Emergence and succession of Carboniferous conodont and ammonoid communities in the Polish part of the Variscan sea

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The end of the carbonate sedimentation of the Famennian *Wocklumeria* limestone in the Holy Cross Mts and Sudetes coincides with the disappearance of a high-diversity warm-water assemblage of ammonoids and conodonts with elaborated platform elements. In replacement, a low diversity ammonoid community of *Acutimitoceras prorsum* and a thin-crown conodont *Protognathodus* fauna migrated to the area. When carbonate sedimentation was re-established in the Tournaisian, the new high-diversity ammonoid and conodont faunas represented again almost the whole range of morphologies known from the Famennian. Migrations into the area from unknown sources dominated, with little contribution from the local phyletic evolution. This characteristic ammonoid-conodont community disappeared with the sea-level rise in the *Siphonodella crenulata* Zone, to emerge at the same time in the North American Midcontinent. The reverse direction of migrations marks the latest Tournaisian *Scaliognathus anchoralis* event. In yet another cycle of the late Viséan, the new high-diversity faunas were not able to develop as elaborate conch or platform element morphologies as before. In a review of the literature it is shown how the Variscan orogenic activity, progressing towards the Northeast, and glaciations in Gondwana influenced the distribution of late Carboniferous ammonoids in Poland. Conodont taxa *Weyerognathus* gen. n., *Neopolygnathus sudeticus* sp. n., and *Siphonodella belkai* sp. n. are proposed.

K e y   w o r d s :   conodonts, ammonoids, apparatuses, taxonomy, biostratigraphy, Famennian, Tournaisian, Devonian, Carboniferous, Hangenberg event.

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Introduction

The conodont chordates and cephalopod molluscs have the most complete fossil record among pelagic organisms of the Palaeozoic. They may thus serve as useful markers of changes that took place in pelagic ecosystems at systemic boundaries and during their fundamental remodellings by catastrophic environmental events. The Variscan orogenic belt abounds in good sections of the Devonian–Carboniferous transition strata. They have been extensively studied for cephalopods and conodonts in the western part of the area (Flajs & Feist 1988; Becker 1993; Korn 1993; Luppold *et al.* 1994), and in southern regions now incorporated in the Alpine orogen (Carnic Alps: Gedik 1971; Schönlaub 1969; Korn 1992). The area in between, bordered on the SW side by the Sudetes and on the NE by the Holy Cross Mountains, remains relatively poorly known. Palaeontological evidence of early Tournaisian conodonts (Szulczewski 1973) involves only mixed faunas derived from fissure fillings (limestone clasts of various ages in a lithologically similar matrix) and some preliminary determinations of Tournaisian conodonts collected in stratigraphic successions (Weyer 1965; Freyer & Żakowa 1967; Chorowska 1974; Chorowska & Radlicz 1984). In both Sudetes and Holy Cross Mountains there are good sections of Famennian and Tournaisian strata, the most complete being Dzikowiec and Kowala, respectively. This provides an opportunity to follow the evolution of pelagic faunas throughout the latest Famennian and early Tournaisian, when a basic rebuilding of the marine ecosystems took place in this and other areas of the world. The record of faunal events becomes more punctuated above the *Gattendorfia* limestone equivalents and fossiliferous outcrops of the Early Carboniferous strata are rather sparse, both in the Sudetes and the Holy Cross Mountains. The only easily accessible exposures of pelagic limestones with well preserved and abundant conodonts are those of the latest Tournaisian and late Viséan strata at Ostrówka (Todowa Grząba) in the Holy Cross Mountains (from both horizons ammonoids are also known) and late Viséan relatively shallow-water limestones at Czerna in the Kraków area. Samples from these localities have been used to identify the composition of the conodont faunas, referring not to a form-taxonomy but to more

biologically meaningful apparatus reconstructions. These faunas are more or less representative of the open-sea conodont faunas of the Viséan, as the published evidence based on other sources (e.g., Bełka 1985, 1995) points to a relative faunal stability over that time span in the area. There is an extensive literature coverage of the Viséan and Namurian conodont and cephalopod faunas, referring mostly to borehole materials from the whole area of Poland. All this will be used to present a provisional picture of the conodont and ammonoid faunal succession, up to their complete disappearance from the area.

A presentation of data on conodonts and ammonoids from the Kowala and Dzikowiec sections and their interpretation in evolutionary and migrational terms is the starting point of this paper. The Chinese section Muhua (Hou *et al.* 1985; Ji *et al.* 1989), sampled by myself, will serve as a reference standard as it is the most complete and fossiliferous. A brief presentation of the latest Tournaisian ammonoids and conodonts from Ostrówka will follow, and some comments and illustrations of conodont apparatuses from the late Viséan, as well as a literature review of ammonoids from the same strata. Literature data on the Namurian (and earliest Westphalian) ammonoids from southern Poland will complete the factual part of the paper.

Illustrated specimens are housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (abbreviated ZPAL), Museum of the Geological Institute of the University of Wrocław (UWR), Polish Geological Institute in Warsaw (IG), Institute of Geological Sciences of the Polish Academy of Sciences in Kraków (ZMS, collection of Dr. Stanisław Czarniecki), and the Museum of Natural History of the Alexander von Humboldt University in Berlin (UB).

Biostratigraphy of the early Tournaisian in Polish sections

Early Tournaisian conodonts are known in Poland from several localities but, as mentioned above, only two sections are complete enough to show the undisturbed original succession of faunas: Kowala in the Holy Cross Mountains and Dzikowiec in the Sudetes (Fig. 1). It seems necessary to start the discussion with a short presentation of the conodont succession there. This will be done from purely a palaeontological viewpoint, aspects of their geology being subject of studies by other authors (e.g., Chorowska & Radlicz 1984; Malec 1995). Both sections have been measured from the top, where the base of the overlying black shales and radiolarites provide an useful marker point.

