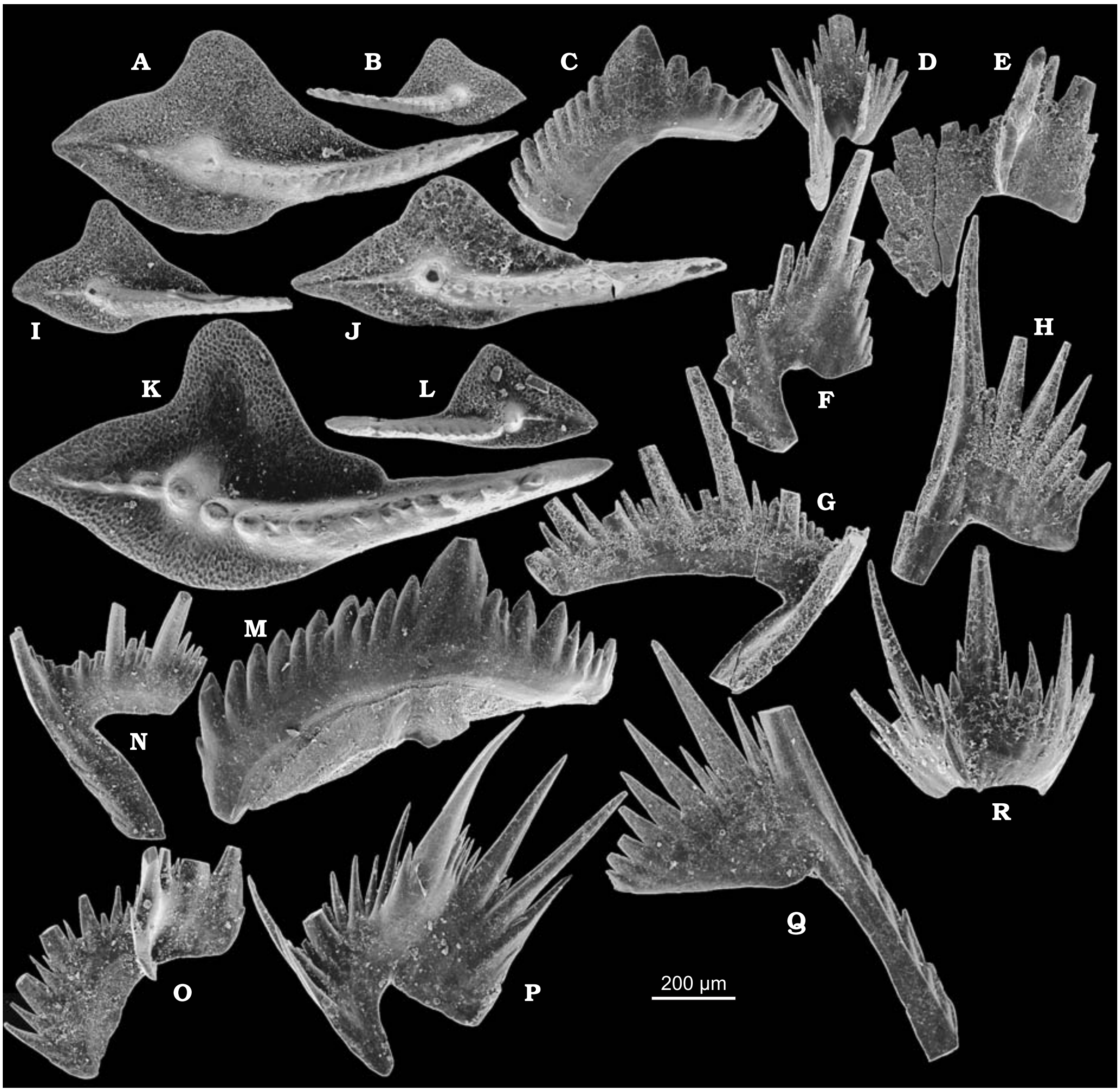


Fig. 91. Late palmatolepidid *Tripodellus lobus* (Helms, 1963) with biramous P_2 elements from the late *K. triangularis* Zone at Wietrznia (I, J, sample Wtr-27), the *K. crepida* Zone at Jabłonna (A–H,) sample J-44, and the late *K. crepida* (with *K. rhomboidea*) Zone at Łagów (K–R, sample Mak-3-4) in the Holy Cross Mountains. P_1 (A, B, I, J, K, L), P_2 (C, M), S_0 (D, R), S_1 (E, O), S_2 (F, P), $S_{3–4}$ (G, N), and M (H, Q) elements; specimens ZPAL cXVI/2742, 2741, 2743–2748, 1423, 1421, 2750, 2749, 2751, 2755, 2753, 2754, 2756, and 2752, respectively.

Diagnosis. — Triramous P_2 element, rhomboidal outline of platform of P_1 almost without any lobe; straight or slightly asymmetric juvenile specimens.

Remarks. — The P_2 element was identified by van den Boogaard and Kuhry (1979). Apparatus was restored by Metzger (1994). P_2 elements with additional process occur rarely but consistently in samples with *T. variabilis*, being probably end-members of population variability expressed mostly in bending of the element. They start to dominate the sample in the Kadzielnia section between samples Ka-3 and Ka-5.

Occurrence. — The *K. crepida* Zone to the earliest *C. quadrantinodosa* Zone at Kadzielnia, Łagów, Jabłonna, Wietrznia, Miedzianka, and Kowala.

Tripodellus donoghuei sp. n.
(Figs 92K–Q and 134)

Holotype: Specimen ZPAL cXVI/2763 (Fig. 92N).

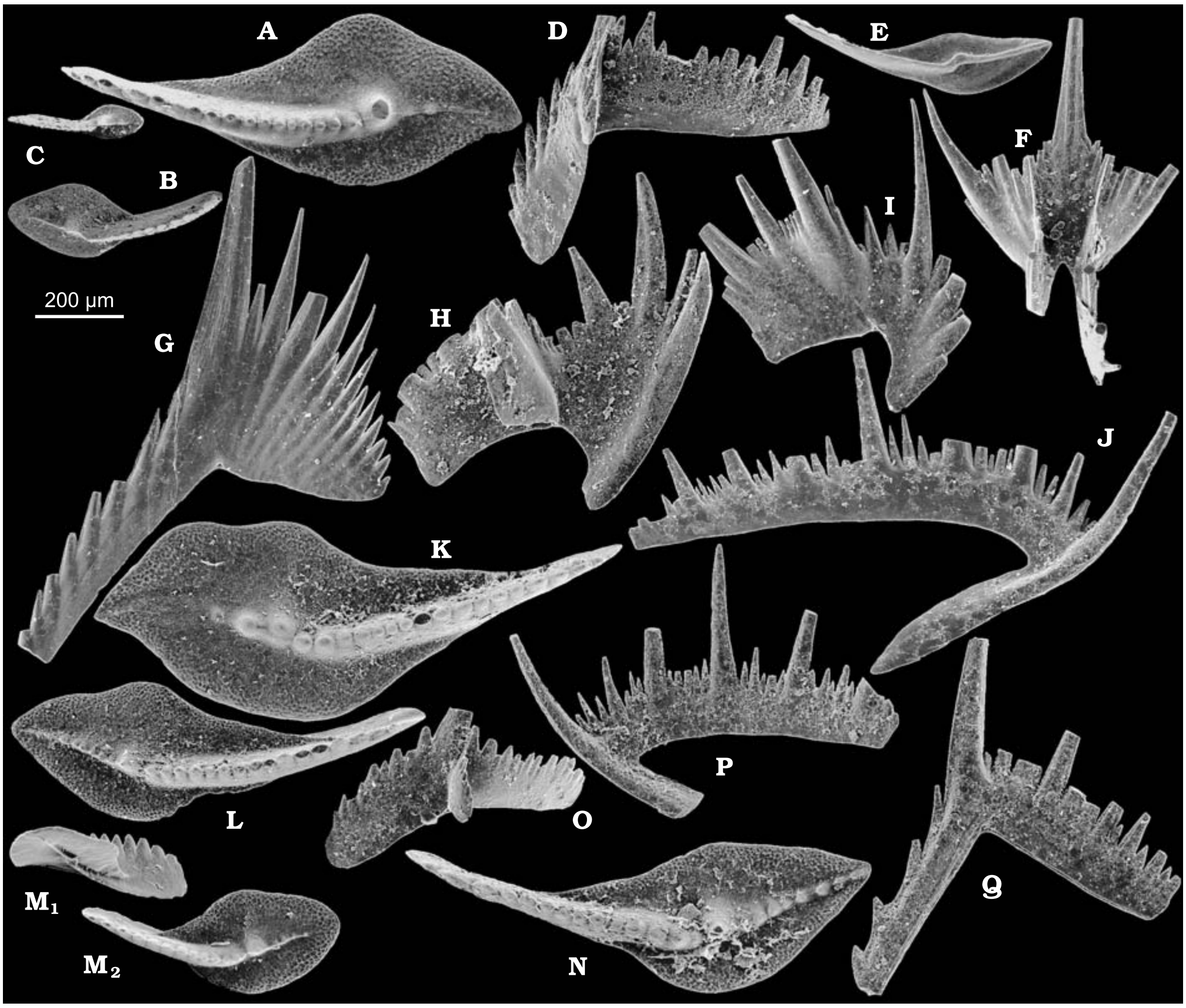


Fig. 92. Species of the palmatolepidid *Tripodellus* with triramous P_2 elements from the Holy Cross Mountains. **A**–**J**. *T. minutus* (Branson *et* Mehl, 1934) from the *C. quadrantinodosa* Zone at Łagów (sample Ł-28). P_1 (A–C, E), P_2 (D), S_0 (F), S_1 (H), S_2 (I), $S_{3–4}$ (J), and M (G) elements; specimens ZPAL cXVI/1402–1405, 2940, 1406, 1410, 1408, 1407, and 1409, respectively. **K**–**Q**. *T. donoghuei* sp. n. from the early *L. styriacus* Zone at Ostrówka (K, M, N, sample Ost-12) and the *P. trachytera* Zone at Jabłonna (L, O–Q, bed 24). P_1 (K–N), P_2 (O), $S_{3–4}$ (P), and M (Q) elements; specimens ZPAL cXVI/2764, 2758, 2762, 2763 (holotype, N), and 2759–2761, respectively.

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

Derivation of name: To honour Philip Donoghue for his contribution to understanding the architecture of conodont apparatuses.

Material. — 391 specimens.

Diagnosis. — Twisted P_1 element with wide, lanceolate platform and minute larval basal cone (pit).

Remarks. — The apparatus of this species was already restored by Schülke (1999) as *Palmatolepis* aff. *Pal. gracilis*. Specimens of similar morphology occur in samples with *T. minutus* but there is no gap in variability separating them from the modal morphology of that species. Such a gap can be identified only in samples with *T. schleizius* and *T. lobus* as associated species, although rarely juvenile specimens of *T. schleizius* of comparable size are associated with *T. donoghuei* in its early populations. The oldest sample with juveniles of *T. schleizius* showing a virtually straight blade have been found in Kadzielnia in sample Ka-7, where *T. donoghuei* is missing.

In the outline of the platform *T. donoghuei* resembles members of the *T. gonioclymeniae* lineage but it lacks the stage of "sinuosa" larva with strongly asymmetric basal cone in P_1 elements. It seems to be a successor of *T. minutus*, which originated allopatrically in respect to *T. schleizius*.

Occurrence. — The late *K. crepida* (with *C. klapperi*) to *L. styriacus* zones at Kadzielnia, Jabłonna, Kowala, and Ostrówka.

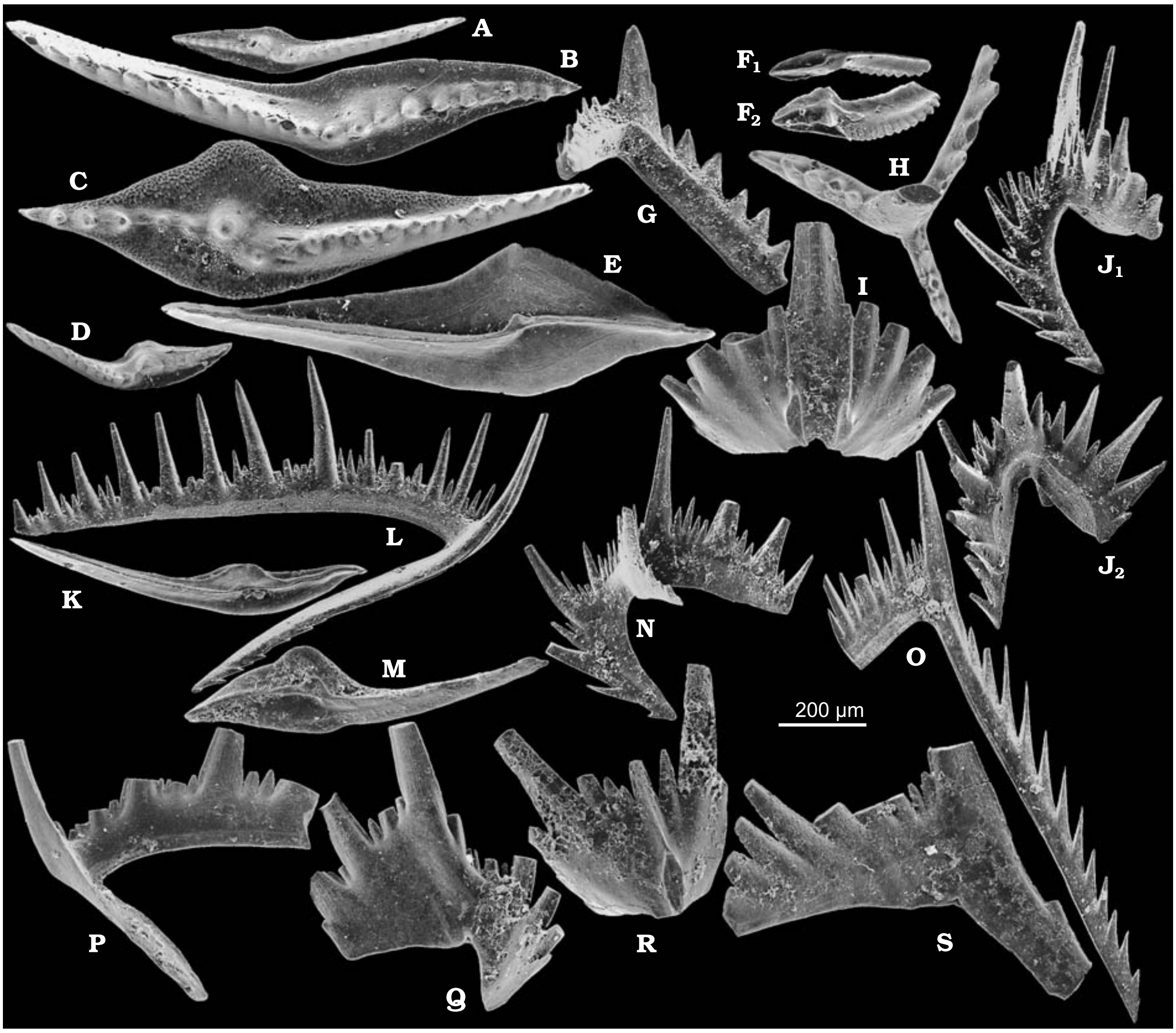


Fig. 93. Palmatolepidid *Tripodellus schleizius* (Helms, 1963) with triramous P_2 elements from the *P. trachytera* Zone at Kowala (B, F, G, J–L, N, O, sample Ko-8a; M, sample Ko-9a) and the early *Lagovignathus styriacus* Zone at Ostrówka (A, C–H, I, P–S, sample Ost-12) in the Holy Cross Mountains. P_1 (A–F, K, M), P_2 (G, H), S_0 (I, J), S_1 (N, R), S_2 (Q), S_{3-4} (L, P), and M (O, S) elements; specimens ZPAL cXVI/2768, 391, 2769, 2766, 2765, 392, 2770, 2771, 393, 2937, 395, 2944, 394, 396, 2774, 2773, 2772, and 2775, respectively.

Tripodellus schleizius (Helms, 1963)
(Figs 9C, 93, and 134)

Type horizon and locality: 6.5 m below the top of the Famennian at Großen Buschteich near Rödersdorf, Thuringia, upper part of the *Platyclymenia* Stufe (Ziegler 1975).

Material. — 5,112 specimens.

Diagnosis. — Clearly separate asymmetric basal cone (pit) and sinuous blade in juvenile P_1 element, platform sometimes disappearing in front of the tip in adults with an angular posterior lobe near the cusp, triramous P_2 element.

Remarks. — The transition from *T. minutus* to *T. schleizius* can be traced through the Łagów section near the base of the *C. quadrantinodosa* Zone. In samples from the Lower Łagów Beds minute specimens of *Tripodellus* are laterally arched and their basal cone remains very small. At the base of the Upper Łagów Beds sigmoidally bent juvenile elements appear with a wide asymmetric basal cone. From some reason in these transitional samples there is a distinct bimodality in size frequency distribution and no intermediate specimens have been found. It looks as if sinuous morphologies had a higher rate of juvenile mortality, perhaps related to metamorphosis at the end of the sinuosa larva stage. The blade is usually more sinuous in adults than it was in older samples but they do not show clear separation of the larval basal cavity. Either it was resorbed, specimens with asymmetry rarely survived to adult stages, or species of two separate lineages co-occurred. The latter possibility seems unlikely, as in samples from somewhat higher beds (e.g., Ł-40) intermediate specimens occur showing continuity between extreme stages of ontogeny. This is the case also with late Famennian samples with *T. gracilis*. They show, however, increased juvenile mortality and are in this respect different from co-occurring conodont species. Perhaps this was an ecologically opportunistic species. In the course of evolution of the lineage within the mid Famennian the basal cavity became wider and wider, as documented in the Kowala section.

The boundary between this chronospecies and its successor *T. gracilis* is difficult to define as the diagnostic characters are very variable in populations and seem to spread gradually in the course of evolution. The type population of *T. schleizius* is uncomfortably close to the end of its range.

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

Tripodellus gracilis (Branson *et* Mehl, 1934)
(Figs 94A–K and 134)

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

Material. — 11,928 specimens.

Diagnosis. — Wide and strongly asymmetric basal cone (pit) of P_1 element, its tip bent posteriorly, rounded lobe near the cusp even in large specimens.

Remarks. — Apparatus was restored by van den Boogaard and Kuhry (1979), and confirmed by myself (Dzik 1991). No specimens of the morphology proposed to be typical for *Tripodellus expansus* (Sandberg *et* Ziegler, 1979) are known from the Holy Cross Mountains but some mature elements with an extremely wide platform approach that morphology (e.g., in sample Ost-5). They share with those from Montana their asymmetric larval basal cavity, which places them in the *T. gonioclymeniae* lineage, but they do not show so strong a widening of the platform and in occlusal view do not differ form *T. gracilis*. In sample Ost-7 the dominant elements with asymmetric larval basal cavity are associated with rare specimens having a wider platform, which do not show a separation of the basal cavity at all, thus being similar in those respects to older populations of *T. gracilis*. In fact, such asymmetry and incipient separation of the basal cone is observable in the population of *T. gracilis* from sample Ost-12, but the basal cone is small and well visible only in juvenile and strongly asymmetric specimens. It seems thus that this stage in the evolution of the *Tripodellus* branch is marked by expansion of juvenile characters to later ontogenetic stages. *Palmatolepis deflectens sigmoidalis* of Ziegler (1962) seems to be based on a juvenile *T. gracilis*.

Possibly, "*Palmatolepis expansa*" is a morphotype within the range of population variability of *T. gracilis*. Perri and Spaletta (1991) classified within "*P. expansa*" specimens that do not show asymmetry of the basal cavity. This indicates how misleading may be the concept of that species and that stratigraphic decisions based on it are of questionable value.

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

Tripodellus mancus (Helms, 1963)
(Figs 94S and 134)

Type horizon and locality: 3 m below the top of the red limestone of the *Platyclymenia* Stufe at Alte Heerstrasse near Oettersdorf, Thuringia (Helms, 1963).

Material. — 12 specimens.

Diagnosis. — Strongly bent P_1 element with obtuse tip of the platform and strongly asymmetric juvenile basal cavity; apparatus unknown.

Remarks. — This is a poorly known species, represented by a few specimens of minute size in all published localities. Perhaps they represent marginal populations of the *T. gonioclymeniae* lineage at the stage of its allopatric separation from the main lineage of *Tripodellus*. Small size of elements seems consistent with apparently paedomorphic evolution of the lineage, marked by expansion of the sinuosa larva stage to the end of ontogeny. The platform of some specimens from Kowala show a pointed dorsal tip, which makes them similar to *T. gonioclymeniae*.

Occurrence. — The early *P. jugosus* Zone at Ostrówka and Kowala.

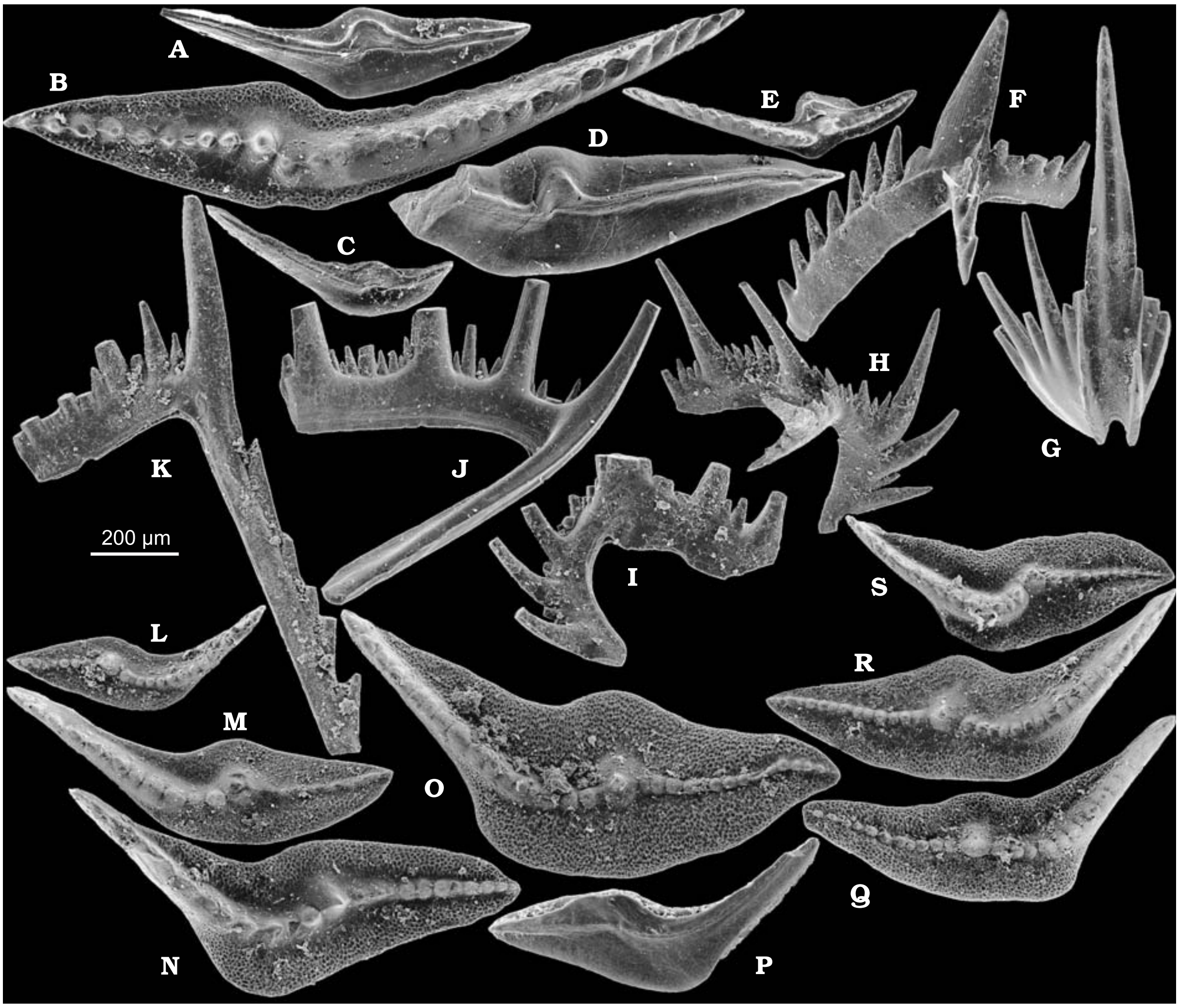


Fig. 94. Late species of the palmatolepidid *Tripodellus* with triramous P_2 elements. **A**–**K**. *T. gracilis* (Branson *et* Mehl, 1934) from the *D. trigonica* (A, sample Ko-166) and *P. jugosus* (C, sample Ko-3) zones at Kowala and the *P. jugosus* Zone at Ostrówka (B, D–K, sample Ost-2). P_1 (A–E), P_2 (F), S_0 (G), S_1 (H), S_2 (I), S_{3-4} (J), and M (K) elements; specimens ZPAL cXVI/2931, 2780, 2934, 2781, 2779, 2782–2787, respectively. **L**–**R**. *T. gonioclymeniae* (Müller, 1956) from the *P. jugosus* Zone at Ostrówka (L, M, Q, sample Ost-2) and Kowala (P, sample Ko-62) in the Holy Cross Mountains and the *P. jugosus* (N, R, sample Dz-8) and the *D. trigonica* (O, sample Dz-7) zones at Dzikowiec in the Sudetes. P_1 elements; specimens ZPAL cXVI/2790, 2777, 2792, 2789, 2788, 2778 an 2791, respectively. **S**. *T. mancus* (Helms, 1963) from the *L. styriacus* Zone at Ostrówka (sample Ost-5). P_1 element; specimens ZPAL cXVI/2776.

Tripodellus gonioclymeniae (Müller, 1956)
(Figs 94L–R and 134)

Type horizon and locality: Grayish brown limestone from the top of Effenberg near Hachen, Rhenish Slate Mountains (Ziegler 1975).

Material. — 243 specimens.

Diagnosis. — Strongly bent P_1 element with platform narrowing to the tip, with its greatest width in the middle length of the element, the asymmetric basal cone continues throughout ontogeny, other elements of the apparatus probably indistinguishable from *T. gracilis*.

Remarks. — No doubt that the lineage *T. mancus* → *T. gonioclymeniae* originated from *T. gracilis*. Sandberg and Ziegler (1979) proposed "*Palmatolepis expansa*" to be the connecting link. As noted above, this morphology is not represented in the Holy Cross Mountains and probably the evolution took place elsewhere, with *T. manca* and *T. gonioclymeniae* being successive immigrants from that source area.

Occurrence. — The late *P. jugosus* to *D. trigonica* zones at Ostrówka, Kowala, aned Dzikowiec.

Genus ***Palmatolepis*** Ulrich *et* Bassler, 1926

Type species: *Palmatolepis perlobata* Ulrich *et* Bassler, 1926 from the “Hardin sandstone” of Tennessee.

Diagnosis. — Apparatus with the symmetry transition series elements bearing weakly developed cusps and irregularly arranged denticles, M element processes in linear arrangement, large P_1 elements with elaborate, usually prominently tuberculated platform.

Palmatolepis initialis sp. n.
(Figs 80H–R, 95, and 135)

Holotype: M element ZPAL cXVI/1261 (Fig. 95Q).

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

Derivation of name: From the initial position of the species in the *Palmatolepis* lineage.

Material. — 2,041 specimens.

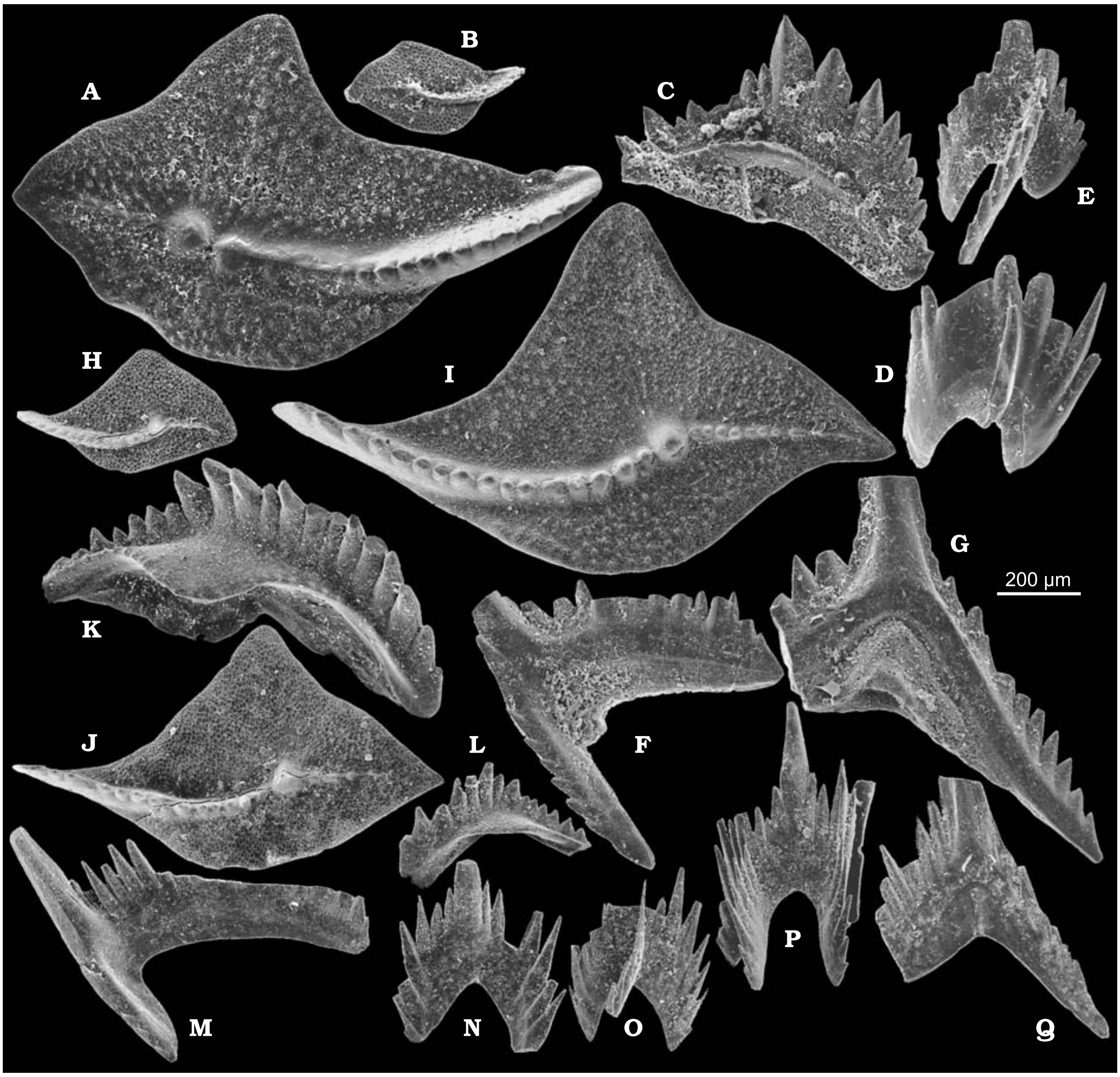


Fig. 95. *Palmatolepis initialis* sp. n. from the late *K. triangularis* Zone at Wietrznia (A–G, sample Wtr-27) and Jabłonna (H–Q, sample J-53) in the Holy Cross Mountains. P_1 (A, B, H–J), P_2 (C, K, L), S_0 (P), S_1 (D, E, O), S_2 (N), $S_{3–4}$ (F, M), and M (G, Q) elements; specimens ZPAL cXVI/1440, 1442–1447, 1252, 1254, 1253, 1256, 1255, 1260, 1259, 1258, a257, and 1261 (holotype), respectively.

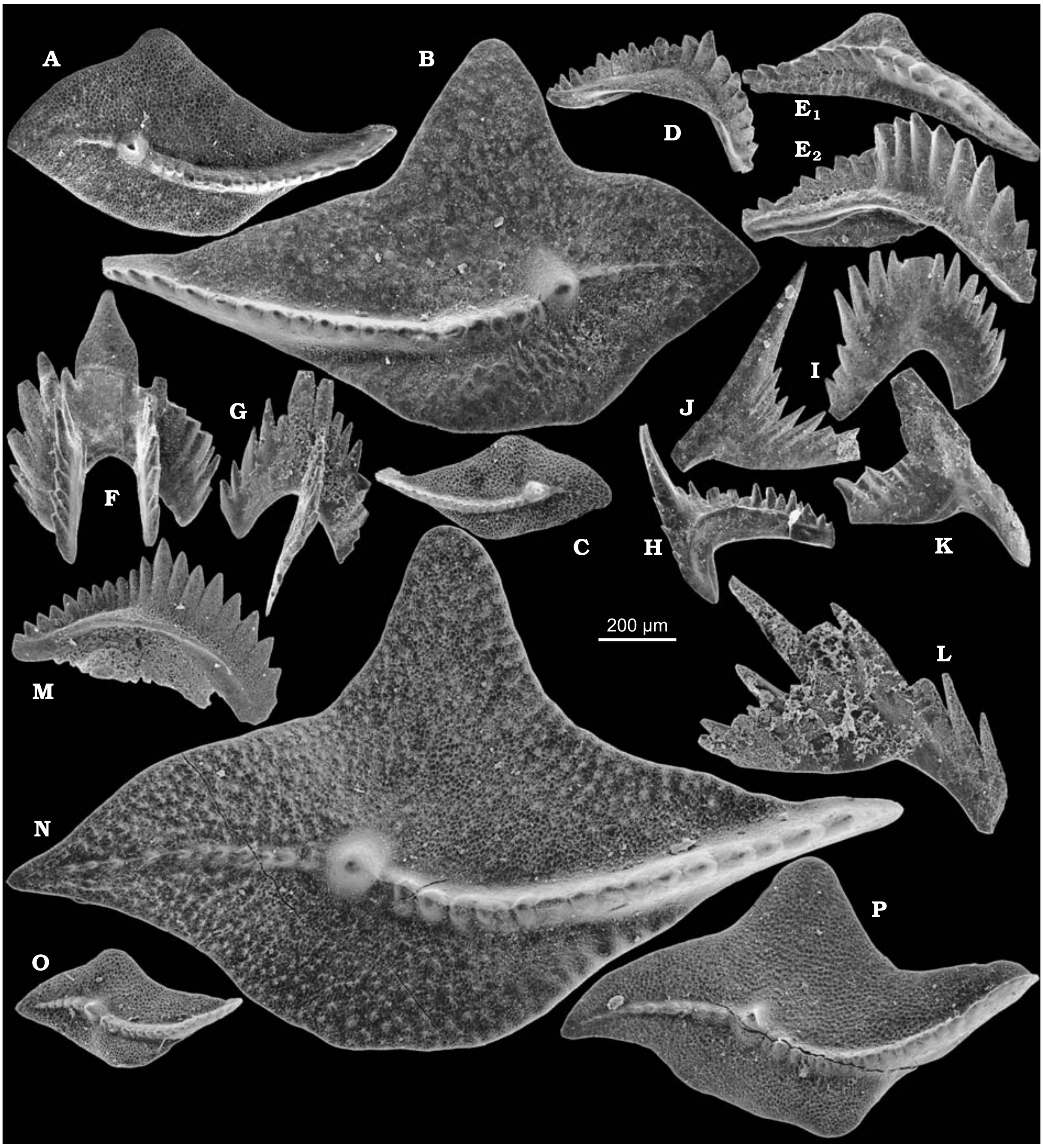


Fig. 96. *Palmatolepis sandbergi* Ji *et* Ziegler, 1993 from the late *K. triangularis* (A–K, sample J-53a) and early *K. crepida* (L, sample J-43; M, O, P, bed 3; N, bed 5) zones at Jabłonna in the Holy Cross Mountains. P_1 (A–C, N–P), P_2 (D, E, M), S_0 (F), S_1 (G), S_2 (I), S_{3-4} (H), and M (J-L) elements; specimens ZPAL cXVI/1280-1284, 1286, 1288, 1285, 1289, 1290, 2884, 2883, 2882, and 2880, 2881, respectively.

Diagnosis. — M element with almost straight cusp and short but well denticulated ventral process forming a wide angle with the prominently denticulated dorsal process.

Remarks. — Schülke (1999) proposed to use the name *Palmatolepis abnormis* (Branson et Mehl, 1934) for this species. However, as pointed out by Klapper *et al.* (2004, p. 382) the P_2 element from the Saverton Shale chosen to be the holotype of this species is undiagnostic and indistinguishable from ones that occur in different apparatus reconstructions (according to Branson and Mehl 1934 there is a “fairy complete gradation” to other P_2 specimens in the sample) and the species is invalid (a *nomen dubium*). It is rather the M element that bears characters diagnostic for the species. In its shape, with slightly reclined cusp, it is transitional between the ancestral morphology of *Klapperilepis* and that of *Palmatolepis* and *Conditolepis*. The population from sample Pł-1 (Fig. 80H–R) is probably the oldest one in my material showing features of *P. initialis* sp. n., but the generally small size of elements makes it similar rather to *Klapperilepis triangularis*. P_1 elements of these two species seem to be indistinguishable.

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

Palmatolepis sandbergi Ji *et* Ziegler, 1993
(Figs 96 and 135)

Type horizon and locality: Lali section, southern China.

Material. — 803 specimens.

Diagnosis. — M element with proclined cusp and short finely denticulated ventral process forming a wide angle with the prominently denticulated dorsal process.

Remarks. — The apparatus was restored by Schülke (1999). Except for the apparent trend towards typical *Palmatolepis* in the morphology of M elements, the apparatus is similar to *Klapperilepis triangularis*.

In bed 3 at Jabłonna P_1 elements somewhat resembling those of *Conditolepis lobicornis*, but with the posterior lobe of the platform differently oriented, co-occur with P_2 and M elements closely similar to those of *P. sandbergi* (Fig. 96M, O, P). Whether the proposed apparatus composition is correct, and then this is possibly a new species of *Palmatolepis*, or the platform elements belong to another genus, has to be tested with a material from another locality.

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

Palmatolepis perlobata Ulrich *et* Bassler, 1926
(Figs 97, 98, and 135)

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

Material. — 320 specimens.

Diagnosis. — Relatively low population variability in P_1 elements with sinuous outline and small posterior lobe of almost smooth platform, sharply denticulated P_2 elements with prominent cusp.

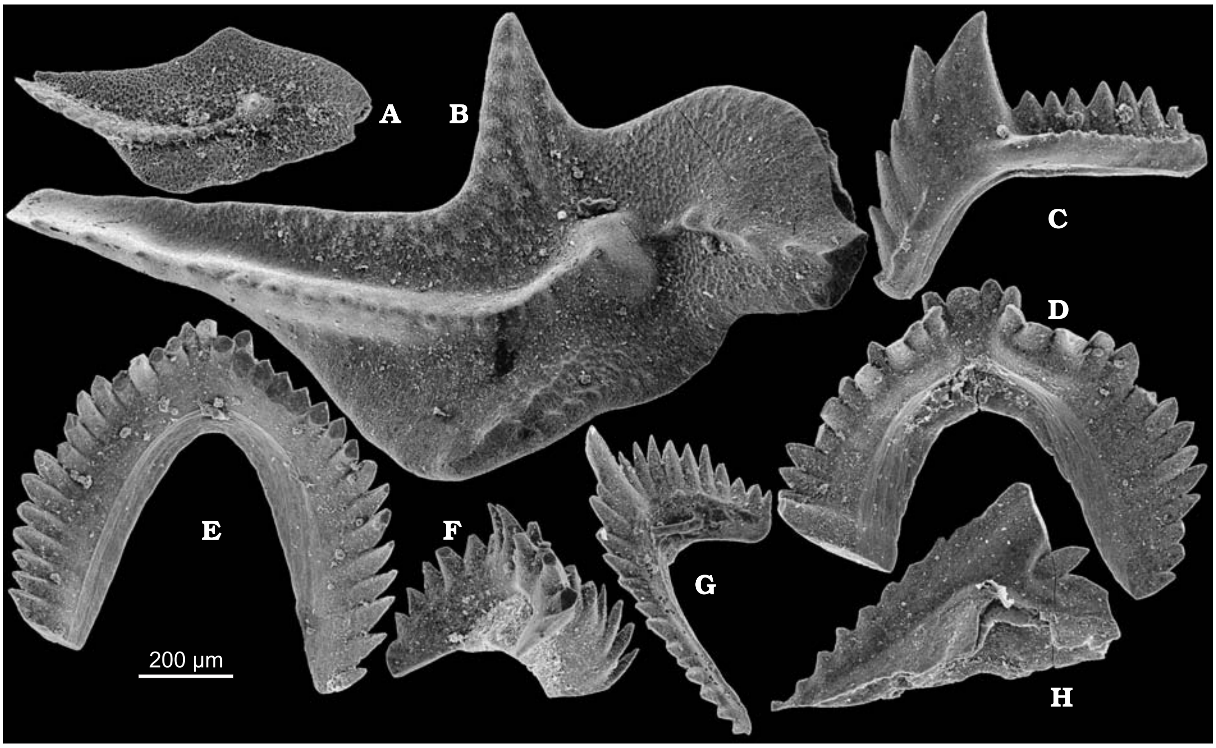


Fig. 97. *Palmatolepis perlobata* Ulrich *et* Bassler, 1926 from the *K. crepida* Zone at Kadzielnia (sample Ka-7) in the Holy Cross Mountains. P_1 (A, B), P_2 (C), S_0 (D), S_1 (E), S_2 (F), $S_{3–4}$ (G), and M (H) elements; specimens ZPAL cXVI/2885–2892, respectively.

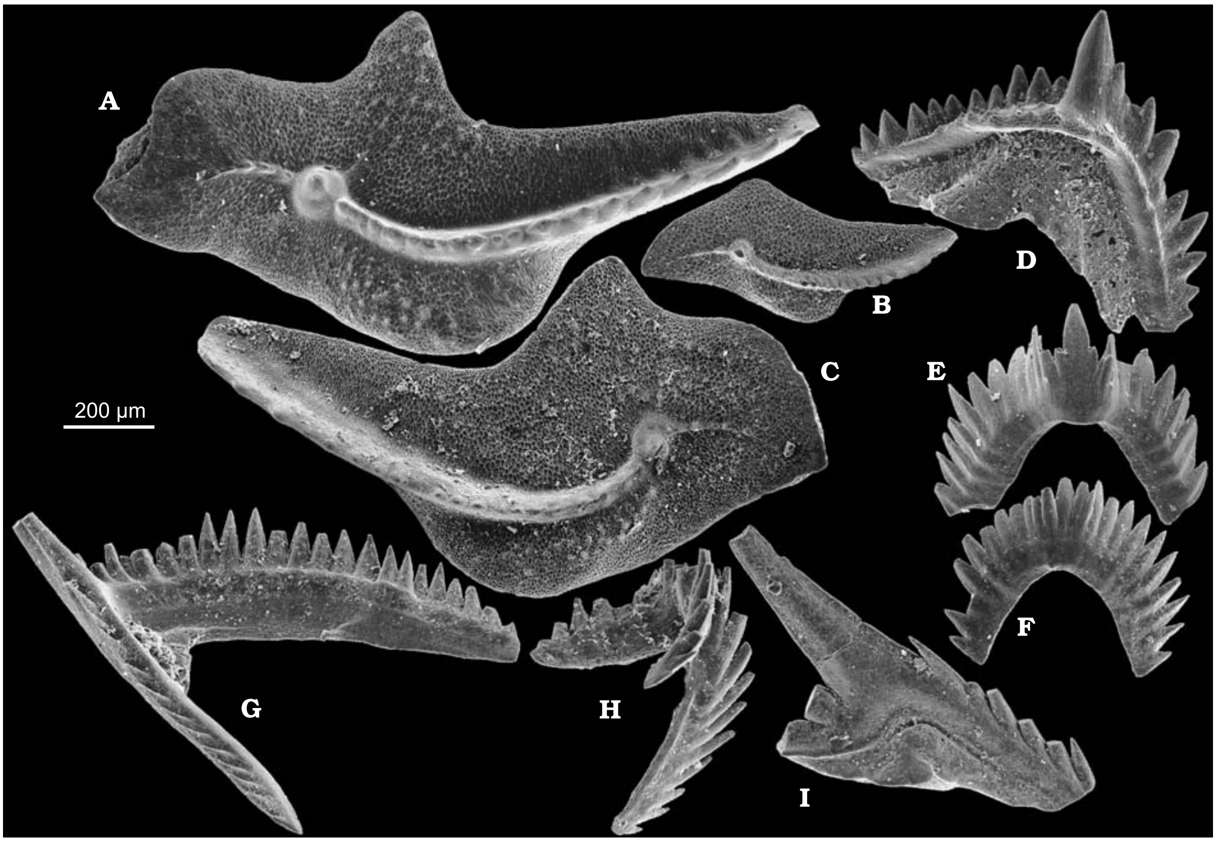


Fig. 98. *Palmatolepis perlobata* Ulrich *et* Bassler, 1926 from the *C. quadrantinodosa* Zone at Łagów (A–D, F–I, sample Ł-28; E, sample Ł-38) in the Holy Cross Mountains. P_1 (A–C), P_2 (D), S_0 (E, F), S_1 (H), $S_{3–4}$ (G), and M (I) elements; specimens ZPAL cXVI/2893, 2894, 1376, 1377, 1414, 1378, 1380, 1379, and 1381, respectively.

Remarks. — Apparatus of the species was restored by Metzger (1994) and the Holy Cross Mountains material supports his interpretation. P_2 elements in samples from Miedzianka frequently show bifurcation of the external process. Their platform may be very wide and broken pieces superficially resemble ancyrognathid P_1 elements.

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

Palmatolepis schindewolfi Müller, 1956
(Figs 99 and 135)

Type horizon and locality: Gray limestone from a breccia with ?*Platyclymenia* from a quarry at Langenaubach near Haiger, Rhenish Slate Mountains (Ziegler 1975).

Material. — 6,378 specimens.

Diagnosis. — Variable shape of P_1 elements with mature elements showing frequently very narrow and sharp lobes of the platform, while juveniles may lack any posterior processes having instead a large rounded anterior lobe.

Remarks. — P_2 elements were identified by van den Boogaard and Kuhry (1979), complete apparatus was restored by Metzger (1994) but with incorrectly attributed M element (actually belonging to *Conditolepis*).

P. schindewolfi is a variable species. Even the very large sample Ost-12, with almost eight hundred P_1 elements has not helped much in identification of possible cryptic species within the observed range of variability. The anterior lobe is semicircular in outline and gently convex in the dominant morphotype (usually classified as *P. maxima*, e.g., Metzger 1994), whereas the posterior lobe is well developed and sharply pointed. The variability extends in three main directions. One of the extreme morphotypes develops a crenulated marginal ridge of the anterior lobe. It is transitional to *P. trachytera* but just a couple of such specimens (*P. perlobata sigmoidea* Ziegler, 1962) have been found and the demarcation of *P. schindewolfi* and *P.*

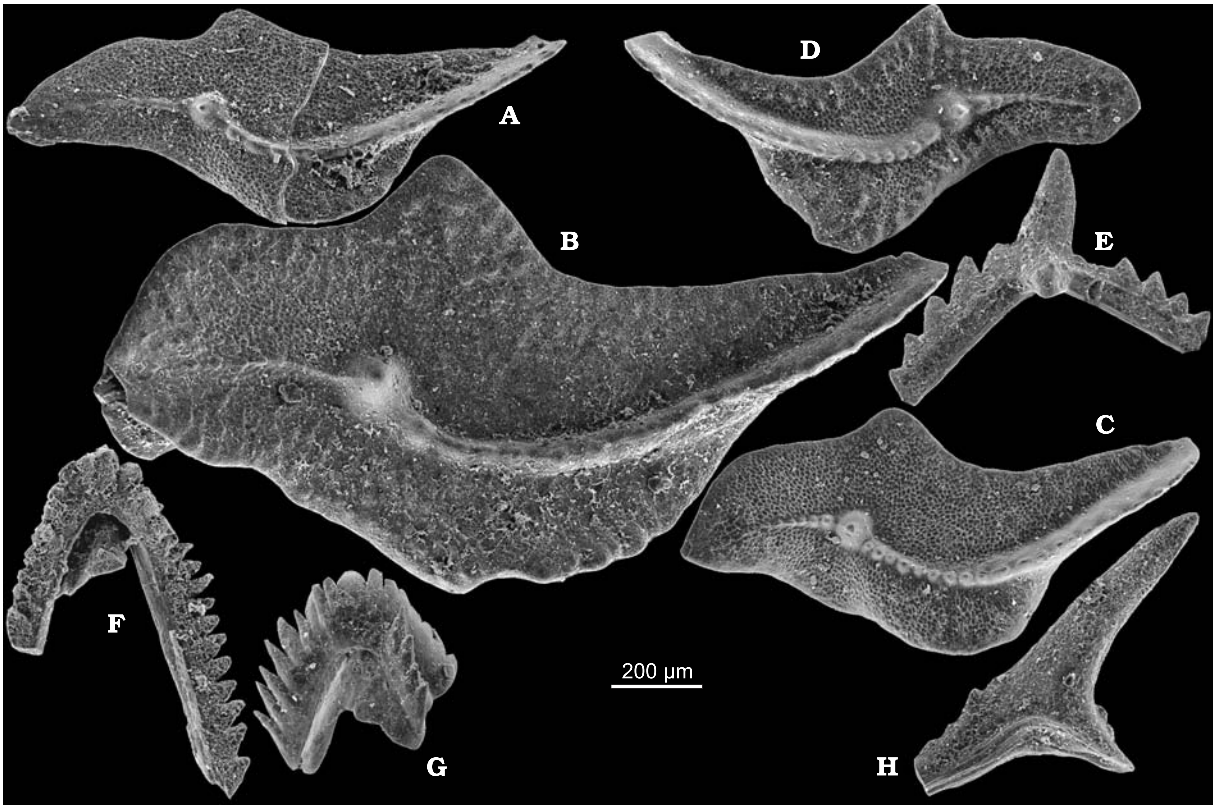


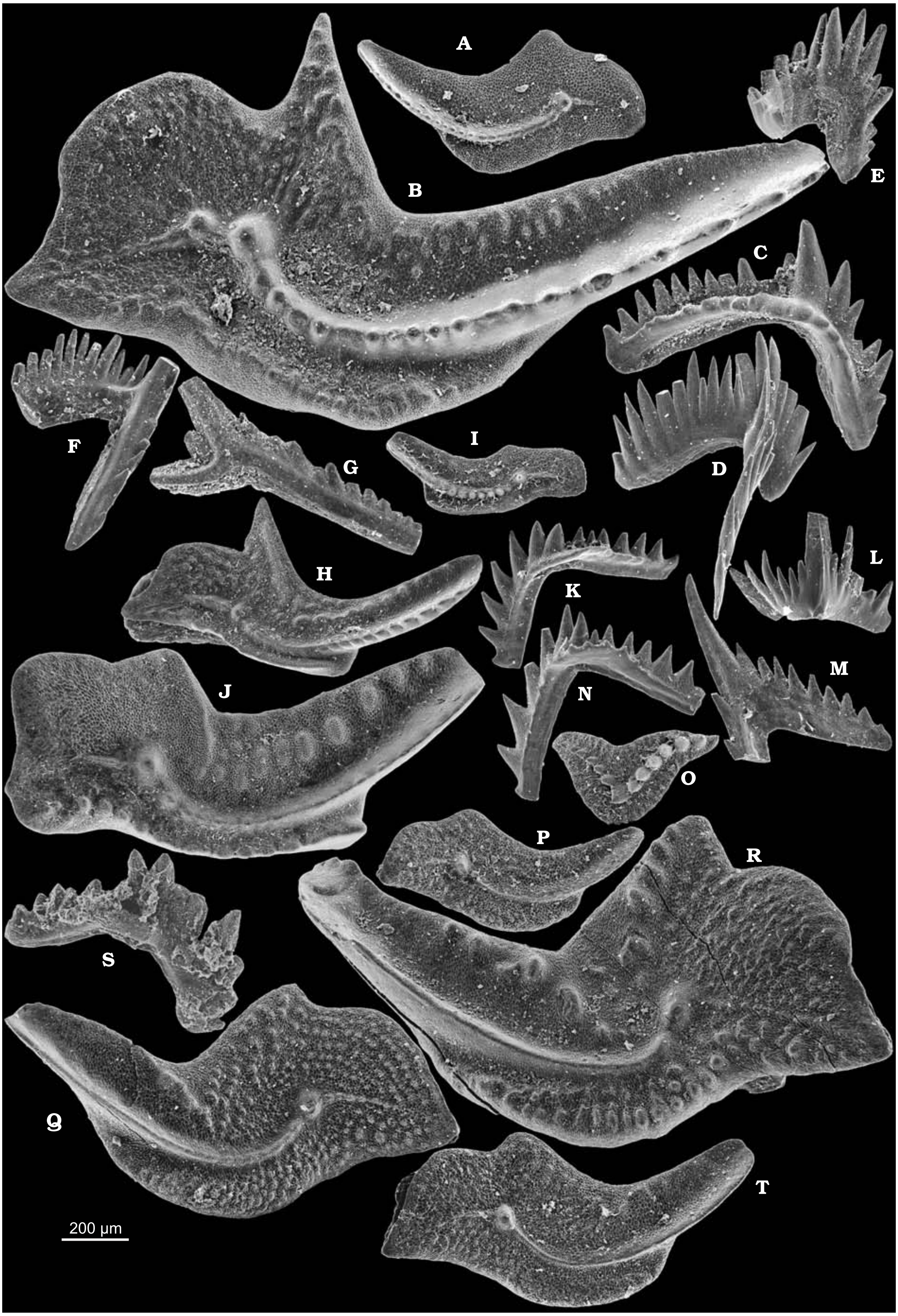
Fig. 99. *Palmatolepis schindewolfi* Müller, 1956 from the *P. trachytera* Zone at Kowala (A, sample Ko-6) and the *P. jugosus* Zone at Ostrówka (B–H, sample Ost-5) in the Holy Cross Mountains. P_1 (A–D), P_2 (E), S_1 (F), S_2 (G), and M (H) elements; specimens ZPAL cXVI/291–298, respectively.

trachytera seems rather objective. A possibility remains, however, that some cross-breeding between them took place. The second extreme morphotype lacks the posterior lobe and the whole platform is triangular in outline (*Palmatolepis perlobata helmsi* Ziegler, 1962). There is a complete gradation connecting it with the modal morphology of the population. No morphologic gap or even a lowering of frequency that would substantiate species distinction has been observed. The third extreme morphotype is the most troublesome. These are also specimens with reduced posterior lobe but the platform margins are roughly parallel and the whole robust element is strongly twisted (*P. perlobata postera* Ziegler, 1960). Their most striking feature is the anterior lobe with its ventral end protruding far from the blade. There is also a complete gradation between this morphology and the modal one but the transitional specimens may not be numerous enough to give a normal distribution of morphologic classes. As the evidence is equivocal, no separate taxon is here recognized.

The P_2 elements are equally variable. They are always highly arched with a dominant cusp. The platform may form a wide asymmetric leaf-like shelf but may be almost lacking in other morphotypes, with robust appearence of denticulation. There is no clear correspondence between these morphologies and size so they probably correspond to ranges of variability in platform extent and robustness in P_1 elements.The external process tends to be bifurcated in late populations.

Elements of the symmetry transition series are very irregular in appearance and variable, which obscures distinctions between locations. Their denticulation is rather robust, with somewhat irregularly sinuous distribution and no dominant cusp. Those virtually symmetrical with subquadrate apical part and arched processes, apparently represent S_0 elements. Similar in shape but somewhat asymmetrical elements with additional process of variable length represent the S_1 location. The process may be incipient and rarely the additional second process developed, which suggests that this morphology overlaps with the neighboring S_0 and S_2 locations. Similarly arched elements without processes are probably typical for the S_2 location.

$S_{3–4}$ elements are strongly asymmetric, with one process almost straight or gently curved, the other sinuous and they diverge at the apex at a narrow angle.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M elements differ from those of *Conditolepis* in the presence of a dominant cusp, weak dorsal denticles and somewhat angular disposition of processes as seen in profile.

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

Palmatolepis ampla Müller, 1956
(Figs 100A–G and 135)

Type horizon and locality: Sample 217 of *Platyclymenia* or *Clymenia* Stufe from Seßacker near Oberscheld in the Rhenish Slate Mountains (Ziegler 1975).

Material. — 562 specimens.

Diagnosis. — Platform of strongly sinuous P_1 elements ornamented with randomly distributed tubercles on its posterior part and transverse rows of small tubercles on the anterior lobe, P_2 elements with low cusp and wide posterior platform.

Remarks. — Apparatus was restored by myself under the name *P. rugosa* (Dzik 1991). The P_1 elements show a relatively narrow range of variability for a *Palmatolepis* species and are easily distinguishable from associated *P. perlobata*.

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

Palmatolepis trachytera Ziegler, 1960
(Figs 100H–O and 135)

Type horizon and locality: Sample 10 of gray cephalopod limestone 0.3 m above layer with *Prolobites delphinus* and *Platyclymenia involuta* (Ziegler 1975).

Material. — 989 specimens.

Diagnosis. — Platform of P_1 elements with sharp ridge or a row of tubercles along its anterior margin.

Remarks. — P_1 elements are flat and sinous in appearance. They vary much in development of the posterior pointed lobe. In early populations the posterior lobe is sharply pointed and elongate (Fig. 100H), whereas in later populations it may be virtually missing.

The P_2 elements bear a minute cusp and denticles in proximity of it are lower than others. The processes meet at an angle in the plane of the platform, which results in its boomerang-like shape. Width and ornamentation of the platform vary and extremely smooth, wide-platform elements resemble somewhat elements of *Conditolepis*.

The symmetry transistion series elements differ from those of *P. schindewolfi* in a more generalized appearance, that is, in usual domination of the cusp, sharp denticulation and their less sinuous arrangement. Otherwise they are similar to those of other *Palmatolepis* species.

Occurrence. — Zone of its own at Łagów, Ostrówka, Miedzianka, Kowala, and Jabłonna.

Palmatolepis rugosa Branson *et* Mehl, 1934
(Figs 100PO–S and 135)

Type horizon and locality: Saverton Shale seven miles north of Monroe City, Missouri (Ziegler 1975).

Material. — 664 specimens.

Diagnosis. — P_1 elements with transversely ribbed anterior lobe.

Remarks. — There is a gap in occurrence between *P. trachytera* and *P. rugosa* in the Holy Cross Mountains but the laterally sinuous shape of P_2 elements suggests a close relationship between these species. In some specimens of late *P. trachytera* the anterior ridge splits into a row of tubercles. There would not be much to change this into the tuberculated anterior field of *P. rugosa*, but the change remains to be domonstrated.

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

← Fig. 100. Advanced species of *Palmatolepis* from the Holy Cross Mountains. **A–G**. *Palmatolepis ampla* Müller, 1956 from the *C. marginifera* Zone at Łagów (sample Ł-5). P_1 (A, B), P_2 (C), S_1 (D), S_2 (E), $S_{3–4}$ (F), and M (G) elements; specimens ZPAL cXVI/2895–2901, respectively. **H–O**. *Palmatolepis trachytera* Ziegler, 1960 from its nominal zone at Łagów (H, sample Ł-40) and Jabłonna (N, bed 24) and the *L. styriacus* Zone at Ostrówka (I–O, sample Ost-12). P_1 (H–J), P_2 (K, N, O), S_1 (L), and M (M) elements; specimens ZPAL cXVI/2902–2909, respectively. **P–T**. *Palmatolepis rugosa* Branson *et* Mehl, 1934 from the *P. jugosus* Zone at Ostrówka (P–S, sample Ost-5) and the late *L. styriacus* zone at Kowala (T, sample Ko-6). P_1 (P–R, T), and P_2 (S) elements; specimens ZPAL cXVI/2919–2922, and 2910, respectively.

Genus **Conditolepis** van den Boogaard *et* Kuhry, 1979

Type species: *Palmatolepis marginifera* Helms, 1959 from the *Cheiloceras* Stufe of the Rhenish Slate Mountains.

Diagnosis. — Apparatus with biramous S_0 elements, laterally sinuous P_2 elements with low cusp and usually uniform distribution of denticles, M element having proclined cusp, linearly arranged processes with radiating denticles of the dorsal process.

Remarks. — *Panderolepis* Helms, 1963 has a priority over *Conditolepis* van den Boogard and Kuhry, 1979 but it was based on the type species *Polygnathus*? *serratus* Hinde, 1879, which was found to be a *nomen dubium* by Huddle (1968).

Conditolepis lobicornis (Schülke, 1995)
(Figs 101A–M and 136)

Type horizon and locality: Bed 29 of Seßacker trench near Dillenburg in the Rhenisch Slate Mountains (Schülke 1995).

Material. — 403 specimens.

Diagnosis. — Smooth P_1 element with a narrow extension of the posterior lobe and gently bent P_2 element with incipient platform and denticles of almost uniform height and size.

Remarks. — Apparatus was restored by Schülke (1999) who identified it as the first member of the branch of palmatolepidids with reduced additional processes in S_0 elements, indicating also its proximity to *K. linguiloba* sp. n. representing a continuation of its lineage. As shown by Schülke (1999) *Klapperilepis subperlobata* (Branson *et* Mehl, 1934 *sensu* Schülke 1999) is ancestral to *C. lobicornis*. Its relationship to, and possible identity with, *K. triangularis* remains to be clarified.

The shape of the platform of P_1 elements is very variable in each of the studied samples, with end-members of transition series approaching *Palmatolepis initialis* sp. n. (Fig. 101 C–E), *C. tenuipunctata* (Fig. 101O), and *C. linguiloba* sp. n. (Fig. 101E). This apparent similarity is the result of a phylogenetic proximity to all these species, in the first case the shared features of the apparatus morphology are plesiomorphic, in two others these could be considered apomorphic for the genus. There is a clear morphologic gap between the ranges of the platform shape variability of the type populations of *C. lobicornis*, *C. linguiloba* sp. n., and *C. tenuipunctata*.

Klapper *et al*. (2004) considered *C. lobicornis* conspecific with *Palmatolepis subperlobata helmsi* Ovnatanova, 1976, here renamed *C. linguiloba* sp. n. However, the holotype of *C. lobicornis* with its narrow posterior lobe is unsimilar to specimens of *C. linguiloba*, and no specimen in the type series (Schülke 1995, pl. 40) fits its morphology. Instead, they tend to be similar in the shape of the platform to underived species of *Palmatolepis*.

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

Conditolepis linguiloba sp. n.
(Figs 101N, O and 136)

Holotype: Specimen ZPAL cXVI/2794 (Fig. 101N).

Type horizon and locality: Sample J-48, early Famennian *K. crepida* Zone at Jabłonna, Holy Cross Mountains.

Derivation of name: Referring to the tongue-like shape of the platform lobe.

Material. — 125 specimens.

Diagnosis. — Smooth P_1 element with a wide tongue-like extension of the posterior lobe.

Remarks. —Although no other element of the apparatus of this species was identified with confidence, co-occurrence of its relatively numerous P_1 elements with species of *Conditolepis* suggests that the P_1 and other elements of their apparatuses were indistinguishable, thus more advanced than those of *C. lobicornis*. *C. lobicornis* probably represents the same lineage but differs in the more pointed tip of the platform lobe in the P_1 elements, its P_2 elements virtually lack a platform, and occur in older strata.

This species has been referred to as *Palmatolepis subperlobata* by i.a., Wolska (1967), Dreesen and Dusar (1974), Helms and Ziegler in Clark (1981, fig. 52), Wang (1989), and Metzger (1994), but it definitely represents a different lineage, as shown both by the morphology of P_1 elements and apparatus composition (Schülke 1999). Klapper *et al*. (2004) used the name *C. lobicornis* for this species as a replacement for *Palmatolepis subperlobata helmsi* Ovnatanova, 1976, a homonym of *Palmatolepis helmsi* Ziegler, 1962.

Occurrence. — The *K. crepida* and *C. quadrantinodosa* zones at Jabłonna, Kowala, Miedzianka, and Łagów.

Fig. 101. Early species of the palmatolepidid *Conditolepis*. **A**–**M**. *Conditolepis lobicornis* (Schülke, 1995) from the late *K. triangularis* Zone at Jabłonna (A, B, F, sample J-65) and Wietrznia (C–E, G–L, sample Wtr-27). P$_1$ (A–E), P$_2$ (F–J), S$_1$ (K), S$_{3-4}$ (L), and M (M) elements; specimens ZPAL cXVI/2875, 2878, 2803, 2804, 2879, 1417, 2801, 2805, 2802, 1418–1420, respectively. **N**, **O**. *C. linguiloba* sp. n. from the *K. crepida* Zone at Jabłonna (sample J-48). P$_1$ elements; specimens ZPAL cXVI/2794 (holotype) and 2793. **P**–**BB**. *Conditolepis tenuipunctata* (Sannemann, 1955) from the *K. crepida* Zone at Jabłonna (sample J-45a). P$_1$ (P–R), P$_2$ (S, T), S$_0$ (U, V), S$_1$ (W), S$_2$ (X, Y), S$_{3-4}$ (Z), and M (AA, BB) elements; specimens ZPAL cXVI/1303, 1301, 1302, 1304–1306, 1311, 1308, 1307, 1309, 1310, and 2829, respectively.

Conditolepis tenuipunctata (Sannemann, 1955)
(Figs 101P–CC and 136)

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

Material. — 3,535 specimens.

Diagnosis. — P$_1$ elements elongate and sinuous, with wide smooth platform bearing rounded triangular extension in the middle.

Remarks. — The species may be related to stratigraphically older *C. lobicornis*, from which it differs in the reduced lobe of the platform. At Wietrznia in sample Wtr-27 an early population of this species occurs with P_2 elements virtually lacking the platform, similar to those of *C. falcata*, that is without a recognizable cusp. Such an element was already attributed to the species by den Boogaard and Kuhry (1979, fig. 8; the specimen on Fig. 7 belongs to *Klapperilepis quadrantinodosolobata*, as pointed out by Schülke 1999). Younger samples with P_1 elements typical for the species contain P_2 elements with very wide, oval platform, closely similar to that in more advanced *Conditolepis* species. I suggest to distinguish early and late forms of the species on this basis. A robust appearance of P_1 elements characterizes populations with the platform of P_2 elements already well developed but not reaching the tip of the inner process (sample Md-27).

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

Conditolepis prima (Ziegler *et* Huddle, 1969)
(Figs 102 and 136)

Type horizon and locality: Reddish limestone at the base of the upper *Cheiloceras* Stufe at Amönau near Marburg, Rhenish Slate Mountains (Ziegler 1975).

Material. — 7,165 specimens.

Diagnosis. — Narrow P_1 elements with short anterior lobe having elevated rounded margin and no posterior lobe.

Remarks. — P_2 elements of the apparatus were identified by van den Boogaard and Kuhry (1979) and Metzger (1994) and its complete restoration was offered by Schülke (1999).

The species is transitional between *C. tenuipunctata* and *C. glabra* but usually is understood in a typological sense. Schülke (1999) synonymized it with *Palmatodella unca* of Sannemann (1955a). However, *C. tenuipunctata* and *P. unca* share the same type locality and there is nothing in the text of their original description (Sannemann 1955a) that would suggest that they occur in different horizons. Moreover, Sanemmann (1955a) illustrated typical *C. glabra* from the same locality. Perhaps Schülke (1999) was in possession

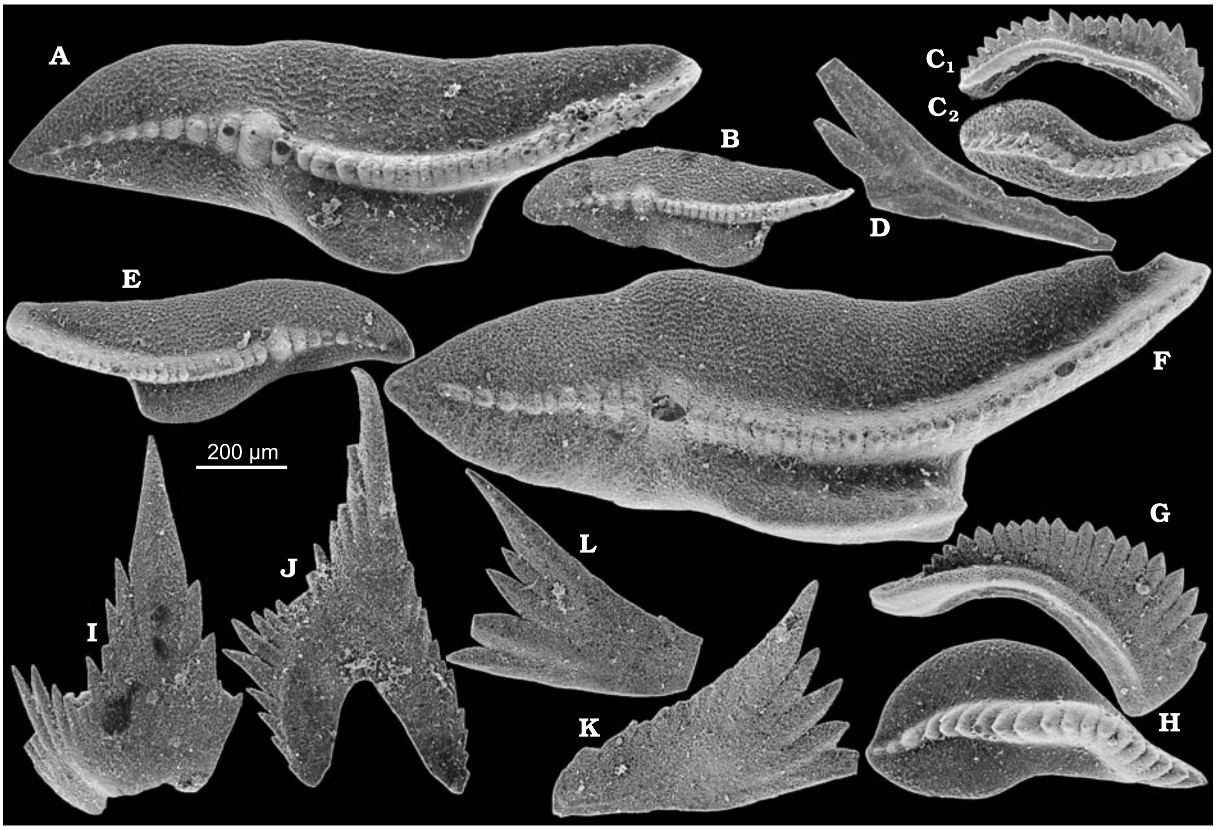

Fig. 102. *Conditolepis prima* (Ziegler *et* Huddle, 1969), an early member of the *C. glabra* lineage, from the *K. crepida* Zone at Jabłonna (I–L, sample J-50) and Kadzielnia (E, F, and H, samples Ka-3; G, I–K, sample Ka-4) in the Holy Cross Mountains. P_1 (A, B, E, F), P_2 (C, G, H), S_0 (I), S_2 (J), and M (K, L) elements; specimens ZPAL cXVI/2831, 2830, 2832, 2833, 2867, 2868, 2871, 2869, 2872–2874, and 2870, respectively.

of additional information that the third species is represented in the same assemblage. In my material apparatuses of *C. tenuipunctata* and *C. glabra*, as well as populations possibly transitional between them, do not differ in their apparatus composition. This refers also to the M elements and the specimen illustrated by Schülke (1999, pl. 3: 18) as belonging to *C. tenuipunctata* may be atypical. Narrow-platform elements classified by Schülke (1999) in *P. unca* co-occur with typical elements of *C. tenuipunctata* in its late samples and the same

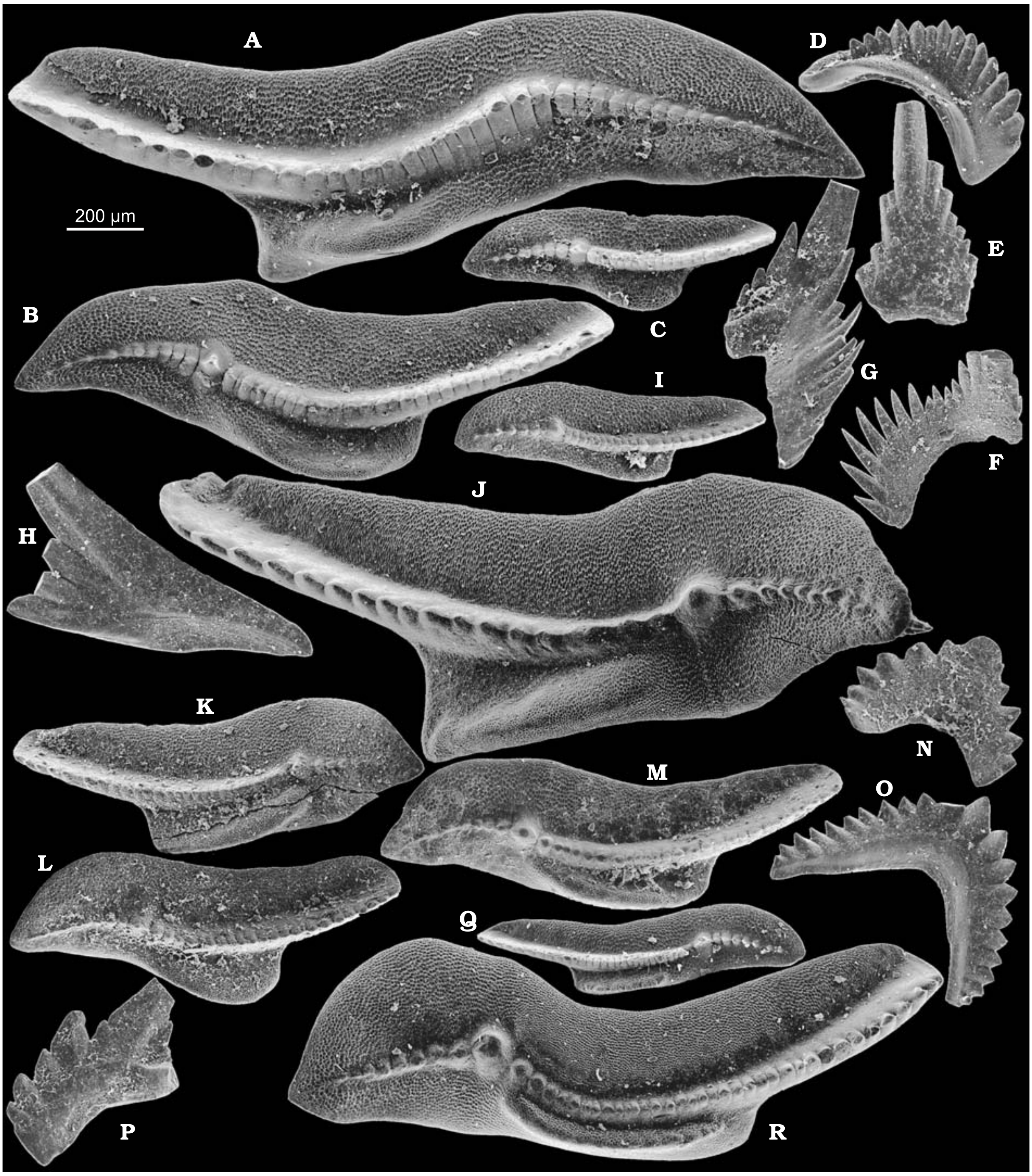

Fig. 103. Advanced species of the palmatolepidid *Conditolepis glabra* lineage from the Holy Cross Mountains. **A**–**P**. *Conditolepis glabra* Ulrich *et* Bassler, 1926 from the *C. quadrantinodosa* Zone at Łagów (A–H, sample Mak-3-4; I, J, sample Ł-26; L–N, sample Ł-28) and Miedzianka (O, P, sample Md-2). P$_1$ (A–C, I–M), P$_2$ (D, N, O), S$_0$ (E), S$_2$ (F), S$_{3–4}$ (G, P?), and M (H) elements; specimens ZPAL cXVI/2837, 2836, 2835, 2838–2842, 2864, 2863, 1394, 1393, 1395, 1397, 2865, 1393, and 2866, respectively. **Q**, **R**. *Conditolepis distorta* (Branson *et* Mehl, 1934) from the *C. marginifera* Zone at Łagów (sample Ł-9). P$_1$ elements; specimens ZPAL cXVI/2850 and 2851.

is in the Montagne Noire material of Schülke (1999, p. 91). This suggests that these are just morphologies within monospecific populations instead of distinct species and that in the course of evolution narrow-platform elements became more and more numerous.

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

Conditolepis glabra Ulrich *et* Bassler, 1926
(Figs 103A–P and 136)

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

Material. — 2,230 specimens.

Diagnosis. — P_1 elements with a ridge along the anterior margin of the platform, ventrally departing from the blade and truncated with an angulation perpendicular to it.

Remarks. — In several large samples studied there is a complete gradation between morphologies traditionally believed to characterize separate species, including “*Palmatolepis*” *prima* (Fig. 103L), “*P.*” *pectinata* (Fig. 103K–M) or “*P.*” *acuta* (Fig. 103J). I consider them variants within population variability, although the type populations of some of them may truly be distinct from *C. glabra*.

Elements of the apparatus of this species are closely similar to those of *C. quadrantinodosa* and it is difficult to separate them in samples. The difference is that in *C. glabra* P_2 elements are more arched and M elements more elongated than in the other lineage.

The species is apparently ancestral to *C. distorta* and probably to *C. falcata*. Evolution from *C. prima* to *C. glabra* and from *C. glabra* to *C. distorta* is connected with increased variability and transitional populations are polymorphic in respect to morphology of P_1 elements. Delimitation of these probable chronospecies is thus rather conventional.

Occurrence. — The *C. quadrantinodosa* Zone at Łagów, Kowala, Jabłonna, and Miedzianka; also in the Dębnik area (Baliński 1995).

Conditolepis distorta (Branson *et* Mehl, 1934)
(Figs 103Q, R and 136)

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

Material. — 890 specimens.

Diagnosis. — P_1 elements elongate and sinusoidal, with narrow platform bearing a prominent anterior ridge, close to the blade along its whole length.

Remarks. — Transition from *C. glabra* to *C. distorta* took place early in the *C. marginifera* Zone. As already shown in the Canning Basin succession in Australia by Glenister and Klapper (1966, text-fig. 3), the change is gradual. Populations intermediate in age show more and more common elements having the narrow furrow between the ridge on the anterior lobe and the blade, including those usually classified as *C. pectinata*.

Occurrence. — Typical populations are common in the *C. marginifera* Zone at Łagów, Kowala, and Miedzianka. Rare specimens from higher horizons at Ostrówka and Miedzianka may be reworked.

Conditolepis falcata (Helms, 1959)
(Figs 104 and 136)

Type horizon and locality: Upper part of bed 5 at Bohlen near Saalfeld, Thuringia (Helms, 1959).

Material. — 41,366 specimens.

Diagnosis. — P_1 elements very elongate and narrow, with triangular, aborally pointing anterior lobe; P_2 elements sinuous, with rudimentary platform, S_0 elements with prominent processes.

Remarks. — P_2 elements of the apparatus were identified by van den Boogaard and Kuhry (1979), the complete apparatus by myself (Dzik 1991). Metzger (1994) confirmed identification of the symmetry transition series but questioned the identification of the M element, transfering it incorrectly to *P. schindewolfi* (this would be the only element of that species different from the apparatus of related *P. perlobata*). *C. falcata* is the most abundant palmatolepidid species in the Holy Cross Mountains and its apparatus reconstruction leaves little doubt. Sample Ost-12 offers the largest material of this species being devoid of any other *Conditolepis* species.

Fig. 104. Palmatolepidid *Conditolepis falcata* (Helms, 1959) from the *C. quadrantinodosa* Zone at Łagów (C, F, I, J, M, and P, sample Ł-28) and the early *Lagovignathus styriacus* Zone at Ostrówka (A, B, D, E, G, H, K, L, N, O, and Q, sample Ost-12) in the Holy Cross Mountains. P_1 (A–C), P_2 (D–F), S_0 (G–I), S_{1-2} (J, K), S_{3-4} (L–N), and M (O–Q) elements; specimens ZPAL cXVI/2852, 2853, 1392, 2854, 2855, 1396, 2857, 2856, 1398, 1399, 2858, 2859, 1400, 2860, 2862, 1401, and 2861, respectively.

The origin of this species remains in doubt. The species emerged from an unknown source in the late *K. crepida* Zone at Kadzielnia together with equally cryptic *C. klapperi*. Although relatively little change is necessary in the morphology of the P_1 element to derive it from that of *C. glabra*, the whole apparatus is quite different. It cannot be excluded that the lack of a platform in P_2 elements is an ancestral feature inherited from *C. lobicornis* and early *C. tenuipunctata* and that the lineage of *C. falcata* is independent of that of *C. glabra*.

Occurrence. — Common from the *C. quadrantinodosa* Zone, most abundant in the *P. trachytera* and *L. styriacus* zones of all studied localities. Rare specimens found together with *P. jugosus* at Ostrówka and Miedzianka may be reworked.

Conditolepis klapperi (Sandberg *et* Ziegler, 1973)
(Figs 105A–G and 136)

Type horizon and locality: 42 m above the base of the West Range Limestone at the Bactrian Mountains, Nevada (Ziegler 1975).

Material. — 2,846 specimens.

Diagnosis. — Anterior margin of the P_1 element with a massive ramp-like ridge, posterior margin of the platform non-lobate, strongly sinuous.

Remarks. — This is the first species of the *C. marginifera* lineage as indicated by its robust appearance with massive anterior ridge of the platform. Similarly to the P_1 element, other elements of the apparatus are of large size, massive appearance and regular distribution of sharp denticles, otherwise they resemble those of other typical *Conditolepis* species.

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

Conditolepis quadrantinodosa (Branson *et* Mehl, 1934)
(Figs 105H–N and 136)

Type horizon and locality: Saverton Shale seven miles north of Monroe City, Missouri (Ziegler 1977, p. 367).

Material. — 139 specimens.

Diagnosis. — Very variable P_1 element, oval in outline with gently convex anterior lobe covered with tubercles or forming a ridge.

Remarks. — The range of population variability of this species encompasses, with completely smooth gradation, morphologies typical of *C. inflexa* (see Dreesen and Dusar 1974; Dreesen 1976) but also *C. marginifera* and *C. inflexoidea*. They separated into distinct biological species somewhat later in their evolution.

Occurrence. — Zone of its own at Łagów, Kowala, and Miedzianka.

Conditolepis marginifera (Helms, 1959)
(Figs 105O, P, S–V and 136)

Type horizon and locality: Bed 13 of reddish limestone with *Cheiloceras enkebergense* in trench II at Seßacker near Oberscheld, Rhenisch Slate Mountains (Ziegler 1977, p. 325).

Material. — 1,430 specimens.

Diagnosis. — Short P_1 element with subcircular dorsal end, bearing a sharp ridge or row of tubercles along the anterior margin in proximity to the blade.

Remarks. — Because of the tremendous morphological variability of the P_1 elements of this species it is difficult to determine it reliably based on single specimens. In fact, the co-occurrence of *C. inflexoidea*, separated by a gap in morphologic variability, gives a helpful hint that one is dealing with a separate species and not with an extreme morphology of the stratigraphically preceding *C. quadrantinodosa*.

Occurrence. — Zone of its own at Łagów, Kowala, Ostrówka, and Miedzianka.

Conditolepis inflexoidea (Ziegler, 1962)
(Figs 105Q, R and 136)

Type horizon and locality: Bed 13 of reddish limestone with *Cheiloceras enkebergense* in trench II at Seßacker near Oberscheld, Rhenish Slate Mountains (Ziegler 1975).

Material. — 145 specimens.

Diagnosis. — Elongate P_1 element with gently convex smooth anterior lobe.

Remarks. — The problem of the evolutionary origin of this species remains to be solved. As shown by Dreesen and Dusar (1974) and Dreesen (1976) there is a tremendous polymorphism in the populations transitional between those with dominant *C. quadrantinodosa* and *C. marginifera* morphologies, which obliterates the true nature of evolutionary change. Whether the genetic barrier developed sympatrically in the whole area of occurrence of the species or, alternatively, an allopatric speciation event not expressed in morphology preceded spatial reunification of the lineage, remains unknown. Perhaps detailed biometrical studies in successions from different places in the world may help in finding an answer to this question.

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

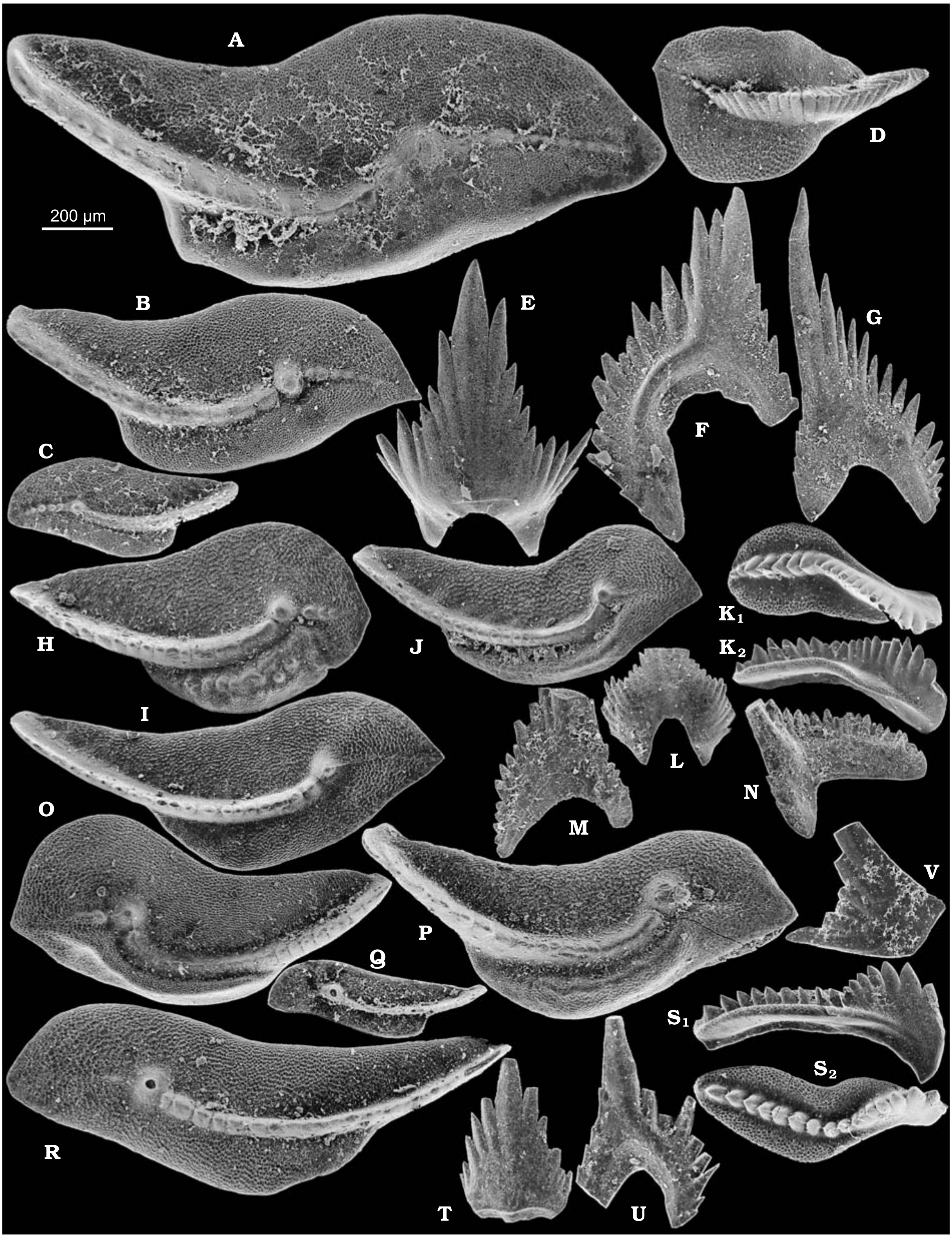

Fig. 105. Palmatolepidids of the *Conditolepis marginifera* lineage from the Holy Cross Mountains. **A**–**G**. *C. klapperi* (Sandberg *et* Ziegler, 1973) from the *K. crepida* Zone at Kadzielnia (sample Ka-10). P_1 (A–C), P_2 (D), S_0 (E), S_{1-2} (F), and S_{3-4} (G) elements; specimens ZPAL cXVI/2845, 2844, 2846, 2847, 2849, and 2848, respectively. **H**–**N**. *C. quadrantinodosa* (Branson *et* Mehl, 1934) from its nominal zone at Łagów (sample Ł-28). P_1 (H–J), P_2 (K), S_0 (L), S_{1-2} (M), and S_{3-4} (N) elements; specimens ZPAL cXVI/1382–1386, 1389, and 1390, respectively. **O**, **P**, **S**–**V**. *C. marginifera* (Helms, 1959) from its nominal zone at Łagów (sample ŁSł73-3). P_1 (O, P), P_2 (S), S_0 (T), S_{1-2} (U), and M (V) elements; specimens ZPAL cXVI/2821, 2825, 2826, 2823, 2827, and 2828, respectively. **R**. *C. inflexoidea* (Ziegler, 1962) from the same sample. P_1 elements; specimens ZPAL cXVI/2825 and 2824.

Family **Cavusgnathidae** Austin *et* Rhodes, 1981

Diagnosis. — P_1 elements with axial symmetry, bearing elaborate icrion or high-positioned platform.

Remarks. — The three Famennian conodont lineages with more or less developed axial symmetry in their platform elements discussed below, probably share their common ancestry in a *Pandorinellina*-like form of early Famennian age. The *Pseudopolygnathus* lineage continued without any drastic morphological changes from the Famennian to the Tournaisian when it diversified significantly (Dzik 1997). *Alternognathus* is apparently only a homeomorph of *Pinacognathus* (sensu Dzik 1994) and early *Siphonodella* (Ziegler and Sandberg 1984; Sweet 1988). *Omolonognathus*, known from the late Famennian of the Cracow area (Baliński 1995) may be an extremely shallow-water offshoot of the *Alternognathus* lineage. As shown by Beinert *et al*. (1971) there is a continuity between the mid Famennian *Scaphignathus* and Tournaisian *Clydagnathus* lineages. It has to be admitted that there is some uncertainty whether the axial symmetry originated only once at the base of the whole clade. Whereas *Pandorinellina* seems to be truly the best root for the *Alternognathus* branch, the oldest member of the *Pseudopolygnathus* lineage (*P. jugosus*) shows expanded basal cone similar rather to *Dasbergina stabilis*, the species stratigraphically preceding the lineage of *Pseudopolygnathus* but not *Alternognathus*. The family defined as above may thus be polyphyletic.

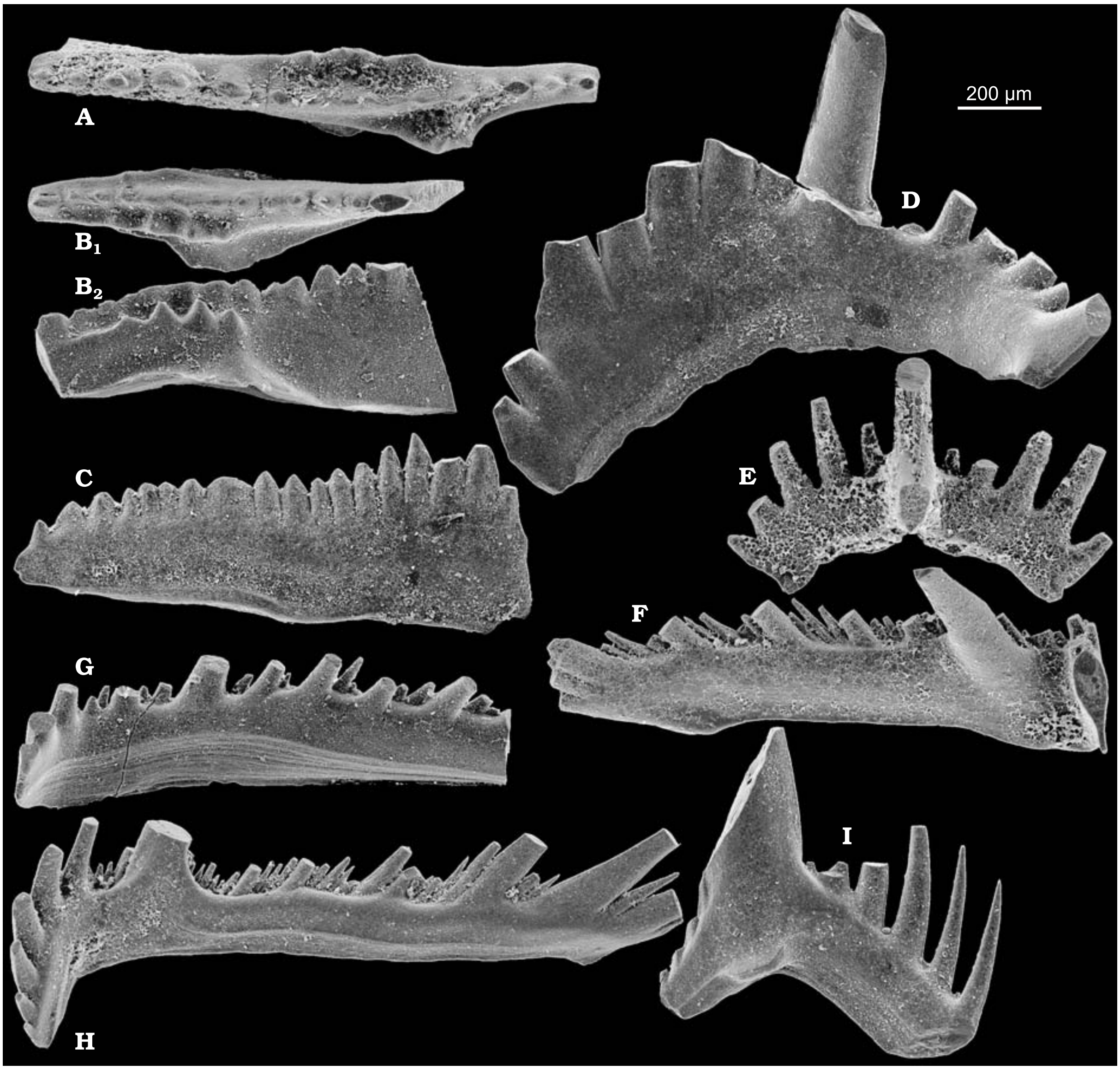

Fig. 106. *Alternognathus pseudostrigosus* (Dreesen *et* Dusar, 1974), probably the earliest cavusgnathid, from the *K. crepida* Zone at Kadzielnia (sample Ka-10) in the Holy Cross Mountains. P_1 (A–C), P_2 (D), S_0 (E), S_1 (F), S_2 (G), S_{3-4} (H), and M (I) elements; specimens ZPAL cXVI/2236–2244 (holotype B), respectively.