Kowala. — A trench dug by Jan Malec (Polish Geological Institute in Kielce) in 1992 represents the most complete section of uncondensed Tournaisian rocks in Poland (Malec 1995 is a preliminary geological description of the section; also Olempska in press). About 32 meters of rock thickness have been exposed (Fig. 2), ranging from the black shale at the base of the *Wocklumeria* Stufe limestones to the black shales and radiolarites of not precisely determined Early Carboniferous age (presumably *Siphonodella crenulata* Zone of the Tournaisian; Malec 1995), which mark the top of the sampled section. The shales with horizons of calcareous nodules in the upper part of the section form a well-defined rock unit that has been identified as the Radlin beds by Malec (1995), the black radiolarites being attributed to the Zaręby Beds. It seems
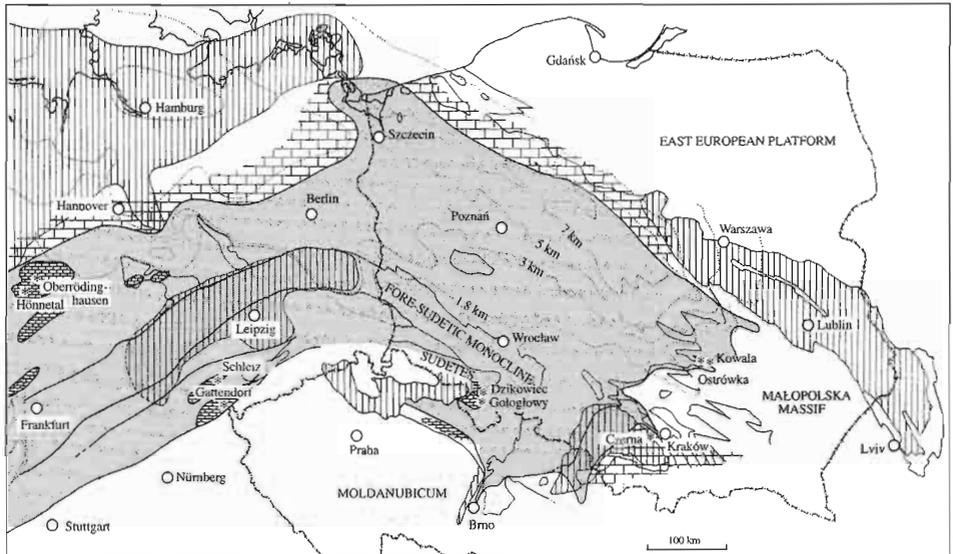
Fig. 1. Locations of the main sections discussed in the text shown on a non-palinspastic map of the central European Variscides (compare with Fig. 47; compiled after Kotas 1972; Zając 1984; Porzycki 1988; Ziegler 1990; Szulczewski *et al.* 1995; Belka *et al.* 1996, and other sources). Isopachytes of post-Variscan deposits are given to show the problems in delimiting the NE margin of the Variscan orogen, which is placed differently by different authors. Because of very limited information for the *Wocklumeria* and *Gattendorfia* limestones (fine brick pattern) sedimentation times, the map content refers to other time horizons, just to give a general impression of the geological evolution of the area. The extent of preserved marine Carboniferous deposits is shown by a continuous thin line; the boundary between relatively deeper water (grey) and the shelf sedimentation (usually carbonate: brick pattern) in the late Viséan represented by the thicker line; areas with thick Late Carboniferous continental deposits are vertically hatched.

unlikely, however, that they are in lithologic continuity with the Radlin beds and Zaręby Beds as identified by Szulczewski & Skompski (1995; see also Szulczewski 1978) in Ostrówka, where they are of latest Tournaisian and early Viséan ages, respectively. A lithological unit that seems to correspond to that in Kowala has been recognised and dated (but not named) in the borehole Bolechowice by Freyer & Żakowa (1967; see also Żakowa & Chlebowski 1984).

The carbonates and shales of the *Wocklumeria* Stufe, containing assemblages of conodonts and ammonoids typical for these strata, end in Kowala about 21.2 m below the radiolarites. The following series, 4.0 m thick (ranging to about 17.0 m below the radiolarites), is represented by clays at the base, tuffites in the middle and laminated marly limestones at the top. The clay immediately following the last limestone bed with *Wocklumeria* contains the same conodont assemblage as that below. Beginning from a tuffaceous shale, located about 20.0 m below the top of the section (1.0 m above the *Wocklumeria* limestone), *Neopolygnathus communis* (see Tables 2–3 and Fig. 5 for sample compositions and p. 78 for taxonomic nomenclature of this and other conodont species mentioned in this chapter), insignificant in strata below, starts to contribute to the assemblage. The tuffite bed 19.6 m below the top contains at its bedding surface numerous crushed specimens of ammonoids probably representing *Acutimitoceras prorsum*. This and following beds are devoid of conodonts. *Protognathodus*, associated elsewhere with these ammonoids, joins *N. communis* and dominates it in the limestone beds higher up, greenish at 17.8 m and reddish at 17.6 m below the top. It disappears immediately above, being replaced in the conodont assemblage by *Pinacognathus? praesulcatus*

(*'Siphonodella praesulcata'*). There seems to be a change (evolutionary?) from *Pseudopolygnathus* (*'Bispathodus'*) *costatus* morphologies to *P. primus* between 15.8 and 15.2 m of the section. In the same interval and slightly above, strongly asymmetric *Pinacognathus* **sp** elements become dominant, which possibly marks the transition from *P.? praesulcatus* to *P. sulcatus*, although data are insufficient to prove this. Between 14.4 and 13.2 m typical *P. sulcatus* occurs and in the interval from 12.8 to 11.4 m an **sp** element transitional to those of *Siphonodella duplicata* has been found (but see comments on taxonomy below). It co-occurs with the first *Weyerognathus inaequalis* population that immigrated to the area and does not show any gradation with presumably ancestral *Pseudopolygnathus primus*.