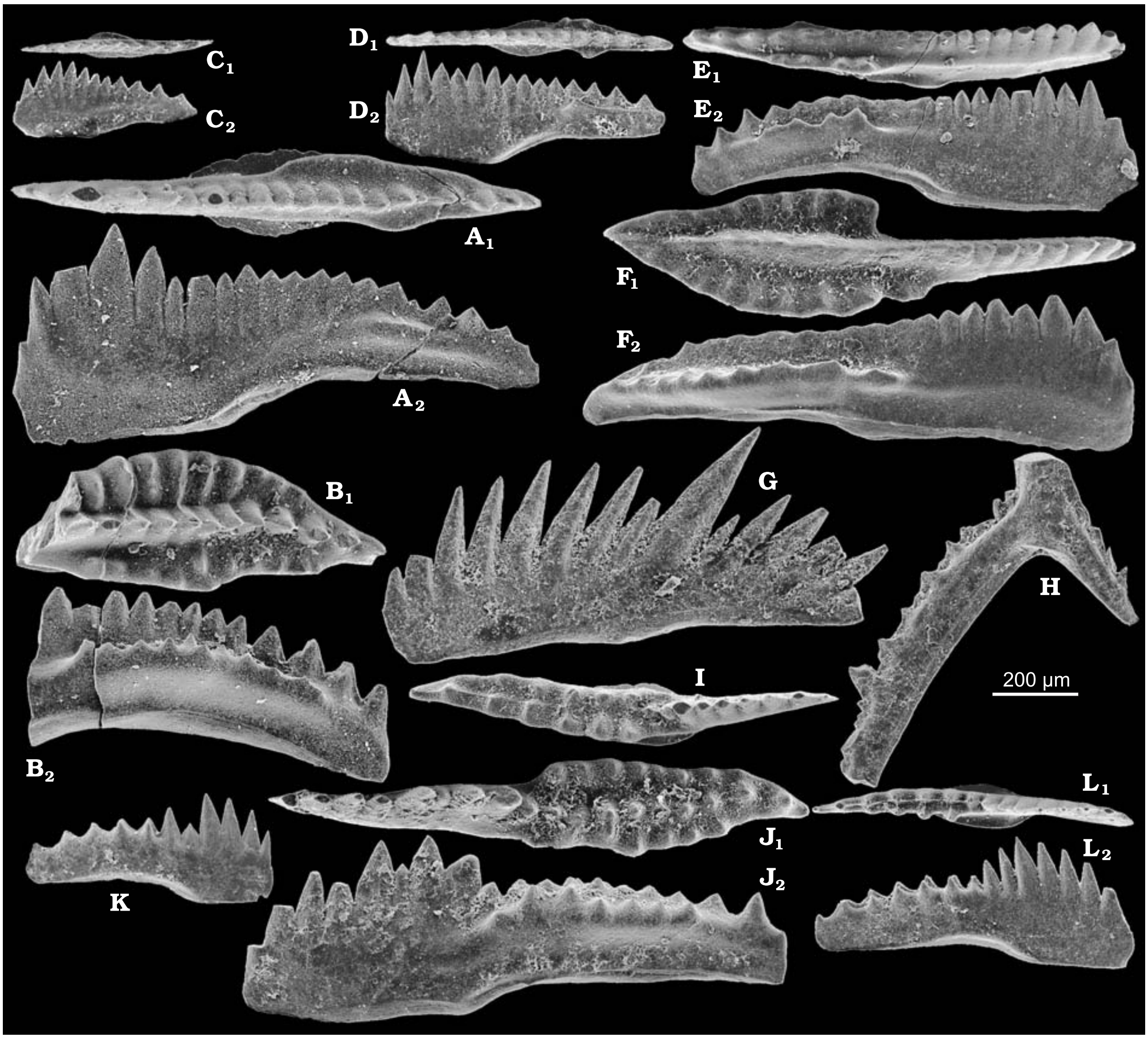

Fig. 107. Early cavusgnathids from the Holy Cross Mountains. **A**, **B**. *Alternognathus pseudostrigosus* (Dreesen *et* Dusar, 1974) from the *C. quadrantinodosa* Zone at Miedzianka (sample Md-2). P_1 elements; specimens ZPAL cXVI/2346, 2347. **C**–**H**. *Alternognathus regularis* Ziegler *et* Sandberg, 1984 from the *P. trachytera* Zone at Jabłonna (bed 24). P_1 (A–F), P_2 (G), and M (H) elements; specimens ZPAL cXVI/2351, 2350, 2349, 2348, 2352, and 2353, respectively. **I**–**L**. *Scaphignathus velifer* Helms, 1959 from the same sample. P_1 elements; specimens ZPAL cXVI/2355–2357 and 2354.

Genus *Alternognathus* Ziegler *et* Sandberg, 1984

Type species: *Alternognathus regularis* Ziegler *et* Sandberg, 1984 from the Famennian Three Forks Formation of Montana.

Diagnosis. — P_1 element with platform developing transverse ridges almost at the same level as the tips of nearby denticles of the blade, distinct shallow larval basal cavity of fusiform outline.

Remarks. — The oldest occurrence of the *Alternognathus* lineage in the Holy Cross Mountains is sample Md-2 from Miedzianka, where it co-occurs with *C.* (*C.*) *inflexoidea*, thus older than the entry of *P. trachytera*. P_1 elements in this sample usually show very weak development of the platform, which remains incipient even in large specimens. A platform-icrion developed stronger on one side of the blade and axial symmetry may be involved there. In bed 24 at Jabłonna the lineage co-occurs with *P. trachytera*, but the platform remains relatively narrow. Mature elements with very wide platform occur abundantly in sample Wzd-10 at Ściegnia. Juveniles are virtually missing there. It remains thus undecided whether the difference in width of the platform between samples results from evolution or only expresses differences in population dynamics.

The P_2 elements of *Alternognathus* differ from those of associated *Pseudopolygnathus*, *Dasbergina* and *Pandorinellina* in a significantly more prominent dorsal process. The differences between these genera in the rest of the apparatus are minor and it is hardly possible to separate them in samples where they occur in similar numbers.

Alternognathus pseudostrigosus (Dreesen *et* Dusar, 1974)
(Figs 106, 107A, B, and 137)

Type horizon and locality: Sample 4 from the Hamoir-Fairon section near Liege, Belgium.

Material. — 114 specimens.

Diagnosis. — Irregular, strongly asymmetric incipient platform located high on the blade slightly below the tips of its denticles in mature P_1 elements; elements of the apparatus robust of *Pandorinellina* type.

Remarks. — This is the earliest of the more or less certain members of the *Alternognathus* lineage. In its stratigraphic occurrence it significantly predates other species of *Alternognathus* and species of *Pseudopolygnathus* with robust icrion. The structure referred to as an incipient platform may approach icrion in some elements and is so irregularly developed that it is hard to say whether axial symmetry is already developed in P_1 elements of this species, or not. There seems to be an evolutionary change in the Holy Cross Mountains material; the stratigraphically younger specimens show a better developed platform originating earlier in the ontogeny and not so high on the blade. The elements are also less robust and somewhat "arthritic" in appearance.

Occurrence. — The late *K. crepida* Zone at Kadzielnia and the *C. quadrantinodosa* Zone at Miedzianka (Md-2).

Alternognathus regularis Ziegler *et* Sandberg, 1984
(Figs 107C–H, 108, and 137)

Type horizon and locality: Top of the Trident Member of Three Forks Formation at Sheep Mountain in Centennian Range of Montana (Ziegler and Sandberg 1984).

Material. — 1,390 specimens.

Diagnosis. — Well developed but rather narrow platform of P_1 element with large nodes along the margin.

Remarks. — The species was referred to as *Scaphignathus subserratus* until Ziegler and Sandberg (1984) questioned the species identity of the lectotype. The incipient axial symmetry of the elements refers only to the shape of the platform and is more clearly visible on juveniles than on large specimens with a wider platform. The blade remains curved in mirror-image pairs.

Occurrence. — The *C. quadrantinodosa* to early *P. jugosus* zones at Łagów, Kowala, Ostrówka, and Miedzianka.

Alternognathus? sp.
(Fig. 110H–L)

Material. — Seven specimens.

Remarks. — Rare P_1 elements from Dzikowiec are of juvenile *A. regularis* size and morphology but their free blade is shorter, resembling thus much more ontogenetically advanced and larger specimens of that species. They may thus represent adults of a separate species.

Occurrence. — The late *P. jugosus* Zone at Dzikowiec in the Sudetes.

Alternognathus beulensis Ziegler *et* Sandberg, 1984
(Figs 9A, 109, and 137)

Type horizon and locality: Top of the Hemberg Limestone at the top of Beul Mountain near Balve in the Rhenish Slate Mountains (Ziegler and Sandberg 1984; Beinert *et al*. 1971).

Material. — 202 specimens.

Diagnosis. — Wide platform ornamented with ridges and nodes.

Remarks. — This is the most advanced species of the *Alternognathus* lineage, probable a successor of *A. regularis* and this is consistent with the stratigraphic succession of these species in the Holy Cross Mountains.

Although the non-platform elements of the *Alternognathus* apparatus are of a rather generalized morphology, P_2 elements with their straight long processes may be of some use in determining the generic affinity.

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

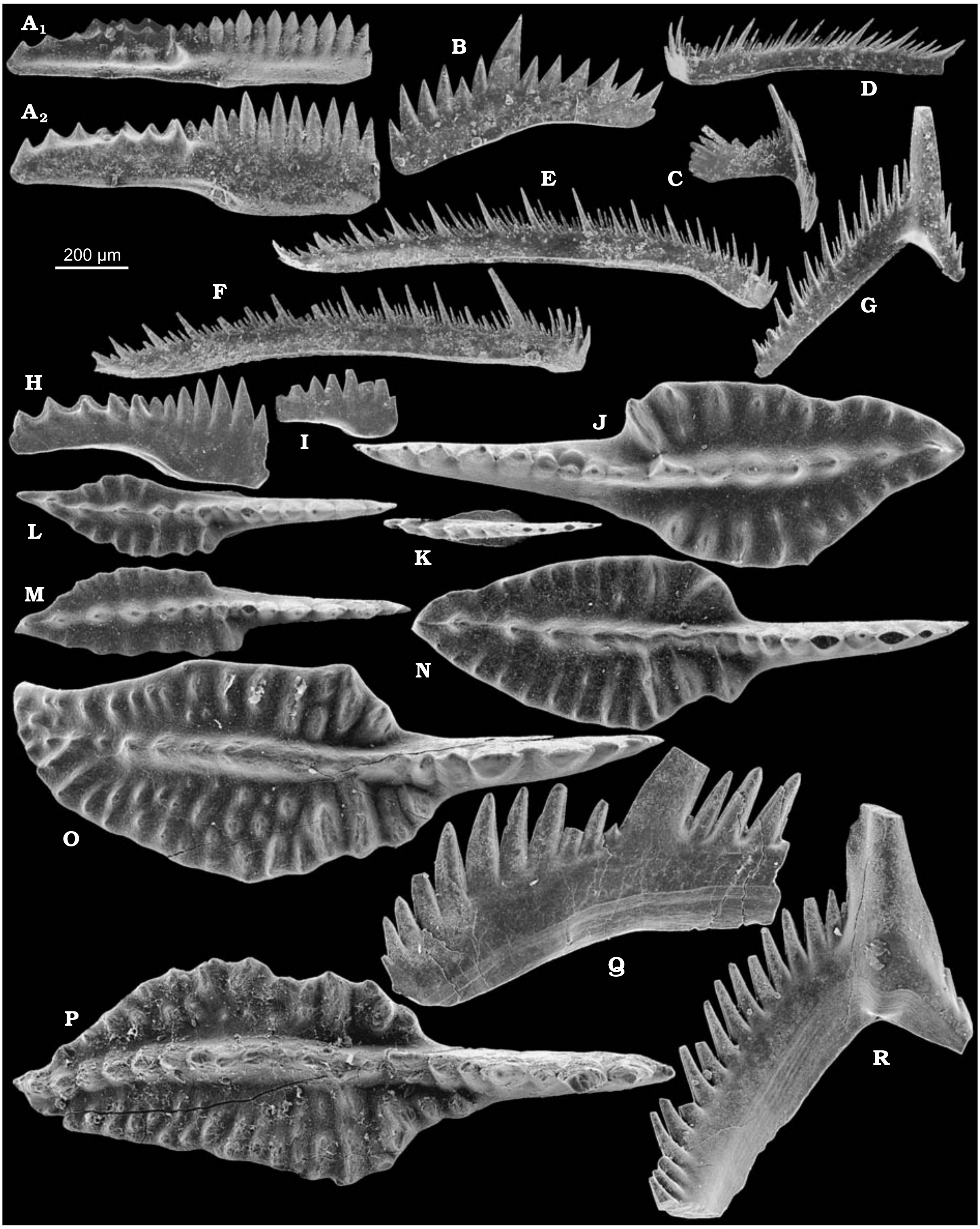

Fig. 108. Cavusgnathid *Alternognathus regularis* Ziegler *et* Sandberg, 1984 from the early *P. trachytera* Zone at Kowala (A–G, sample Ko-8a) and the *L. styriacus* Zone at Miedzianka (H–R, sample Md-14) in the Holy Cross Mountains. P_1 (A, H–P), P_2 (Q), and M (R) elements; specimens ZPAL cXVI/527, 528, 531–533, 535, 534, 2358, 2360, 2365, 2359, 2367, 2368, 2366, 2364, 2361, 2363, and 2362, respectively.

Genus ***Scaphignathus*** Helms, 1959

Type species: *Scaphignathus velifera* Helms, 1959 from the mid Famennian of the Saalfeld area.

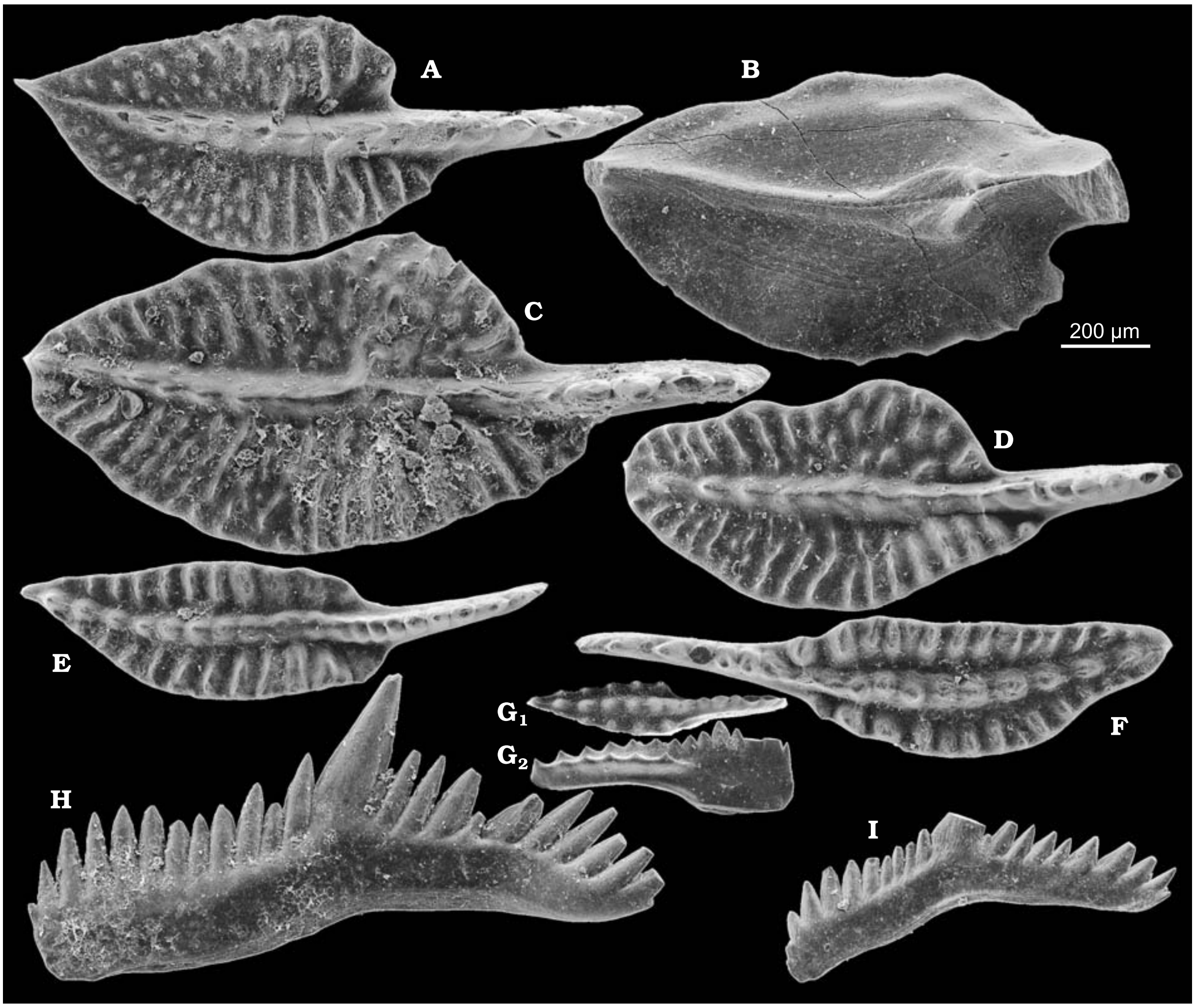

Fig. 109. Cavusgnathid *Alternognathus beulensis* Ziegler *et* Sandberg, 1984 from from the *P. trachytera* Zone at Ściegnia (Wzdół Plebański; sample Wzd-10; homeomorph of the species?) and the *L. styriacus* Zone at Miedzianka (A, B, sample Md-14) and Ostrówka (C–I, sample Ost-15) in the Holy Cross Mountains. P_1 (A–G) and P_2 (H, I) elements; specimens ZPAL cXVI/2370–2376, 2378, and 2377, respectively.

Diagnosis. — Strongly asymmetric icrion in P_1 elements, with tubercles of lateral and middle rows at approximately the same level, high free blade.

Remarks. — *Scaphignathus* differs from *Alternognathus* mainly in virtually equal height of tubercles of the platform and those of the corresponding part of the blade. In fact, at early stages of the ontogeny this is not a true platform but rather an icrion. This difference is apparent even in the geologically oldest samples with species of those genera co-occurring (e.g., J-24), although some specimens remain difficult to tell apart. There was probably no difference in the apparatus structure between those erliest members of the lineage. In geologically younger samples two kinds of P_2 elements seem to occur, one with a rather generalized morphology belonging to *Alternognathus* and the other with a very regular and low denticulation, probably representing *Scaphignathus*. Early occurrences of *Scaphignathus* in the Holy Cross Mountains differ from those from younger strata in a much narrower icrion. In the icrion being developed dorsally mostly on one side, the P_1 elements exhibit an axial symmetry, although some bending of the blade allows recognition of particular members of the mirror image pair.

Scaphignathus velifer Helms, 1959
(Figs 110G and 137)

Type horizon and locality: 4.5 m below the top of the finely nodular limestone Unit 5 at Bohlen, assemblage dominated by *Palmatolepis schindewolfi* and *Conditolepis falcata* (Helms 1959).

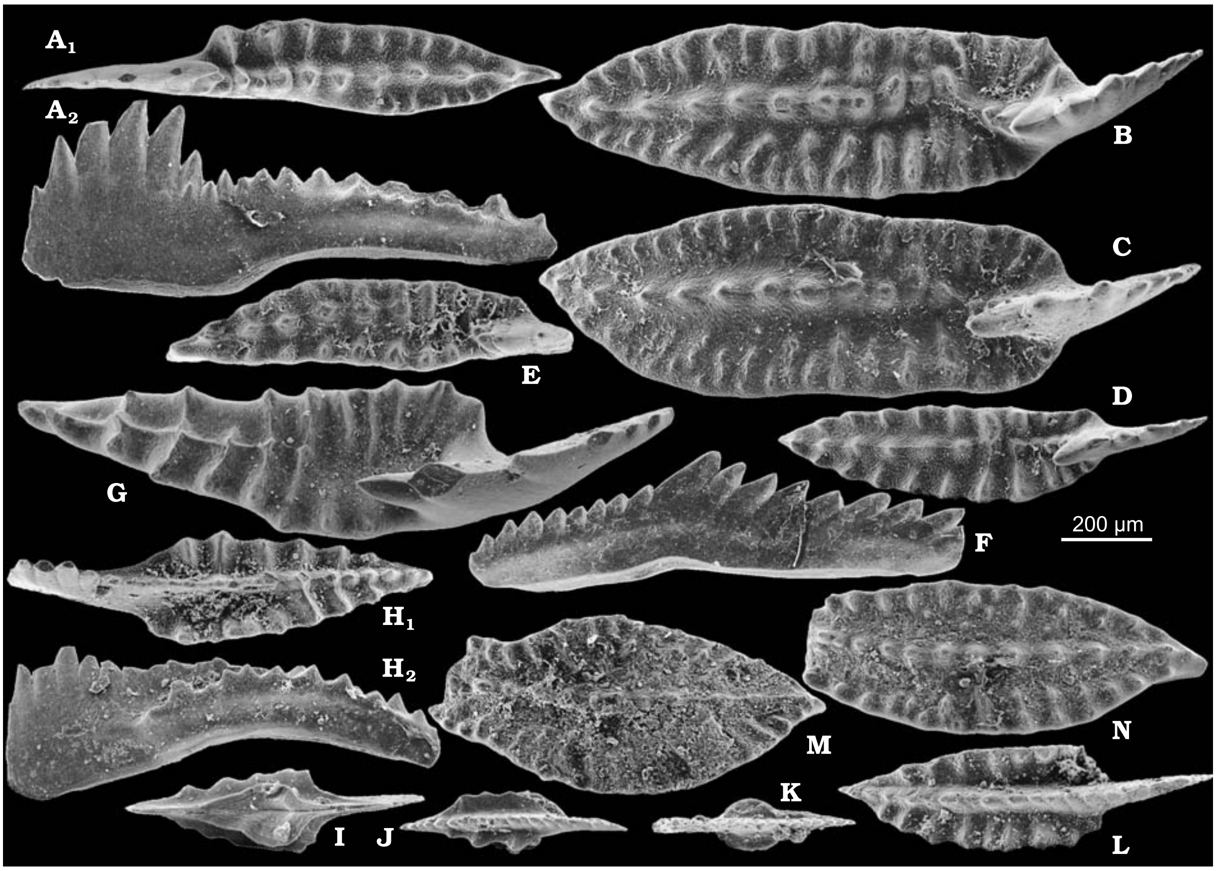

Fig. 110. Cavusgnathids. **A**–**F**. *Scaphignathus leptus* (Ziegler *et* Sandberg, 1984) from the *L. styriacus* Zone at Miedzianka (sample Md-14, A) and Ostrówka (B, D–F, sample Ost-12; C, sample Ost-1a) in the Holy Cross Mountains. P_1 (A–E) and P_2 (F) elements; specimens ZPAL cXVI/2369, 2379, 2504, and 2380–2382, respectively. **G**. *Scaphignathus velifer* Helms, 1959 from the *C. marginifera* Zone at Łagów (G, sample Ł-5) in the Holy Cross Mountains. P_1 element; specimen ZPAL cXVI/2503. **H**–**L**. *Alternognathus*? sp. from the *P. jugosus* Zone at Dzikowiec (H, sample Dz-10; I–L, sample Dz-54) in the Sudetes. P_1 elements, specimens ZPAL cXVI/2387, 2990–2992, and 2989. **M**, **N**. *Pinacognathus*? *praesulcatus* (Sandberg, 1972) from the *D. trigonica* Zone at Kowala (sample Ko-166) in the Holy Cross Mountains. P_1 elements, specimens ZPAL cXVI/2389 and 2390.

Material. — 50 specimens.

Diagnosis. — Icrion in P_1 elements gradually tapering dorsally, with narrow tip.

Remarks. — *Alternognathus costatiformis* of Matyja (1993), with its virtually equal height of lateral and medial denticles in the icrion and a distinct separation of icrion from the free blade, is so similar to *Scaphignathus* that it probably belongs in this genus.

Occurrence. — The *C. quadrantinodosa* to *P. trachytera* zones at Łagów and Jabłonna.

Scaphignathus leptus Ziegler *et* Sandberg, 1984
(Figs 110A–F and 137)

Type horizon and locality: Upper trachytera Zone, Hemberg Limestone at Ballberg near Balve (Ziegler and Sandberg 1984).

Material. — 77 specimens.

Diagnosis. — Parallel margins of the icrion and relatively blunt dorsal end in mature P_1 elements.

Remarks. — Because of significant changes in the ontogeny of P_1 elements and population variability the available material of relatively few specimens from many samples is too small to be sure of species distinctions in this genus. The proposed diagnoses remain thus provisional until a more precise picture of their evolution is achieved.

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

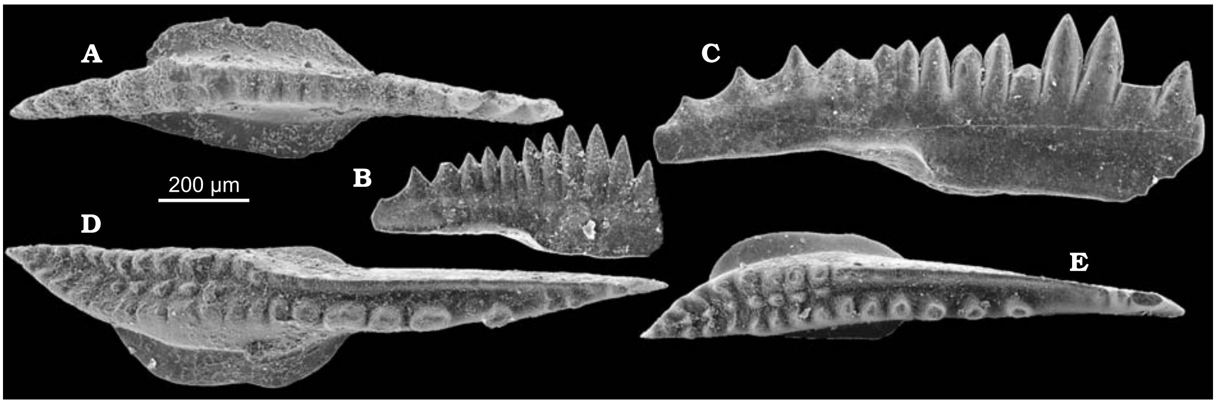

Fig. 111. Early probable cavusgnathid *Pseudopolygnathus jugosus* (Branson *et* Mehl, 1934) from its nominal Zone at Jabłonna (A–C, bed 27) and Ostrówka (D, E, sample Ost-185) in the Holy Cross Mountains. P_1 elements; specimens ZPAL cXVI/2212, 2211, 2210, 2295, and 2296, respectively.

Genus ***Pseudopolygnathus*** Branson *et* Mehl, 1934

Type species: *Pseudopolygnathus prima* Branson *et* Mehl, 1934 from the Tournaisian of Missouri.

Diagnosis. — Icrion in P_1 elements composed of rows of tubercles and frequently a longitudinal ridge, basal cavity wide and shallow.

Remarks. — The Devonian species attributed here were classified in *Bispathodus* Müller, 1962, although its type species *Spathodus spinulicostatus* E. R. Branson, 1934 is of Early Carboniferous age. Its holotype, similar to that of *S. costatus*, is probably the end member of the variability range of the co-occuring type species of *Pseudopolygnathus*, *P. primus*, as suggested by samples from elsewhere (Dzik 1997). Whatever is the real nature of this specimen, these genera are clearly closely related and there is no way to distinguish them in a satisfactory way.

According to Ziegler *et al*. (1974), the icrion developed independently in the branch of *P. jugosus* and *P. ziegleri* from the ancestral situation of *P. stabilis*. I have not been able to confirm or exclude this. However, *P. ostrovkensis*, with its robust and wide icrion, appears earlier at Kowala than *P. jugosus*, much less advanced in this respect. Perhaps *Pseudopolygnathus*, as understood here, is truly polyphyletic and the *P. jugosus* lineage should be classified in *Dasbergina*.

Pseudopolygnathus jugosus (Branson *et* Mehl, 1934)
(Figs 111, 112, and 137)

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

Material. — 3,111 specimens.

Diagnosis. — Icrion in the dorsal part of mature P_1 element composed of two rows of denticles and additional medial row of minute denticles.

Remarks. — Icrion developed in this species by widening denticle tips in juveniles and shows axial symmetry owing to asymmetric position of the sharp ridge along the ventral portion of the blade. Mirror-image symmetry is still clearly expressed in curvature of the blade.

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

Pseudopolygnathus ostrovkensis sp. n.
(Figs 113 and 137)

Holotype: Specimen ZPAL cXVI/2298 (Fig. 113F).

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

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

Material. — 2,927 specimens.

Diagnosis. — Usually wide icrion of P_1 elements; in the dorsal part composed of three rows of robust denticles, the medial row being of the same height as the lateral ones.

Remarks. — P_1 elements of this species from the borehole Kowala have already been illustrated as *Bispathodus ultimus* by Nehring-Lefeld (1990, pl. 2: 13, 14). Probably also specimens identified with the

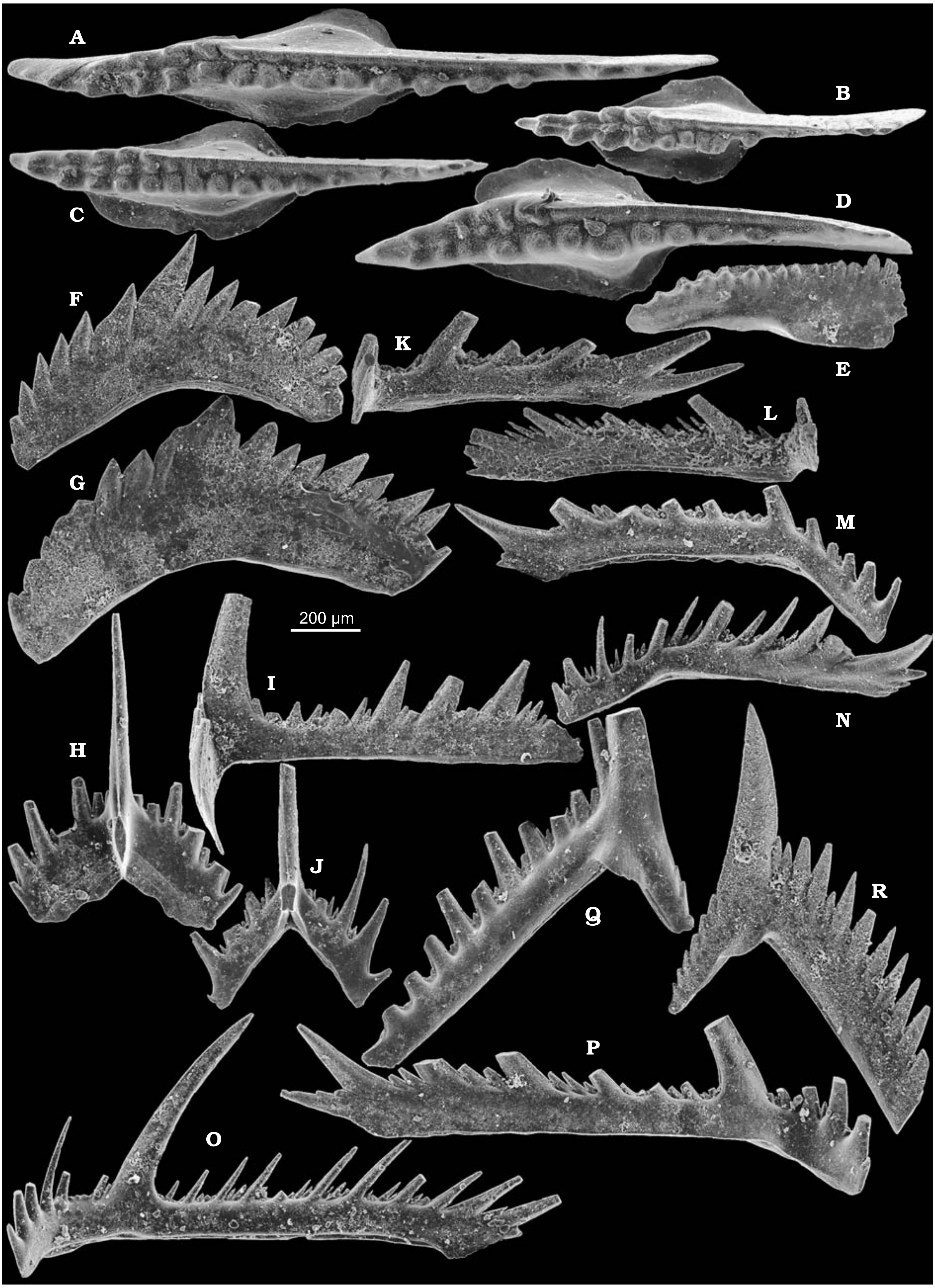

Fig. 112. Advanced probable cavusgnathid *Pseudopolygnathus jugosus* (Branson *et* Mehl, 1934) from its nominal Zone at Jabłonna (sample J-51) in the Holy Cross Mountains. P_1 (A–E), P_2 (F, G), S_0 (H–J), S_1 (K, L), S_2 (M, N), S_{3-4} (O, P), and M (Q, R) elements; specimens ZPAL cXVI/2225, 2226, 2286–2288, 2227, 2289, 2290, 2228, 2229, 2230, 2291, 2231, 2292, 2232, 2293, 2233, and 2294, respectively.

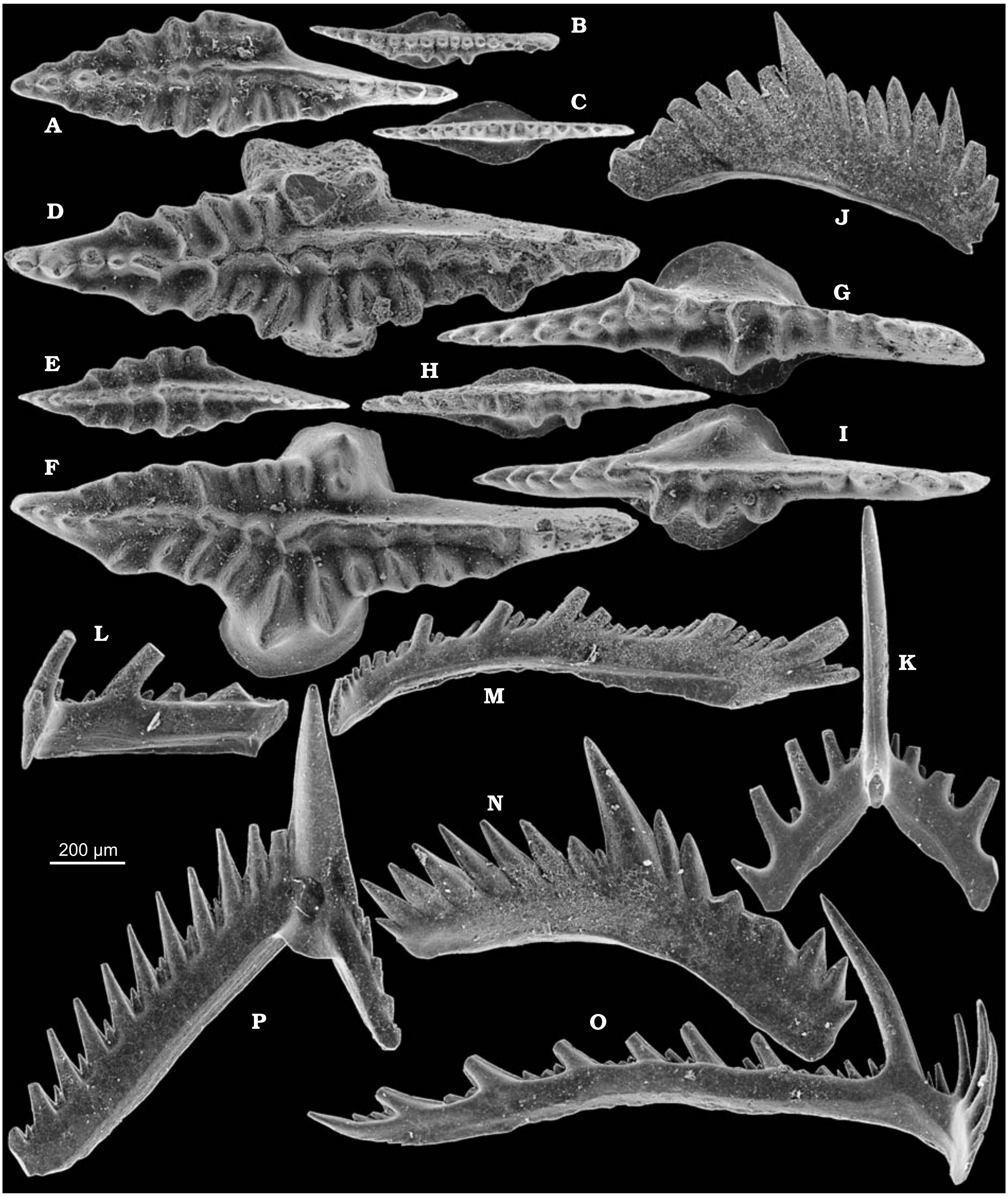

Fig. 113. Probable cavusgnathid *Pseudopolygnathus ostrovkensis* sp. n. from the *P. jugosus* Zone at Ostrówka (sample Ost-185) in the Holy Cross Mountains. P_1 (A–I), P_2 (J, N), S_0 (K), S_1 (L), S_2 (M), S_{3-4} (O), and M (P) elements; specimens ZPAL cXVI/2213, 2214, 2303, 2297, 2301, 2298 (holotype, F), 2299, 2302, 2300, 2215, 2305–2307, 2304, 2308, and 2309, respectively.

Tournaisian *Pseudopolygnathus vogesi* by Dreesen *et al*. (1976, pl. 4: 1–5) from the Famennian of Belgium are conspecific. There is a possibility that this is the beginning of the *P. primus* lineage, as suggested by findings of populations morphologically close and transitional in time (e.g., Bouckaert and Groessens 1976; Sanz-López *et al*. 1999). However, an independent origin of the Carboniferous *Pseudopolygnathus* from a less elaborate latest Famennian *Pseudopolygnathus* seems more likely because of the substantial gap in continuity in the late Famennian and much wider population variability of *P. primus* (covering also morphologies typical for the late Famennian) than is observed in *P. ostrovkensis* sp. n.

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

Pseudopolygnathus aculeatus (Branson *et* Mehl, 1934)
(Figs 114A–D and 137)

Type horizon and locality: Probably the Saverton Shale near Monroe City, Missouri (Ziegler 1975, p. 17).

Material. — 1,014 specimens.

Diagnosis. — Denticles developed only on one side of the sharp ridge formed by the blade; left and right elements only slightly differ in their axial symmetry.

Remarks. — This is probably a successor of *P. jugosus*, but it apparently originated as a result of allopatric speciation and their ranges partially overlap in Polish sections. They probably were adapted to different environment, but the nature of these differences remain to be clarified.

Occurrence. — Late *P. jugosus* to the end of the Famennian in all studied localities.

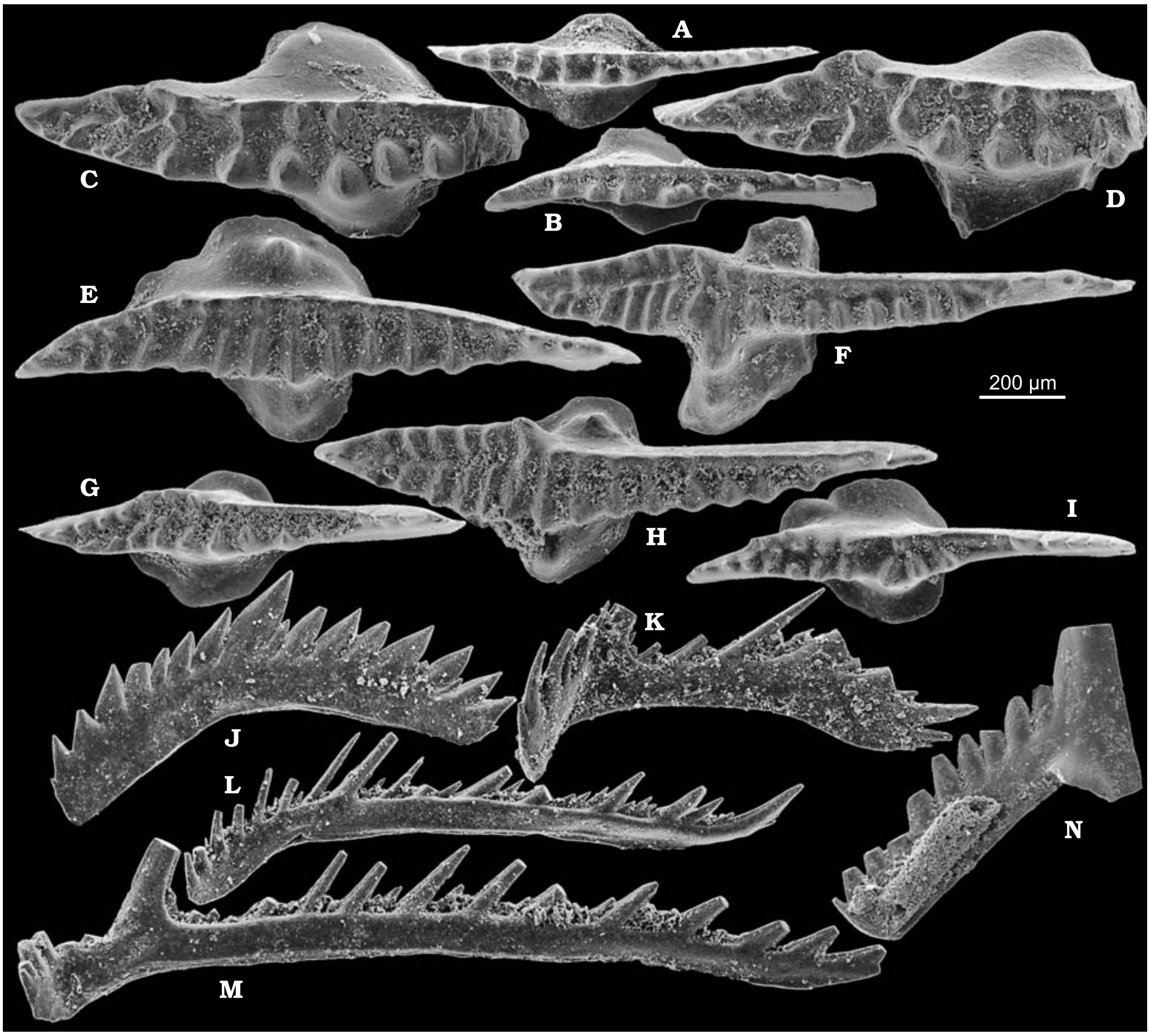

Fig. 114. Probable cavusgnathids *Pseudopolygnathus* in the Holy Cross Mountains. **A**–**D**. *P. aculeatus* (Branson *et* Mehl, 1934) from the *P. jugosus* (A, B, sample Ko-54) and *D. trigonica* (C, D, sample Ko-110) zones at Kowala. P_1 elements; specimens ZPAL cXVI/2332, 2333, 2321, and 2320, respectively. **E**–**N**. *P. ziegleri* (Rhodes, Austin *et* Druce, 1969) from the *D. trigonica* Zone at Ostrówka (sample Ost-3). P_1 (E–I), P_2 (J), S_0 (K), S_2 (L), S_{3-4} (M), and M (N) elements; specimens ZPAL cXVI/2322, 2324, 2325, 2323, and 2326–2331, respectively.

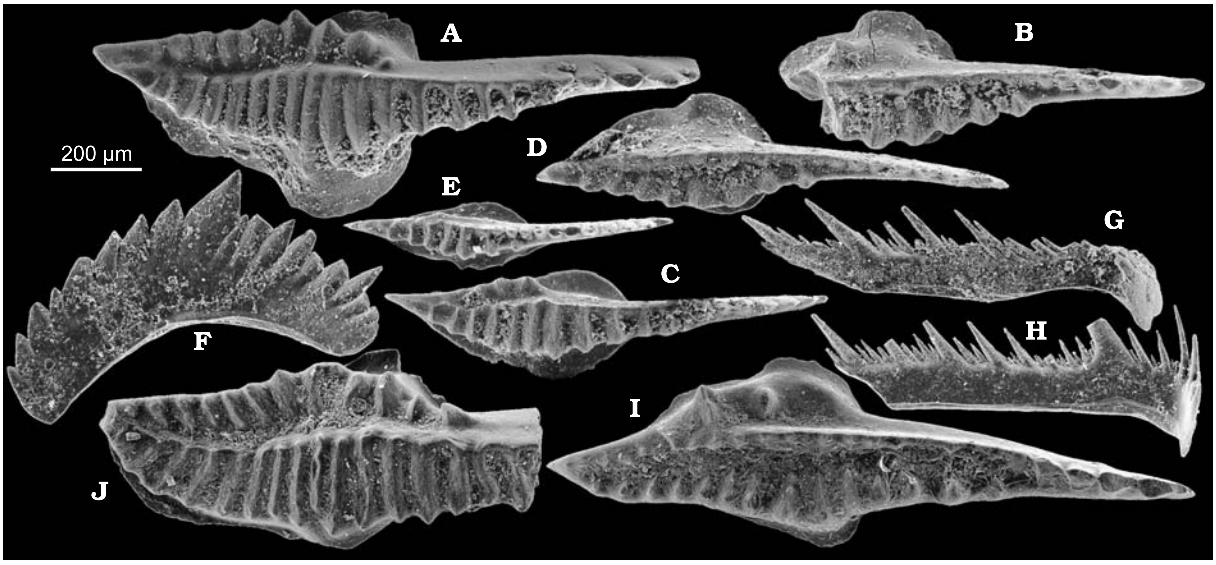

Fig. 115. Probable cavusgnathid *Pseudopolygnathus ultimus* (Bischoff, 1957) from the *P. jugosus* Zone at Dzikowiec (A–H, sample Dz-17) in the Sudetes and the *D. trigonica* (I, J, sample Ko-110) Zone at Kowala in the Holy Cross Mountains. P_1 (A–E, I, J), P_2 (F), S_2 (G), and S_{3-4} (H) elements; specimens ZPAL cXVI/2310–2319, respectively.

Pseudopolygnathus ziegleri (Rhodes, Austin *et* Druce, 1969)
(Figs 114E–N and 137)

Type horizon and locality: Upper costatus Zone in the Hönnetal road cut near Balve, Rhenish Slate Mountains (Ziegler 1975).

Material. — 112 specimens.

Diagnosis. — Icrion in the dorsal part of P_1 elements composed of three rows of denticles; the medial higher than the lateral ones that tend to develop transverse ridges.

Remarks. — Left and right elements show different morphology of the icrion, as already shown by Ziegler and Sandberg (1984) classifying the latter under the name of *Bispathodus ultimus*. In Kowala *P. ziegleri* was replaced by *P. ultimus* between deposition of strata represented by samples Ko-114 and Ko-113, thus after emergence of *D. trigonica*, whereas at Dzikowiec *P. ultimus* appears before *D. trigonica*. Probably this change was controlled ecologically and not directly related to evolution, as suggested by the re-appearance of *P. ziegleri* before the end of the Famennian at Kowala.

Occurrence. — The late *P. jugosus* Zone at Kowala, Ostrówka, and Dzikowiec.

Pseudopolygnathus ultimus (Bischoff, 1957)
(Figs 115 and 137)

Type horizon and locality: The type locality of the *Wocklumeria* beds at Wocklum, Rhenish Slate Mountains (Bischoff 1957; Ziegler 1975).

Material. — 1,333 specimens.

Diagnosis. — The lateral rows of denticles in the dorsal part of the icrion of P_1 elements transformed into wide transverse ridges separated in the middle by a longitudinal escarpment, sometimes forming also a low crest.

Remarks. — Left and right elements differ in width of icrion and prominence of its ribbing. The species seems to be a direct successor of *P. ziegleri* but the transition was probably long-lasting and population variability wide. It is thus hardly of much correlative value in stratigraphy.

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

Family **Elictognathidae** Austin *et* Rhodes, 1981

Diagnosis. — Secondarily lost axial symmetry in P_1 elements.

Remarks. — Classification of *Siphonodella* in this family was proposed by Sweet (1988) based on the assumption that its apparatus P_2 location was occupied by elements earlier classified as *Elictognathus*. This was followed by myself (Dzik 1994), although only one of the *Siphonodella*-like Tournaisian conodonts may possibly fit such an apparatus concept. P_2 elements of *Elictognathus* morphology co-occur with ramiform elements classified in *Dinodus*, the generic name having priority. The Devonian elements with a morphology resembling *Dinodus* can hardly belong to an apparatus related to the *Siphonodella* lineage and probably are rather of prioniodinid affinities (*Guizhoudella*). The derived morphology of apparatus elements of *Siphonodella* probably did not originate before the Tournaisian. Possibly, the earliest elictognathids were quite different and their roots are to be looked for in *Immognathus*. All this introduces much uncertainty to classification of those conodonts and requires clarification.