The typical *S. duplicata* is known up to the level of 9.8 m below the top and at 9.4 m it is replaced (by evolution?) by *S. carinthiaca*. A little below, at 9.8 m, *S. belkai* sp. n. appears; it is a species of *Siphonodella* that is very characteristic and surprisingly advanced morphologically for this horizon. This is the only species of the genus at 9.0 m. Some rare **sp** elements of *Siphonodella* with transversely arranged tuberculation at the anterodorsal area of the platform, thus resembling *S. carinthiaca* but without any widening of the denticle tips which is the diagnostic feature, and with additional ridges, have been encountered 8.8 m below the top of the section. At 8.0 m the tuberculation of this area in *Siphonodella* is irregular and the ridges merge with the posterior margin of the platform in its widest part. Perhaps this population belongs to *S. cooperi*. At 7.2 m it is replaced by another population, with ridges paralleling the platform margin and the tuberculation arranged in longitudinal rows, possibly a form of *S. sandbergi*. This marks a discontinuity in the Kowala succession of *Siphonodella*. It remains unclear whether it resulted from a stratigraphic condensation in a record of otherwise continuous evolutionary transition or from an immigration of an allopatric lineage. *S. sandbergi* seems to continue at least to 2.5 m below the top, where *Dinodus lobatus* (*Siphonodella lobata*) first appears.

In the next productive sample, 1.3 m below the top, the *S. cooperi* lineage seems to reinvade the area, being then represented by a more advanced chronospecies with a smooth central part of the platform. In the topmost conodont-bearing level 0.6 m below the radiolarites the smooth central part of the platform appears narrower and with irregular tubercles. At 2.6 m below the top of the section, *Weyerognathus triangulus* appears, without any evidence of direct evolutionary connection with the preceding and ancestral (as documented in the Chinese Muhua section) *W. inaequalis*. This is thus an immigration event. The lower Tournaisian part of the Kowala section terminates with a single bed of an unstratified rock (possibly a weathered tuffite) devoid of conodonts.

Dzikowiec. — A precise location of the sampled Tournaisian sections (Fig. 2) in the abandoned Dzikowiec (Ebersdorf) quarry are given by Mazur (1987). Tournaisian ammonoids were described for the first time from this locality (as Devonian) by Tietze (1871) and then by Frech (1902). Schindewolf (1920) attributed the topmost limestone unit exposed in the quarry to the *Gattendorfia* Stufe, and a description of the whole ammonoid fauna represented in museum collections was published by Weyer (1965). He also dissolved a few limestone pieces for conodonts, identifying species typical of the *Siphonodella duplicata* Zone. Conodonts from the unit have been later studied by Chorowska (1974) and photographs of several stratigraphically important species have been published (Chorowska & Radlicz 1984).