Genus ***Pinacognathus*** Branson *et* Mehl, 1934

Type species: *Pinacodus profundus* Branson *et* Mehl, 1934 from the Bushberg Sandstone of Missouri.

Diagnosis. — P_1 elements with lanceolate, flat or inverted basal cavity separated by an escarpment from the rest of the platform base; ramiform elements with relatively short processes.

Pinacognathus? *praesulcatus* (Sandberg, 1972)

(Figs 110M, N and 129)

Type horizon and locality: Top of the Sappington Member of Three Forks Formation at Lick Creek Road, Little Belt Mountains, Montana.

Material. — 17 specimens.

Remarks. — Material at my disposal is rather poor and only sample Ko-116 contains enough specimens of various ontogenetic age to see their variability. It appears that juveniles have a platform usually separated from the blade by a deep depression and the element has the greatest width at the dorsal end of the platform. In mature specimens the middle part of the platform is the widest and it is almost flat with the denticles of the blade somewhat elevated. Elements show mirror symmetry that makes unlikely any relationship to *Alternognathus*. Also the flat or somewhat inverted basal cavity makes it different from *Alternognathus*, where the base remains slightly concave and the margin of the basal cone remains sharp. Variability is expressed mostly in more or less robust transverse ribbing of the platform and in the dorsal margin of the platform, in juveniles being thin and wide or rather narrow and robustly tuberculated. The apparatus remains unknown.

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

Family **Idiognathodontidae** Harris *et* Hollingsworth, 1933

Diagnosis. — Generalized late Palaeozoic conodonts with wide basal cavity in P_1 elements and tendency to develop a platform at the basal cone or icrion in the dorsal part of the element; in post-Devonian forms the external process of S_{3-4} elements is arched and recurved.

Genus ***Protognathodus*** Ziegler, 1969

Type species: *Gnathodus kockeli* Bischoff, 1957 from the *Gattendorfia* Stufe in the Rhenish Slate Mountains.

Diagnosis. — Widely gaping and rather deep basal cavity reaching the dorsal tip of P_1 element, gently arched profile of the blade.

Protognathodus kockeli (Bischoff, 1957)

(Figs 116M, N and 138)

Type horizon and locality: Lower part of the *Gattendorfia* Limestone at Wocklum in the Rhenish Slate Mountains.

Material. — 42 specimens.

Remarks. — Specimens from the topmost Famennian strata at Kowala are difficult to clean from clayish cover and thus are not suitable for SEM photography. They show tuberculation of the basal cone typical of the early Tournaisian populations of *Protognathodus* (e.g., Dzik 1997).

Occurrence. — Terminal Famennian at Kowala (samples Ko-51 and Ko-24; Dzik 1997) and Dzikowiec (Dz-75).

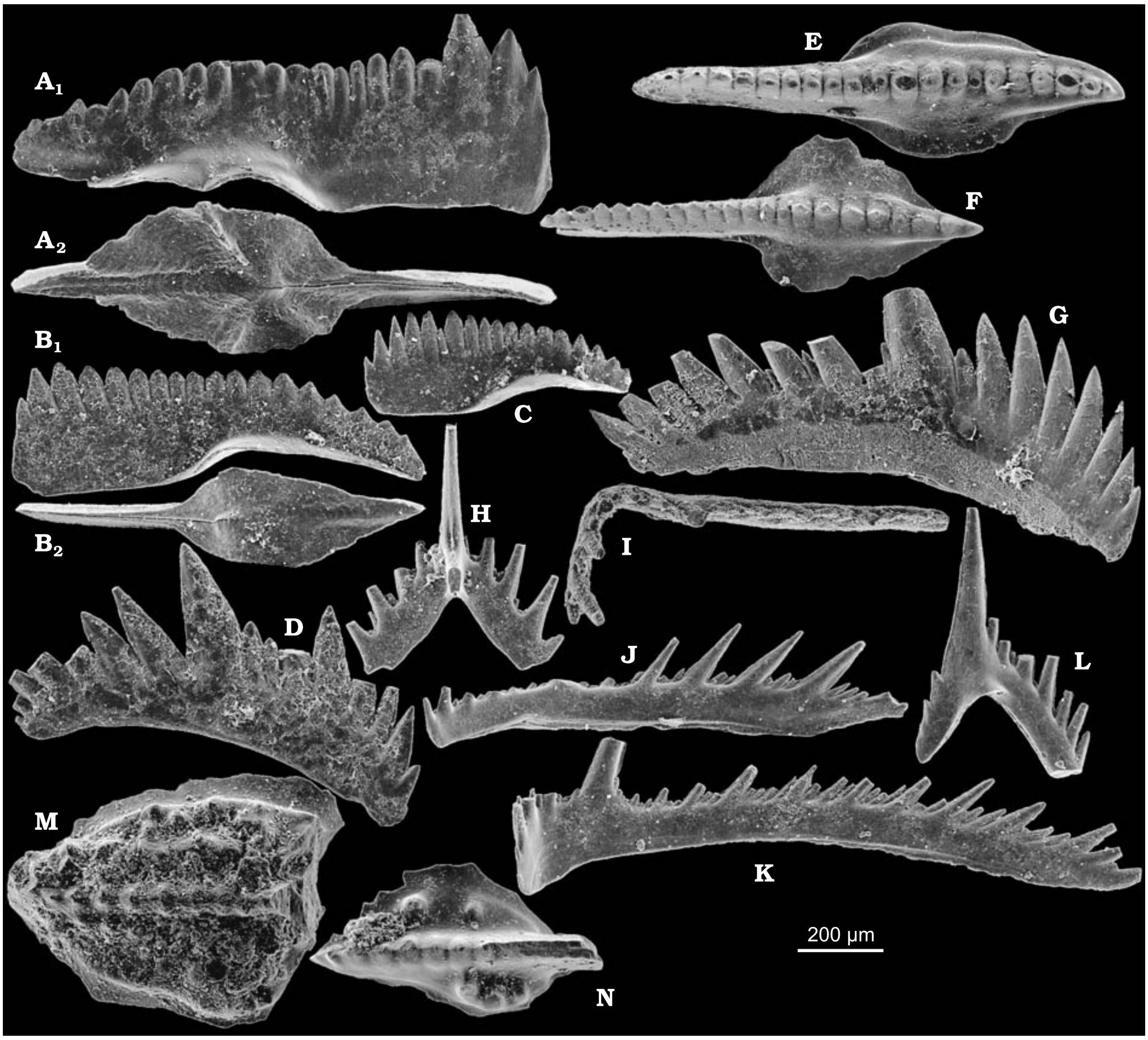

Fig. 116. Early idiognathodontids. **A–L**. *Dasbergina stabilis* (Branson *et* Mehl, 1934) from the *P. jugosus* Zone at Jabłonna (A–D, bed 27) and Ostrówka (E–L, sample Ost-185) in the Holy Cross Mountains. P_1 (A–C, E, F), P_2 (D, G), S_0 (H), S_1 (I), S_2 (J), $S_{3–4}$ (K), and M (L) elements; specimens ZPAL cXVI/2206–2209 and 2261–2268, respectively. **M**, **N**. *Protognathodus kockeli* (Bischoff, 1957) from Dzikowiec (sample Dz-75). P_1 elements, specimens ZPAL cXVI/2965 and 2964.

Genus ***Dasbergina*** Schäfer, 1976

Type species: *Dasbergina ziegleri* Schäfer, 1976 from the bed 93 of a trench at Dasberg, lower costatus Zone.

Diagnosis. — Very shallow conical basal cavity, variously developed platform around the basal cone, apparatus of generalized morphology.

Remark. — Early species of the genus, with weakly developed platform, are transitional to the probably ancestral species of *Pandorinellina*, *P. vulgaris*. The difference between transitional populations is only in the width of the basal cone, in fact, very variable.

Dasbergina stabilis (Branson *et* Mehl, 1934)
(Figs 116 and 138)

Type horizon and locality: Probably the Saverton Shale near Monroe City, Missouri (Ziegler 1975, p. 47).

Material. — 4,491 specimens.

Diagnosis. — P_1 element lacking platform, almost flat cavity of the basal cone with eye-drop outline, continuing to the dorsal tip of the blade.

Remarks. — The apparatus of the species was restored by Over (1992). The basal cavity varies from being virtually flat to distinctly conical. Specimens with very flat base differ from those of *Pandorinellina vulgaris* in their much lower blade and a tendency to develop an incipient platform of low elevation continuing to the tip of the element. From associated juvenile specimens of *Dasbergina micropunctata* such elements differ in having their base (and "platform") gradually narrowing to the tip while in *D. micropuntata* the base has a pear-like outline and terminates significantly in front of the element tip.

The oldest specimens of *D. stabilis* in the densely sampled part of the Kowala section have been found in sample Ko-187. Unfortunately specimens classified in *P. vulgaris* from the sample immediately below are fragmentary, hampering biometrical presentation of the change.

Occurrence. — The *P. trachytera* to *D. trigonica* zones at Jabłonna, Ostrówka, Kowala, and Miedzianka, the Holy Cross Mountains, and Dzikowiec, the Sudetes.

Dasbergina micropunctata (Bischoff *et* Ziegler, 1956)
(Figs 117 and 138)

Type horizon and locality: Dark limestone of toV from the "Rote Scheid" quarry near Marburg (Bischoff and Ziegler 1956).

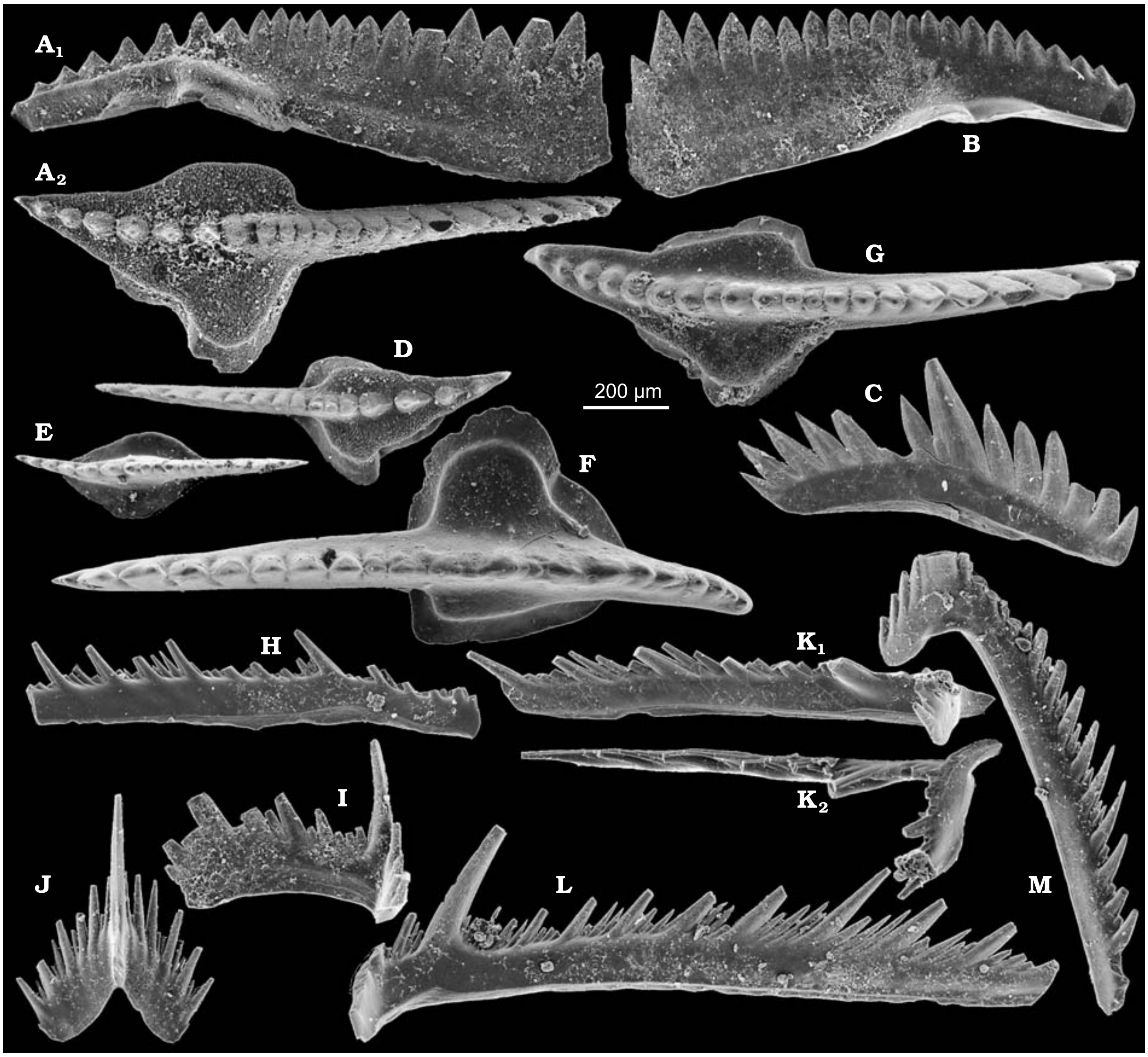

Fig. 117. Idiognathodontid *Dasbergina micropunctata* (Bischoff *et* Ziegler, 1956) from the *P. jugosus* Zone at Jabłonna (A–C, sample J-52) and Ściegnia (D–L ,sample Wzd-13) in the Holy Cross Mountains. P_1 (A–F), P_2 (G), S_0 (I, J), S_1 (K), S_2 (H), S_{3-4} (L), and M (M) elements; specimens ZPAL cXVI/2235, 2197, 2196, 2234, 2251, 2250, 2252, 2254, 2256, 2255, 2253, and 2257, 2258, respectively.

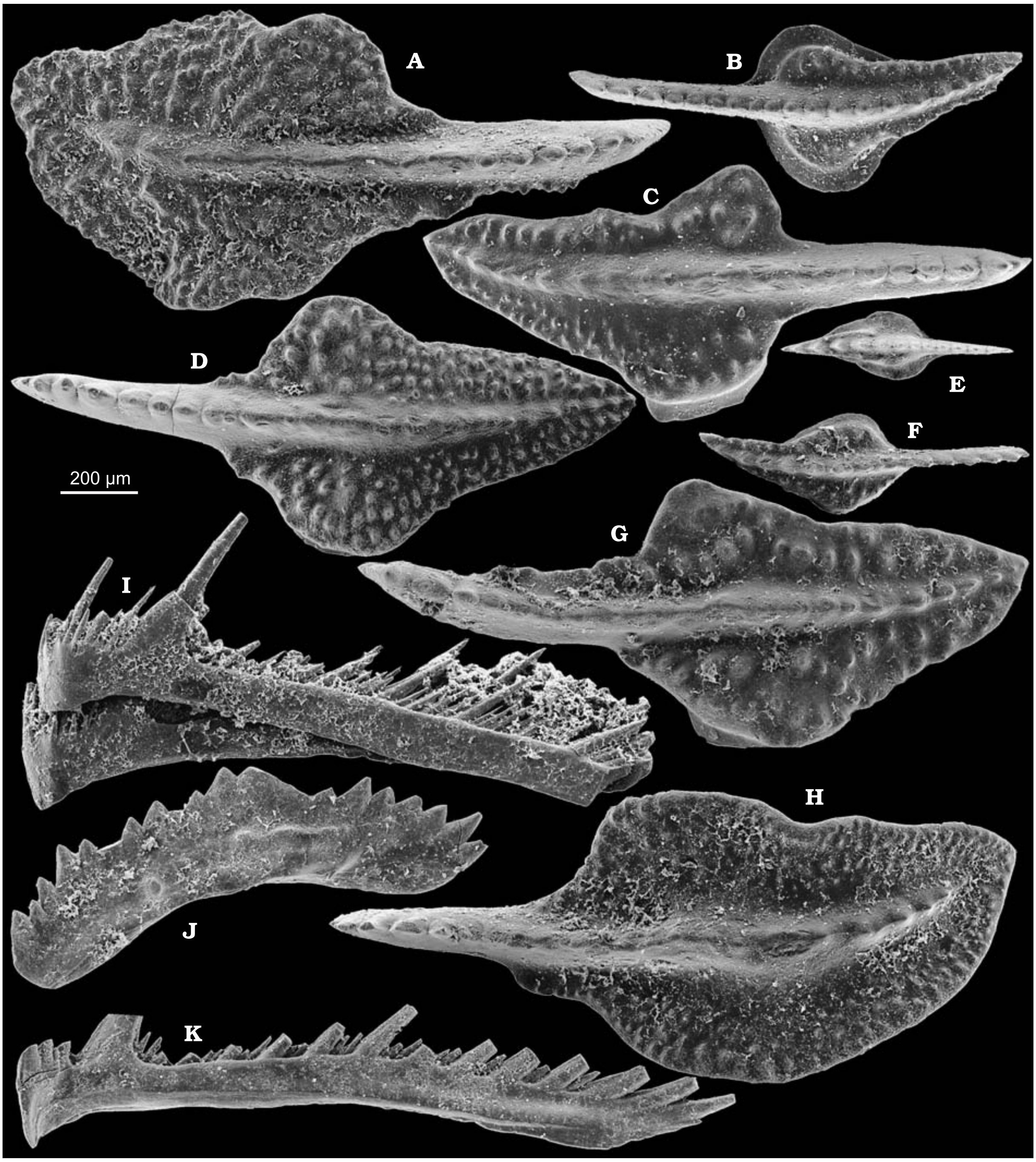

Fig. 118. Idiognathodontid *Dasbergina granulosa* (Ziegler, 1962) from the *L. styriacus* Zone at Ostrówka (A–C, I–K, sample 1a; D–H, sample Ost-12) in the Holy Cross Mountains. P_1 (A–H), P_2 (J), and S_{3-4} (I, cluster of two elements, K) elements; specimens ZPAL cXVI/2271, 2270, 2269, 2275, 2278, 2276, 2277, 2274, 2345, 2272, and 2273, respectively.

Material. — 1,733 specimens.

Diagnosis. — The basal cone of P_1 element with a smooth triangular platform, basal cavity narrows in front of the dorsal tip of the blade.

Remarks. — Some P_1 elements have platform with a completely smooth surface, others show the reticulate pattern of ameloblast imprints. The meaning of this difference is unclear. Triramous S_1 elements may belong to this species.

Occurrence. — The *L. styriacus* to *D. trigonica* zones at Jabłonna, Ostrówka, Kowala, Miedzianka, the Holy Cross Mountains, and Dzikowiec, the Sudetes.

Dasbergina granulosa (Ziegler, 1962)
(Figs 118 and 138)

Type horizon and locality: Bed 0 in the Sessacker II trench, *P. trachytera* Zone.

Material. — 1,732 specimens.

Diagnosis. — The platform of irregularly angular shape ornamented with numerous tubercles, basal cavity forms lobes on both sides of the P_1 element.

Remarks. — This is one of the most robust and largest Famennian conodonts. Mature P_1 elements bear a very wide platform but the conical basal cavity grows to maturity. Some specimens from Kowala and Dzikowiec, with very variable ornamentation and the platform extending far outside the basal cone, but restricted to the center of the element, may be transitional to *Dasbergina* sp. aff. *D. kayseri*.

Occurrence. — The *P. trachytera* to *P. jugosus* zones at Jabłonna, Ostrówka, Kowala, Miedzianka, the Holy Cross Mountains, and Dzikowiec, the Sudetes.

Dasbergina kowalensis sp. n.
(Figs 119A–C and 138)

Holotype: Specimen ZPAL cXVI/2256 (Fig. 119B).

Type horizon and locality: Sample Ko-1, late Famennian early *P. jugosus* Zone at Kowala, Holy Cross Mountains.

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

Material. — 27 specimens.

Diagnosis. — Incipient platform of irregularly angular shape ornamented with a few large tubercles, basal cavity forms wide lobes on both sides of the P_1 element.

Remarks. — This seems to be the oldest member of the *D. trigonica* lineage, perhaps a successor of *D. stabilis*, although the transition has not been demonstrated. The basal cone ornamented with tubercles makes the species similar to *Protognathodus*. This is probably only a convergence; the difference is that the basal cavity is expanded only in proximity to the cusp and strongly narrows dorsally.

Occurrence. — The early *P. jugosus* Zone at Kowala.

Dasbergina marburgensis (Bischoff *et* Ziegler, 1956)
(Figs 119D–I and 138)

Type horizon and locality: Dark limestone of toV unit from the quarry NE Weitershausen in the Rhenish Slate Mountains.

Material. — 190 specimens.

Diagnosis. — Triangular platform of P_1 element ornamented with robust marginal denticles, tending to form irregular transverse rows near the element center; transversely elongated lobes of basal cavity with parallel margins.

Remarks. — Perhaps the most characteristic feature of the species is the basal cavity of the P_1 element. Its narrowly elongated anterior lobe has a rounded tip, whereas the posterior lobe varies from narrowly rounded to angular, with the ventral angle more prominent.

Occurrence. — The late *P. jugosus* Zone at Ostrówka, Kowala, and Dzikowiec.

Dasbergina trigonica (Ziegler, 1962)
(Figs 119J–N and 138)

Type horizon and locality: Sample 3a from the Hönnetalstraße section in the Rhenish Slate Mountains.

Material. — 204 specimens.

Diagnosis. — The basal cavity of P_1 element bifurcates anteriorly.

Remarks. — In successive samples in the upper part of the Dzikowiec section the anterior lobe of the basal cavity of the P_1 element, originally round (Dz-18), gradually becames more angular (Dz-10, Dz-17, Dz-20b) and then its tip narrows and the lobe bifurcates (Dz-19, Dz-47, Dz-4). This marks the transition from *D. marburgensis* to *D. trigonica*. This character shows a significant population variability and juveniles may show angular wide lobes even in samples from high above in the section (e.g., Dz-8).

The species occurs in the borehole Kowala, as shown by Nehring-Lefeld (1990).

Occurrence. — Zone of its own at Kowala and Dzikowiec.

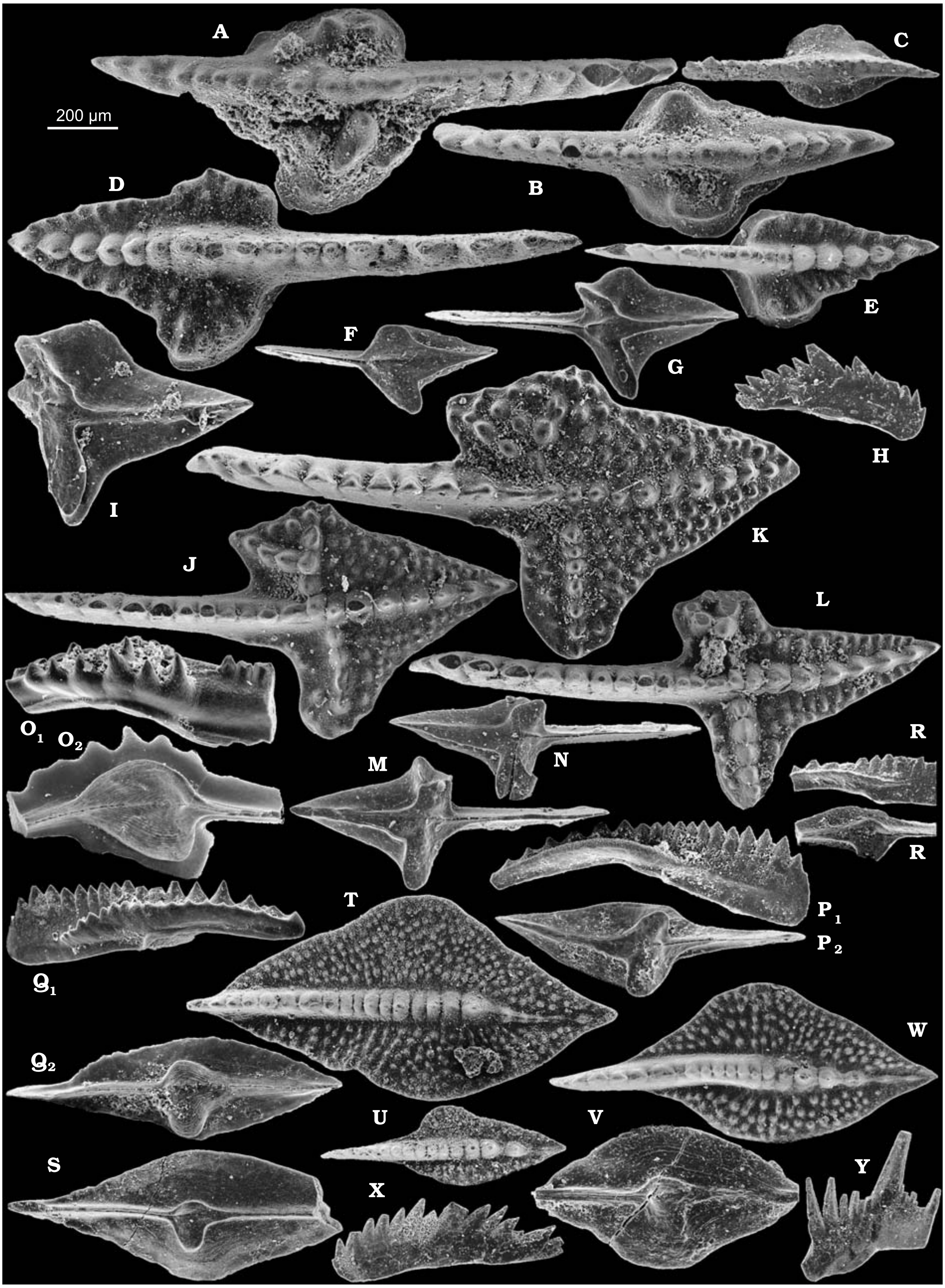

Fig. 119. Idiognathodontids of the *Dasbergina trigonica* and *D. kayseri* lineages. **A–C**. *D. kowalensis* sp. n. from the early *P. jugosus* Zone at Kowala (sample Ko-1). P_1 elements; specimens ZPAL cXVI/2245–2247 (holotype, B). **D–I**. *Dasbergina marburgensis* (Bischoff and Ziegler, 1956) from the late *P. jugosus* Zone at Ostrówka (D, E, sample Ost-185) and Dzikowiec (F–I, sample Dz-10; late form). P_1 (D–G, I) and P_2 (H) elements; specimens ZPAL cXVI/2280, 2279, 2977–2980, and 2979,

→

Dasbergina sp. aff. *D. kayseri* (Bischoff *et* Ziegler, 1956)
(Fig. 119O, P)

Remarks. — At Kowala below the occurrence of *Dasbergina kayseri* an unnamed species occurs with a wide asymmetric basal cavity resembling that of adult *Dasbergina granulosa* and with a higly variable tuberculation of the platform that may be almost smooth in juveniles (e.g., Perri and Spalletta 1991, pl. 9: 5). It even seems that in successive samples the basal cone became smaller and more asymmetric, although too few specimens are known to be sure that this is not a case of very wide population variability. A possibility thus emerges that the latest Famennian *D. keyseri* lineage is an outshoot of *Dasbergina*, homeomorphic with the early Famennian ancyrognathids.

Dasbergina kayseri (Bischoff *et* Ziegler, 1956)
(Figs 119Q–Y and 132)

Type horizon and locality: Dark limestone of toV from the quarry NE Weitershausen near Marburg (Bischoff and Ziegler 1956).

Material. — 80 specimens.

Diagnosis. — Relatively large, asymmetric basal cone (pit); rhomboidal outline of platform in P_1 element reaching almost the ventral end of the blade in mature specimens.

Remarks. — One specimen from Kowala (Fig. 119Q) shows a large basal cavity, transitional in size and shape between that in the preceding species and typical *D. kayseri*. Rare ramiform elements associated with P_1 elements typical of the species are too generalized to prove its generic affiliation, but their morphology does not contradict affinities with advanced *Dasbergina*.

Occurrence. — The *P. jugosus* Zone at Ostrówka and Kowala.

Dasbergina brevipennata (Ziegler, 1962)
(Figs 120A–U and 138)

Type horizon and locality: Sample 1327 from the road section at Hönnetal, late *L. styriacus* Zone.

Material. — 782 specimens.

Diagnosis. — Platform of P_1 element with regularly angular outline and flat surface ornamented with numerous tubercles.

Remarks. — Juvenile P_1 elements of the species show a more lanceolate outline of the platform than preceding species and in this respect they are rather similar to juveniles of *D. ziegleri*.

Occurrence. — The *L. styriacus* Zone at Jabłonna, Kowala, and Ściegnia.

Dasbergina ziegleri Schäfer, 1976
(Figs 120V–Y and 138)

Type horizon and locality: Bed 93 in a trench at Dasberg, lower costatus Zone

Material. — 310 specimens.

Diagnosis. — Wide robust platform extending almost to the whole length of P_1 element, ornamented with robust tubercles and ridges.

Remarks. — *Pseudopolygnathus controversus* Sandberg *et* Ziegler, 1979 is probably conspecific with this species. Notably, the early population of *D. ziegleri* from the *L. styriacus* Zone (Fig. 120V, W), with a rather angular outline of the platform and its fine tuberculation, resembles *D. brevipinnata*. The late population from the *P. jugosus* Zone (Fig. 120X, Y) is similar in those respects rather to *Pseudopolygnathus*

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respectively. **J**–**N**. *Dasbergina trigonica* (Ziegler, 1962) from its nominal zone at Ostrówka (J, K, sample Ost-3) in the Holy Cross Mountains and Dzikowiec (L, sample Dz-7; M, N, sample Dz-74) in the Sudetes. P_1 elements; specimens ZPAL cXVI/2281–2283, 2966, and 2967. **O**, **P**. *Dasbergina* sp. aff. *kayseri* (Bischoff *et* Ziegler, 1956) from the *P. jugosus* Zone at Kowala (sample Ko-192), possible transitional forms from underived *Dasbergina* with wide basal cone to *D. kayseri*. P_1 elements; specimens ZPAL cXVI/2996 and 2997. **Q**. *Dasbergina kayseri* (Bischoff *et* Ziegler, 1956) early form with wide basal cavity from the *P. jugosus* Zone at Kowala (sample Ko-197). P_1 element; specimen ZPAL cXVI/2995. **R**–**Y**. Typical *Dasbergina kayseri* (Bischoff *et* Ziegler, 1956) from *P. jugosus* Zone at Ostrówka (H, K, sample Ost-2; I, J, L, M, sample Ost-185) and Kowala (N, O, sample Ko-198) in the Holy Cross Mountains. P_1 (R–W), P_2 (X), and $S_{3–4}$ (Y) elements; specimens ZPAL cXVI/2998, 2603, 2598, 2599, 2999, and 2600–2602 respectively.

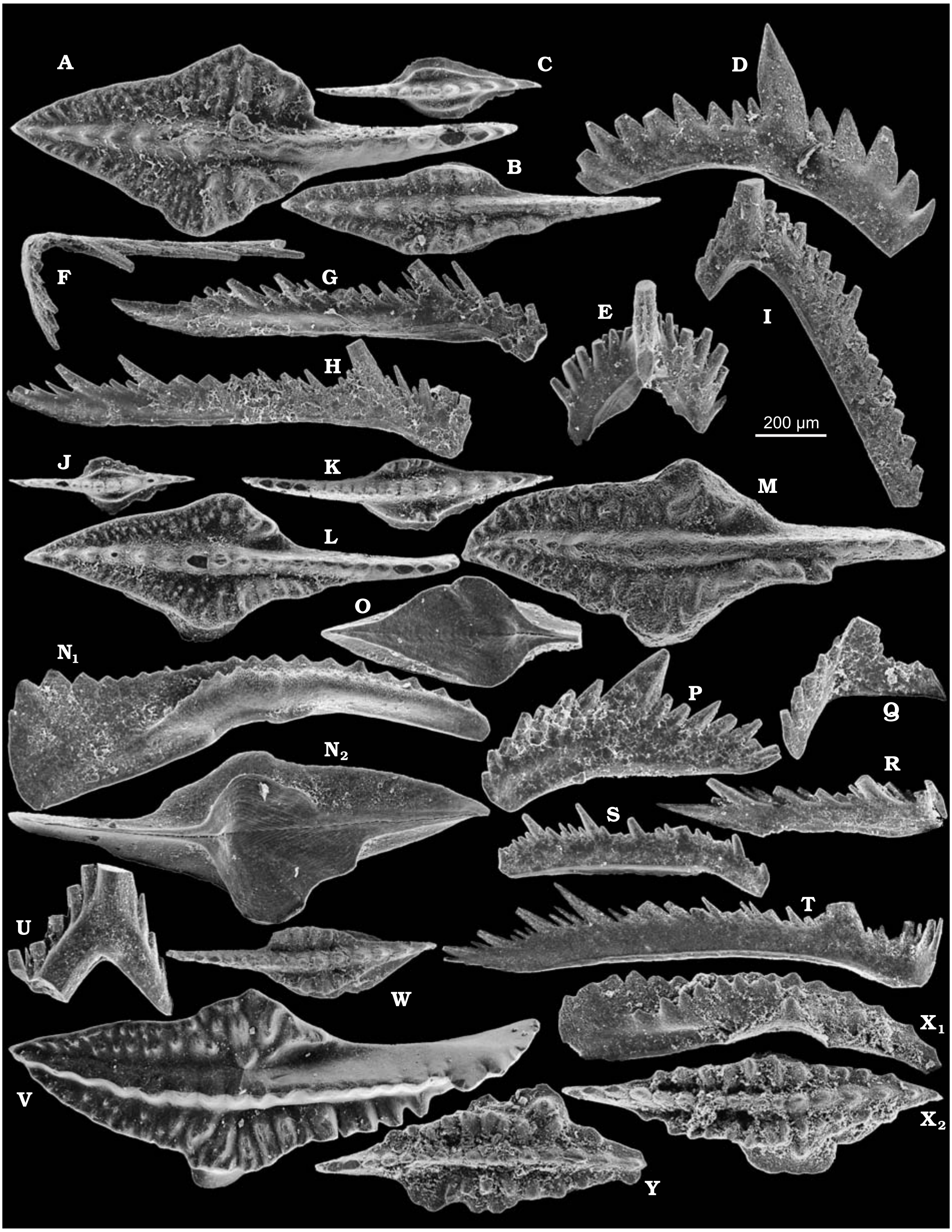


Fig. 120. Idiognathodontids of the *Dasbergina ziegleri* branch from the Holy Cross Mountains. **A–U**. *Dasbergina brevipennata* (Ziegler, 1962) from the early *P. jugosus* Zone at Jabłonna (A–I, bed 27) and the late *L. styriacus* Zone at Kowala (J–U, sample Ko-191). P_1 (A–C, J–O), P_2 (D, P), S_0 (E, Q), S_1 (F, R), S_2 (G, S), S_{3-4} (H, T), and M (I, U) elements; specimens ZPAL cXVI/2216–2224, 3000–3011, respectively. **V–Y**. *Dasbergina ziegleri* Schäfer, 1976 from the *L. styriacus* Zone at Ostrówka (V, W, sample Ost-7) and the early *P. jugosus* Zone at Kowala (X, Y, sample Ko-1). P_1 elements; specimens ZPAL cXVI/2284, 2285, 2248, 2249.

ostrovkensis. It seems thus that this is an outshoot of the *Dasbergina* lineage homeomorphic with *Pseudopolygnathus* (in fact, both are closely related).

Occurrence. — The *P. jugosus* Zone at Kowala and Ostrówka.

FAUNAL DYNAMICS OF THE FAMENNIAN CONODONTS IN POLAND

While reviewing distribution of particular groups of fossil organisms one has to face the conflict between ecology and phylogeny. Obviously, the supraspecific taxonomic units are by definition based on evolutionary (that is, genetic) relationships among species, which do not need to be related to their environmental preferences. However, many Famennian conodont taxa seem to preserve some ecological coherencey and the review in the introductory chapters of this work presenting conodont ecostratigraphy in the area (Fig. 5, 6) may serve as an useful approximation. To extract the unbiased evidence on the evolution of local environments it would be necessary to address distribution of each species separately. This kind of evidence is offered by quantitative data on their frequency distribution in the part of the work showing the stratigraphic distribution of species (Figs 121–138). Some general comments on the global environmental change as seen from a Polish perspective are presented. This will be followed by a review of the Famennian evolutionary diversification of conodonts, with an attempt to be free as much as possible from its preservational and ecological bias.

SUCCESSION OF THE FAMENNIAN CONODONT FAUNAS

Conodont species with apparatuses containing platform elements represent only a fraction of the complete late Devonian conodont diversity. This is to a great degree obliterated by unbalancing of fossil samples, that is their enrichment in robust platform- or icrion-bearing elements as a result of hydrodynamic sorting and/or fragmentation of fragile ramiform elements of the apparatus. To restore the original numerical contribution of species to the biological productivity of the conodont community this bias should be removed. Let us attempt to do this by replacing counts of platform elements to a selected sample by numbers derived from counts of non-platform elements of the same species. In the standard conodont apparatus with 15 elements, the P_1 elements represent approximately 13% of all elements. To compensate for the possibly greater fragility of ramiform elements in such apparatuses in respect to those without platforms, lets assume that the number of P_1 elements actually found represents 25 % of their original number prior to taphonomic distortion. For rare species known only from platform specimens and for *Icriodus* their number in the count below has been only halved.

If reinterpreted in this way, the terminal Frasnian Kellwasserkalk sample Pł-391 represented by 17,804 specimens (see Dzik 2002) gives a not especially impressive picture of biological diversity of the community (more precisely: its biological production). Only three species significantly contributed to this: the dominant *Polygnathus webbi* (including its variety informally listed as *P.* "*tuberculatus*", do not related to true *P. tuberculatus* Hinde, 1879) with almost 35% of all elements, *Icriodus iowaensis* with about 30% (perhaps more, as the way in which this estimate was done is especially unreliable in this case), and the palmatolepidid *Lagovilepis bogartensis* with 20% contribution. Five species contributed from 1.5 to 3.9% each, so some of them had a chance to be represented in samples of standard size (species of *Ctenopolygnathus*, *Ancyrodella*, *Klapperilepis*, *Ligonodina* and *Dyminodina*). All the remaining seven species of this high-diversity community even after such compensation are represented by less then 1%. They are thus unlikely to be identified in a standard conodont sample taken for stratigraphic purposes (species of *Pelekysgnathus*, *Pluckidina*, *Mehlina*, *Ancyrognathus*, and the palmatolepidids *Manticolepis winchelli*, *M. rhenana* and "*Conditolepis*" *linguiformis*).

All this shows also how unreliable ranges of vertical distribution of taxa may be, even in situations where the fossil record is complete.

Frasnian–Famennian boundary event. — The dramatic change at the Frasnian–Famennian boundary seen from this perspective fades very much (cf. House 2002; Bambach *et al.* 2004; Racki 2005). It is still a significant decrease in diversity, but not unprecedented in the Frasnian record. The three earliest Famennian samples (Pł-20, Pł-16, and Pł-15; Dzik 2002), counted together in the same way to compensate for unbalancing, give a surprisingly similar community structure. Again, only three species dominate: *Icriodus* (different species than in the Frasnian, *I. alternatus*) with its 39% contribution, *Polygnathus* (*P. praecursor*, possibly a successor of the Frasnian *P. webbi*) contribution about 30% and the only palmatolepidid *Klapperilepis ultima* continuing from the Frasnian, of almost 20% share in the community structure. Also other lineages probably continue from the Frasnian, with two of reasonable contribution (*Ctenopolygnathus*, about 10% and *Mehlina* 4%). *Pelekysgnathus*, *Ligonodina*, *Dyminodina* and *Pluckidina* all have below a 1% contribution. It appears thus that except for the termination of *Lagovilepis bogartensis* and replacing one species of *Icriodus* by another, nothing truly unusual happened at this allegedly "one of the greatest extinction events in the World history", in contrast to the internationally-accepted definition of the F–F mass extinction boundary (see references above). In the Holy Cross Mountains, where the stromatoporoid-coral reef communities of the Frasnian are especially well represented, their growth terminated significantly below this change in conodont communities. There is hardly any reason to believe in a sudden catastrophic event of extraterrestrial cause at the Frasnian–Famennian boundary. No doubt, however, that a profound rebuilding of marine ecosystems and long-distance migrations of pelagic communities took place that time, suggestive of a deep change in the global climate (e.g., Dzik 2002; Joachimski and Buggisch 2002; Joachimski *et al.* 2001, 2004).

Within-Famennian environmental changes. — The earliest Famennian strata in the Płucki section differ from those below in the increased contribution of black shale intercalations. It is thus instructive to compare the first Famennian conodont community with that representing a similar environment of black shale in the mid Famennian. Sample Ko-8a of 1058 specimens from the limestone concretions, collected immediately above the black "paper" shale exposed in the Kowala quarry representing the *Platyclymenia annulata* event, offers such an opportunity (Fig. 4, 6). Counted in the same way it shows an overdomination of the prioniodinid (or the earliest non-platform gondolellid) *Branmehla* (57%), two other species, the palmatolepidid *Tripodellus schleizius* and the cavusgnathid *Alternognathus regularis* contributed 12% and 10%, respectively. All other species (of genera *Icriodus*, *Mitrellataxis*, *Idioprioniodus*, *Vogelgnathus*, *Pandorinellina*, *Mehlina*, *Polynodosus*, *Hemilistrona*, and *Neopolygnathus*) are of insignificant importance in the community. Less then half of them had platform elements in their apparatuses.

Paradoxically, a much more profound rebuilding of the conodont community occurred in time slices not so well noted in connection with purported catastrophic events. The first such fundamental transformation of the conodont communities in the Holy Cross Mountains during the Famennian took place near the end of the *K. triangularis* Zone. Many new lineages immigrated at that time, but most of the preceding diversity survived the change. Obviously, this was connected with a transgressive event immediately after the sea level drop (Johnson *et al.* 1985) that in the Holy Cross region resulted in the submersion of the earlier eroded massive limestone at Kadzielnia, the sedimentary discontinuity surface at Wietrznia, and the redeposition of limestone pebbles at Miedzianka.

Less apparent and generally stepwise changes in composition of the conodont community by immigration of some and disappearance of other lineages took place within the *C. quadrantinodosa* and *C. marginifera* zones. Also these events were related to periodic lowering of sea level, as suggested by the sedimentary discontinuity within this time span in the Łagów section. The change was not connected with competition between members of different lineages but resulted rather from lateral shifts of ecosystems as a result of global environmental changes.

Several events of the sea level rise and increase in biological productivity marked by bituminous shale deposition (see Walliser 1996; House 2002) are well displayed in the Kowala section. These were identified with the *Platyclymenia annulata*, Epinette and Hangenberg events by myself (Dzik 1997). They did not cause any dramatic change in the conodont community. The changes in their relative contribution were not more significant than in the whole upper part of the section, where cyclicity of probably Milanković nature seems to be recorded (Fig. 6). There was a series of two sudden drops in diversity of conodonts near the end of the Famennian. The first one corresponds to the beginning of the *D. trigonica* Zone; from this moment the icrion-bearing *Pseudopolygnathus* dominated the assemblages. The whole pelagic faunal diversity was reduced to a catastrophic level at the time of sedimentation of the Hangenberg black shale (Dzik 1997; see also Brand *et al.* 2004).

In some aspects this situation is similar to that at the Frasnian–Famennian transition. The faunal replacement was even more significant near the end of the Famennian and the new dominant taxa (*Protognathodus kockeli* and *Acutimitoceras*) seem to mark an incursion of cold waters to the area (Dzik 1997). No doubt, however, that elsewhere several Famennian lineages survived and participated in restoring the warm-water

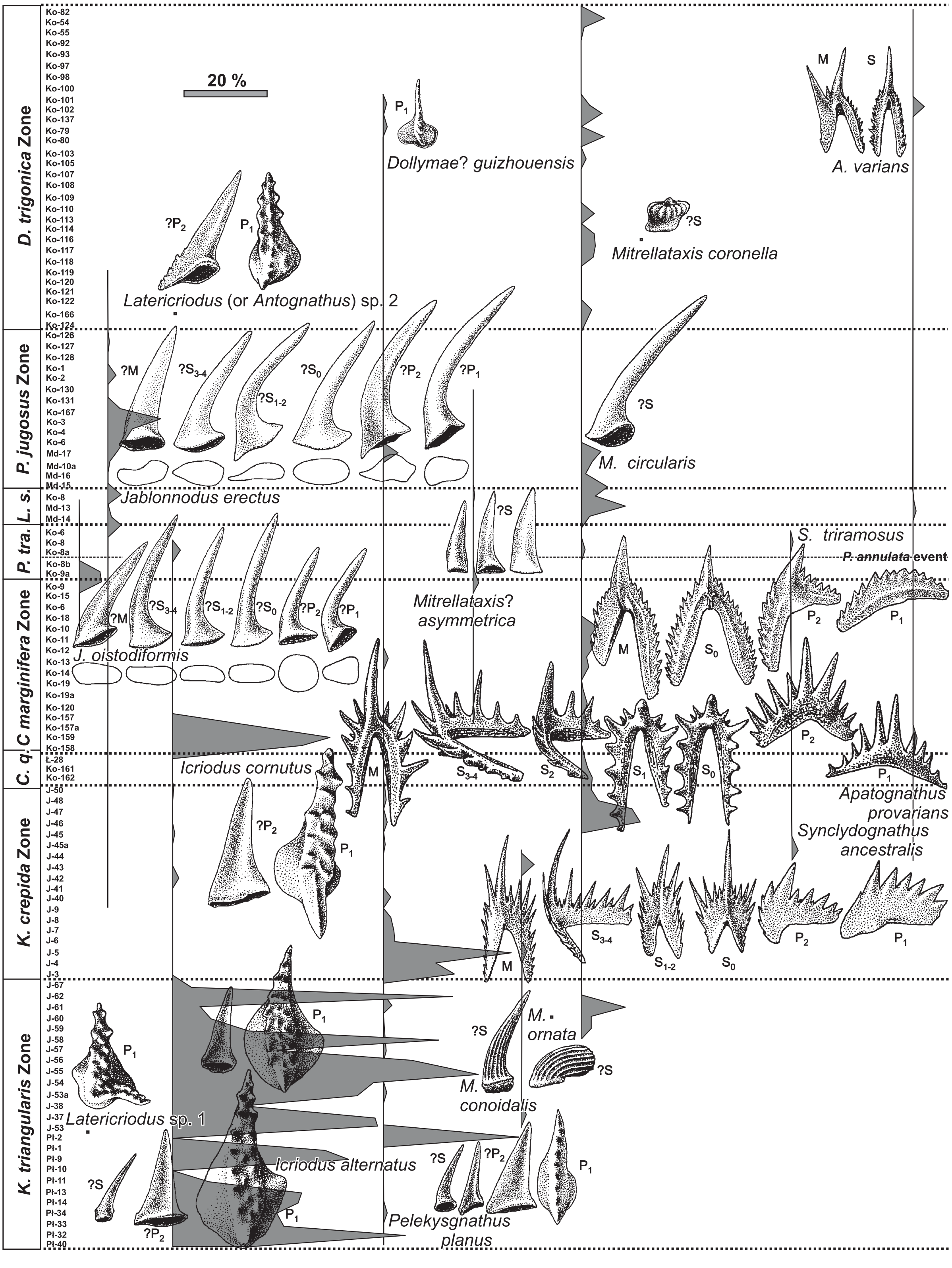


Fig. 121. Stratigraphic distribution of the possible protopanderodontid *Jablonnodus*, icriodontids, and spathognathodontids in the Polish Famennian. Percent contribution to samples in a composite succession assembled with representative sections in the Holy Cross Mountains (sample numbers given in the left column; for species not represented in these sections only vertical line denotes their distribution) and diagrammatic representation of identified apparatus elements is shown. Probable chronospecies of the same lineage are arranged in the same line; bases of lines correspond to immigration events. Note highly irregular frequency distribution of elements in particular lineages, which makes observed extent of ranges very sensitive to differences in sample size and usually not truly meaningful.