The bluish, weathering to yellow, slightly silicified limestone of the *Gattendorfia* Stufe is exposed in several sites along the wall of the abandoned quarry in Dzikowiec. This rock unit was named Wapnica beds by Żakowa (1963). The most complete exposure is located at the southern end of the quarry (Fig. 2), to the right and above the gallery (Mazur 1987: fig. 9). The black shales of the Gołogłowy unit of unknown thickness, perhaps more than one meter, overlie about 3 m of thick Tournaisian limestone, in contact with the underlying Famennian strata (Fig. 2, second column). It is described below in descending order as only the top parts of particular exposures within the quarry can be matched with some certainty, the base being apparently diachronous.
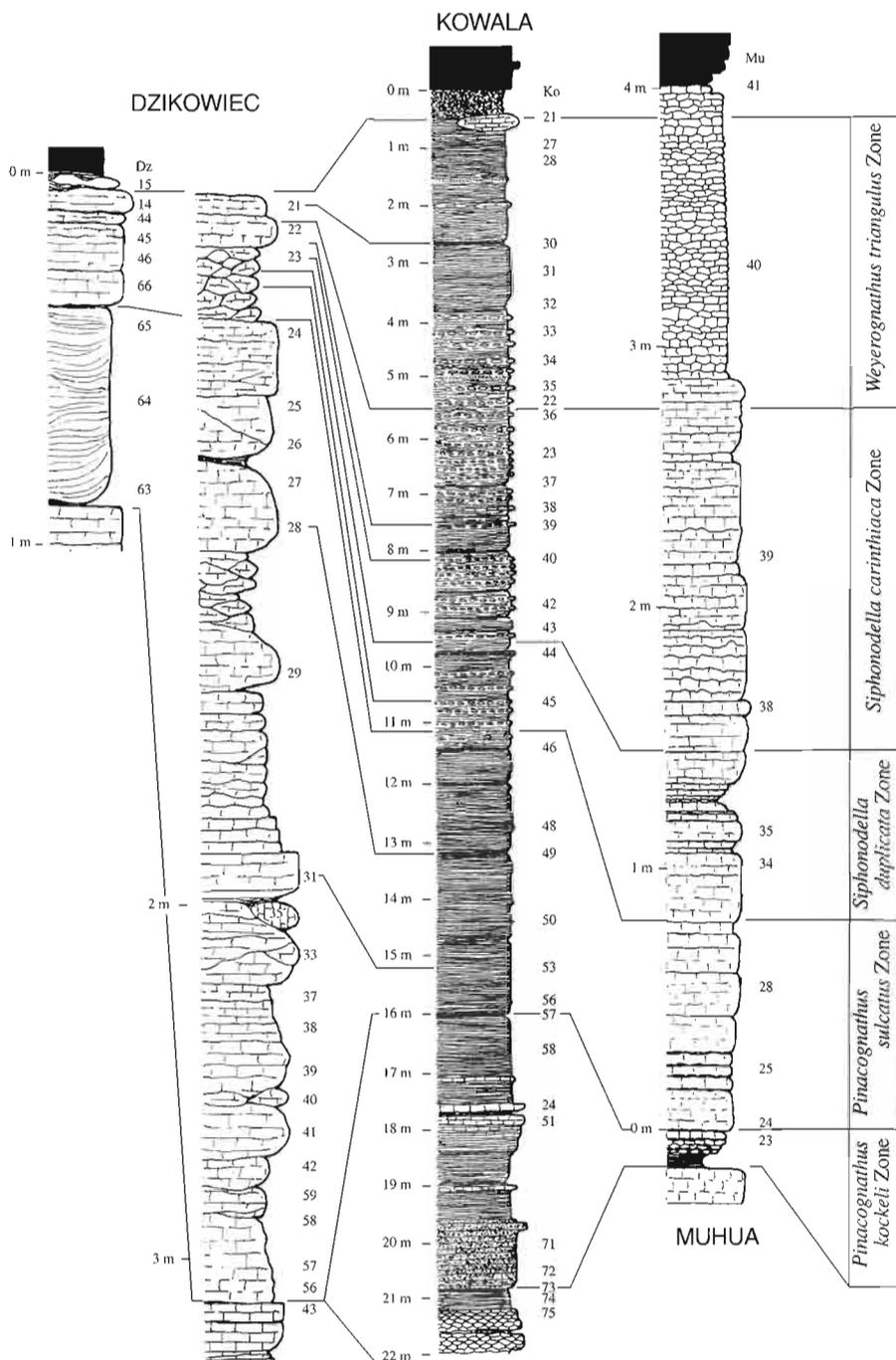
Fig. 2. Correlation of the Dzikowiec sections of the Wapnica beds from the northern and southern ends of the quarry with those of Kowala and Muhua and their proposed conodont zonation. Note different scales. Sample numbers to the right of each column. The top rock unit (shown in black) in Dzikowiec represents the Gołogłowy Formation, in Kowala an unnamed radiolarite, and in Muhua the Muhua Formation.

At the northern end of the quarry (Fig. 2, first column; see also Mazur 1987), there is only a few centimetres of the black shale intercalation separating the *Gattendorfia* limestone from the overlying gneissic sandstone of the Nowa Wieś Formation, dated as latest Tournaisian (Głuszak & Tomaś 1993). Close to the limestone, the shales become yellowish and a discontinuous 3–5 cm thick irregular limestone bed occurs within these shales. It contains (sample Dz-15; see Table 1) *Siphonodella* cf. *cooperi* and a *Weyerognathus* population that shows no close similarity to the preceding stratigraphically *W. triangulus* but, instead, seems transitional morphologically between much older *W. inaequalis* and the late Tournaisian *W. pinnatus*. No corresponding layer has been traced in the southern part of the quarry.

The bed immediately below, 6–7 cm thick, is recognisable both in the northernmost and southernmost ends of the quarry. Not so productive, samples Dz-14 and Dz-21 (see Table 1) taken there contain another *Siphonodella* species resembling in shape American specimens of *S. obsoleta*, with ridges gently approaching the platform margin and the narrow inner area of the platform in **sp** elements covered with rare irregular tubercles. The bed is rich in ammonoids, represented by an advanced new species of *Eocanites*, *Pseudarietites silesiacus* (Fig. 3), and *Gattendorfia*.

Further below in the section (samples Dz-22 from a 9 cm thick layer at S end and Dz-44 from a 3 cm thick layer at N end; also the loose block Dz-50, collected at the southern end, seems to come from the same bed) *Siphonodella* **sp** elements have their central parts usually smooth. Elements with such a morphology are classified as *S. isosticha* in North America (see Klapper 1971, 1973), but those from Dzikowiec are definitely older in age and hardly conspecific. Rare *Gattendorfia* specimens occur there.

Even lower (sample Dz-45 from 4 cm thick layer), along with a *Siphonodella* species similar to that above, the very characteristic *S. carinthiaca* occurs. It is abundant in the next bed below (sample Dz-46 and 23), being associated with *S. belkai*, known also from the Kowala section. This apparently advanced species is preceded in Dzikowiec by unsimilar *S. duplicata* (in sample Dz-66), ancestral rather to *S. carinthiaca*. This is the lowest horizon with abundant conodonts in the northern part of the quarry, below there is only a laminated limestone, deformed by slumps(?), with very rare *Protognathodus* specimens. The maximum thickness of the *Gattendorfia* limestone in the northern exposure is 0.9 m.