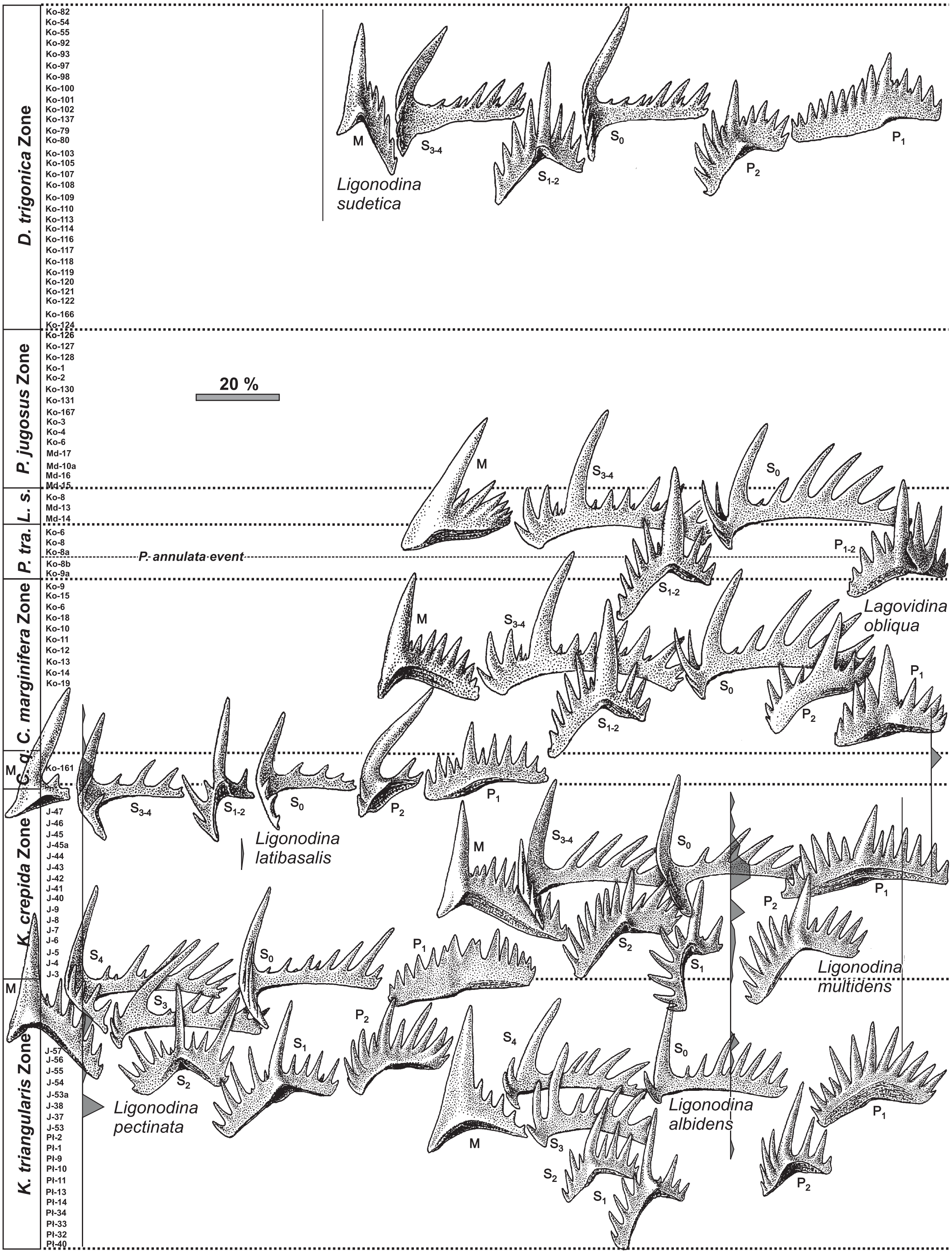


Fig. 122. Stratigraphic distribution of the prioniodinids *Ligonodina* and *Lagovidina* in the Polish Famennian (the same kind of presentation as on Fig. 121).

high-productivity communities of the *Gattendorfia* Limestone (Dzik 1997). Their exact course of evolution remains to be traced.

EVOLUTION OF THE FAMENNIAN CONODONTS

Most of the change in the faunal dynamics of conodonts in the Famennian of Poland appears thus to be caused by migrations, not unlike other examples of the fossil record in tropical environments. Only in a few cases a phyletic evolutionary change is recorded clearly enough to enable quantitative stratophenetic description. It is beyond the scope of the present work to use stratophenetics to show the evolution of the fauna. Its main goal is to present apparatus reconstructions. Their knowledge is still in so early a stage that more basic questions on their relationships haves to be clarified first. However, it has to be pointed out that the available evidence supports a generally gradual pattern of evolution, unless it was truncated by sudden changes in ecological conditions or non-deposition events (Dzik 2005; compare with Donoghue 2001). A brief overview of probable phylogeny of particular Famennian conodont taxa is given below.

Mitrellataxids. — The first coniform *Mitrellataxis* emerges in the Holy Cross Mountains together with *Palmatolepis initialis*. More elaborate *M. ornata* followed soon and this may be an evolutionary succession. It occurred in proximity of the Karczówka mudmound analogous to the Frasnian belodellids. The order in appearance of smooth "simple cones" is from *M. circularis*, through *Jablonnodus erectus* to *J. oistodiformis* (Fig. 121). The end member of the *Jablonnodus* lineage is probably the unnamed late Famennian species with geniculate elements illustrated by Sandberg and Dreesen (1984). If taken literally this would suggest that the morphological distinctions within the apparatus typical of the last species developed gradually. However, no real transition has been demonstrated and this succession may have beeen controlled ecologically. The main lineage of *M. circularis*, although relatively well represented throughout the succession, is too indifferent morphologically to be interpreted in evolutionary terms. Anyway, a secondary homeomorphy with the Ordovician distacodontids remains a valid alternative to inheritance of ancient characters in a lineage of "living fossils".

Icriodontids. — Such "living fossils" are probably the most archaic Famennian icriodontids *Latericriodus*, episodic immigrants from an unknown source area.

The population of the earliest Famennian *Icriodus alternatus* (sample Pł-16) differs morphologically from the latest Frasnian *I. iowaensis* population, and may have roots somewhat deeper in the Frasnian (Dzik 2002). The representation of *Icriodus* throughout the early and mid Famennian is not completely continuous (these shallow-water conodonts were very sensitive to local environmental changes) but it is almost certain that the change from *I. alternatus* to *I. cornutus* was gradual. Also the succession of *Pelekysgnathus*, which replaced *Icriodus* in times of its low frequency and was apparently an open-sea animal, is of that kind. The low number of specimens and their disjunctive occurrence leaves some uncertainty whether *Dollymae*? *guizhouensis* is in the direct ancestor-descendant relationship to older *Pelekysgnathus* or immigrated from another region.

Devonian spathognathodontids. — Biramous symmetrical elements in the apparatus are an ancient feature of the ozarkodinid conodonts. At the beginning of the Silurian in the prioniodinid lineage, and at the beginning of the Devonian in polygnathids, a medial process developed in the S_0 element to be preserved almost without any significant change to the end of the Triassic. Reversal to the biramous condition was recognized only in the Frasnian lineage of the palmatolepidids (Dzik 2002). Therefore it was puzzling that throughout the Carboniferous and Permian the lineage of *Synclydognathus* and *Hindeodus* occurred with an apparatus groundplan closely similar to that of the Silurian spathognathodontid *Ozarkodina*. It was proposed by myself that they represent the same clade (Dzik 1991) and this has found support in the significant reduction of the stratigraphi gap as a result of finding *Synclydognathus* in the early Famennian of the Holy Cross Mountains. This finding disclosed also the affinity of *Apatognathus*, earlier classified among prioniodinids. There is a tendency towards reducing morphologic differences between elements in the apparatus in this lineage. Occurrences of the spathognathodontids remain few and stratigraphically isolated and it is thus difficult to resolve their phylogeny.

Prioniodinids and ancestral gondolellids. — Among the prioniodinids only two lineages seem to display phyletic evolution *in situ*, all others show a disjunctive, ecologically punctuated distribution. The most impressive case of evolutionary transformation is offered by *Lagovidina*. Its origin from earlier *Ligonodina* remains to be demonstrated, but is likely. Like other prioniodinids, these conodonts show a great variability that hampers evolutionary studies with low-number samples, but the latest populations of the lineage show rather stable organization of the apparatus.

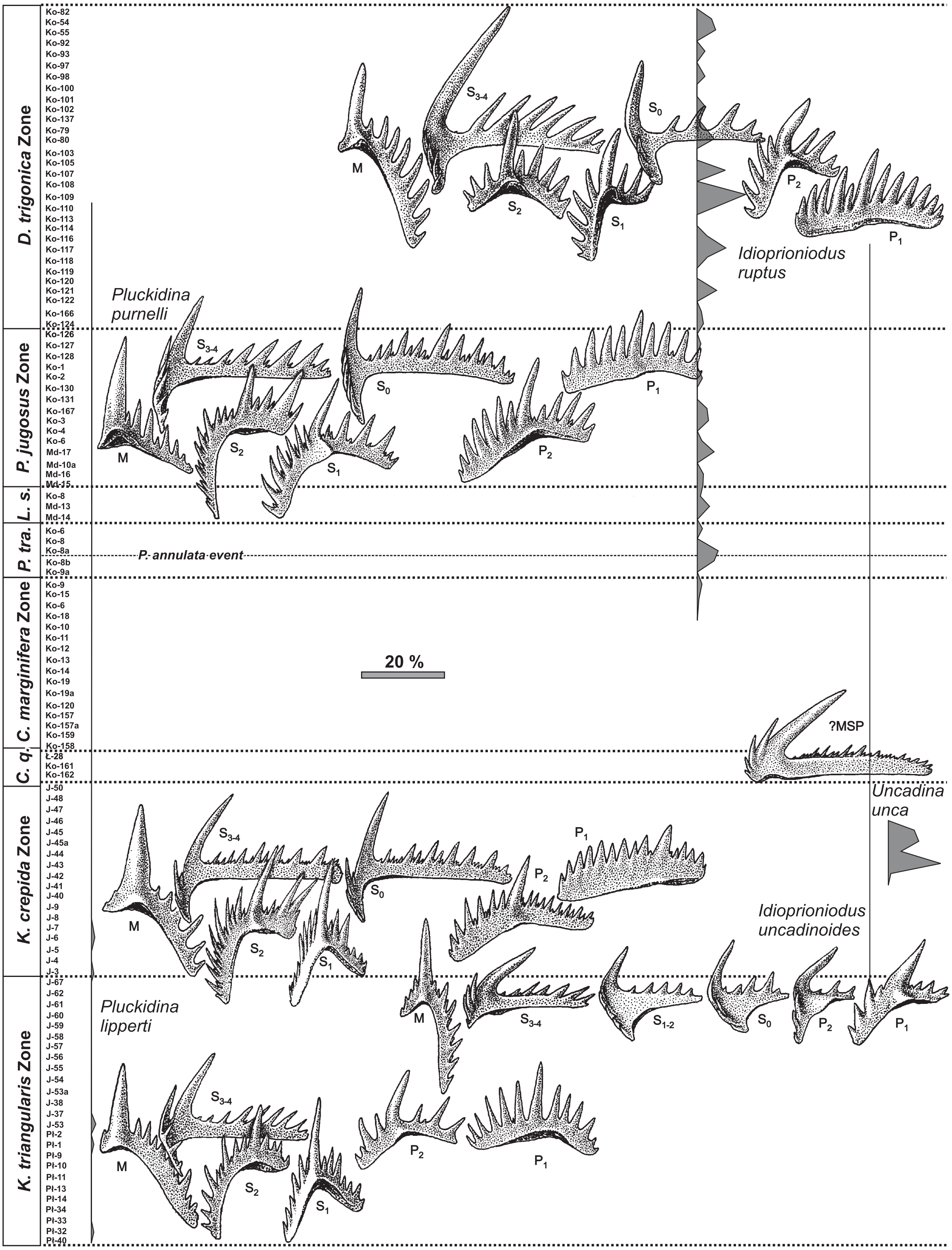


Fig. 123. Stratigraphic distribution of the prioniodinids *Pluckidina*, *Idioprioniodus* and *Uncadina* in the Polish Famennian (same kind of presentation as on Fig. 121).

The Famennian part of the lineage of *Pluckidina* seems to lead towards a gracile appearance of elements with a sharp, delicate denticulation. Unfortunately, only in a few samples are they represented in reasonable number. The late Carboniferous to Triassic branch of the gondolellids (Orchard 2005) for a long time was

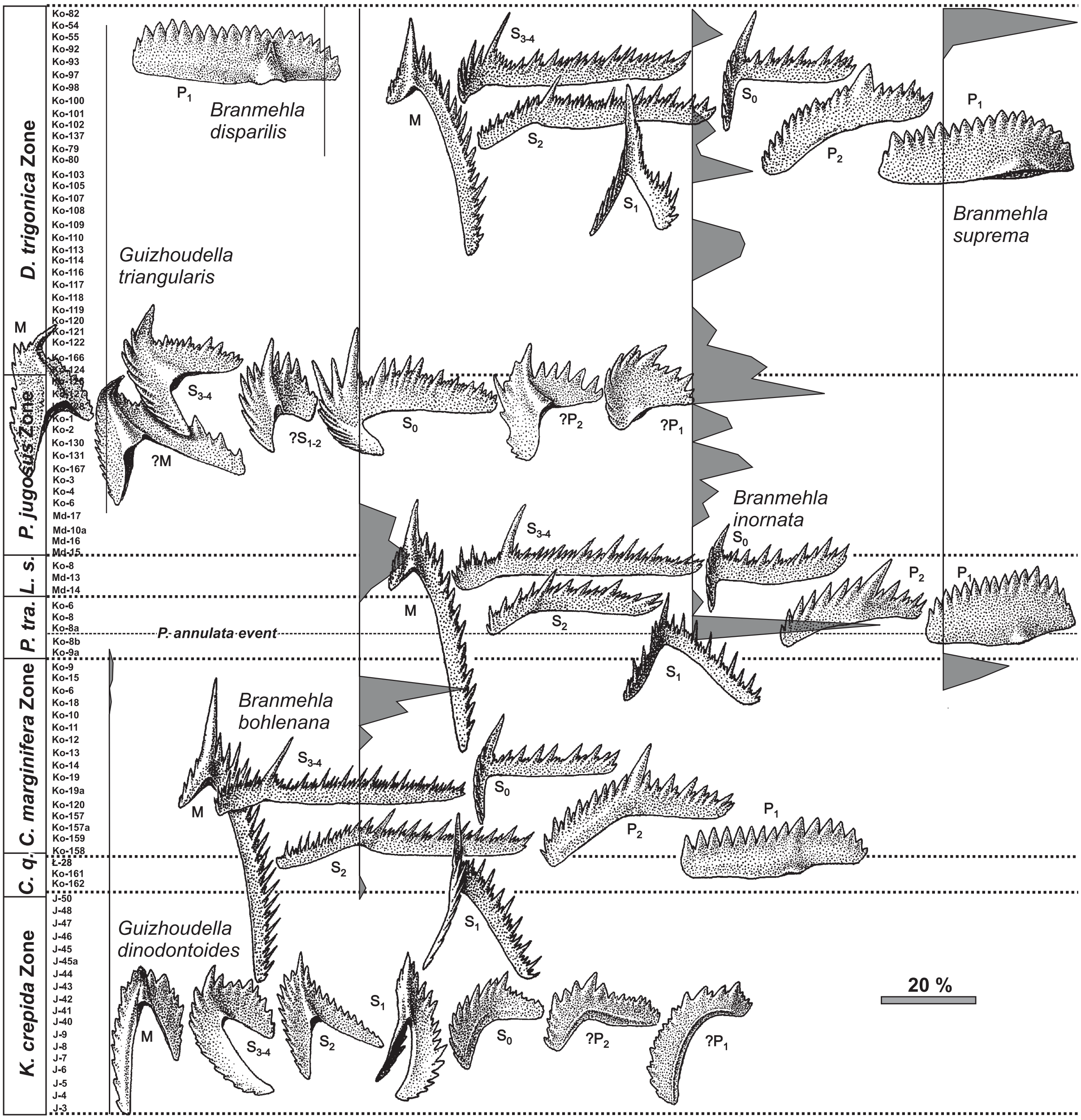


Fig. 124. Stratigraphic distribution of the advanced prioniodinid *Guizhoudella* and earliest gondolellid *Branmehla* in the Polish Famennian (the same kind of presentation as on Fig. 121).

considered to be of cryptic origin. The most characteristic aspect of their apparatus is the unusual shape of the S_1 element ("enantiognathus"), a reduced dorsal process in the P_1 elements, and extremely gracile appearance of other elements. These are features of the latest Devonian members of *Branmehla*. Its origin from *Pluckidina* is likely and it is only a matter of convenience where to place the boundary between the prioniodinids and gondolellids.

The most bizarre lineage of probable prioniodinids is represented by *Uncadina* of unknown origin and geographic source area. Some poorly known species of *Idioprioniodus* show remote similarity but the complete lack of any morphologic differentiation of elements in the apparatus was probably an evolutionary novelty.

Francodinids. — The most unexpected result of this apparatus study is recognition of a whole branch of conodonts with apparatus composition ranging from minute forms of almost Silurian appearance (*Vogelgnathus*, earlier known only from the Carboniferous) to robust apparatuses with elements mimicking the Car-

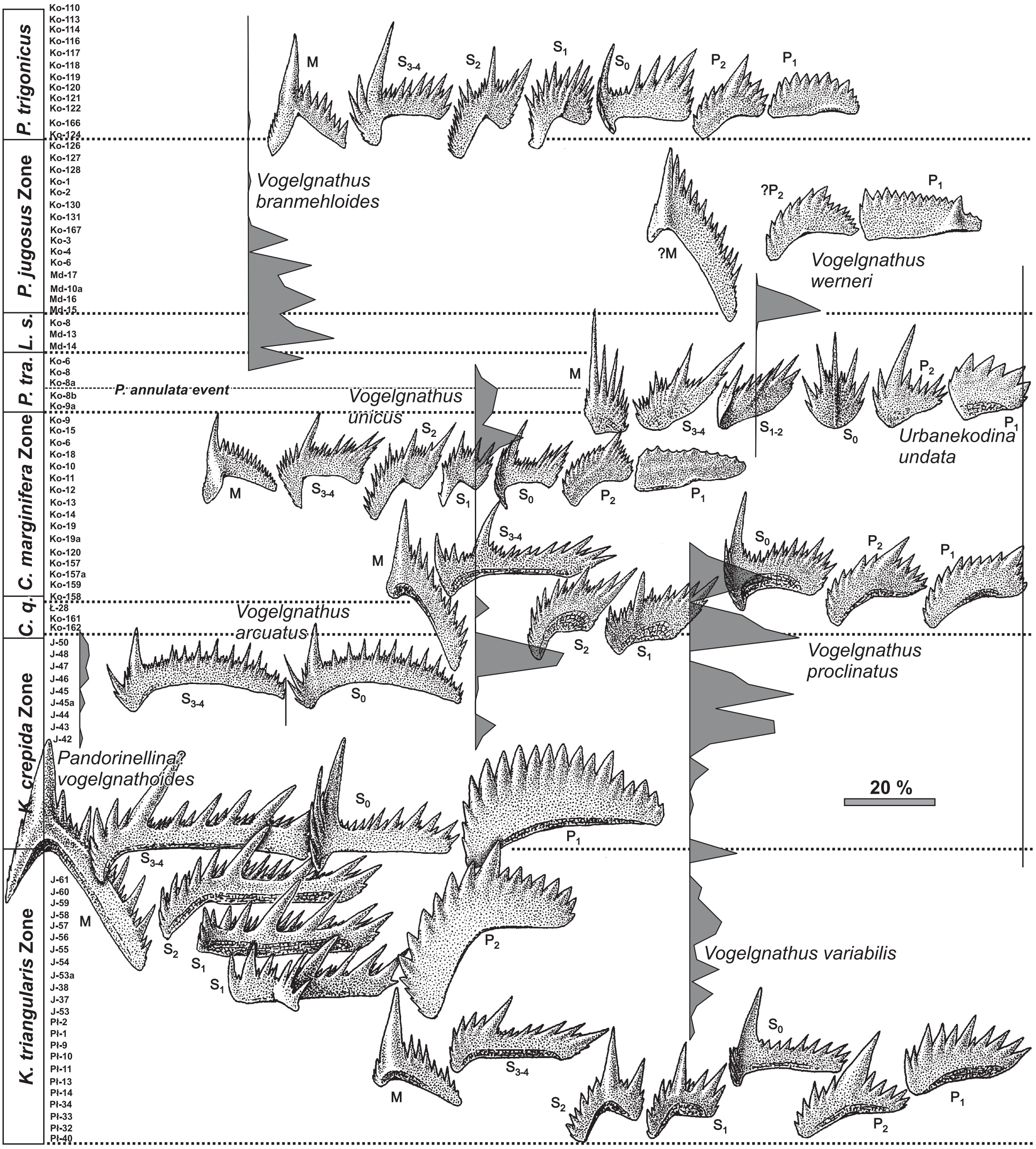


Fig. 125. Stratigraphic distribution of paedomorphic francodinids in the Polish Famennian (the same kind of presentation as on Fig. 121).

boniferous prioniodinid *Kladognathus* (*Planadina*). They share a tendency to paedomorphic shapes and are probably monophyletic, although the earliest stages of their evolution remain unknown. All of several lineages of the family, except for that of *Vogelgnathus variabilis* → *V. proclinatus*, represent brief incursions of exotic, environmentally sensitive forms. Morphologically the most intriguing is the lineage of *Urbanekodina*, long-ranging only at Miedzianka, with extremely small and simplified elements. A fundamental reorganization of the ground plan of the M element, otherwise the most stable in the evolution of conodonts, is offered by the *Francodina* → *Sweetodina* → *Planadina* succession, unfortunately punctuated by migrations and allopatric speciation events.

Mehlinid origin of ornate platforms. — Another unexpected aspect of the evolution of the Famennian conodonts is the probable central role of *Mehlina* in the evolution of platform-bearing polygnathids. A key

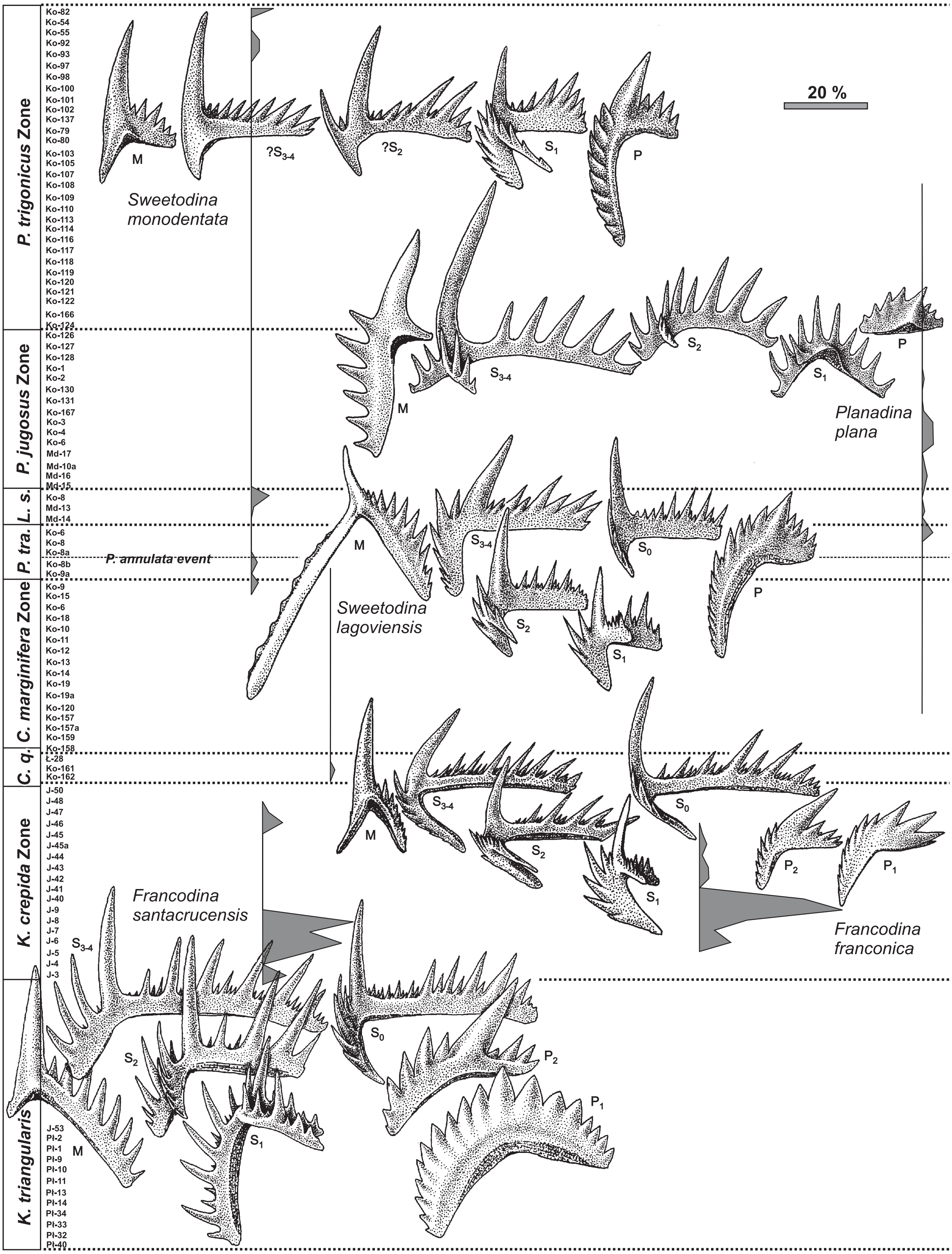


Fig. 126. Stratigraphic distribution of large francodinids in the Polish Famennian (the same kind of presentation as on Fig. 121).

to understanding their relationship was offered by the development of a brush-like peniculus in the early histogeny of the P_2 elements. This character discloses relationships of several lineages of *Polynodosus*, earlier placed in the ancient platform-bearing *Polygnathus* branch. It remains to be resolved how far this

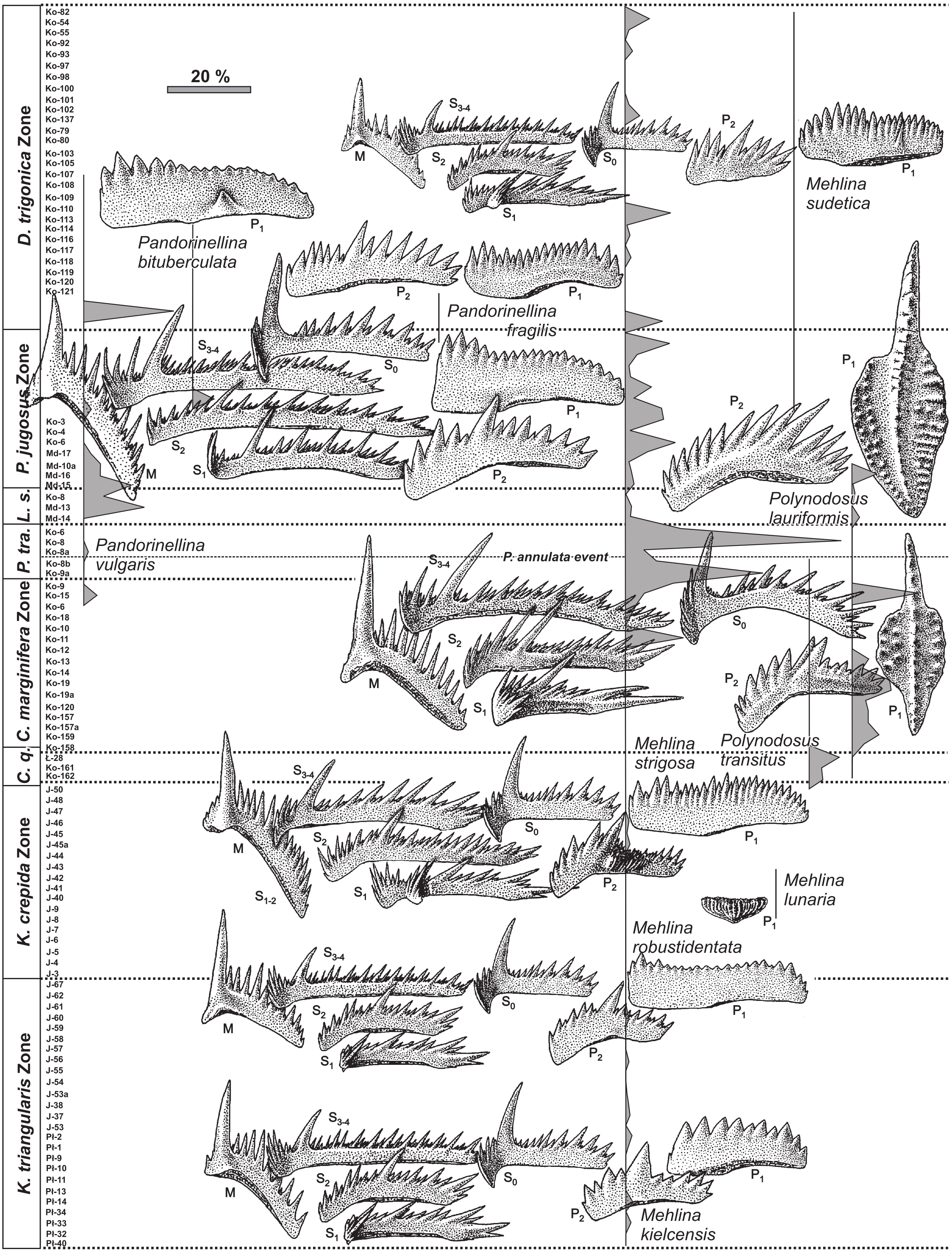


Fig. 127. Stratigraphic distribution of the non-platform polygnathids and the least derived platform-bearing *Polynodosus* species in the Polish Famennian (the same kind of presentation as on Fig. 121).

reached and whether the even more elaborate *Hemilistrona* also belongs there. The end member of this branch is of bizarre morphology with almost completely reduced blades of both types of the P elements (Fig. 128).

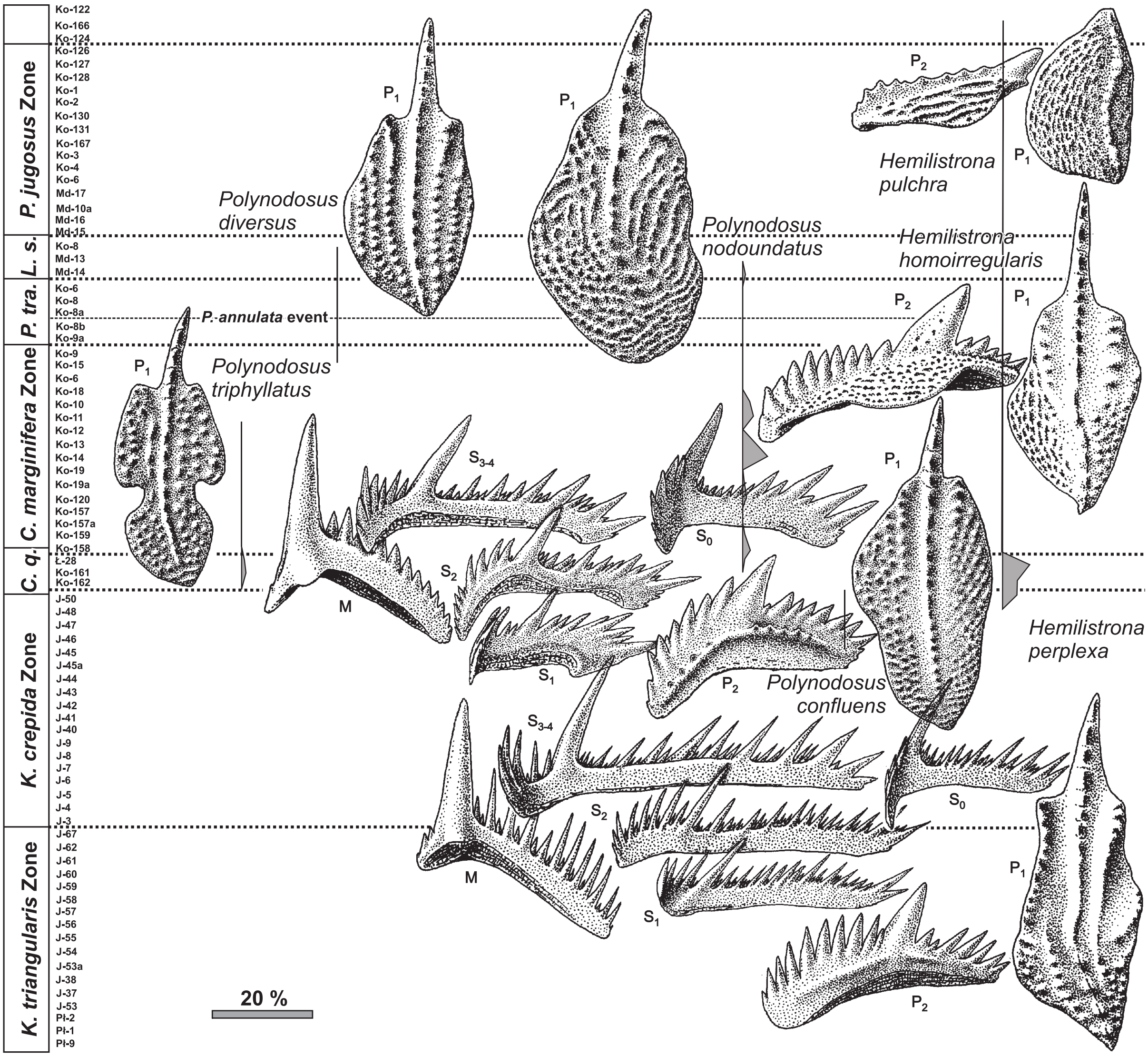


Fig. 128. Stratigraphic distribution of the advanced *Polynodosus* species and *Hemilistrona* in the Polish Famennian (the same kind of presentation as on Fig. 121).

There is a hope that increase in knowledge of the apparatus structure will introduce a long-awaited order in the phylogeny of ornate platform-bearing polygnathids. Studies on the evolution of the *Polygnathus*-group conodonts are difficult because they are highly sensitive environmentally and have punctuated distribution hampering recognition of phyletic evolutionary changes. Moreover, their population variability is high. Unfortunately, apparatuses of the polygnathids are morphologically generalized and usually only the P_2 elements are of significance in diagnosing species. However, a distinct apparatus composition allows separation of the *P. extralobatus*–*P. znepolensis* group and proves that *Polylophodonta* (actually a relative of *Ancyrognathus*) has little to do with the *Polynodosus confluens* → *P. triphyllatus* lineage.

Probable ctenopolygnathid roots of siphonodellids. — There is much uncertainty regarding relationships of the late Famennian and Tournaisian conodonts with a fusiform flat basal cavity in the platform elements. They are believed to be of crucial importance in delimiting, on an evolutionary basis, the Devonian–Carboniferous boundary. Unfortunately, the apparatus reconstructions of various siphonodellids are no more than provisional (Dzik 1997) and even relationships within the clade (classified in the Elictognathidae, based on the assumed controversial apparatus interpretation) are not clear. It may be, however, of importance that the preliminary apparatus reconstructions of the earliest siphonodellids (Dzik 1997)

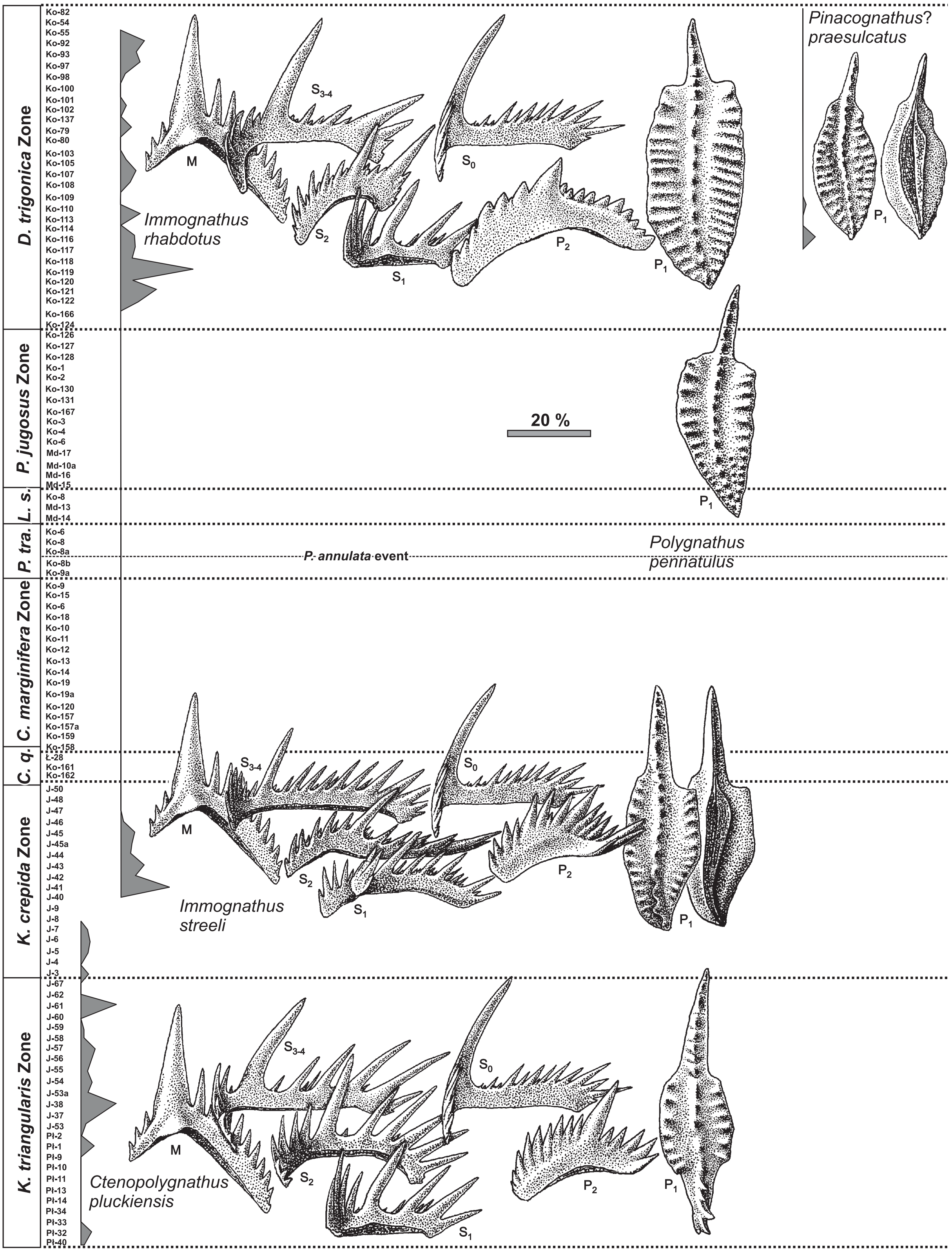


Fig. 129. Stratigraphic distribution of the robust polygnathids *Ctenopolygnathus* and *Immognathus* and possible elictognathid species in the Polish Famennian (the same kind of presentation as on Fig. 121; drawing of *Polygnathus pennatulus* of possible relationship to the *Immognathus* lineage added).

resemble the apparatus of the mid and late Famennian derivative of the robust polygnathid *Ctenopolygnathus*, here named *Immognathus*. In this lineage the peculiar form of *Siphonodella*-like base developed

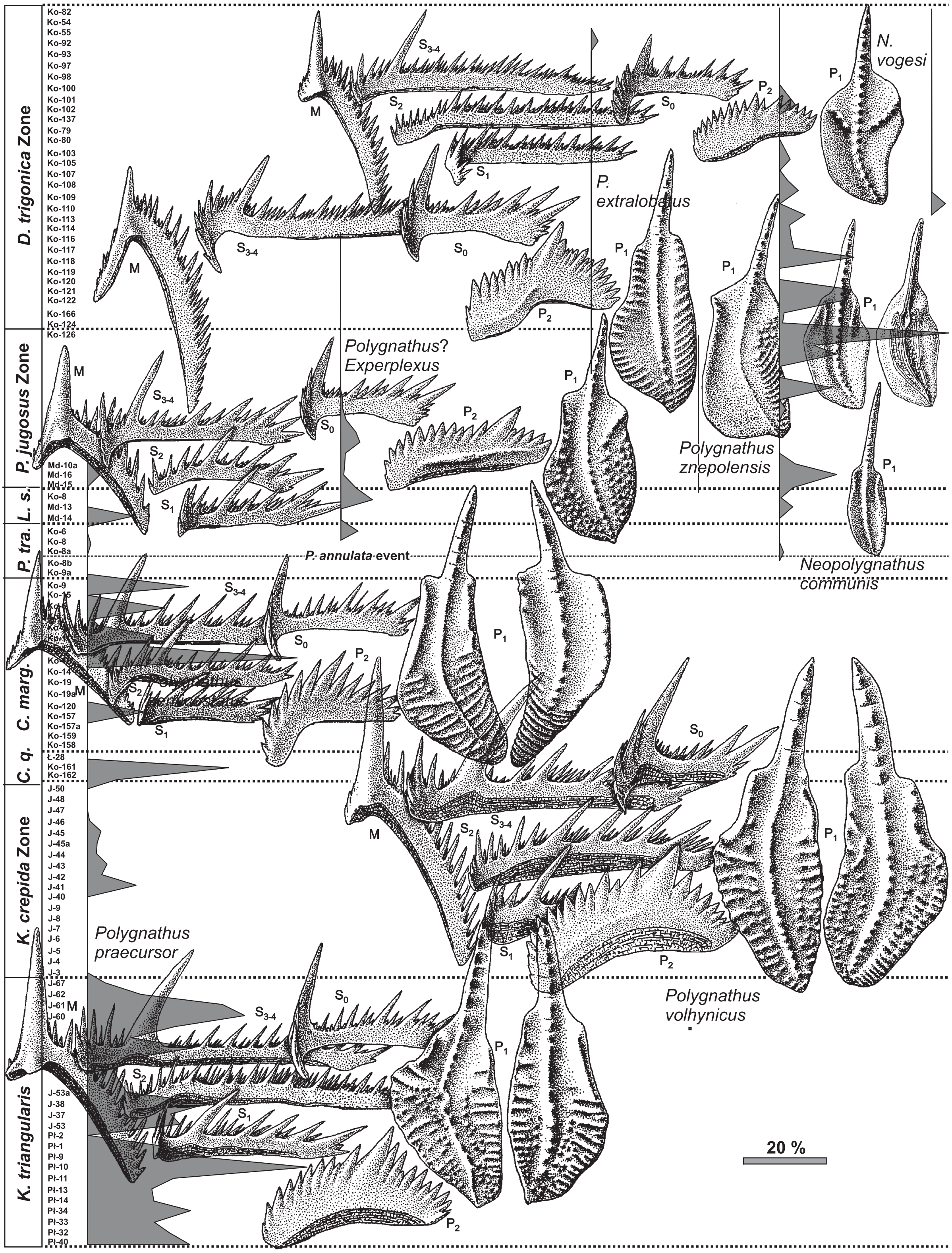


Fig. 130. Stratigraphic distribution of the polygnathids *Polygnathus* and *Neopolygnathus* in the Polish Famennian (the same kind of presentation as on Fig. 121).

independently of the Famennian *Alternognathus*. The latter genus, with its incipient axial symmetry in the P_1 pair, is an unlikely relative of the siphonodellids, being rather ancestral to the Carboniferous cavusgnathids.

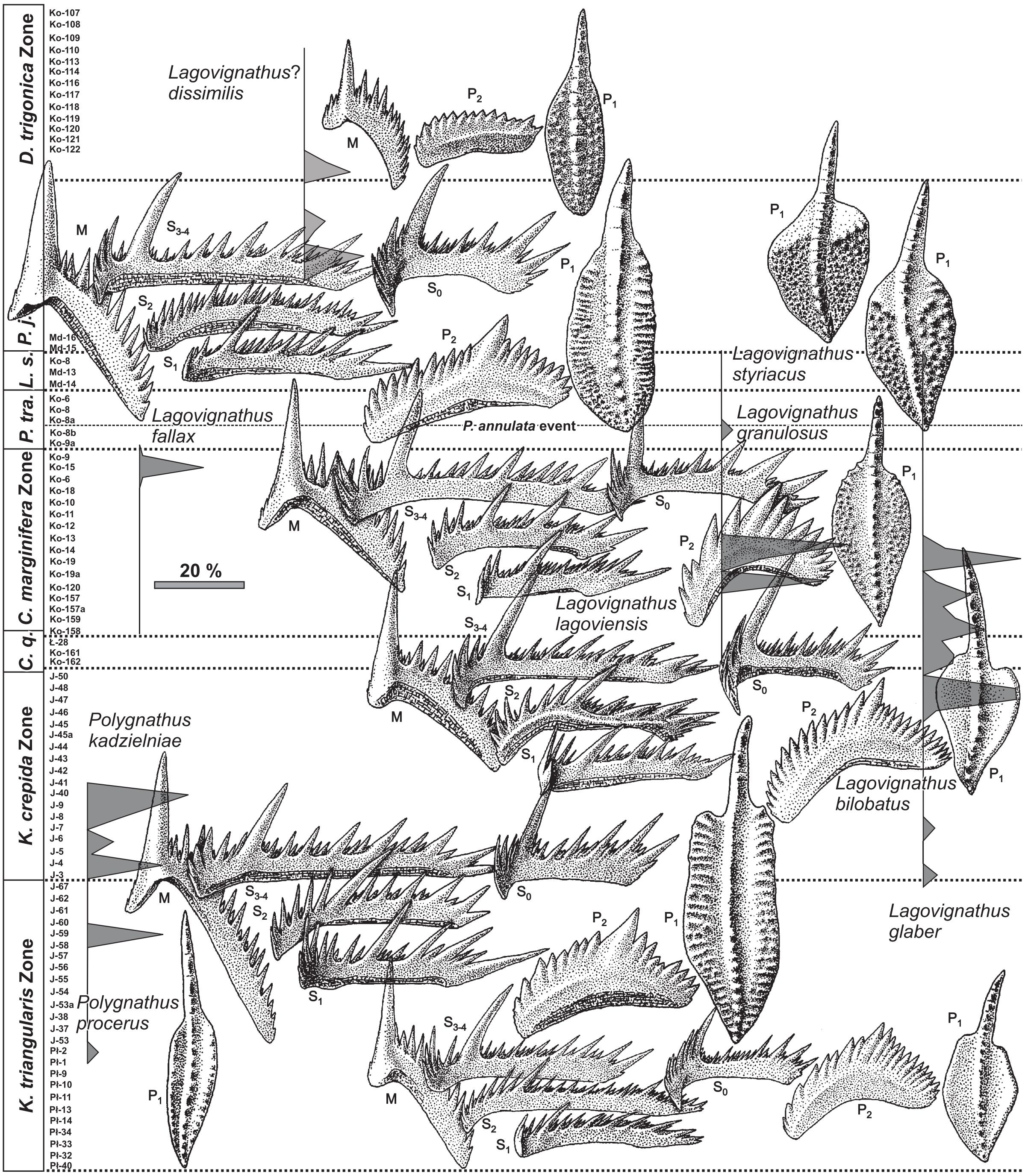


Fig. 131. Stratigraphic distribution of the polygnathid *Lagovignathus* and its possible relatives among *Polygnathus* species in the Polish Famennian (the same kind of presentation as on Fig. 121).

The problem of *Neopolygnathus*. — The common early Carboniferous genus *Neopolygnathus* has Devonian roots. It is difficult, however, to indicate its exact ancestry because its earliest populations show a great population variability and the morphology of its elements is generally degenerative, marked by deep simplification of the unknown original morphology. Their P_1 elements are of small size and simple morphology but, paradoxically, a tendency towards simplification and developing a smooth platform (but with imprints of ameloblasts) characterizes one of the most robust polygnathids of the Famennian, *P. semicostatus*. Notably, unusually high population variability is a feature of this species. It seems thus that the characteristic concave base of P_1 elements of *Neopolygnathus* is also a degenerative feature, an effect of lowered mineralization of the platform base.

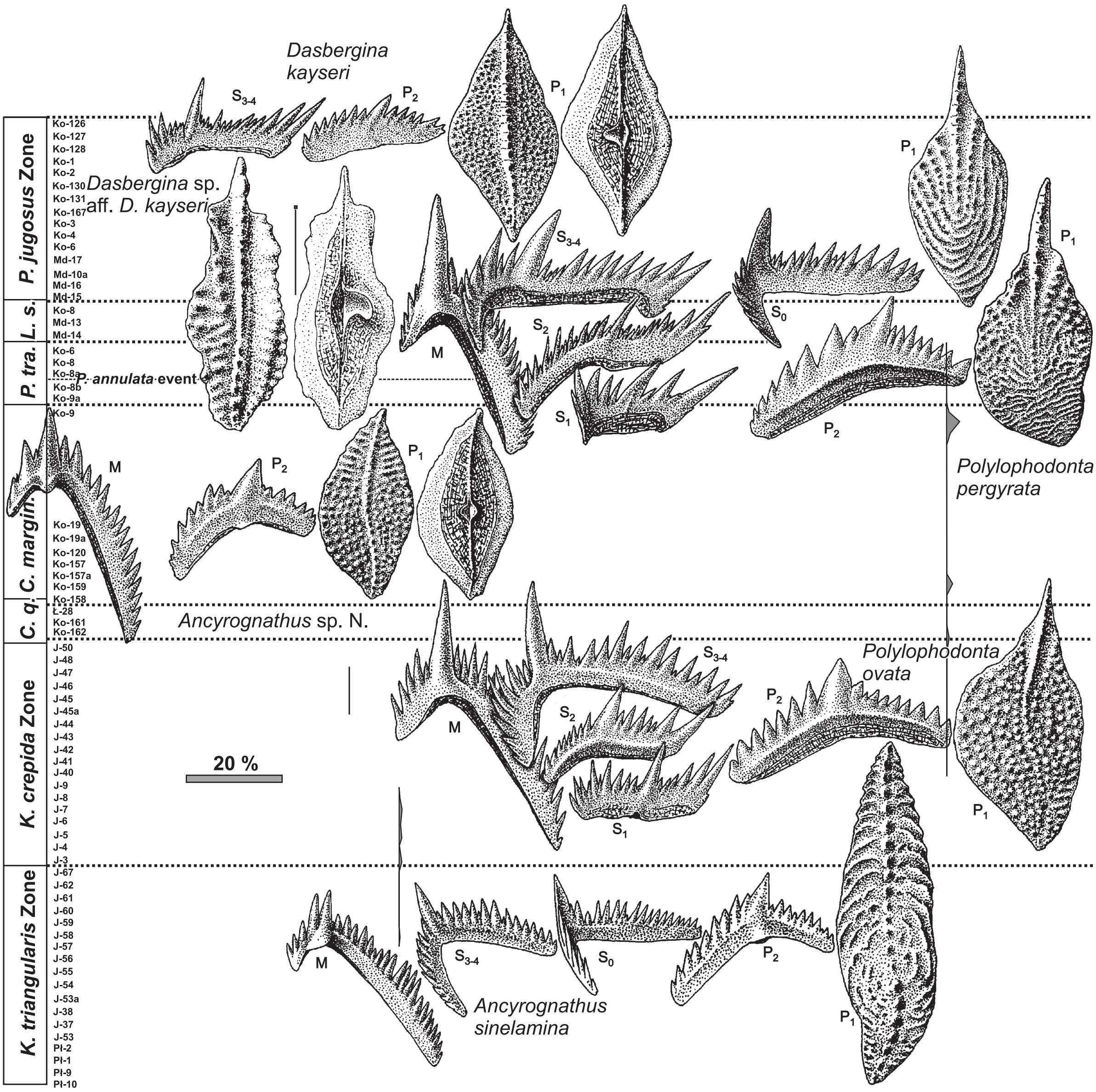


Fig. 132. Stratigraphic distribution of the ancyrognathids and their idiognathodontid homeomorphs in the Polish Famennian (the same kind of presentation as on Fig. 121).

Advanced Carboniferous species of *Neopolygnathus* are almost homeomorphic to another, unrelated polygnathid lineage, here classified in *Lagovignathus*. Several lineages of these conodonts with a thin platform in the P_1 elements occur in the mid Famennian, mostly of ecologically punctuated distribution. Their origin remains unknown but possibly the earliest Famennian *Polygnathus procerus* may connect them with the Frasnian species characterized by an almost symmetrical, thin platform. Only two lineages show a probably phyletic evolution *in situ*. One of them *L. fallax* → *L.*? *dissimilis* is incompletely demonstrated. The other, *L. lagoviensis* → *L. granulosus* → *L. styriacus*, offers a succession of great correlative value.

Palmatolepidids. — Only one local lineage of Famennian palmatolepidids was represented at the beginning of the Famennian. The environmental change that resulted in the disappearance of the typically Frasnian lineages of *Lagovilepis* and *Manticolepis* had no detectable influence on the phyletic evolution of the *Klapperilepis* lineage except for a somewhat delayed increase in its population variability (Dzik 2002). This seems to be a result of a released selection pressure earlier generated by competition of other palmatolepidid species. New lineages emerged sequentially by immigration from their places of origination. The apparent decrease in population variability of *K. ultima* was probably caused by the appearance in the area of species

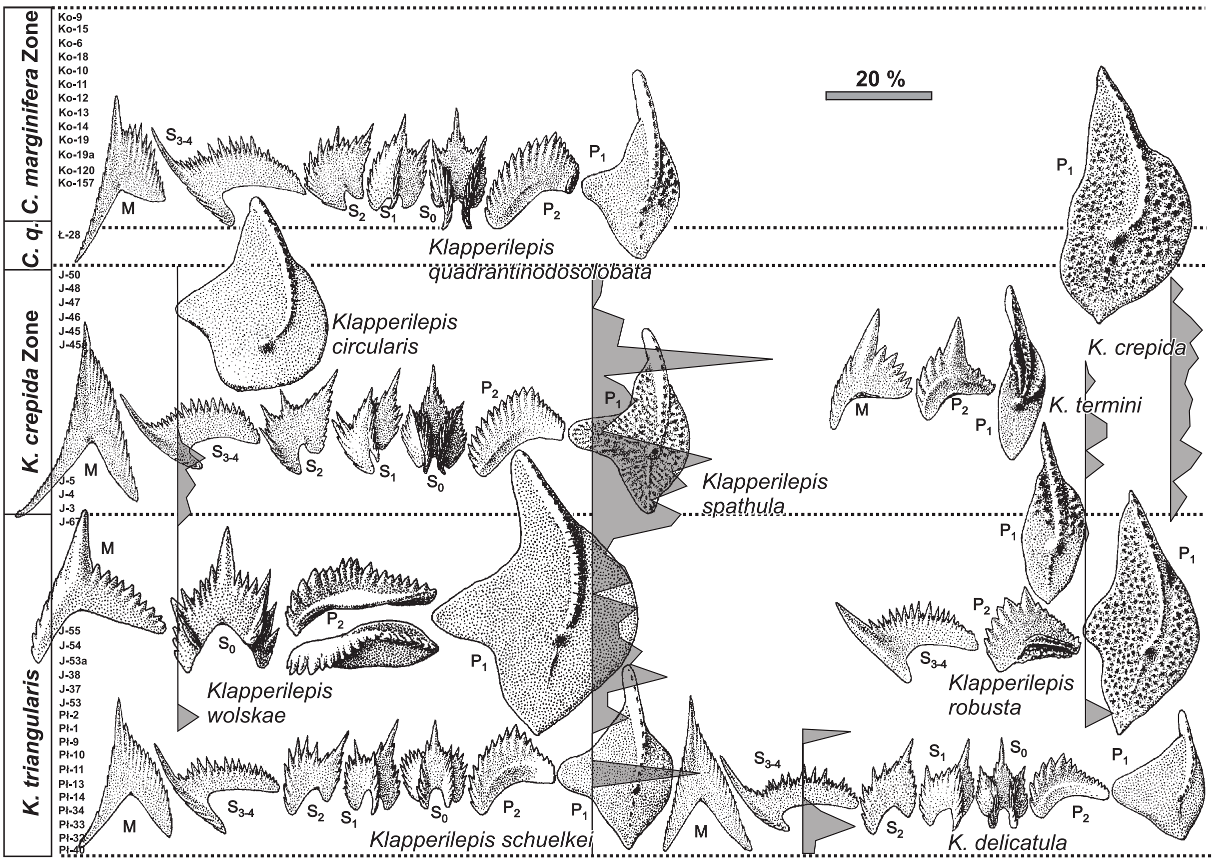


Fig. 133. Stratigraphic distribution of advanced species of the palmatolepidid *Klapperilepis* in the Polish Famennian (the same kind of presentation as on Fig. 121).

that still had similar ecological preferences. Remarkably, the platform elements of the species new in the area only a little increased the total range of shapes earlier represented in the single species, *K. ultima*. However, under the competition from other sympatric species they all had to reduce their variability. Probably the local population was forced to accommodate to the new conditions of partially overlapping ecological niches (the phenomenon of character displacement). The subsequent phylogeny of the Famennian palmatolepidids was reviewed by myself elsewhere (Dzik 2005). The early Famennian is marked by allopatric diversification and the subsequent geographic merging of several lineages of *Klapperilepis*. They preserved an underived apparatus structure but with various morphologies of the P_1 elements.

In the mid Famennian they were replaced by a few lineages of the gradually diversifying branch of *Conditolepis*, with secondarily biramous S_0 elements of the apparatus. The branches of *Palmatolepis* and *Tripodellus* continue throughout the Famennian, usually with not more than two lineages sympatric. Phyletic evolution has been observed in several lineages of the Famennian palmatolepidids. Among those of *Klapperilepis* the most extensive is represented by the lineage *K. schuelkei* → *K. spathula* → *K. quadrantinodosolobata*. The succession *K. wolskae* → *K. circularis* is also rather complete but the observed morphologic change is not profound. A similar extent of transformations characterizes the lineage *K. robusta* → *K. crepida*, the lineage covering early and late, rather different *K. termini*, and the stratigraphically rather punctuated lineage *K. protorhomboidea* → *K. rhomboidea*.

The main lineage of *Tripodellus* offers probably the most extensive morphologic change and complete record (Fig. 134). Apparently gradual and continuous is also the change in the long lineage from *Palmatolepis initialis* up to *P. schindewolfi*. Less continuous but likely to be gradual is the series *P. ampla* → *P. trachytera* → *P. rugosa*. In *Palmatolepis* and *Conditolepis* the processes of the M elements acquired a position closely similar to that in the Frasnian *Manticolepis*. It appears thus that the pelagic palmatolepidids, unlike the generally shallow-water polygnathids, offer a much more complete record of their evolution.

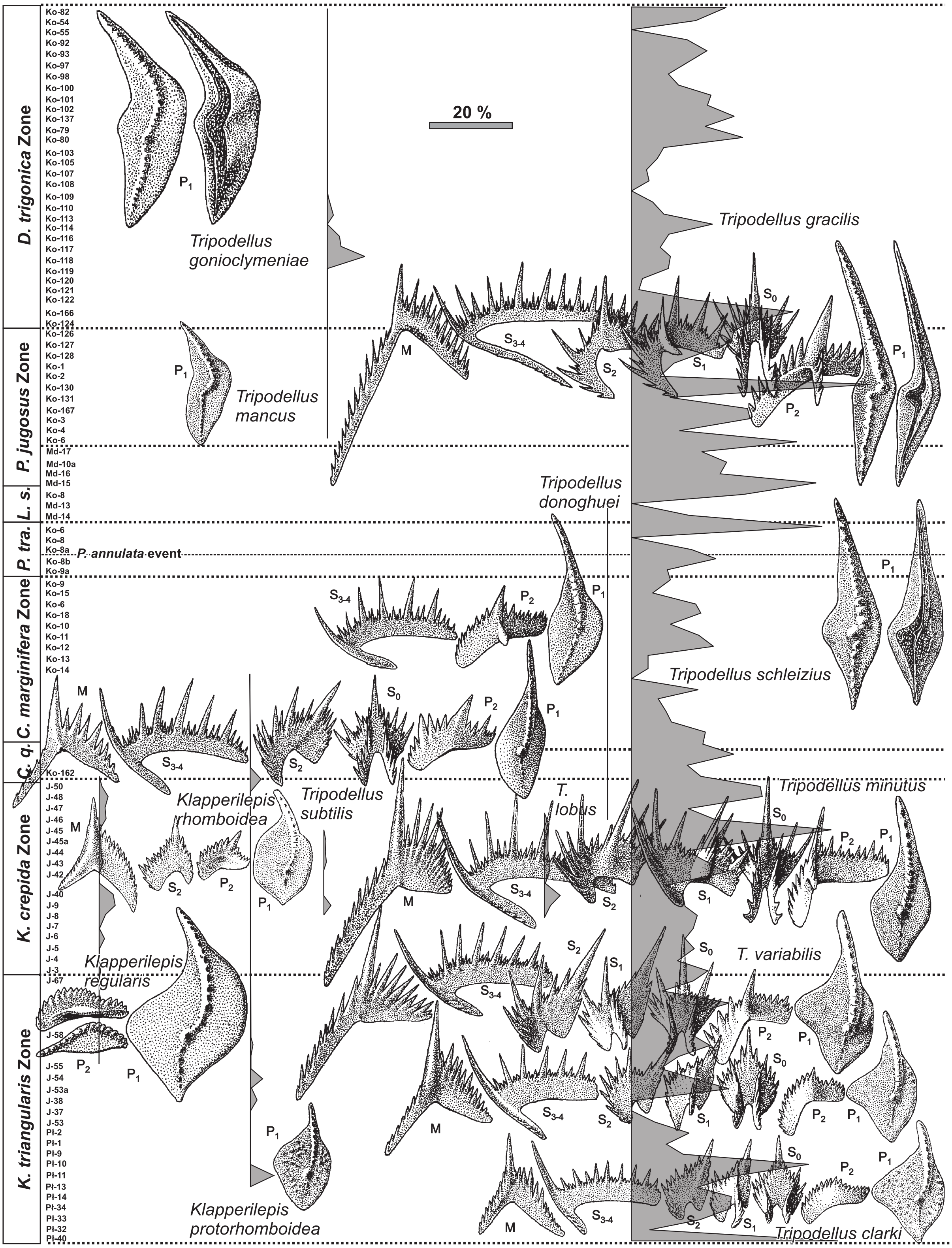


Fig. 134. Stratigraphic distribution of advanced species of the palmatolepidid *Tripodellus* and some *Klapperilepis* species in the Polish Famennian (the same kind of presentation as on Fig. 121).

Origin of axial symmetry of elements. — Left and right elements of many conodonts are not mirror images. This apparently improved their fit in occlusion. In rare cases, however, this tendency went as far as to develop left and right elements of virtually the same shape, seemingly not forming pairs. This is a case of ax-

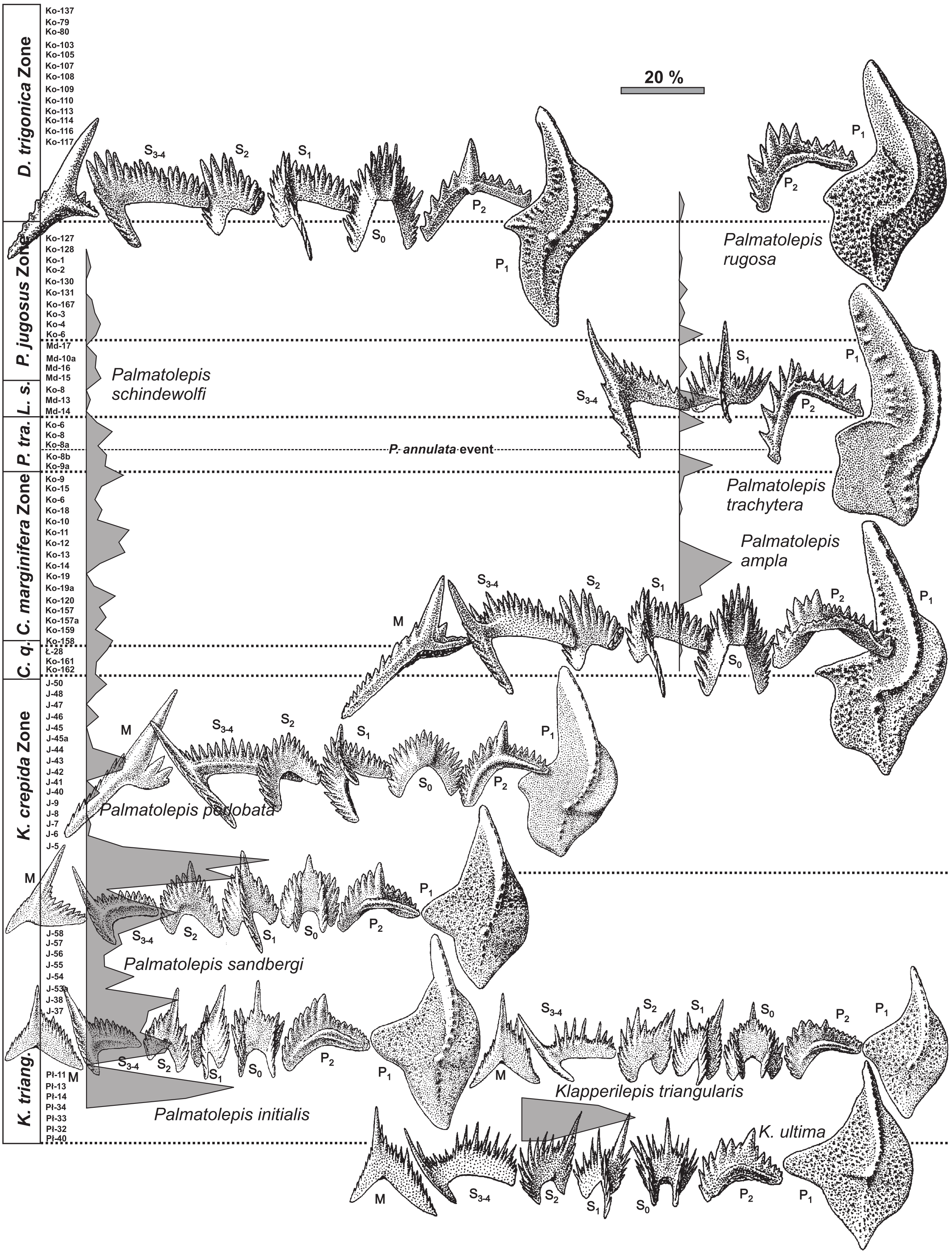


Fig. 135. Stratigraphic distribution of the palmatolepidid *Palmatolepis* and its ancestral *Klapperilepis* species in the Polish Famennian (the same kind of presentation as on Fig. 121).

ial symmetry. Virtually all the conodonts with the P_1 elements of this kind occur in the late Devonian and early Carboniferous. One may thus wonder whether the axial symmetry developed once in the evolution of conodonts or several times independently. The earliest Famennian case of undoubted axial symmetry is rep-

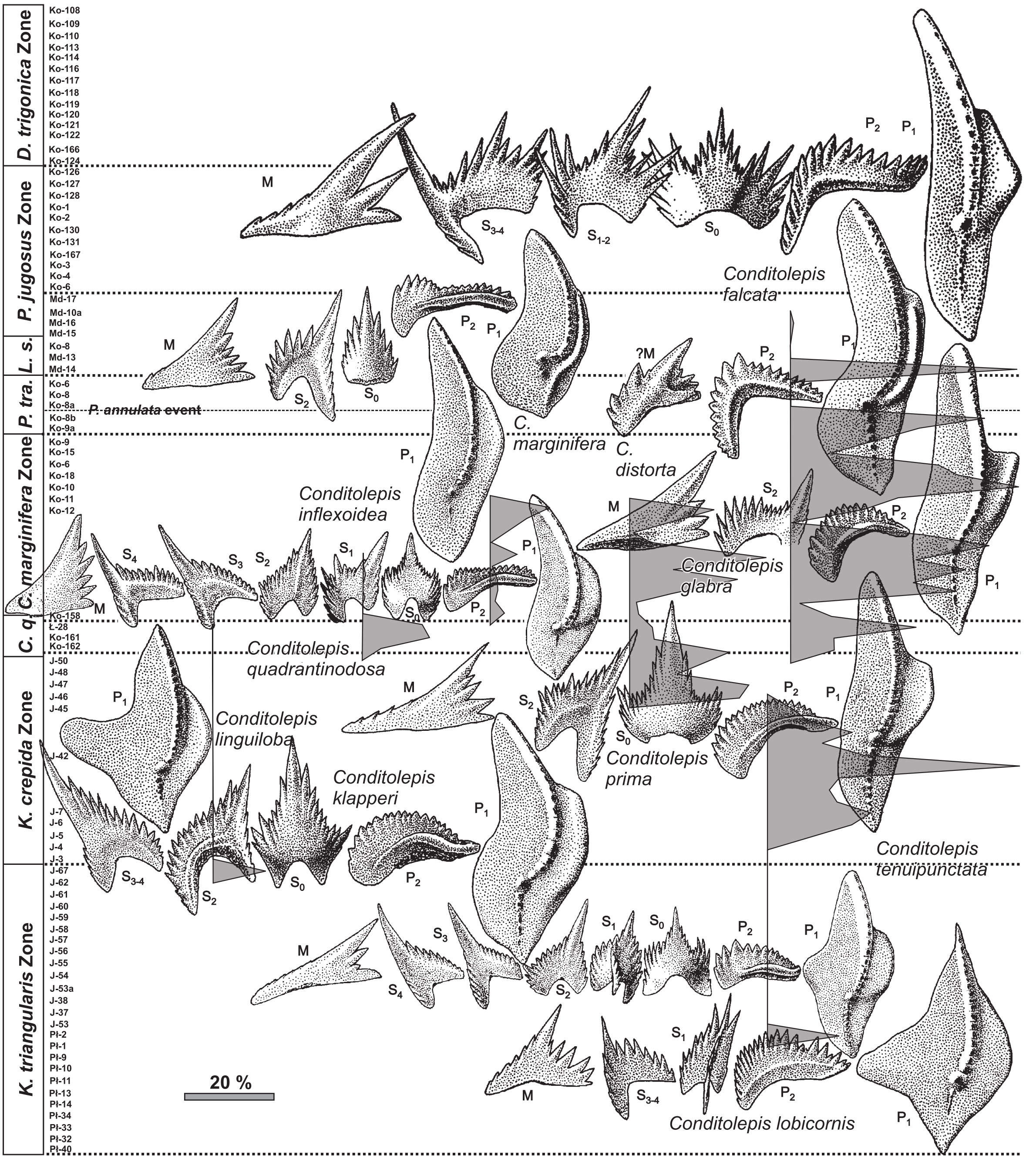


Fig. 136. Stratigraphic distribution of the palmatolepidid *Conditolepis* in the Polish Famennian (the same kind of presentation as on Fig. 121).

resented by the mid Famennian *Scaphignathus*, a branch of the *Alternognathus* lineage with an incipient asymmetry of elements. There is no doubt that *Scaphignathus* gave rise to the Carboniferous branch of *Cavusgnathus* and *Mestognathus*, the model cases of axial symmetry.

There is another group of conodonts with axial symmetry of their P_1 elements. Their basal cavities are basically different from that of *Alternognathus*, resembling rather *Dasbergina* in this respect. However, the exact ancestry of this lineage has not been traced and the situation resembles that among the Carboniferous cavusgnathids. The problem has to be clarified, which may not be so easy, however, because the *Pseudopolygnathus* species are environmentally sensitive and their evolution is poorly recorded. Perhaps the most complete succession is that of the *P. ziegleri* → *P. ultimus* lineage.

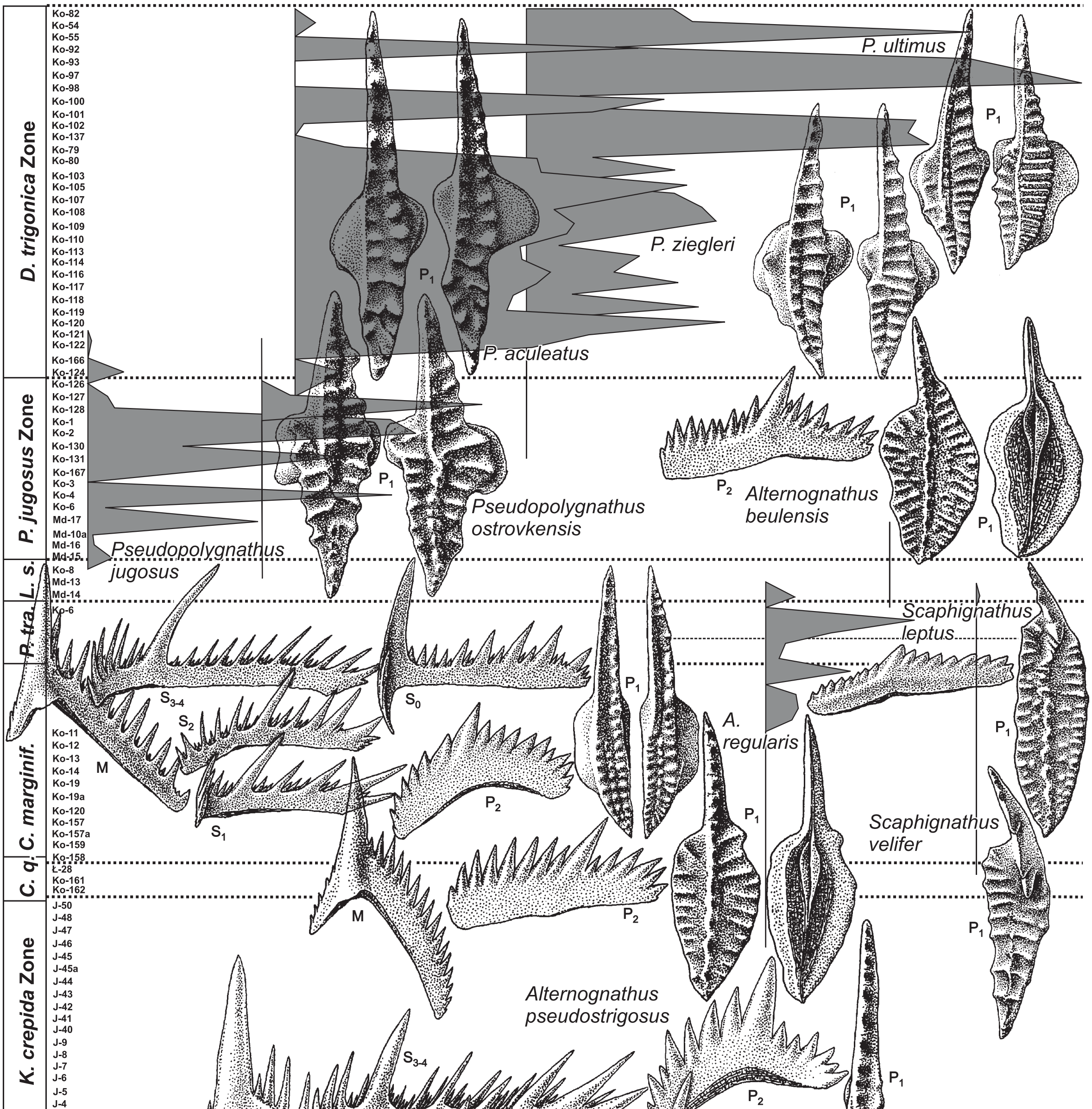


Fig. 137. Stratigraphic distribution of the cavusgnathids in the Polish Famennian (the same kind of presentation as on Fig. 121).

The Devonian roots of the idiognathodontids. — A crucial role in the evolution of the late Paleozoic conodonts was played by a mid Famennian relative of the most generalized polygnathid lineage of that age, *Pandorinellina vulgaris*. This was *Dasbergina stabilis*, the only derived feature of which was the expanded base with a shallow but wide cavity. In several lineages that emerged from *D. stabilis*, the basal cone developed tuberculation or a kind of tuberculated platform. Two relatively fast evolving lineages are of importance in this group. The *D. brevipinnata* → *D. ziegleri* lineage developed an elaborate platform with rows of tubercles. In the *D. kowalensis* → *D. marburgensis* → *D. trigonica* lineage, the originally coarsely tuberculated platform gradually changed into a characteristic ramified structure.

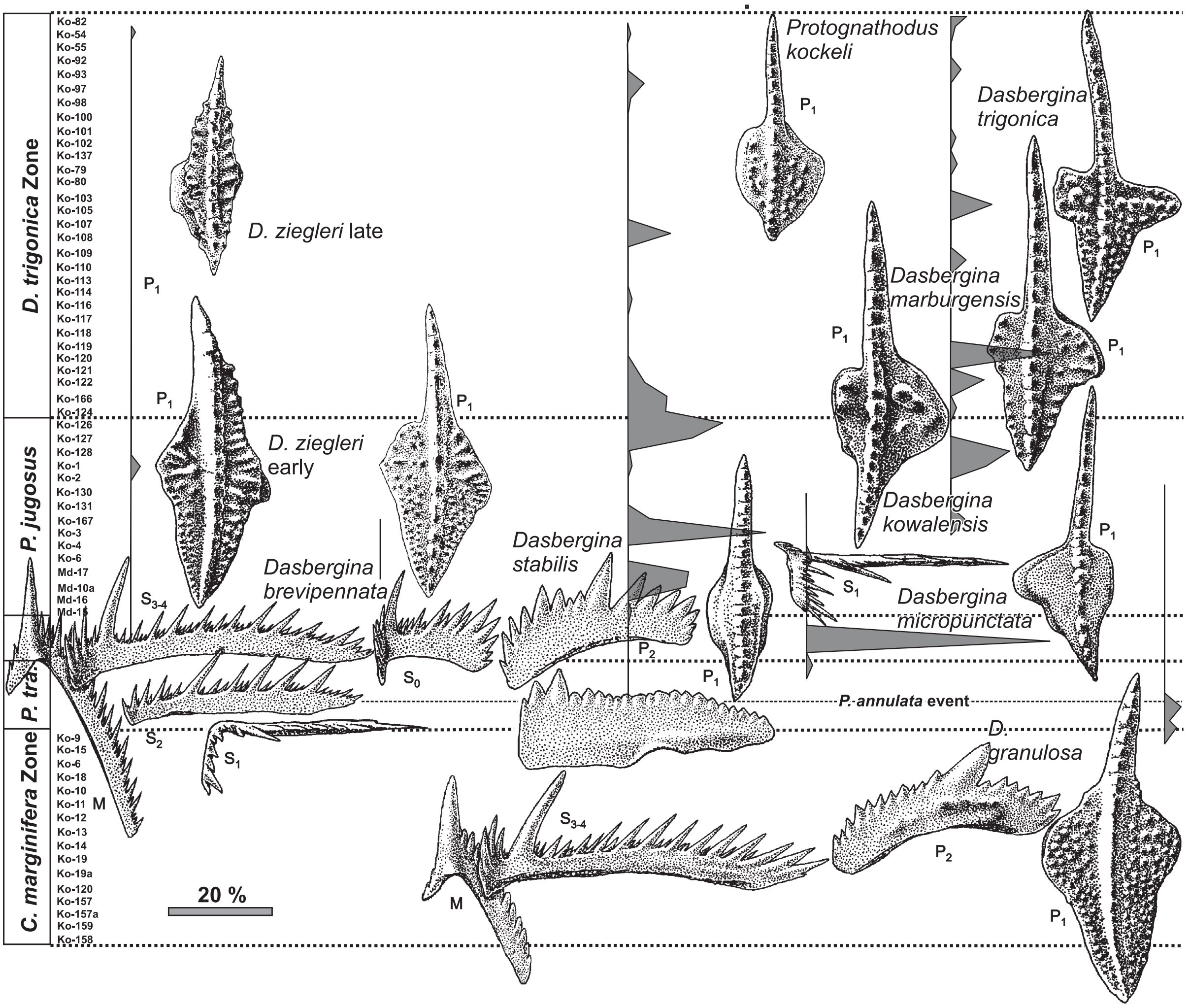


Fig. 138. Stratigraphic distribution of advanced species of the idiognathodontids in the Polish Famennian (the same kind of presentation as on Fig. 121).

Apparently from *Dasbergina* originated also *Protognathodus*, which appeared near the end of the Devonian from an unknown source. Its lineage probably diversified later into the main group of open-sea Carboniferous conodonts, the idiognathodontids. An important change in the ramiform elements of its apparatus took place in the Viséan (Dzik 1997).

Conclusion. — The number of 142 conodont species says more about the nomenclatorial history of their research than about their faunal history. The count of identifiable lineages is somewhat more informative in this respect. Usually they represent brief segments of evolution labelled with a single species name, in some examples being a case of the more extensive record of their evolution, corresponding to a few chronospecies. There are 101 such lineages in the material available to me, 31 of them showing more or less apparent evolutionary change. In the majority of cases the record is not comletely continuous and it is not always clear whether a lineage completely disappeared from the area for some time or is not represented in some samples only because of its locally or periodically small contribution.

The diagrams depicting their time distribution are not calibrated in real time as the length of particular units expresses only completeness of sampled geological sections. Anyway, if so crudely estimated ranges are compared on the basis of their length, it appears that the succession showing more or less certain evolutionary transformations represent almost half (46%) of the summarized observed ranges of conodont lineages in the Holy Cross Mountains and the Sudetes. Their record is not complete and probably not more than half of it is suitable for stratophenetic studies. This is much less than in the temperate climatic zone record represented by the Ordovician succession in the same area (Dzik 1994), but this seems to be a distinction typical of equatorial successions of various ages (Dzik 1983, 1997).

It is a controversial issue how to estimate the complexity of living forms but probably in all aspects that can be considered, the Famennian was the epoch of the greatest anatomical and species diversity of conodonts, comparable with only a few episodes in their earlier history (e.g., Llanvirn to early Caradoc; late Llandovery to early Wenlock), and only one after the Famennian (late Tournaisian). The number of sympatric species (well defined morphological species, not arbitrarily selected morphotypes!) was commonly higher than 25. The Famennian experienced also an invasion of pelagic environments with efficiently swimming large predators. For the first time acanthodians, sharks, and ganoid fishes started to co-occur with conodonts (earlier they inhabited mostly near-shore environments not accessible to conodonts; e.g., Blieck *et al*. 2000). The Famennian marine pelagic fish show some species diversity and significant participation in biological productivity of the pelagic community. Concavicarid and angustidontid crustaceans, with grasping appendages mimicking conodont elements but an order of magnitude larger, were also represented by phosphatized mandibles and carapaces (see below). Both fish and large pelagic crustaceans probably fed also on conodonts (Rolfe and Dzik 2007). Perhaps this was a factor contributing to their late Palaeozoic decline.

AMMONOID CONCHS AND JAWS

The aspects of the ammonoid conch morphology easiest to access are the general geometry and the contact of septa with the conch wall (suture line), well discernible on internal moulds. Growth increments on the conch surface are less commonly preserved because the aragonitic conch wall is rarely transformed into calcite with enough precision. Even less commonly preserved, but of much biological and taxonomic value, are initial whorls of the conch. In the Late Palaeozoic goniatites and Mesozoic ammonites the first whorl of the conch has a smooth surface devoid any marks of growth increments Kulicki *et al*. 2002). This is generally accepted as the evidence of its formation within the egg covers and the ammonitella developmental stage preceding the primary shell constriction is considered embryonic. However, in the orthoceratid nautiloids (Dzik 1981, 1885), bactritids (Doguzhaeva 2002), and earliest ammmonoids (e.g., Klofak *et al*. 1999) the conch development stage corresponding to ammonitella bears distinct growth increments. Apparently juvenile early cephalopods were free living. The transition from free-living larva to development of the larva inside the egg until its metamorphosis was probably gradual and proceeded independently in many lineages, like other molluscs. In some goniatites with a smooth ammonitella conch, adult morphological features develop suddenly, showing that the change was connected with a metamorphosis of anatomy, not just a retardation of growth resulting from hatching. Therefore I prefer to apply the term “larval” to conchs at the pre-metamorphosis stage of the development, equipped with two first septa. In the material from the Holy Cross Mountains a few phosphatized larval conchs have been found, the larval stage is also discernible in pyritic internal moulds found in conodont samples.

Little data are available on the anatomy of the Devonian ammonoids. Rarely discernible muscle scar attachments are known (Richter 2001, 2002; Richter and Fischer 2002). Only in a few cases the conchs can be matched with jaws.

ANAPTYCHI AND APTYCHI

The ammonoid jaws functioned simultaneously also as opercula (Dzik 1981). To be preserved, the mostly organic jaws of the Devonian ammonoids required anoxic conditions of sedimentation, represented by the black shale facies. The only horizon in the Holy Cross Mountains where ammonoid jaws occur in significant number is the calcareous shale at Kowala of earliest Famennian (possibly also latest Frasnian) age.

Unfortunately, no determinable cephalopod conch has been found in association with them, so it can only be speculated, to which ammonoid taxa they belonged. A few single-piece lower jaws (anaptychi) do not differ in outline from those identified in the living chamber of the gephyroceratid *Crickites* by Matern (1931) or closing aperture in *Sphaeromanticoceras* (Clausen 1969). Although the specimens were collected from the scree, it is likely that they come from strata of latest Frasnian age. At Kowala, the cephalopod lower jaws split

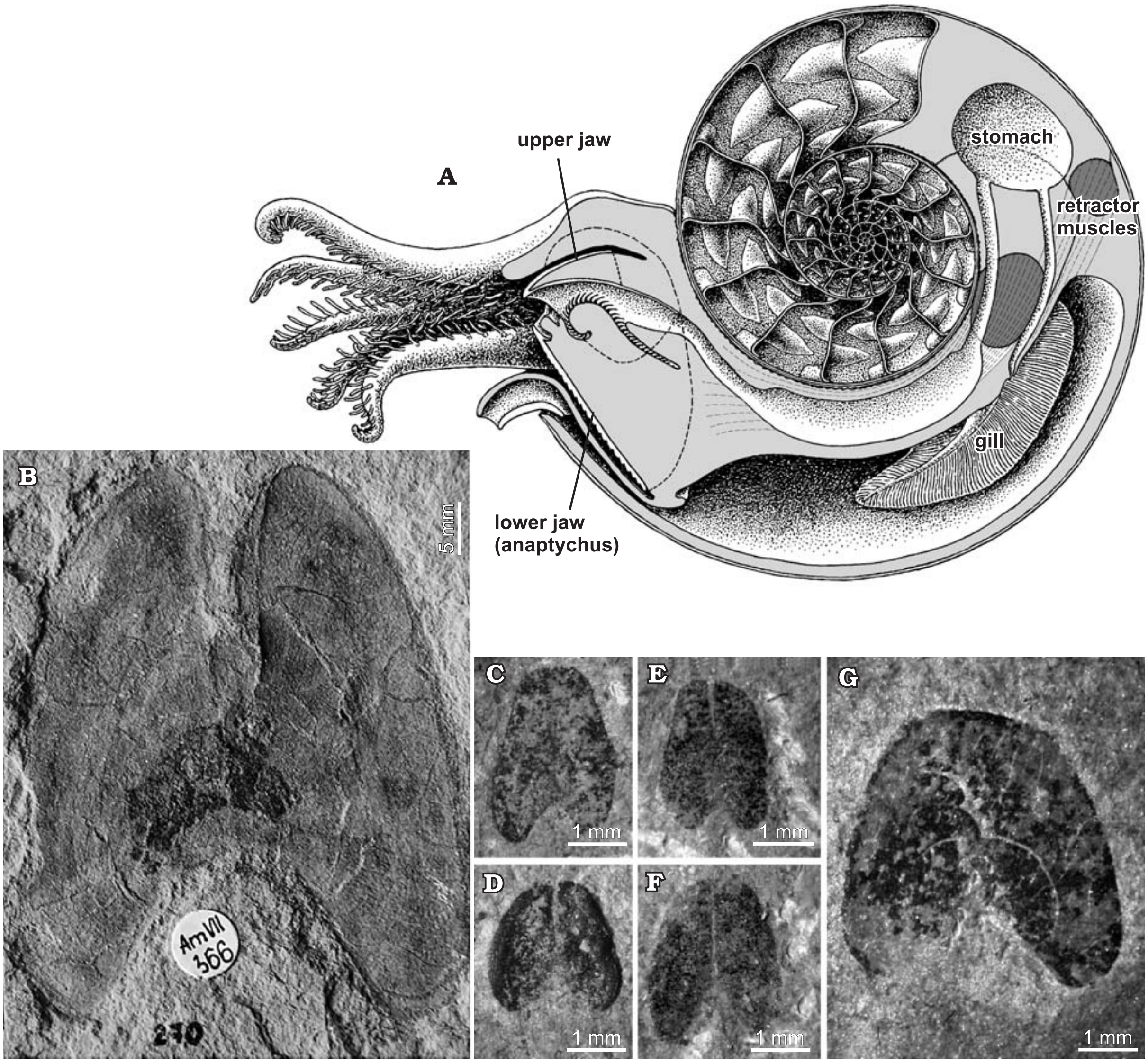


Fig. 139. Probable ammonoid jaws from the Late Devonian at Kowala in the Holy Cross Mountains. **A**. Hypothetical medial section of an advanced tornoceratid showing position of the jaws. **B**. Large aptychus with separated valves from the same stratum, specimen ZPAL AmVII/366. **B**–**F**. Juvenile anaptychi possibly belonging to *Tornoceras*, from the earliest Famennian with the organic chitinous tissue carbonized or pyritized (C), specimens ZPAL AmVII/370, 371, 374, and 373. **G**. Carbonized anaptychus, possibly from the latest Frasnian and belonging to a gephyroceratid, specimen ZPAL AmVII/367.

medially into two valves (aptychi) are much more common. Their occurrence in the Devonian is surprising, as true aptychi are confined to the late Mesozoic, except for those of the Silurian arionoceratid nautiloids. The possibility that the fossils from Kowala represent bactritoid or orthoceratid jaws can be rather excluded because of the size of the largest specimens, many times exceeding that of the late Devonian bactritids (Fig. 139B). Their association with the tornoceratids, the only ammonoids known from strata of this age in Europe, is more plausible. The lower jaw of the early Carboniferous goniatitid *Girtyoceras* (Doguzhaeva *et al*. 1997), as well as its late Carboniferous relative *Eoasianites* (Closs 1967), significantly differ in its shape, being similar rather to the jaws of the nautilids. Whether there were several reversals in the evolution of ammonoid beaks or rather the goniatitids represent a side branch of the main ammonoid lineage, remains to be clarified. The pentagonal shape of the probable anaptychus *Libodiscus* from the early Tournaisian Exshaw Shale of Alberta (Dzik 1997, p. 126) support the idea of continuity between the Frasnian and post-Carboniferous ammonoid jaws with opercular function. Anaptychi of a somewhat similar pentagonal shape have been described from the early *Clymenia* Stufe of the Rhenish Slate Mountains by Korn (2004*b*) and the Cleveland Shale of Ohio (Frye and Feldmann 1991).

The names introduced for ammonoid jaws are valid from the nomenclatorial point of view, and might potentially compete for priority with names based on conchs. This approach has been executed already by Matern (1931), who identified the jaw (anaptychus) *Spathiocaris koeneni* Clarke, 1884 in the living chamber of *Crickites holzapfeli* Wedekind, 1913. The type specimens of both taxa are from the same horizon and region, so their biological identity raises little doubt. This is not so apparent in the case of the type species of *Spathiocaris*, *S. emersonii* Clarke, 1882 from the Frasnian Portage Formation at Naples, Ontario (Clarke 1882). Potentially, *Spathiocaris* may appear to be a senior synonym of, say, *Manticoceras* Hyatt, 1884, but it would not be practical to enforce this nomenclatorial action because of rather indifferent morphology of the Devonian ammonoid mandibles. Fortunately, no such problem is connected with the Famennian ammonoids discussed below.

GROWTH AND FUNCTION OF THE CONCH

It is generally believed that the cephalopod septum geometry is of functional importance, especially when it shows convex areas acting as vaulting in the generally concave septum (when seen from the conch aperture). This is why in the ammonoid and nautiloid taxonomy much value is given to the course of the suture line – a planar representation of the contact between septum and the conch wall. However, the correspondence between the suture line and geometry of the septum is not straightforward and similar sutures may express different patterns of convexities and concavities of the septum. In the simplest situation, the visceral sac of an ammonoid body behaves as a balloon under pressure of internal fluids and its end develops a hemispherical shape in a cylindrical body chamber of the conch (Seilacher 1975). If the cross section of the chamber, determined by the secretive action of the mantle margin at its aperture, is laterally flattened, wide lateral sinuses may develop in the suture line. More complex outlines may produce a quite sophisticated pattern of lobes and saddles without any change in the concavity of the septum (Seilacher 1975; Dzik 1984; Korn 1992, 1999; Dzik and Gaździcki 2002). The situation becomes more complex if the body is locally attached to the shell wall with muscles, which hamper its fast withdrawal. Lobes not related to the conch cross-section may then develop, frequently pointed, and marginal parts of the septum may finally develop vaulting (Seilacher 1975). Yet another mechanism of vaulting and complex septal geometry may be related to non-uniform stiffness of the free surface of the visceral sac. This could have been caused by the translocation of some internal organs towards the venter as a result of increased involuteness of the conch.

The conch involuteness and the whorl expansion rate are independent aspects of the conch geometry. Involute and evolute conchs may have the same whorl expansion rate, and *vice versa*. The whorl expansion rate varied very much among the early ammonoids being clearly connected with their swimming abilities (Klug *et al.* 2004). The Agoniatitina, Gephuroceratina, Prolecanitida and Paraceltitina generally show a high whorl expansion rate and significant control of ontogeny, while Anarcestina, Pharciceratina, Tornoceratina, and Goniatitina show a low expansion rate (Korn and Klug 2001). This is not an evolutionary stable character and within the Tornoceratina there was a change from the tornoceratids with relatively high whorl expansion rate to cheiloceratids with low expansion rate, the character subsequently inherited by the Goniatitina, but changed again during the evolutionary history of the Prolecanitina (Korn 1994).

Wrinkle layer. — The wrinkle layer of the ammonoid shell wall (House 1971) was secreted by the dorsal surface of the animal head while it extended from the living chamber. This is quite clearly shown, among others, by the specimens of *Tornoceras typum* from Jabłonna with preserved intact aperture (Fig. 141A_3). The extent of the wrinkle layer is there clearly delimited. It formed a lobe outside the aperture. The area was in contact with the body only when withdrawn from the conch. The secreting organ was thus rather the animal's head than a specialized part of the mantle. This suggests that the wrinkle layer is homologous to the "black layer" of the nautilids and ceratites, occurring in exactly the same region near the conch aperture (Klug *et al.* 2004).

Korn (2000) compared irregular meandering protrusions on the shell surface of some Famennian ammonoids with the wrinkle layer, using this as the evidence of their conchs being covered with mantle during life. These structures resemble mineralized periostracum protrusions, the feature of conchs of many mollusks, including the Mesozoic ammonites.

Internal thickenings and constrictions of the conch. — Internal thickenings are specific for many Famennian cheiloceratids and a high diagnostic value was attributed to them by Sobolew (1914). It is thus important to understand their origin before their use in taxonomy is supported or abandoned. As shown by some mature specimens of *Cheiloceras subpartitum* from Łagów, which died immediately after developing the last internal thickening of the shell, the thickening was produced at the margin of the aperture or immediately behind it. As a result, in underived cheiloceratids the thickenings tend to follow the growth increments. In *Prionoceras*, there is even a connection between irregularities at the conch surface and the thickening below. In more derived cheiloceratids such a correspondence has disappeared and in their conchs the apertural sinus may co-occur with constrictions forming a prominent ventral saddle (e.g., *Cheiloceras inversum*). Apparently, the place of formation of the thickenings moved behind aperture, although most probably its most distal part was still initiated at, or near, the aperture. This is suggested by the unity of external and internal shell wall features in *Balvia*. The mechanism controlling development of such constrictions remains unknown. It could have been similar to that responsible for the divaricate shell ornamentation in other mollusks, that is the zone of formation of the constriction migrated along the aperture margin with its growth (this does not seem especially likely) or a linear narrow zone of increased secretion of the lamellar aragonite layer of the conch extended across the mantle, initially in connection with its margin.