In contrast, the lower part of the southern Dzikowiec section shows a well documented succession of early *Pinacognathus*. A few horizons with numerous *Protognathodus* interfinger with those characterised by more diverse conodont assemblages. Throughout the lower part of the section, species of *Neopolygnathus*, mostly *N. subplanus*, are the dominant conodonts. The lower meter of the *Gattendorfia* limestone at this site contains reworked Devonian conodonts of a preservation not different from the associated indigenous fossils. Presumably this exotic fraction comes from extraclasts. One such extraclast containing exclusively Famennian conodonts has been collected at 2.0 m below the top (Fig. 2). The oldest sample with dominant Tournaisian conodonts is Dz-59; it contains only a few reworked specimens of *Tripodellus sigmoidalis*. Closer to the base of the formation, the Famennian conodonts become dominant – in the lowest sample Dz-56 contributing more than 96 per cent to the assemblage. Most of the rock there seems to be represented by Devonian material although generally high productivity of Devonian extraclasts may also give such relationships among conodonts. That the stratum already represents the Tournaisian is indicated by the presence of relatively advanced *Pseudopolygnathus primus* – in the Muhua section comparable forms occur beginning from sample Mu-24. The topmost part of the well-bedded *Kalloclymenia* limestone, immediately below, represented by sample Dz-43, contains only Famennian species.

Biostratigraphic correlation. — Similar morphologies in populations of early *Siphonodella* species allow correlation of the lower parts of Kowala and Dzikowiec sections (Fig. 2). Thus, sample Ko-53 seems to be coeval with Dz-31, Ko-48 with Dz-28, and Ko-45 with Dz-66. The occurrence of the highly characteristic species, *S. carinthiaca*, in samples Ko-43 and Dz-46, as well as even more characteristic *S. belkai* in samples Ko-44, 42 and Dz-46, 23 allows rather firm correlation of the corresponding levels.
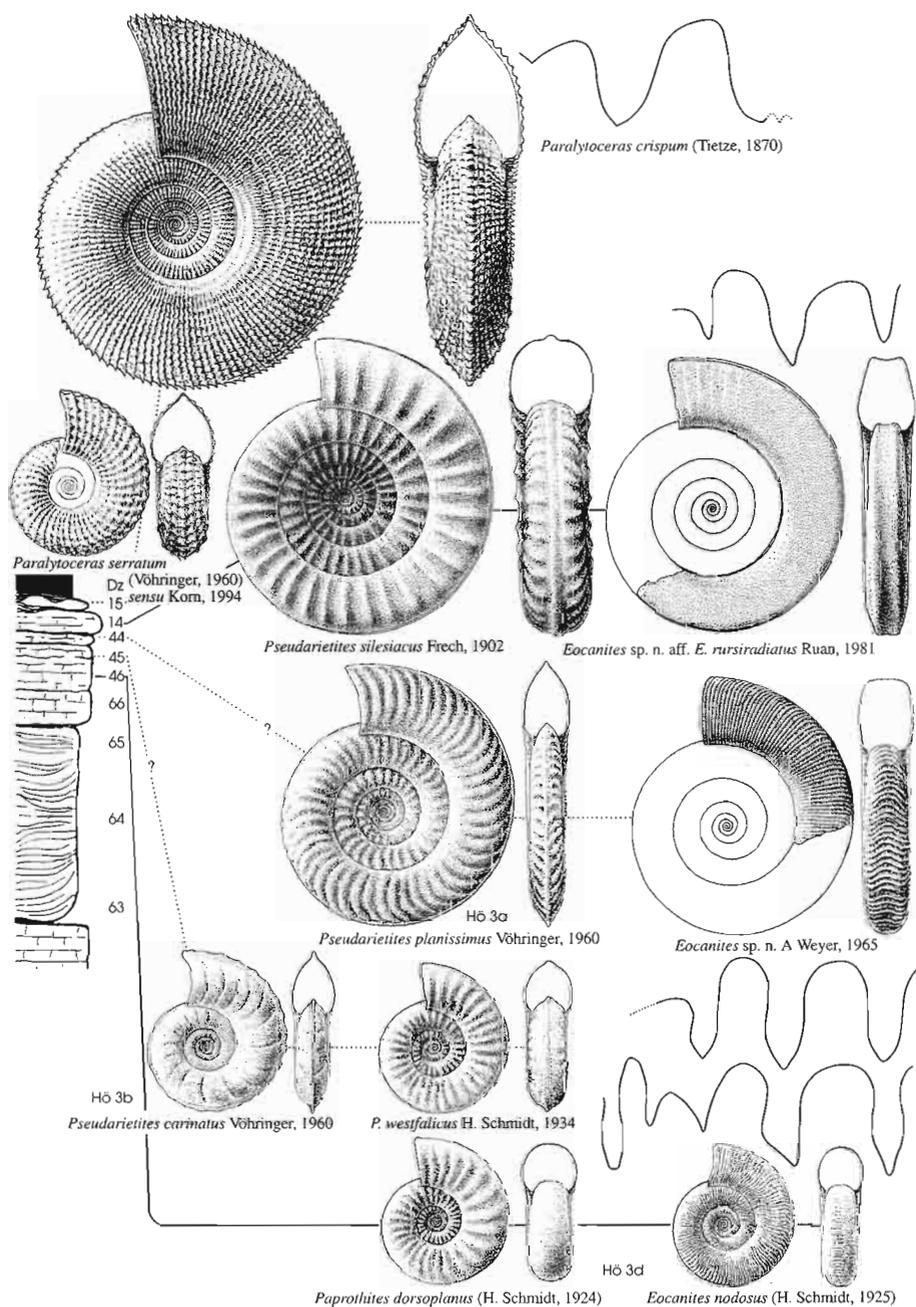
Fig. 3. Stratigraphic distribution of evolute ammonoids in the Wapnica beds at Dzikowiec quarry. Figures of species with well established position in the rock section are connected with appropriate beds by continuous lines; those described by Weyer (1965), with position inferred from their relationships in the Hönnetal section of Vöhringer (1960; bed numbers given), are connected with probable parent beds by pointed lines. Suture lines of *Eocanites* sp. n. A and *Paralytoceras crispum* redrawn from Weyer (1965).