Terminalized conch growth. — It is generally assumed that a crowding of septa and growth increments near the aperture is sufficient to prove maturity of the ammonoid conch (e.g., Makowski 1991). Actually, these features of the conch are just reflections of delayed growth, which may be accidental, seasonal or connected with spawning, and may thus be misleading. Regrettably, an alternative to this potentially simplistic reasoning is offered in the Famennian only by the conch geometry of the prolobitid goniatites and wocklumeriid clymenias. In both groups the mature body chamber shows a profound change in its cross-section and develops periapertural modifications. Unlike the post-Triassic ammonites, this does not seem to be an expression of sexual dimorphism. The body chamber modification of *Prolobites*, with a constriction near the aperture strengthened with an internal thickening, seems to be a protection agains predators. The mature conch shape of the wocklumeriids probably improved their hydrodynamic properties.

DESCRIPTION AND CLASSIFICATION OF THE AMMONOIDS

In this work a review of the ammonoid faunal dynamics in the Famennian of the Holy Cross Mountains and Sudetes is presented rather than a formal description of the taxa. A reliable taxonomic research, as exemplified by works of Korn (e.g. 1994) and Becker (e.g., 1993b), would require access to the mostly German type and topotype material. In the case of the taxa based on materials from Poland, very few type specimens survived the World War II and these were already reillustrated by earlier authors. The types of Sobolew (1914) and Dybczyński (1913) have not been traced in known museum collections and are probably all lost. Their type strata are no longer accessible (with a few exceptions which were attempted by myself to exploit). In the former Dzieduszycki's Museum collection in Lvov there are many specimens collected by Dybczyński at Sieklucki' brickpit (located in the western part of Kielce, no longer accessible). The pyritized ammonoid specimens occurred there, together with numerous concretions, in the Quaternary sand covering the Famennian shale excavated in the pit (Sobolew 1912a). They were washed out from various stratigraphic units of the Famennian (possibly even Frasnian, if *Beloceras acutodorsatum* Dybczyński, 1913 truly represents the genus) in the Pleistocene and are obviously heterogenous from the stratigraphic point of view. It is potentially possible to select neotypes from this material but these would be of little use, as they in fact lack any stratigraphic information. Fortunately, a closely similar material has been recovered from black shale within the *C. marginifera* Zone at Kowala, which suggests that most (but not all) of the Sieklucki's brickpit material was derived from this horizon.

Most of the evidence presented below is derived from macroscopic internal moulds of the ammonoid conchs with fragments of the original shell preserved. Camera lucida drawings of the suture and growth lines, together with photographs of specimens whitened with ammonia chloride illustrate taxonomic descriptions below. Whenever there is enough evidence, the geometry of the septum is reconstructed in a diagrammatic way.

Taxonomic nomenclature of the Famennian ammonoids. — The type species of the three representative genera of Paleozoic ammonoids, *Cheiloceras*, *Prionoceras*, and *Imitoceras* all have obliquely convex profile of the conch aperture, as well as the same or closely similar shape of the conch and the external part of the suture. They differ in a degree of folding of the dorsal part of the septum and in the distribution or lack of the internal conch thickenings, features do not considered to be diagnostic for high rank ammonoid taxa and distinguishing rather species within particular genera. Yet, these are types of their own superfamilies! This traditional approach is an expression of a general trend in the evolution of taxonomy towards extreme splitting of taxa and rising their ranks. As a result of professional specialization and low number of taxonomists in particular areas of research (in the case of Devonian ammonoids rarely exceeding a few students involved in research at the same time) there is little interest in standardizing taxa. The difference between traditional taxonomy of the Famennian tornoceratine ammonoids (several superfamilies) and that of the coeval palmatolepidid conodonts (single genus), both including a similar numbers of sympatric species, exemplifies this very well.

These differences in classification methodologies would be probably of little importance if not the value that is given to counting taxa in hope to disclose patterns in the evolution of the living world. Moreover, the too deep discrepancy in attitudes makes the Linnean taxonomy methodologically weak and prone to destruction by followers of more radical philosophies of taxonomy. I believe that to make taxonomy truly useful in its main function as a measure of diversity (even if it is unavoidably subjective) some kind of standardization is necessary. This can be achieved by keeping in mind that too many taxa within a taxon of higher rank make classification impractical, difficult to memorize and to use. Approximately similar range of morphologic variability should also be allowed within taxa of the same rank. Obviously, this cannot be done too rigorously. I believe that a controlled subjectivity is still a much better solution than to go into the illusion that taxonomy can be done in a strict and completely objective way (Dzik 2005).

Nomenclatorially invalid “generic” names of Sobolew (1914), cited in the text, are not italicized.

Phylum **MOLLUSCA** Linné, 1758

Class **CEPHALOPODA** Cuvier, 1795

Subclass **AMMONOIDEA** Zittel, 1884

Order **GONIATITIDA** Hyatt, 1884

Suborder **TORNOCERATINA** Wedekind, 1918

Remarks. — The tornoceratine goniatites inherited a low conch expansion rate after their anarcestine ancestors (Korn and Klug 2001). The conchs are generally involute with the area of the septum on both sides of the preceding whorl vaulted in the dorso-ventral plane.

Much value is given to the profile of aperture in the tornoceratine goniatites and an elaborate terminology for various shapes of growth lines and ribs is available. To make the text comprehensible also to non-specialists I avoid such terms and refer only to prominence of ventrolateral protrusions of the aperture (auricles) and depth of the ventral infundibular sinus. Schematic drawings of growth lines offer enough information on their exact course. Also while describing sutures possibly neutral descriptives are used in hope that this will be understandable to followers of various notation systems.

Family **Tornoceratidae** von Arthaber, 1911

Diagnosis. — Conch aperture with auricles and relatively high whorl expansion rate, septum of simple geometry developing only small lateral vaultings (expressed as one set of flank lobes in the suture) with a tendency to simplification in secondarily evolute forms.

Remarks. — The main difficulty with the taxonomy of generalized tornoceratids is the simplicity of their external conch morphology and geometry of the septum. To interpret the latter it seems enough to invoke the “balloon concept” of the cephalopod septum as an interplay of the whorl cross-section and uniformly distributed hydraulic pressure within the animal soft body (Seilacher 1975). Only in more advanced tornoceratids vaulted areas in the septum developed, suggestive of a more complex pattern of muscular attachments of the body to the internal conch wall. The septal and conch morphology of early tornoceratids seems to be sensitive of evolutionary reversals and homeomorphy an thus of low taxonomic value. In fact, the conch shape and the suture line controlled by it seem variable in both the early Frasnian (Bogoslowsky 1971) and latest Frasnian (Dzik 2002) species represented by a large number of specimens.

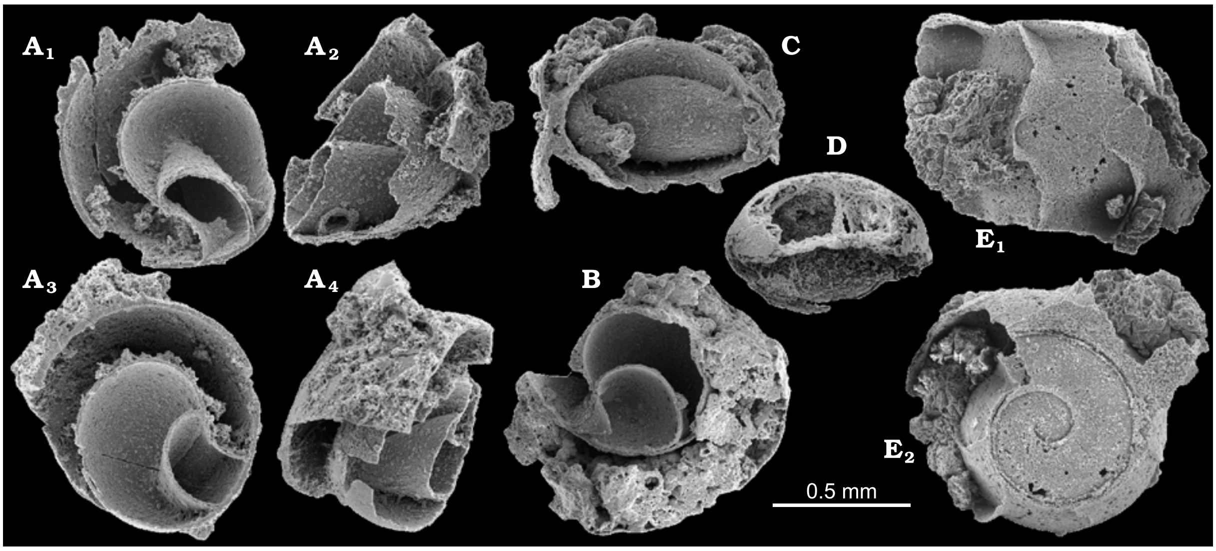


Fig. 140. Silicified juvenile ammonoid conchs from the latest Frasnian at Miedzianka, samples Md-18 (A) and Md-21 (B–E) in the Holy Cross Mountains. **A**. Almost medially split protoconch of a tornoceratid (probably *Linguatornoceras*, the only genus convincingly identified from strata of that age in the area; Dzik 2002) showing swollen first chamber, parts of specimen ZPAL AmVII/1808 in medial and septal views. **B**. Similarly preserved specimen ZPAL AmVII/1810. **C**. First septum of specimen ZPAL AmVII/1811. **D**. Specimen preserved as a partial internal mould of the first chamber, ZPAL AmVII/1812. **E**. Protoconch of a gephyroceratid in lateral view and its ventral surface with remains of septa on the second coil, ZPAL AmVII/1813.

In such a situation the morphology of the first larval septum, deeply concave in at least some tornoceratids (Ruzhentcev 1962; Bogoslovsky 1969) may be of much taxonomic value, because of its uniqueness. The first septum is very different from the succeeding septa and apparently originated under different conditions of secretion. One may speculate that this was a result of secretion of the phragmocone chamber liquid being delayed in respect to secretion of the septal tissue. The volume of the first regular phragmocone chamber was much smaller than that of the protoconch, so subsequent septa originated in a more regular rhythmic pattern. Anyway, this peculiar morphology of the larval (ammonitella) conch may be a useful diagnostic character (synapomorphy) for the least derived trornoceratids.

The problem thus emerges when this concave first septum originated and how long it persisted in the evolution of the tornoceratids. This character was first identified in a typical *Tornoceras* species from the early Frasnian Domanik Formation of Timan (Ruzhentcev 1962; Bogoslovsky 1969). House (1965), while interpreting pyritized protoconchs of the type species of the genus from the Givetian Alden Marcasite horizon within the Ledyard Shale of New York, suggested the presence of an unusually large caecum. It seems possible that this was actually the first septum which developed such a swollen structure. If true, this character might define the origin of the tornoceratid clade more precisely than the conch morphology.

This bizarre first septum morphology is shown by silicified tornoceratid specimens from the topmost Frasnian strata at Miedzianka in the Holy Cross Mountains (Fig. 140) associated with a normally developed (not swollen) siphuncle. Among postlarval tornoceratids of generalized conch morphology only *Linguatornoceras* has been identified in these strata (Dzik 2002). A similar, but not so strongly concave first septum characterizes a tornoceratid from the significantly younger Upper Łagów Beds at Dule (sample Ł-38). Associated protornoceratids show normal development of the first septum. This suggests a gradual disappearance of this character and explains why the clymeniids do not show any signs of its presence, despite their probable tornoceratid ancestry.

Genus *Tornoceras* Hyatt, 1884

Type species: *Goniatites uniangularis* Conrad, 1842 from the latest Givetian Leicester Pyrite of New York.

Diagnosis. — Involute discoidal conch with closed umbilicus; the main subventral area of the septum concave, without lateral vaultings; the first septum deeply concave and swollen.

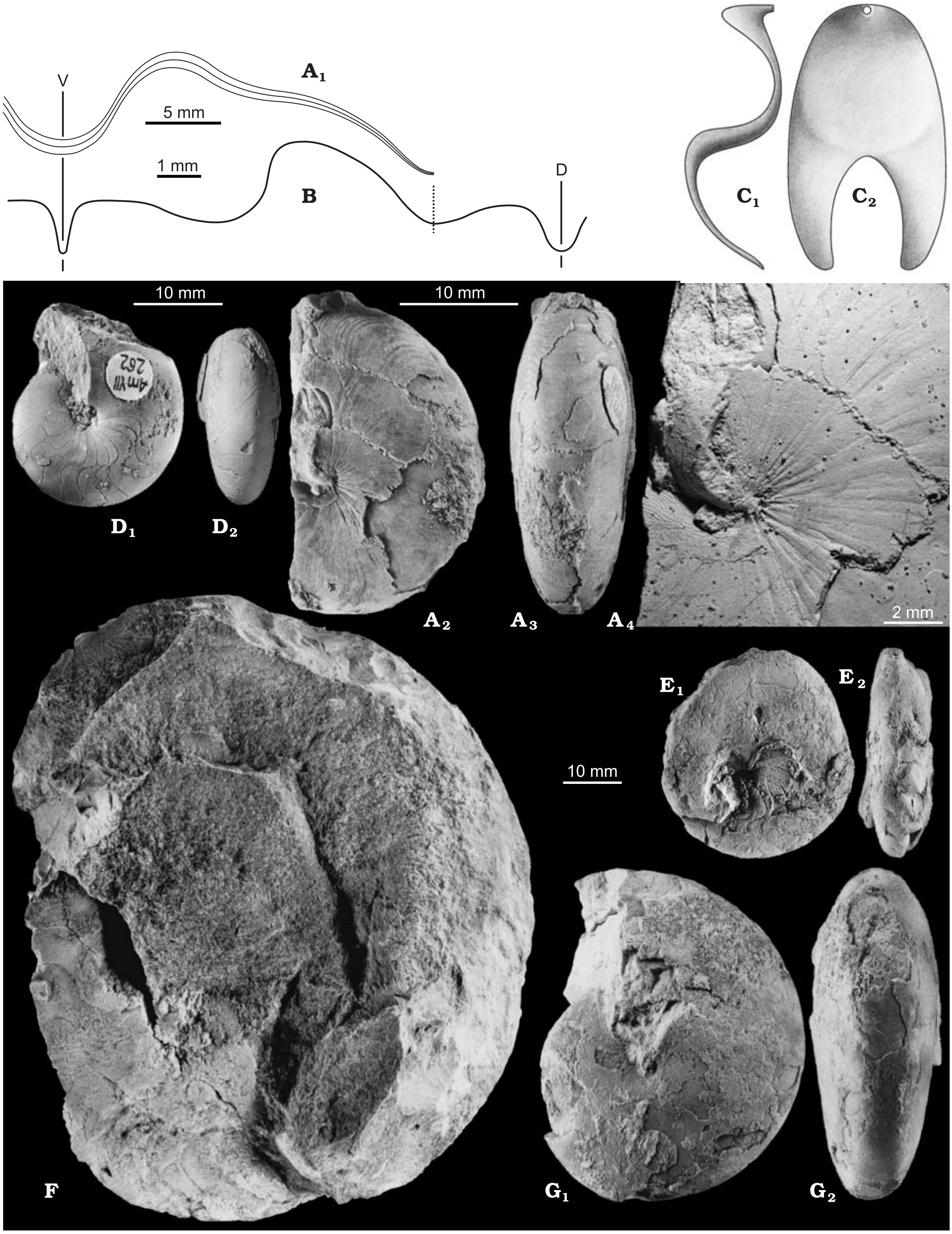


Fig. 141. The most generalized tornoceratid *Tornoceras typum* (Sandberger *et* Sandberger, 1851) from the early Famennian *K. crepida* Zone at Jabłonna (A, B, D, F), Kadzielnia (C, G), and Wietrznia (E) in the Holy Cross Mountains. Growth lines and views of the conch with preserved shell and complete aperture, magnified to show the extend of wrinkle layer (A, bed 7), specimen ZPAL AmVII/299; suture (B) of AmVII/259 (external part; bed 7) and 301 (internal part; bed 6); septal geometry (C) based on specimens AmVII/266 (bed 8) and 301 (bed 6); mature male? conch with exfoliated shell (D, bed 5) ZPAL AmVII/262; internal mould of subadult conch (E, beds with *Concavicaris*) ZPAL AmVII/1692; mature female? conch (F, bed 9) ZPAL AmVII/364; possible macroconch phragmocone(G) with coarsely recrystallized shell ZPAL AmVII/458.

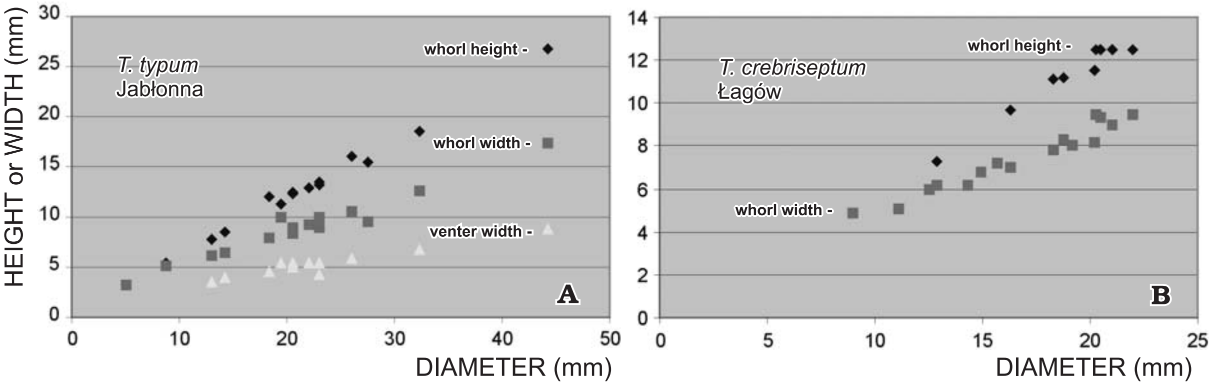


Fig. 142. Variability of conch dimensions of *Tornoceras* **A**. *T. typum* (Sandberger *et* Sandberger, 1851) from the early Famennian *K. crepida* Zone at Jabłonna (beds 5, 6, and 7). **B**. *T. crebriseptum* Raymond, 1909 from the mid Famennian *C. marginifera* Zone at Łagów (samples Ł-5, 28, 29, 30, 31, and 33, probably all from the same bed).

Remarks. — The Frasnian populations of the main lineage of *Tornoceras* differ from those of the Givetian in a less acute outline of the ventral saddles (Bogoslovsky 1971) and from those from the early Famennian in suture lobes restricted to the subventral part of the whorl.

The septum geometry of *Tornoceras* is extremely simple, simpler than one may infer from the relatively complex course of the suture line. There are only concavities in the septum that fits closely the baloon model of Seilacher (1975). The difference between the central concavity located ventrally of the preceding whorl and concavities on its side apparently resulted from different ease of withdrawal of the body while developing a new chamber. This may have been related to the animal's anatomy. One may guess that the internal organs of higher stiffness (liver?) occupied the ventral part of the whorl, resisting the cameral liquid pressure more than the dorsolateral parts.

Tornoceras typum (Sandberger *et* Sandberger, 1851)

(Figs 139B–E?, 141, 142A, and 159)

Type horizon and locality: Probably Frasnian at Seßacker in the Dillenburg region in the Rhenish Slate Mountains (Becker 1993b).

Material. — 23 specimens.

Diagnosis. — Smooth, involute, discoidal conch, deep gently concave flank lobe of the suture line.

Remarks. — This species is usually referred to as *T. simplex* (von Buch, 1832) the original drawing of the type of which shows a specimen with open umbilicus and is a *nomen dubium* (Becker 1993a, p. 182). *T. incrassatus* (Gürich, 1896), based on a specimen from the early Famennian of Karczówka is probably available as a valid name. Although the depository of the original specimen remains unknown, pieces of the rock with ammonoid conchs are preserved in the collection of Dymitr Sobolew in Kharkov, Ukraine.

According to Becker (1993a) this mostly early Famennian species is close to the Frasnian *Linguatornoceras linguum* (Sandberger *et* Sandberger, 1851), the only tornoceratid preceding it stratigraphically in the Holy Cross Mountains (Dzik 2002). Makowski (1991; followed by Becker 1993b) classified the early Frasnian tornoceratids from the Holy Cross Mountains in *T. frechi* (Wedekind, 1918) proposed to be the type species of the new genus *Phoenixites* by Becker (1993b). Unfortunately, similarly as in the case of *T. typum*, the type horizon of *P. frechi* is uncertain. Originally the species was based on an early or mid Frasnian material (Wedekind 1918) and Becker (1993a) proposed the neotype from Seßacker near Oberscheld, probably also of Frasnian age. This would require that these two closely similar tornoceratid lineages co-occurred in both the Frasnian and Famennian, crossing the boundary between these ages. The diagnostic feature of *Phoenixites* is the presence of ventrolateral furrows at the juvenile growth stages. Nothing like that has been recognized in the specimens available to me, their smallest diameter being 5 mm.

There is a significant variation in the conch geometry and suture line within particular samples. In some specimens the flank lobe is strongly concave (as typical for the species), in others shallow, almost approaching the status typical of the mid Famennian *T. crebriseptum*. Juvenile specimens may have rather flat or, instead, globose conchs. Serial ventral thickenings of the aperture, considered by Becker 1993b to define his

Phoenixites sulcatus and *P. varicatus* (Wedekind, 1918), co-occur with those without thickenings (in Jabłonna beds 7 and 24).

The tornoceratids show an apparent bimodality in size frequency distribution interpreted as a case of sexual dimorphism (Makowski 1962, 1963, 1991). Already in the early Frasnian Domanik Formation of the Timan specimens of diameter about 35 mm with densely distributed terminal septa co-occur with conchs of at lest 90 mm diameter (Bogoslowsky 1971). In my material from Jabłonna, a still not mature specimen of 115 mm conch diameter co-occurs with mature specimens of 27 mm size. Makowski (1991) proposed to distinguish a separate chronosubspecies *T. frechi parvum* based on the allegedly small size of macroconchs but the illustrated specimens do not show convincing evidence of growth termination and may be actually juveniles.

In the laminated marls of the earliest Famennian at Kowala, numerous cephalopod jaws occur. Their elongated shape suggests that the conch aperture to which they were fit was rather compressed, with a rounded venter. This would fit the morphology of *Tornoceras*, the only lineage expected to occur in strata of this age. The most unexpected aspect of these jaws is that they show a medial suture; these were actually aptychi (Fig. 139B–E). Minute specimens, probably juvenile, show sometimes an iron mineralization suggestive of substantial original thickness of valves in their marginal parts. Large, probably mature specimen is split along the suture and the ventral tips of valves are rounded also admedially.

Distribution. — Probably the late *K. triangularis* Zone at Karczówka, the early *K. crepida* Zone at Wietrznia, Kadzielnia, Jabłonna (beds 5–7), and Janczyce (Makowski 1991).

Tornoceras subacutum Makowski, 1991
(Figs 143A–H and 159)

Type horizon and locality: Bed 3 of the early Famennian at Janczyce, Holy Cross Mountains.

Material. — 15 specimens.

Diagnosis. — Macroconchs with narrowly trapezoidal cross section of the venter; microconchs with rounded venter (Makowski 1991).

Remarks. — The evolutionary position of the species within the continuous phyletic lineage running from *T. typum* to *T. sublentiforme* was presented by Makowski (1991). Sutures in three specimens (diameters 26 to about 30 mm) show a terminal condensation. The pyritized minute specimen of Gomi-monomeroceras (*Tornoceras*) *kielcense* Sobolew, 1914, from Sieklucki's brickpit may belong to this species although its suture shows a rather unusual symmetrical shape of the flank lobe.

Distribution. — The *K. crepida* Zone at Janczyce (bed 3 of Makowski 1991) and Kadzielnia.

Tornoceras sublentiforme (Sobolew, 1914)
(Figs 143I–N and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — Eight specimens.

Diagnosis. — Acute or very narrowly tabulate venter of adult specimens; generalized tornoceratid suture.

Remarks. — This is the end member of the lineage of *Tornoceras subacutum* as shown by Makowski (1991). Relatively large specimen MD 11090 from Kadzielnia in the collection of the former Dzieduszyckis' Museum in Lvov, about 70 mm in diameter, and mature specimen ZPAL AmVII/991 in my collection, of diameter 57 mm, have an almost acute venter with a very narrow tabulation. The complete lineage seems to be represented at Kadzielnia, but the material comes from loose blocks and the exact stratigraphic position of particular specimens is hard to determine.

Distribution. — The *K. crepida* Zone at Janczyce (beds 4–5 of Makowski 1991), Jabłonna (beds 10, 11, 14), and Kadzielnia; reworked at Sieklucki's brickpit in Kielce.

Tornoceras crebriseptum Raymond, 1909
(Figs 142B, 144A–D and 159)

Type horizon and locality: Mid Famennian (probably *Platyclymenia annulata* Zone) Three Forks Shale north of Three Forks, Montana (D. Korn, personal communication 2005).

Material. — 33 specimens.

Diagnosis. — Relatively shallow flank lobe of the suture.

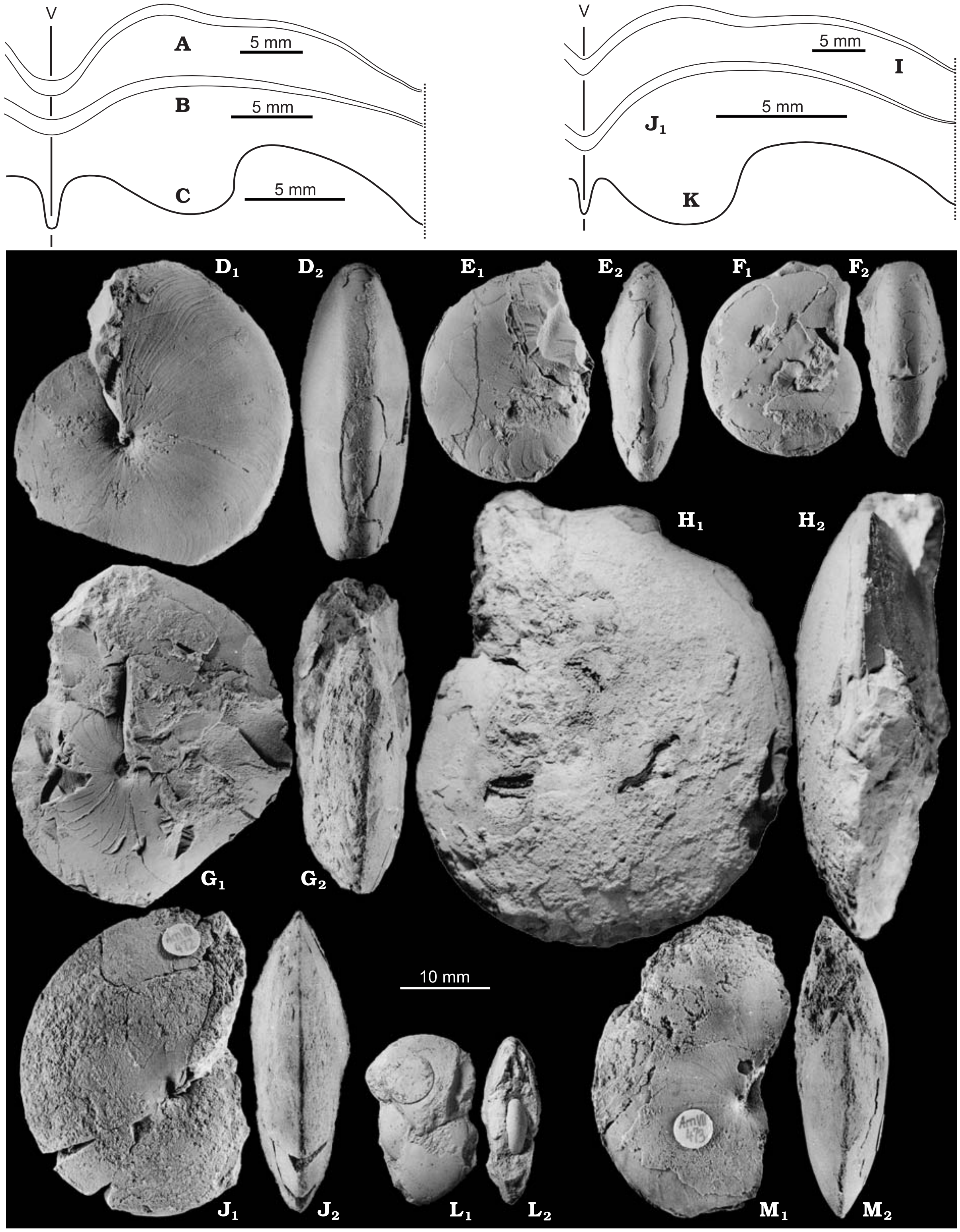


Fig. 143. Tornoceratids with acute conch venter from the early Famennian *K. crepida* Zone of the Holy Cross Mountains. **A–H**. *Tornoceras subacutum* Makowski, 1991 from Kadzielnia; growth lines based on unnambered probable macroconch from Makowski's collection (A) and microconch ZPAL AmVII/287 (B), suture line based on specimen ZPAL AmVII/286 (C); probable microconchs ZPAL AmVII/990, 999, and 987 (D–F) and macroconchs ZPAL AmVII/991 (G) and MD 11090 (H). **I–N**. *Tornoceras sublentiforme* (Sobolew, 1914) from Janczyce (I, bed 5 of Makowski 1991) and Jabłonna (J–N); growth lines based on unnambered probable macroconch from Makowski's collection (I) and microconch ZPAL AmVII/473 (J, bed 11; also views of the specimen), suture line based on specimen ZPAL AmVII/477 (K, bed 11); juvenile ZPAL AmVII/482 (L, bed 14), and probable microconch ZPAL AmVII/ 472 (M).

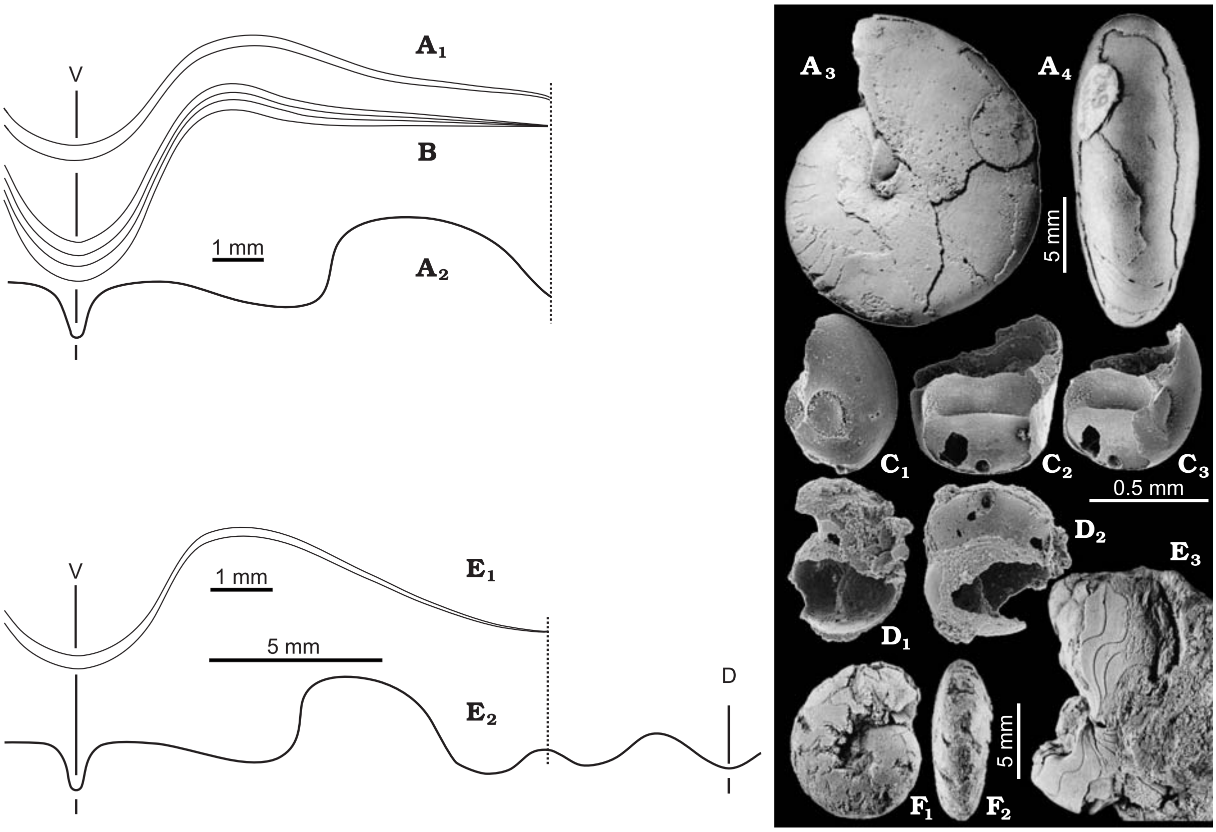


Fig. 144. Late species of *Tornoceras* from the mid Famennian of the Holy Cross Mountains. **A**–**D**. *T. crebriseptum* Raymond, 1909; growth lines traced from imprints on the conch internal mould, suture, and views of specimen ZPAL AmVII/642 from the *C. marginifera* Zone at Łagów-Dule (A, sample Ł-5), growth lines of specimen ZPAL AmVII/646 from the *P. trachytera* Zone at Jabłonna (B, bed 24) with numerous ventral shell thickenings, but do not showing suture, possibly belonging to the same species; and larval (ammonitella) conchs AmVII/1916 and 1614 from the same zone (C, D, sample Ł-38). **E**, **F**. *T. pseudobilobatum* Dybczyński, 1913 from the mid *C. marginifera* Zone at Kowala; growth lines traced from imprints on the conch pyritic internal mould, suture, and views of specimens ZPAL AmVII/1004 (E) and ZPAL AmVII/112 (F).

Remarks. — *Tornoceras applanatus* (Gürich, 1896) based on a specimen from the Upper Łagów beds (Sacculus-Bank) probably refers to the same species. All available specimens are minute in size, up to 22 mm in diameter, three of them with a condensation of sutures suggestive of maturity. Perhaps also Gomire-monomeroceras (*Tornoceras*) *simplicius subacutum* Sobolew, 1914 from the clymeniid limestone at Łagów-Dule belongs to this species, although only the shape of aperture makes it different from associated *Protornoceras simplicius*. In the Czarnocki's collection housed at the State Geological Institute there is a probably adult specimen IG 284 II.290 about 52 mm in diameter, collected from the grey "Laevigites" limestone (*Nodosoclymenia* bed?) at Ostrówka. Its suture is characteristically simple but growth lines are not recognizable.

Another question is whether the North American type population of *T. crebriseptum* is truly conspecific with the Holy Cross Mountains material. Specimens from the Three Forks Shale are pyritic internal moulds with open umbilicus, which may express an increased thickness of the shell forming a kind of umbonal callus (see Fig. 144A). This character was used by Korn and Titus (2006) to substantiate transfer of the species to *Pernoceras* Schindewolf, 1922, the type species of which is *Protornoceras kochi* (Wedekind, 1908. The Montana specimens show a conical depression around umbo, resembling the Polish species of *Protornoceras* from Kowala in this respect but difficult to compare with specimens from Łagów and Jabłonna having the original shell preserved. The species may truly be related to *P. kochi*.

Distribution. — The *C. marginifera* (samples Ł-5, 28, 29, 30, 31, and 33) and possibly the *P. trachytera* zones at Łagów-Dule and Jabłonna (bed 24), perhaps *L. styriacus* Zone at Ostrówka; reworked at Sieklucki's brickpit in Kielce.

Tornoceras pseudobilobatum Dybczyński, 1913
(Figs 144E, F and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — Six specimens.

Diagnosis. — Suture with incipient dorsolateral lobe and relatively straight course of the ventrolateral saddle, otherwise generalized tornoceratid conch.

Remarks. — In the two best preserved relatively large specimens, the siphuncle position is somewhat asymmetric. Juvenile whorls are gently rounded, any relationship to *Falcitornoceras bilobatum* is thus unlikely, contrary to attribution of this species to *F. falcatum* by Becker (1993*b*). This is probably rather an advanced member of the *Tornoceras* branch.

Distribution. — The mid *C. marginifera* Zone at Kowala; reworked at Sieklucki's brickpit in Kielce.

Genus ***Polonoceras*** Dybczyński, 1913

Type species: *Polonoceras planum* Dybczyński from the Famennian of Kielce, Holy Cross Mountains.

Diagnosis. — Acute auricles of the aperture, involute discoidal conch with small umbilicus, flat sides and more or less tabulate venter; weak ventro-lateral vaultings may develop in the septum.

Remarks. — The incipient vaultings of the septum seems to be an expression of locally delayed withdrawal of the visceral sac, attached to the shell with muscles.

Polonoceras sandbergeri (Foord *et* Crick, 1897)
(Figs 145A and 159)

Type horizon and locality: Probably early Famennian at Nehden, Rhenish Slate Mountains (Becker 1993b).

Material. — Two specimens.

Diagnosis. — Auricles of the aperture with relatively blunt, parabolic profile.

Remarks. — The complex nomenclatorial history of the species was clarified by Becker (1993b) who classified it as *Truyolsoceras sandbergeri*. It seems that it represents an early part of the *P. planum* lineage and I find such generic distinction redundant. Perhaps Gomi-monomeroceras (*Tornoceras*) *dorsoplanum avaricatum* Sobolew, 1914 from the Lower Łagów Beds represent this species, although its somewhat wider umbo may suggest affinities to the *Protornoceras* lineage.

Distribution. — The early *K. crepida* Zone (bed 6) at Jabłonna.

Polonoceras bashkiricum Bogoslovsky, 1971
(Figs 145B–D and 159)

Type horizon and locality: Upper part of the *Cheiloceras* Stufe, 200 m from the mouth of the Ishikay River, South Urals (Bogoslovsky 1971).

Material. — Three specimens.

Diagnosis. — Acute tips of auricles of the aperture; distinctly tabulate venter of mature specimens, rounded in juveniles.

Remarks. — The Frasnian-style suture and the subtrapezoidal cross section of the whorl make this specimen similar to the holotype of *Linguatornoceras linguum* (see Becker 1993b, pl. 3: 13, 14). Conchs of the Famennian species attributed to the genus by this author are, however, different from the Łagów specimen in having a very narrow flank lobe of the suture and rounded margins of the umbilicus. In the latter aspect, the specimen discussed resembles the stratigraphically older species attributed here to *Gundolficeras korni* (Becker, 1993) and *Protornoceras simplicius*, being different in the subtrapezoidal whorl section and deep flank lobe of the suture. Specimens from sample Ł-14 tentatively attributed to the latter species may also belong here, as well as the specimen from the Upper Łagów Beds illustrated by Sobolew (1914) as *Tornoceras escoti* Frech, 1902. The species seems both morphologically and stratigraphically transitional between *P. sandbergeri* and *P. planum*.

Distribution. — The late *K. crepida* (bed 15) and probably the *C. marginifera* (bed 17) zones at Jabłonna; the *C. marginifera* Zone at Łagów-Dule; possibly also reworked at Sieklucki's brickpit in Kielce.

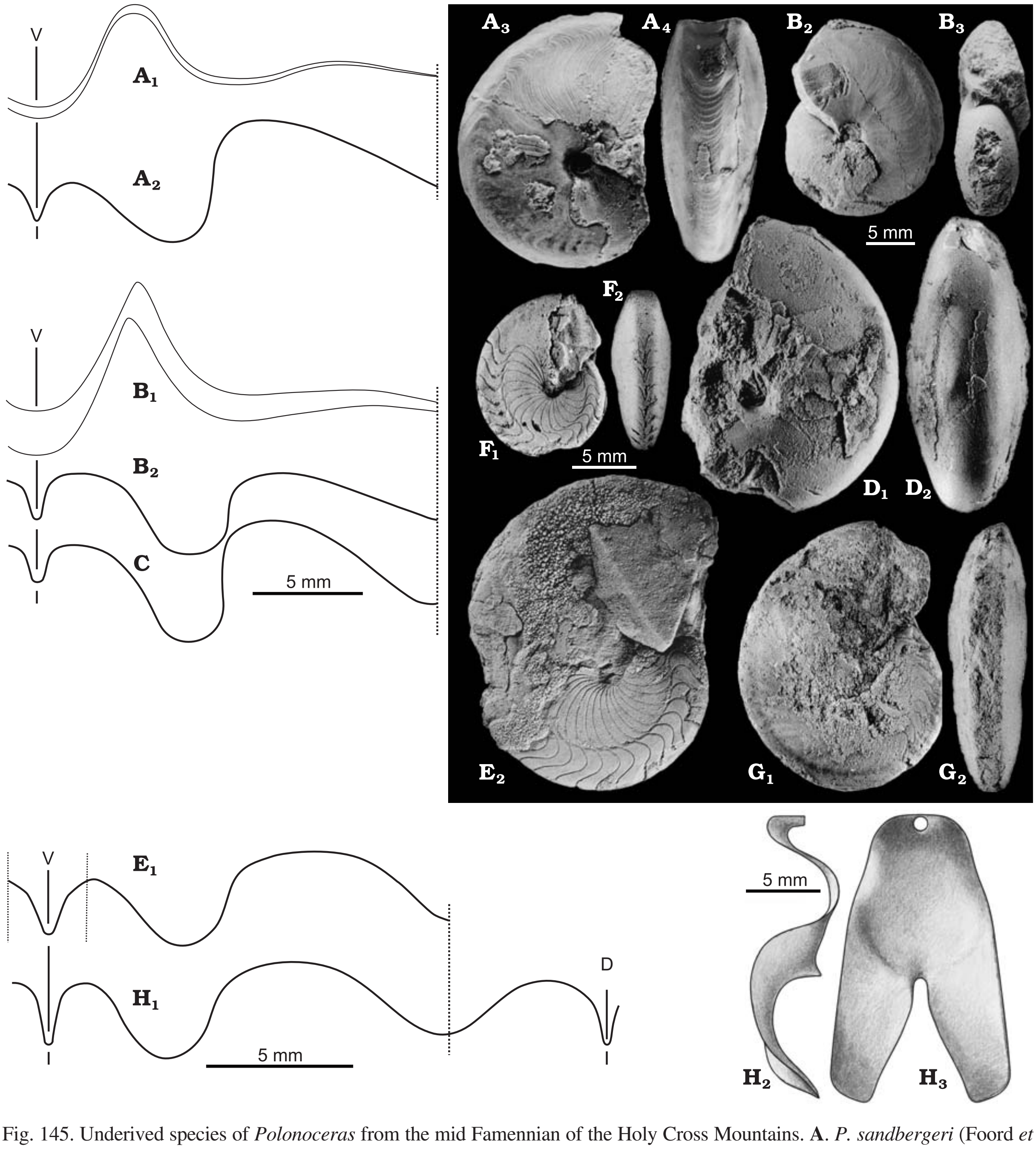


Fig. 145. Underived species of *Polonoceras* from the mid Famennian of the Holy Cross Mountains. **A**. *P. sandbergeri* (Foord *et* Crick, 1897); growth lines, suture, and views of specimen ZPAL AmVII/340 from the *K. crepida* Zone at Jabłonna (bed 6). **B**–**D**. *P. bashkiricum* Bogoslovsky, 1971 from the *C. marginifera* Zone; growth lines and views of specimen ZPAL AmVII/354 from Jabłonna (B, bed 17), suture of ZPAL AmVII/264 (C, bed 15), and views of ZPAL AmVII/1093 from Łagów (D). **E**–**H**. *Polonoceras planum* Dybczyński, 1913 from the mid *C. marginifera* Zone at Kowala; suture and view of specimen ZPAL AmVII/1009 (E), views of ZPAL AmVII/951 and 952 (F, G), suture and septum of ZPAL AmVII/1010 (H).

Polonoceras planum Dybczyński, 1913
(Figs 145E–H and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — 12 specimens.

Diagnosis. — Distinctly tabulate venter even in juvenile specimens, narrow umbilicus.

Remarks. — Tips of auricles are located somewhat dorsally to the tabulate venter, where they sometimes leave a shallow furrow on the phragmocone internal mould. In this respect the species is different from *P. dorsoplanum*, its probable successor.

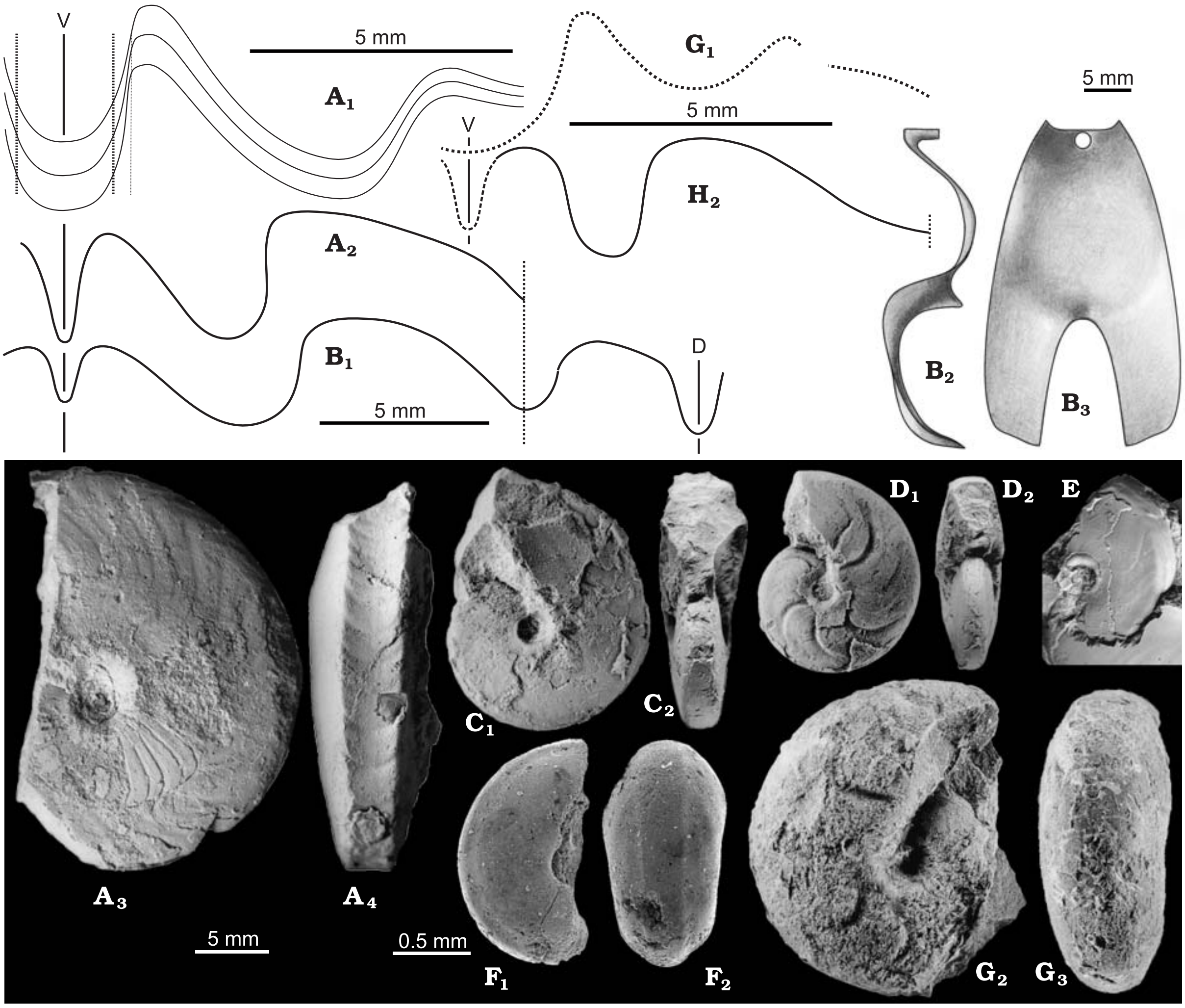


Fig. 146. Advanced species of *Polonoceras* from the Famennian of Poland. **A–E**. *P. dorsoplanum* (Sobolew, 1912) from the *C. marginifera* Zone at Łagów; growth lines, suture, and views of specimen ZPAL AmVII/343 (A), suture and septum of ZPAL AmVII/350 (B), views of specimens ZPAL AmVII/359, 358, and 351, respectively (C–E). **F**. Specifically undeterminable larval (or embryonic) specimen ZPAL AmVII/1837 from the *L styriacus* Zone at Kowala (sample Ko-174) in the Holy Cross Mountains. **G**, **H**. *P. sudeticum* (Renz, 1914) from the *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec in the Sudetes; constriction of the conch and views of ZPAL AmVII/151 (G) and suture of ZPAL AmVII/090 (H).