The morphology of *Siphonodella* elements from sample Ko-21 is comparable to that in Dzikowiec sample Dz-14. *S. sandbergi* seems to be missing in Dzikowiec but a significant part of its occurrence in Kowala may correspond to a gap at Dzikowiec, where advanced species appear immediately above the sample Dz-23 containing *S. duplicata* and *S. carinthiaca*.

If this correlation scheme is correct (Fig. 2), only the topmost thin and irregular bed of the Dzikowiec section, already within shales, cannot be matched with the Kowala section on the basis of conodonts. Presumably, the black shales were already deposited at that time in the Kowala area.

Tournaisian assemblages with *Siphonodella* have been reported also from the Kraków area by Gromczakiewicz-Łomnicka (1979) but, unfortunately, without illustrations which might allow their evaluation. Bełka (1985) identified from borehole material apparently reworked specimens of morphologies occurring in the *Gattendorfia* limestone elsewhere. Matyja & Narkiewicz (1979) identified *Siphonodella obsoleta* and *Gnathodus punctatus* reworked in an assemblage of latest Viséan (possibly even earliest Namurian) age in the topmost sample of the marine Early Carboniferous in borehole WG-94 near Olkusz. The shallow-water record seems to have been preserved in some areas of the East European Platform (Matyja 1976; Avchimovitch & Turnau 1994), as well as in the central part of the Małopolska Massif (Zając 1984). Juvenile platform elements of *Siphonodella* from chert pebbles in the Tenczynek Conglomerate topping the Orzesze Beds (Westphalian B) have been determined as *S. isosticha* by Urbanek (in Paszkowski *et al.* 1995) which suggests *S. crenulata* Zone age for the basinal source sediments in the area between the Upper Silesian Massif and the Sudetes.

Paradoxically, although the Dzikowiec section does not have too much in common with that of Kowala, it can be easily correlated with the Carnic Alps successions (Schönlaub 1969). The *Siphonodella* population from the topmost bed of the limestone series at Krohnhof Graben (sample 438) seems to be identical with that from the topmost limestone layer in Dzikowiec (sample Dz-15). Similarly, *S. carinthiaca* and *Dinodus lobatus* appear in both sections together (sample 437, Dz-22 and Dz-45, respectively). Probably also the older parts of the Carnic Alps sections, not so precisely sampled, are similar to that of the Sudetes.

The classic Hönnetal section of Voges (1959) can be correlated with Dzikowiec only with some difficulties. *Weyerognathus triangulus* from the bed 10 and *W. inaequalis* from Ha 9 at Hönnetal, match with the Dz-46–Dz-45 pair of samples. The conodonts from the bed Ha 11 illustrated by Voges (1959) resemble those occurring in Kowala from the sample Ko-38 upwards. Perhaps the Hönnetal section is more complete than Dzikowiec in its upper part. First *S. duplicata* has been recorded in Hönnetal sample Ha 5 (Bed 4 of Vöhringer 1960, according to Ziegler 1988, who places the base of the *S. duplicata* Zone a little lower) which may thus correspond to Dz-66 and Ko-45.

Any comparison with the North American sections is rather problematic because of inconsistent conodont taxonomy. The lower part of the Hannibal Shale of Missouri contains *S. sulcata* in association with *Protognathodus*, while in the middle part of the same formation the first appearance of *S. duplicata* is reported (Canis 1968), it thus corresponds to the nominative *Siphonodella* zones in central Europe. Correlation of younger units is more difficult, but there is no reason to object to the generally accepted
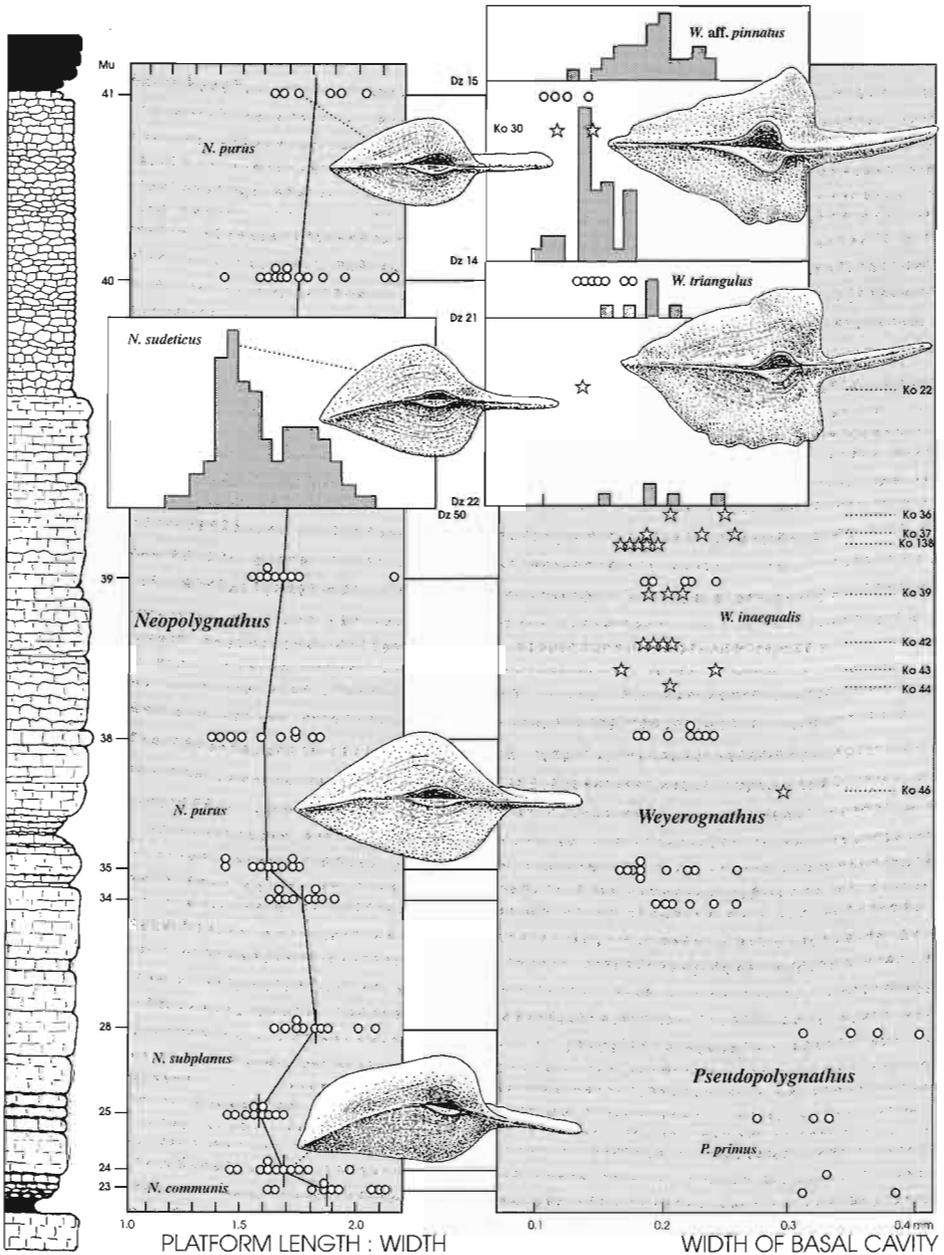
Fig. 4. Evolutionary changes in morphology of **sp** elements in the stratigraphically most important early Tournaisian conodont species from Dzikowiec, Kowala, and Muhua. Histograms showing frequency distribution in classes of platform elongation (measured as ratio of its length to width) in *Neopolygnathus sudeticus* sp. n. from sample Dz-50 (left) and width of the basal cavity in *Weyerognathus* species from samples Dz-22 to Dz-15 (right) are here superimposed on scattergrams of the same characters for the Muhua section. Data on *Weyerognathus* from Kowala samples (asteriscs) are fitted in the right diagram, the resulting correlation being shown in Fig. 5.

assumption that the main transgressive event in the Early Carboniferous of North America is coeval with the transition from the Hangenberg Limestone to the Alum Shales in Europe.

Conodont zonation of the Tournaisian

Although it is commonly assumed that any conodont zone is a time unit referring to some evolutionary originations of species, I prefer to make a distinction between a local-range biostratigraphic correlation based on environmentally controlled distribution of species and long-range time correlation based on documented evolutionary transitions. Therefore some comments are necessary explaining the methodological basis for the units used in this paper (Figs 2, 5). There are problems in the application of the currently used conodont zonation of the Tournaisian to the sections studied. Both the Tournaisian (Sandberg *et al.* 1978) and Viséan (Lane *et al.* 1980) zonal schemes are based on conodont species that are defined vertically (typologically). Moreover, the American type specimens of the early Tournaisian zonal species were almost invariably collected from reworked sediments. The problem thus arises whether morphologic similarity of specimens is enough to identify species. In fact, such specimens in America and Europe may belong to different populations and thus represent completely different biological units. As explained below (p. 70) in taxonomic work, results of which are presented here, I strictly followed a populational approach to species identifications, which may have resulted in some inconsistencies with the definitions used in the current zonation of the Tournaisian.

To avoid misunderstanding, instead of attempting to fit the earlier proposed zonal schemes to the sequence observed in the Polish part of the Variscan belt, I will use provisional time units based on phyletic evolutionary transitions (each referring to a correlative datum), at least in intention based on the populational approach to species. In some respects it is a return to the zonation once proposed by Voges (1959). There seems to be a consensus regarding validity of the phyletic transitions of the most important conodont lineages and they seem relatively well documented. Several such transitions seem to be observable in the most complete Muhua section, representing a rather stable environment of sedimentation (see Ji *et al.* 1989). My sampling of this section in 1995 has supplemented the results of Chinese students and the material has been used to test apparatus reconstructions and evolutionary transitions proposed on the basis of Polish sections (Fig. 4).

A datum can be used to define a chronologically understood zone. It defines the beginning of its nominative zone (in the meaning used throughout the text), the end of it being delimited by the next datum. Obviously, in virtually all rock sections only a fraction of the complete time range of such defined chronozones, which are theoretical concepts, can be found.