Distribution. — The mid *C. marginifera* Zone at Kowala; reworked at Sieklucki's brickpit in Kielce.

Polonoceras dorsoplanum (Sobolew, 1912)
(Figs 146A–E and 159)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains (Sobolew 1912b).

Material. — 21 specimens.

Diagnosis. — Deep conical umbilicus with raised margins, acute tips of auricles demarcate the tabulate venter.

Remarks. — Some specimens show periodic constrictions on the conch flanks.

Distribution. — The *C. quadrantinodosa* (samples Ł-28 and 33), *C. marginifera*, and *P. trachytera* zones at Łagów-Dule.

Polonoceras sudeticum (Renz, 1914)
(Figs 146G, H and 159)

Type horizon and locality: Clymeniid limestone at Dzikowiec, the Sudetes.

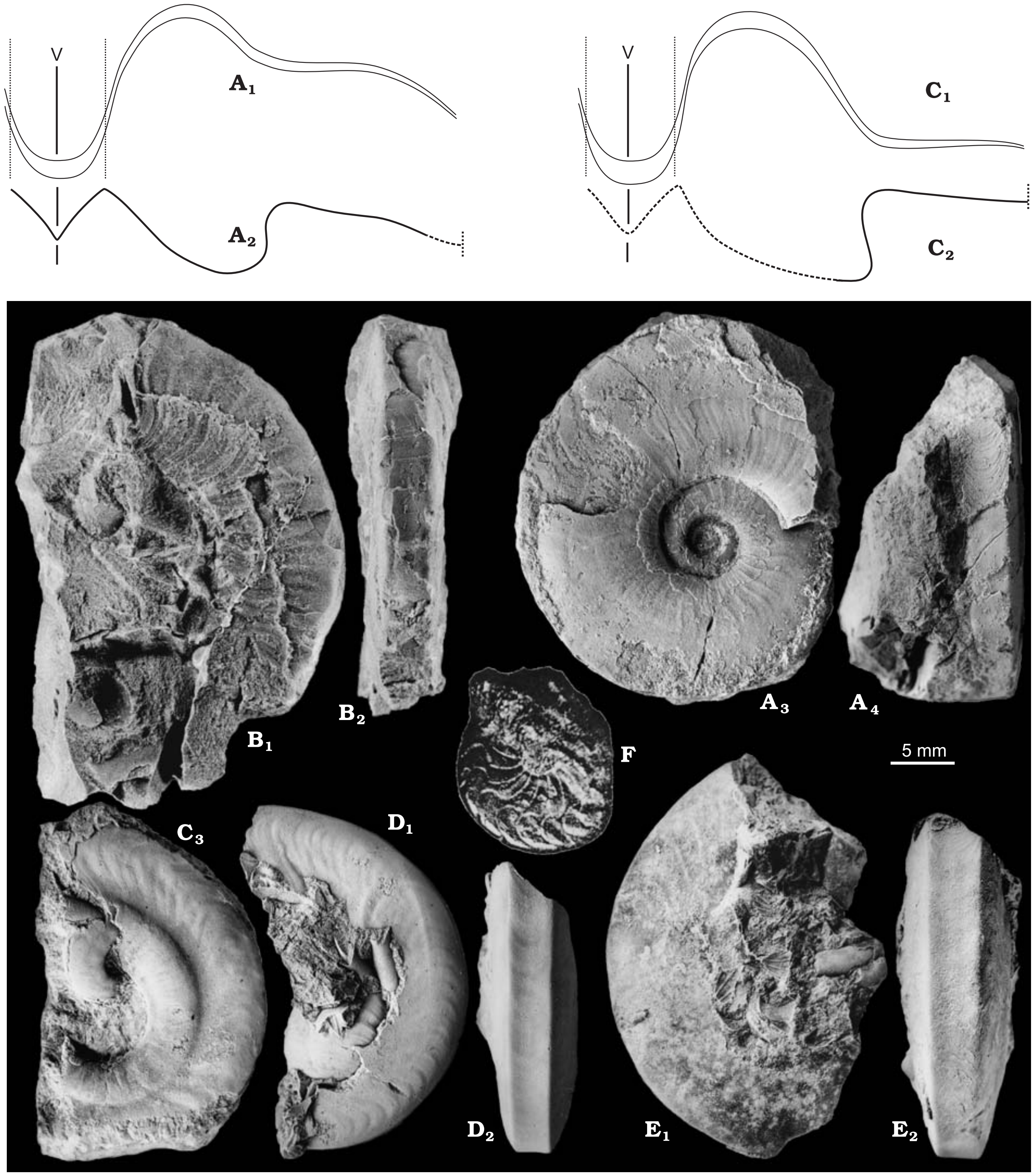


Fig. 147. Species of *Armatites* from the mid Famennian of Poland. **A**, **B**. Early *A. lateroconcavus* (Dybczyński, 1913) from the early *P. trachytera* Zone at Jabłonna (bed 25); growth lines, suture, and views of specimen ZPAL AmVII/341 (A, bed 21), and views of probably mature living chamber ZPAL AmVII/166 (B). **C**–**E**. Late *A. lateroconcavus* (Dybczyński, 1913) from the *L. styriacus* Zone at Jabłonna (A, bed 26) and the late *P. trachytera* Zone at Łagów-Dule (D, E); growth lines, suture, and view (C) of specimen ZPAL AmVII/342, views of fragmentary living chambers ZPAL AmVII/356 and 349 (D, E). **F**. Type specimen of *A. lewinskii* (Dybczyński, 1913) from Quaternary deposits at Sieklucki's brickpit in Kielce (reproduced after Dybczyński 1913, pl. 2: 10).

Material. — Three specimens.

Diagnosis. — Closed umbilicus of conical appearance demarkated by a spiral ridge; roundly tabulate venter; serial constrictions on conch flanks parallel to the aperture, which bears acute auricles; suture with a deep, narrow flank lobe.

Remarks. — Renz (1914) identified his only specimen from Dzikowiec lacking any suture as a new variety of *Oxyclymenia ornata*. The constrictions (not internal thickenings!) in its conch, expressed both on nuclei and the conch surface, are so characteristic that there is little doubt that the newly collected topotype specimens are conspecific. The acute auricles and deep lobe of the suture point to *Polonoceras dorsoplanum* as the ancestor of the species.

Distribution. — The *P. jugosus* (or *D. trigonica*) Zone at Dzikowiec.

Genus ***Armatites*** Becker, 1993

Type species: *Goniatites planidorsatus* Münster, 1839 from the Famennian of Gattendorf in Franconia (Becker 1993b).

Diagnosis. — Conch with tabular or bicarinate venter and flat sides, open umbilicus, generalized tornoceratid suture and aperture with wide, gently rounded auricles.

Remarks. — Among specimens classified in various species of the genus by Becker (1993b) only the lectotype fits the specific morphology of the members of the lineage represented in the Holy Cross Mountains, attributed to *Armatites* here. He later created the new genus *Planitornoceras* for species with a similar apertural profile but a *Protornoceras*-like suture.

Armatites lewinskii (Dybczyński, 1913)
(Figs 147F and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Diagnosis. — Conch with rounded venter and small umbilicus.

Remarks. — The description by Dybczyński (1913) suggests that this may be an early member of the *Armatites* lineage, as indicated by flat flanks and semicircular appearance of flank lobes. Unfortunately, his description and illustrations remain the only source of data on this species. The illustrated specimen is a juvenile and its generalized appearance (especially the rounded venter) may be partly due to the early ontogenetic stage. Both its morphology and probable stratigraphic origin (*C. marginifera* Zone) suggest its ancestral position in respect to other species of *Armatites*.

Distribution. — Reworked at Sieklucki's brickpit in Kielce.

Armatites lateroconcavus (Dybczyński, 1913)
(Figs 147A–E and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — Seven specimens.

Diagnosis. — Flanks of the conch subdivided into two zones by a spiral furrow or escarpment.

Remarks. — Unlike the studied specimens, in the lectotype of *A. planidorsatus* (Becker 1993b, pl. 11: 10) the spiral elevation is restricted to near the umbilicus. All of them show rounded tips of apertural auricles, which makes them different from other specimens attributed to the genus by Becker (1993b). Most of the specimens from Łagów are represented only by ventral parts of the body chamber, only one of them preserved the whole conch flank, with the lateral furrow. This situation seems to be similar to that in the holotype, as described by Dybczyński (1913). The specimen of Petter (1959, pl. 15: 30) from Gourara in Algeria, reillustrated by Becker (1993b) and classified by him in his *A. nudus*, shows a similar aperture to the Polish *A. lateroconcavus*, but narrower umbilicus.

There is an apparent evolutionary change in the lineage. The umbilicus is relatively wide in the geologically oldest specimens from Jabłonna (beds 21–25), with gently rounded margin and flat sides of the conch. In the somewhat younger material from Łagów (sample Ł-14), a shallow furrow in the middle of the flanks developed, achieving the form of a prominent escarpment in the youngest specimen from Jabłonna (bed 26). Closely similar form occurs also in the *Prolobites* horizon in vicinities of the village Spasskij in the South Urals (Perna 1914, pl. 2: 9).

Distribution. — Probably the late *C. marginifera* Zone at Jabłonna (bed 21), the *P. trachytera* Zone at Łagów-Dule (e.g., sample Ł-14) and Jabłonna (beds 23–25); and the *L. styriacus* Zone at Jabłonna (bed 26); reworked at Sieklucki's brickpit in Kielce.

Genus ***Protornoceras*** Dybczyński, 1913

Type species: *Protornoceras polonicum* Dybczyński, 1913 from the Famennian of Kielce.

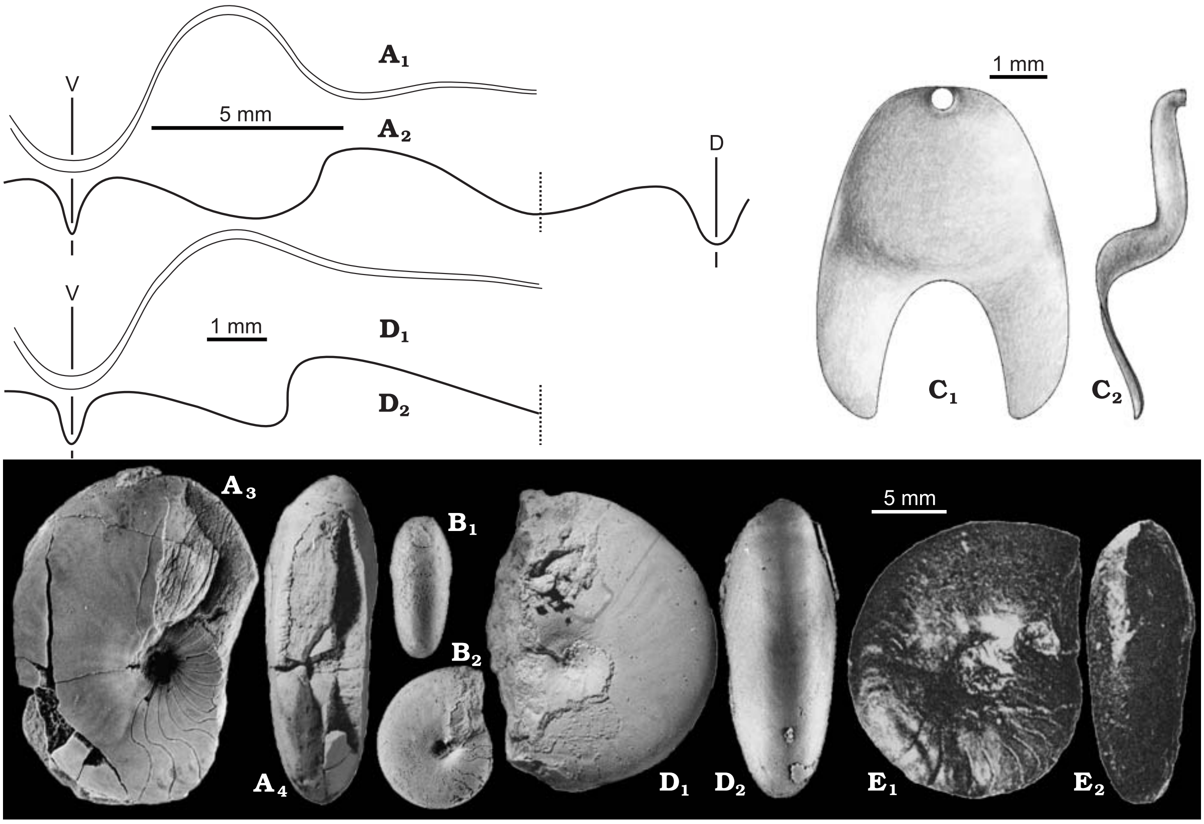


Fig. 148. Species of *Protornoceras* with narrow umbilicus from the Famennian of Poland. **A**–**C**. *P. aphyllitiforme* Dybczyński, 1913 from the mid *C. marginifera* Zone at Kowala; growth lines inferred from wrinkles on the surface of pyritic internal mould, suture, and views of specimen ZPAL AmVII/173 (A), views of specimen ZPAL AmVII/1007 (B), and septum of ZPAL AmVII/956 (C). **D**. *Protornoceras simplicius* (Sobolew, 1914) growth lines, suture, and views of specimen ZPAL AmVII/508 from the *P. trachytera* Zone at Łagów-Dule (sample Ł-9). **E**. *Protornoceras simplificatum* (Sobolew, 1914) from Sieklucki's brickpit in Kielce (reproduced from Sobolew 1914, pl. 9: 27, 28).

Diagnosis. — Simplified suture with a very shallow flank lobe and usually almost straight course of its ventrolateral part; weak ventro-lateral vaultings may develop in the septum; open umbilicus.

Remarks. — This seems to be a separate branch of the tornoceratids evolving towards the clymenoid appearance of the conch and suture. Various forms occur together in the black shale with pyritized ammonoids at Kowala, which suggests their immigration to the Holy Cross Mountains area with the sea transgression of the *C. marginifera* Zone (perhaps at its later stage). Probably the least derived of them is *P. aphyllitiforme*, with almost closed umbo, the most derived is *P. mirabile*. House (1970) proposed the genus *Tornia* for the latter. Perhaps it would be truly reasonable to put the protornoceratids with narrow and wide umbilicus into different genera, but the type species of both *Protornoceras* and *Tornia* are widely umbilicate. Because of the high population variability, their separation seems superfluous. The phylogenetically closest *Kirsoceras* differs in the subventral position of the siphuncle (Bogoslovsky 1971).

Protornoceras aphyllitiforme Dybczyński, 1913
(Figs 148A–C and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — 14 specimens.

Diagnosis. — Narrow umbilicus with the flat adjoining wall of the conch giving it a conical appearance, prominent rounded auricles of the aperture.

Remarks. — The holotype suture is similar to that in juvenile specimens from Kowala. Adult suture (in specimens up to 34 mm in diameter) is more tornoceratid, but it is highly variable. The sample is evidently homogenous, being taken from a single black clay intercalation in the stratigraphically uncondensed, thick rock sequence. An angulation at the dorsal slope of the flank lobe makes some of the Kowala specimens similar to the holotype of *Polonoceras latum* Dybczyński, 1913, which may appear conspecific. Other specimens show a dorsally located indentation in the lobe, having its oblique ventral slope almost straight. This indentation corresponds to a small vaulted area of the septum, a situation closely similar to that in the open-umbilicate *Protornoceras siemiradzkii* Dybczyński, 1913. However, these are distinct species different in the diameter of umbo, the trait less variable than the course of suture in the Kowala material. *Tornoceras obliquum* Perna, 1914 from the *Prolobites* horizon of the Urals shows a similar conch form and suture but unsimilar, pointed auricles of the aperture.

Distribution. — The mid *C. marginifera* Zone at Kowala; reworked at Sieklucki's brickpit in Kielce.

Protornoceras simplicius (Sobolew, 1914)
(Figs 148D and 159)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains.

Material. — 13 specimens.

Diagnosis. — Weakly developed auricles of the aperture; closed conical umbilicus.

Remarks. — Specimens from sample Ł-14, probably representing the type horizon, do not show suture and may be clymenias. In the holotype, the suture is more *Tornoceras*-like than in specimens from the *C. marginifera* Zone (sample Ł-9) but it fits well within the range of variability shown by the stratigraphically somewhat older species from Kowala.

Distribution. — The *C. marginifera* (sample Ł-9) and *P. trachytera* (sample Ł-14) zones at Łagów-Dule, the *L. styriacus* Zone (trench rIVc of Żakowa *et al*. 1986) at Jabłonna.

Protornoceras simplificatum (Sobolew, 1914)
(Figs 148E and 159)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains.

Diagnosis. — Evolute conch with umbo about one fifth of its diameter; oval cross section of the whorl; more or less simplified suture.

Remarks. — No specimen of this morphology has been found by myself in the topotype stratum. Possibly some other taxa by Sobolew (1914) based on Sieklucki's brickpit material belong here: Gomi-re-monomeroceras (*Tornoceras*) *flexuosum* and G. (*T.*) *simplicius rotundatum*.

Distribution. — The *P. trachytera* Zone at Łagów-Dule; possibly also reworked at Sieklucki's brickpit in Kielce.

Protornoceras polonicum Dybczyński, 1913
(Figs 149A–G, 150A, and 159)

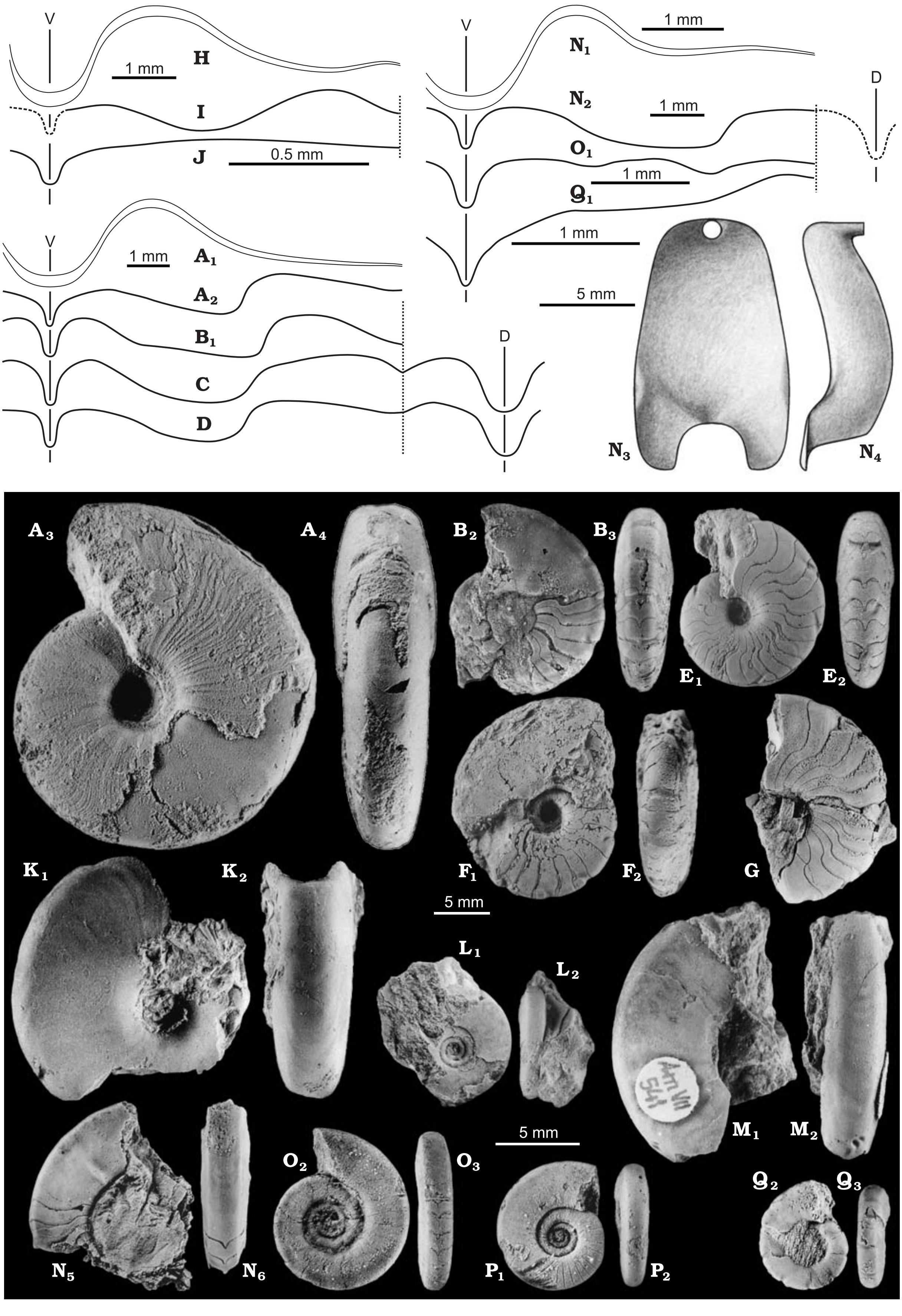
Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — 33 specimens.

Diagnosis. — Open umbilicus of diameter about one tenth of that of mature conch; subtrapezoidal cross section of the whorl; rounded auricles of the aperture.

Remarks. — Similarly to other species of *Protornoceras*, the suture is very variable, especially in respect to concavity of the flank lobe, even within the same specimen. Width of the umbo seems to be of a higher taxonomic value, although it is variable, too (note that all earlier illustrated specimens are pyritic internal moulds). Several species proposed for specimens from Sieklucki's brickpit by Dybczyński (1913), including *P. siemiradzkii*, *P. bilobatiforme*, *P. kielcense*, *P. ornatum*, and *P. zuberi*, and by Sobolew (1914), such as Gomi-re-monomeroceras (*Tornoceras*) *genulobatum planum*, G. (*T.*) *planilobum*, G. (*T.*) *planilobum angulatolobatum*, G. (*T.*) *planilobum avaricatum*, and G. (*T.*) *dorsatum*, may belong here. The holotype of *P. polonicum* is a juvenile specimen with not fully developed suture.

Distribution. — The mid *C. marginifera* Zone at Kowala and Łagów Słupecka 73 (sample ŁSł73-4); reworked at Sieklucki's brickpit in Kielce. Specimens with a similar conch form but the suture not exposed occur in the clymeniid limestone at Łagów-Dule.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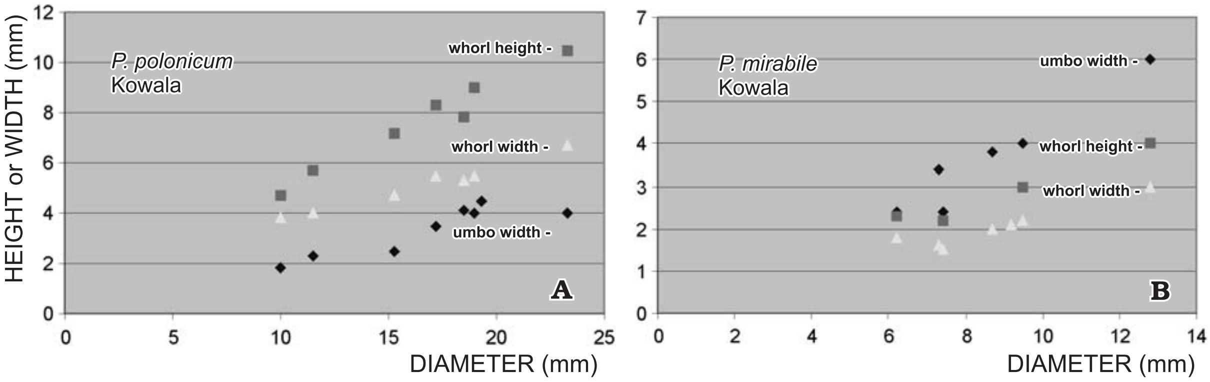

Fig. 150. Variability of conch dimensions (based on measurements of pyritic internal moulds) of *Protornoceras* from the mid *C. marginifera* Zone at Kowala.**A**. *P. polonicum* Dybczyński, 1913. **B**. *P. mirabile* Dybczyński, 1913.

Protornoceras curvidorsatum (Sobolew, 1914)
(Figs 149H-M and 159)

Type horizon and locality: Black clymeniid limestone at Łagów-Dule, Holy Cross Mountains.

Material. — Ten specimens.

Diagnosis. — Evolute conch with umbo width approaching one third of its diameter; subtrapezoidal cross section of the whorl; more or less simplified suture.

Remarks. — In my material only juvenile specimens exhibit suture, which appears to be extremely simplified. Growth lines are prominent, in one specimen numerous apertural thickenings developed along its venter. From the geologically older *P. mirabile* the species differs in the narrower umbo and higher whorls. Possibly some other taxa based by Sobolew (1914) on the Łagów-Dule clymeniid limestone belong here: Gomi-re-monomeroceras (*Tornoceras*) *planilobum arcuatolobatum*, G. (*T.*) *sinuvaricatum*, and G. (*T.*) *umbilicatoides*.

Distribution. — The *P. trachytera* Zone (sample Ł-14) at Łagów-Dule; possibly also reworked at Sieklucki's brickpit in Kielce.

Protornoceras mirabile Dybczyński, 1913
(Figs 149N–P, 150B, and 159)

Type horizon and locality: Reworked to Quaternary sediments at Sieklucki's brickpit in Kielce, Holy Cross Mountains.

Material. — Nine specimens.

Diagnosis. — Evolute conch with the umbo width approaching half of its diameter; subtrapezoidal cross section of the whorl; more or less simplified suture.

Remarks. — This is the type species of *Tornia* House, 1970. The holotype shows a moderately evolute conch, almost straight course of the suture and marks of prominent rounded auricles. In my material the shape of aperture is difficult to trace. However, similarly to other species of the genus, *P. mirabile* population from Kowala shows a tremendous variability in the suture and also, although not so wide, in umbilical width. The whorl cross section shows a remarkable variability ranging from almost tabulate venter and flat flanks to a quite weak angulation. This makes likely conspecificity of some other taxa by Sobolew (1914) based on

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← Fig. 149. Species of *Protornoceras* with wide umbilicus from the Famennian of the Holy Cross Mountains. **A–G**. *P. polonicum* Dybczyński, 1913 from the *C. marginifera* Zone at Łagów locality Słupecka 73 (A, sample ŁSł73-4; with preserved shell wall) and Kowala (B–G; pyritic internal moulds); growth lines, suture, and views of specimen ZPAL AmVII/971 (A), suture and views of ZPAL AmVII/081 (B), sutures of specimens ZPAL AmVII/158 and 909 (C, D), and views of ZPAL AmVII/1006, 1001 and 158 (E–G), respectively. **H–M**. *P. curvidorsatum* (Sobolew, 1914) from the *P. trachytera* Zone at Łagów-Dule (H–J, L, M, sample Ł-14; K, loose specimen), growth lines of specimen ZPAL AmVII/565 lacking suture and of questionable affinity (H), sutures of ZPAL AmVII/705 and 543 (I, J), views of specimens ZPAL AmVII/ 558 and 541 (L, M, sample Ł-14). **N–P**. *P. mirabile* Dybczyński, 1913 from the mid *C. marginifera* Zone at Kowala; growth lines inferred from wrinkles on the surface of pyritic internal mould, suture, and views of specimen ZPAL AmVII/146 (N), suture and views of specimen ZPAL AmVII/114 (O), views of specimen ZPAL AmVII/114 (P), and suture and views of juvenile specimen ZPAL AmVII/120 (O).

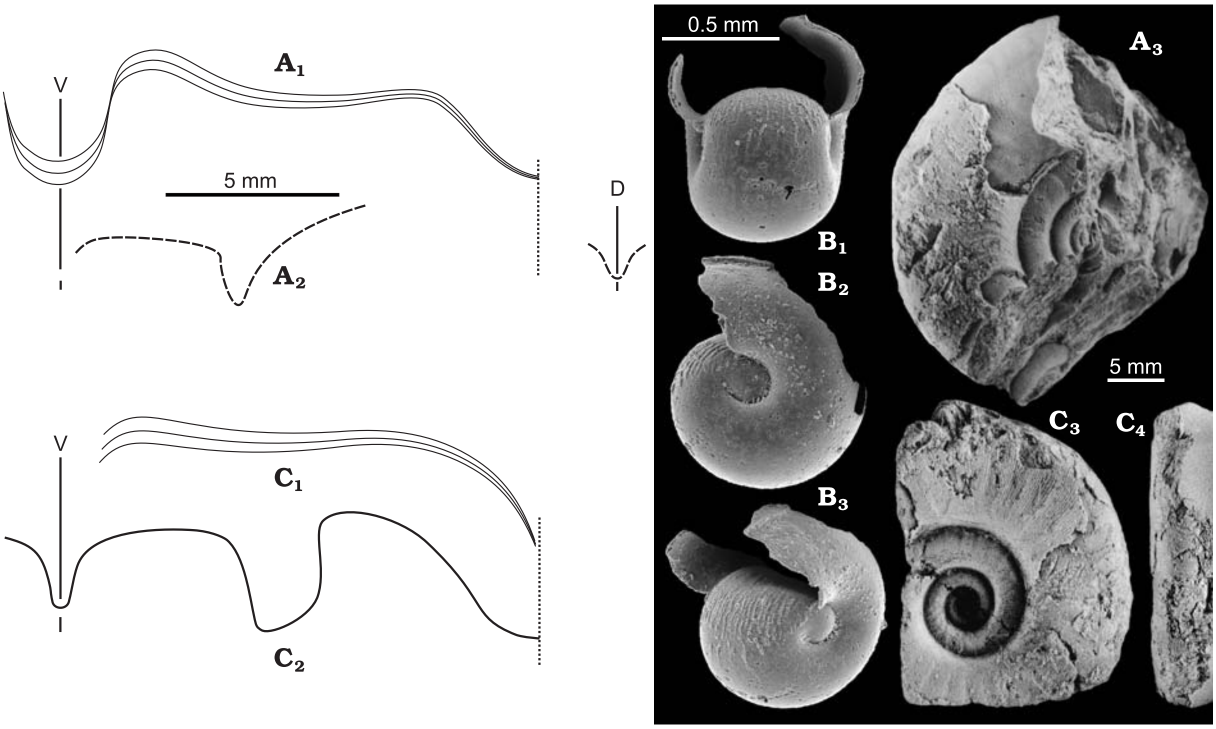

Fig. 151. Species of *Pseudoclymenia* from the Famennian of the Holy Cross Mountains. **A**, **B**. *Pseudoclymenia dillensis* (Drevermann, 1901) from the *C. marginifera* Zone at Łagów-Dule (sample Ł-38); growth lines, suture, and views (A) of specimen ZPAL AmVII/1801 and larval (or embryonic) conch ZPAL AmVII/1818. Note the disposition of wrinkle layer near the aperture and the sudden change in apertural morphology (emergence of auricles) indicating a metamorphosis from the larval conch to teleoconch. The lack of growth increments on the larval conch suggests that the larval development took place completely within the egg covers and that the metamorphosis may have been simultaneous with hatching. **C**. *Pseudoclymenia fundifera* (Perna, 1914) from the *P. trachytera* Zone at Ostrówka, growth lines, suture, and views of specimen IG 284.II.56.

Sieklucki's brickpit material: Gomi-re-protomeroceras *alobatum*, Gomi-re-monomeroceras *umbilicatum*, G. *umbilicatoides*, G. (*Tornoceras*) *simplificatum rotundatum*, and G. (*T.*) *s. subacutum*.

Distribution. — The mid *C. marginifera* Zone at Kowala; reworked at Sieklucki's brickpit in Kielce.

Genus ***Pseudoclymenia*** Frech, 1897

Type species: *Clymenia pseudogoniatites* Sandberger, 1856 from the Famennian of the Rhenisch Slate Mountains.

Diagnosis. — *Aturia*-like flank lobe and incipient dorsolateral lobe of the suture, evolute conch.

Pseudoclymenia dillensis (Drevermann, 1901)

(Figs 151A, B and 159)

Type horizon and locality: Block of clymeniid limestone from a volcanic breccia at Langenaubach near Haiger, Rhenish Slate Mountains.

Material. — One specimen.

Diagnosis. — Somewhat tabulate venter of evolute conch with umbo reaching more than one third of the conch diameter.

Remarks. — The suture in the only available specimen is incomplete, but pointed tip of the flank lobe indicates that this is a species of *Pseudoclymenia*. Its flattened venter suggests species identity with the material of Bogoslovsky (1971; but not Petersen 1975). The originals of Drevermann (1901, pl. 14: 4a, b) are internal moulds and the venter of the specimen illustrated by him is rounded. The relatively narrow umbo (11.5 mm at the conch diameter 30 mm) fits the specimen from Łagów. Larval (or embryonic) and early postlarval phosphatized conchs from the same sample (Ł-38) may also represent this species. Gomi-monomeroceras (*Tornoceras*) *evolutum* of Sobolew (1914) from Sieklucki's brickpit may also represent this or a less derived species of the genus, assuming that the minute original is a juvenile with the suture somewhat worn out.

Distribution. — The *C. marginifera* Zone (sample Ł-38) at Łagów-Dule; possibly also reworked at Sieklucki's brickpit in Kielce.

Pseudoclymenia fundifera (Perna, 1914)
(Figs 151C and 159)

Type horizon and locality: *Prolobites* horizon, Ural River shore 6 km north of the village Kirsy, southern Urals.

Material. — One specimen.

Diagnosis. — Convex ventrolateral lobe of the suture; indistinct auricles of the aperture; oval whorl cross section.

Distribution. — The *P. trachytera* Zone at Ostrówka.

Genus ***Ostrovkites*** gen. n.

Type species: *Ostrovkites numismalis* sp. n.

Derivation of name: From Ostrówka hill, the type locality of the type species.

Diagnosis. — Suture with pointed flank lobe and small secondary ventral lobes; discoidal conch with a tendency to develop longitudinal (spiral) striation.

Remarks. — Suture of the type species is similar to that of the praeglyphioceratid *Lagowites nivae* (Sobolew, 1914) but the auricles of the conch aperture are a tornoceratid feature. The stratigraphic position suggests that the subventral lobation of the suture originated independently of that in advanced *Maeneceras* species.

Ostrovkites numismalis sp. n.
(Figs 152 and 159)

Holotype: Specimen IG 284.II.33 (Fig. 152C).

Type horizon and locality: Black clymeniid limestone of the *P. trachytera* Zone at Ostrówka, Holy Cross Mountains.

Derivation of name: From Latin *numisma* – coin, referring to small size and flat shape of the conch.

Material. — Eight specimens.

Diagnosis. — Minute conch with serial internal thickenings following the aperture on its whole extend, suture with an additional narrow ventral lobe developed on the slope of ventrolateral saddle.

Remarks. — There is a possibility that Sobolew's (1914) Oma-monomeroceras (*Cheiloceras*) *sinuvaricatum* from the Lower Łagów Beds represents the same lineage. The course of internal thickenings in the single known specimen (Sobolew 1914: pl. 7: 10) is similar to that in specimens from Ostrówka, although they

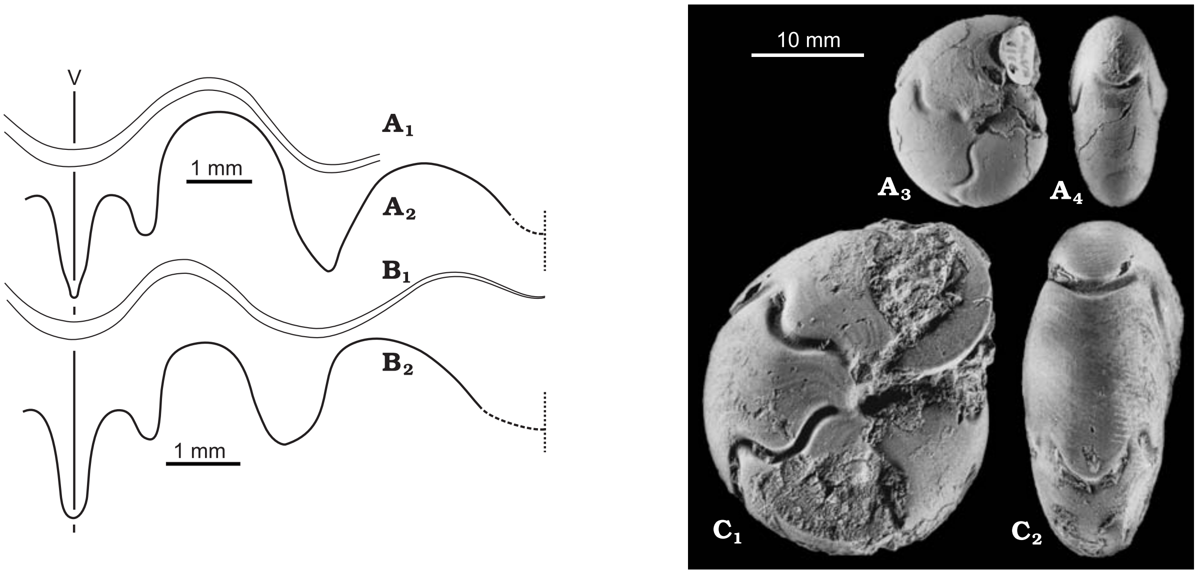

Fig. 152. *Lagowites*-like tornoceratid *Ostrovkites numismalis* sp. n. from the *P. trachytera* Zone at Ostrówka, Holy Cross Mountains; growth lines, suture, and views of specimen ZPAL AmVII/1116 (A, sample Ost-16), growth lines and suture of specimen ZPAL AmVII/016 (A, sample Ost-10), views of the holotype IG 284.II.33 (C).

are less sinuous. Unfortunately, the suture was poorly preserved in the Sobolew's specimen, which is probably lost.

Distribution. — The *P. trachytera* Zone at Ostrówka (samples Ost-10 and Ost-16).

Family **Posttornoceratidae** Bogoslovsky, 1962

Diagnosis. — Suture line with secondary umbonal lobe and a tendency to develop additional ventrolateral lobes (VLU_1:ID → V L^1LU_1UID); conch aperture with auricles; relatively high whorl expansion rate.

Remarks. — Early ontogenetic stages of *Discoclymenia* identified by Becker (1995, fig. 8c, d) show that the dorsolateral lobe in advanced forms is homologous to that in *Gundolficeras*, thus U_1 in Ruzhentcev's notation.

Genus ***Gundolficeras*** Schindewolf, 1936

Type species: *Lobotornoceras bicaniculatum* Petter, 1959 from the Famennian of Algeria.

Diagnosis. — Generalized tornoceratid conch with ventrolateral furrows at early developmental stages; suture with a deep, symmetrical flank lobe and a tendency to developed dorsolateral lobe.

Remarks. — House and Price (1985) questioned relationships between the Famennian tornoceratids with complex suture traditionally classified in *Lobotornoceras* Schindewolf, 1936 and the type species of the genus, *Goniatites ausavensis* Steininger, 1856 from the mid Frasnian Büdesheim Shale of the Eifel Mountains (House 1978). Following this suggestion, Becker (1993*b*) transferred the Famennian species with ventrolateral furrows at early ontogenetic stages to *Falcitornoceras*. They differ rather substantially from the type species of that genus in having rounded auricles and lacking the characteristic juvenile ornamentation. Later (Becker 1995) introduced the genus *Gundolficeras* for some members of this branch. It seems to be the first link in the tornoceratid lineage leading to more and more complex suture, terminating in the acutely discoidal *Discoclymenia*.

Gundolficeras korni (Becker, 1993)
(Figs 153A and 159)

Type horizon and locality: Early Famennian Nehden Shale at Nehden-Schurbusch, Rhenish Slate Mountains.

Material. — Five specimens.

Diagnosis. — Closed umbilicus with the flat adjoining wall of the conch giving it a conical appearance, rounded flank lobe of the suture of otherwise generalized tornoceratid type.

Remarks. — The suture, well visible in two juvenile specimens, fits well that of the type specimen. In the smallest one, indistinct ventrolateral furrows are represented. An adult incomplete specimen with body chamber, of estimated diameter about 55 mm, shows indistinct growth lines with typically tornoceratid rather rounded prominent auricles of the aperture. The conch geometry makes this species similar to *Protornoceras simplicius*, which has a rather simplified and variable suture. Becker (1993b) included it into *Falcitornoceras* although its juvenile conch ornamentation remains unknown. Because of the shape of umbilicus and a rather advanced tornoceratid suture I suggest that this is not *Falcitornoceras*, but is rather related to the *Polonoceras* branch at the stage preceding development of acute auricles.

Distribution. — Probably the *K. crepida* Zone at Jabłonna (wells w150a, b, c dug by Żakowa *et al.* 1984).

Gundolficeras bilobatum (Wedekind, 1908)
(Figs 153B–D and 159)

Type horizon and locality: Early Famennian at Enkeberg, Rhenish Slate Mountains.

Material. — Eight specimens.

Diagnosis. — Narrow ventrolateral saddle, shallow dorsolateral lobe, and very deep and narrow dorsal lobe of the suture; closed umbilicus.

Remarks. — Becker (1993b) included this species into *Falcitornoceras*, referring to furrows on pyritic internal moulds, although its juvenile conch ornamentation remains unknown. Such furrows, preserved also on a juvenile conch from Łagów, are typical of several earliest Famennian tornoceratids and may just be a primitive (plesiomorphic) feature. *Gundolficeras rotersi* Korn, 2002 from the *Platyclymenia annulata* Event

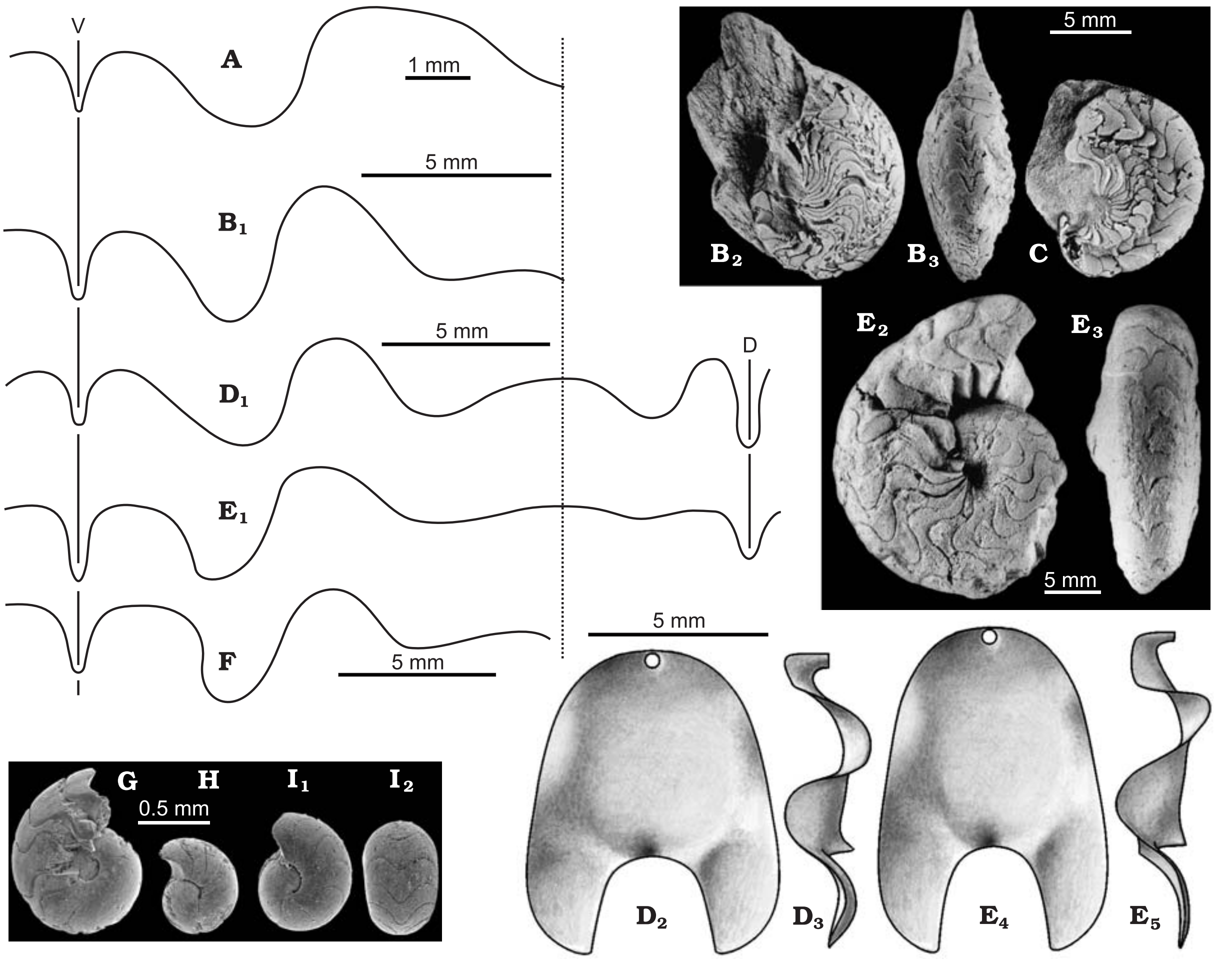

Fig. 153. *Lobotornoceras*-like tornoceratid *Gundolficeras* from the Holy Cross Mountains. **A**. *Gundolficeras korni* (Becker, 1993) from the early Famennian at Jabłonna (probably the *K. crepida* Zone); suture of specimen ZPAL AmVII/659 from well w150c dug by Żakowa *et al*. (1984). **B–D**. *Gundolficeras bilobatum* (Wedekind, 1908) from the mid *C. marginifera* Zone at Kowala (B, C) and probable *C. quadrantinodosa* Zone at Łagów-Dule (D); suture and views of specimen ZPAL AmVII/169 (B), view of specimen ZPAL AmVII/078 (C), suture and septum of specimen ZPAL AmVII/1864 (D, sample Ł-30). **E–I**. *Gundolficeras* sp. n. aff. *G. delepinei* Petter, 1959 from the late Famennian at Kowala (probably the *P. jugosus* Zone), suture and views of specimen IG 284.II.860 (E), suture of unnambered specimen from the same collection (F) and larval (or embryonic) conchs ZPAL AmVII/1833, 1834 (G, H, sample Ko-187, the *P. jugosus* Zone), and 1836 (I, sample Ko-174, the *L. styriacus* Zone) possibly representing the same lineage.

stratum at Kattensiepen in the Rhenish Slate Mountains does not differ from the Holy Cross Mountains material in conch form an suture. Growth lines are not preserved in my material and this precludes reliable comparison.

Distribution. — The mid *C. marginifera* Zone at Kowala; probably the *C. quadrantinodosa* Zone (samples Ł-29, 30, and 34) at Łagów-Dule; reworked at Sieklucki's brickpit in Kielce (Sobolew 1914).

Gundolficeras sp. n. aff. *G. delepinei* Petter, 1959
(Figs 153E–I and 159)

Material. — Two specimens.

Remarks. — Two specimen from the Czarnocki's collection are similar to *Gundolficeras* from the much older strata at the same locality but differ in having a rather wide ventrolateral saddle and shallow dorsal lobe. The first feature is even more apparent in *G. delepinei* from the late Famennian of Algeria (Petter 1959), which may represent the end member of the same lineage (see Becker 1995).

Distribution. — Probably the *P. jugosus* (or the late *L. styriacus*) Zone at Kowala.