(1) *Protognathodus kockeli* Datum. Corresponds to the development of base tuberculation in **sp** elements of the *Protognathodus* lineage. The process seems to be traceable in Kowala but one has to keep in mind that the *Protognathodus* apparatus is extremely generalised and, in fact, difficult to separate from other morphologically simple conodont genera.
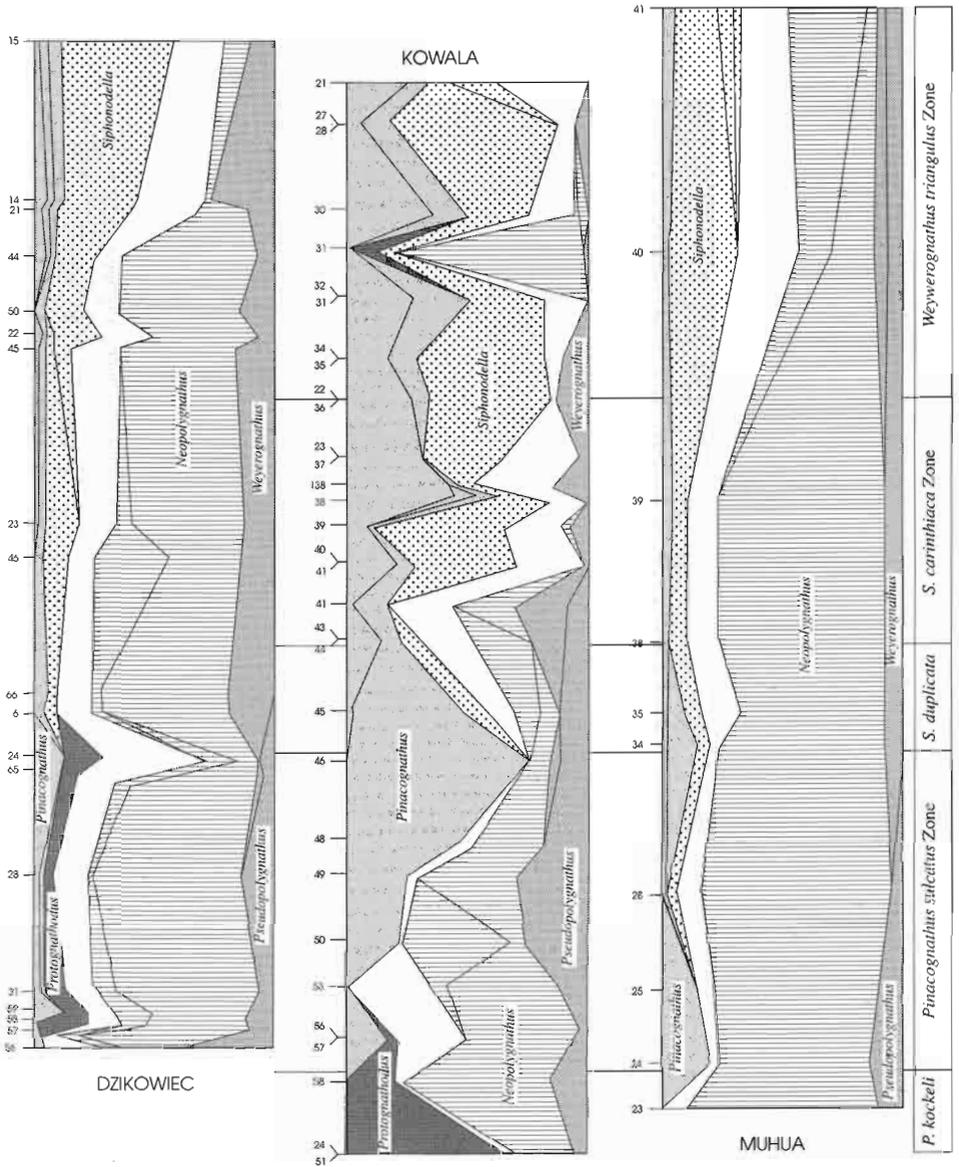
Fig. 5. Logs of per cent contribution of the most important conodont genera to samples in sections at Dzikowiec, Kowala, and Muhua (position of samples standardised in respect to that in Kowala, according to the correlation in Fig. 4). Note that, taking into account differences in spacing of samples, the sections differ basically not only in relative contribution of particular genera, but also in general patterns of faunal dynamics, the Muhua section being the most uniform and stable in this respect, and the Kowala succession being disturbed by at least two events.

(2) *Pinacognathus sulcatus* Datum. Marked by the development of a strong asymmetry and spatulate platform shape in **sp** elements and robust appearance of the inner process in **oz** elements of the *Pinacognathus* lineage (*P. praesulcatus* → *P. sulcatus*

transition). Although allegedly documented in the La Serre section (Flajs & Feist 1988) on the basis of **sp** elements, the evidence provided there, with application of vertical species concept and statistically insignificant numbers of elements taken from re-worked assemblages, is hardly convincing. A precise dating of the transition in a continuous sequence remains to be done.

(3) *Siphonodella duplicata* Datum. Corresponds to the development of ridges parallel to the carina in **sp** elements of the *P. sulcatus → S. duplicata* lineage. This datum is even more problematic than the previous one as there seems to be a rather basic difference in the apparatus structure between these genera. *S. duplicata*, as understood currently, is probably a heterogeneous taxon (in the Muhua section mor-phologically indistinguishable **sp** elements of this kind appear twice, being associated with very different ramiform elements of their apparatuses). The exact dating of the transition also remains to be documented.

(4) *Siphonodella carinthiaca* Datum. Corresponds to the widening of the main row of denticles in adult **sp** elements in the *Siphonodella* lineage. Transitional populations are known from the Dzikowiec and Muhua sections. Generally, the *Siphonodella* successions in studied sections are mostly controlled by migrations and replacements of one species by another. At least five independent lineages are involved in this patchwork. Until apparatuses are better known, enabling unequivocal determinations of the species, it is not recommended to use *Siphonodella* in time correlation.

(5) *Weyerognathus triangulus* Datum. Marked by the reduction in size of the basal cavity and widening of the adult platform in *Weyerognathus ('Pseudopolygnathus') inaequalis → W. triangulus* lineage. Well documented in the Muhua section (Fig. 4).

(6) *Gnathodus punctatus* Datum. Corresponds to the development of radial tuber-culated ridges in adult **sp** elements of the *Protognathodus delicatus → G. punctatus* lineage. The evolution of *Gnathodus* does not seem to be especially useful in zonal definitions because of the wide population variability of early species of the genus, but in most sections *Gnathodus* seems to be the only lineage that shows any recognisable time changes at all. The transition seems to be recorded in the American sections, but it remains unclear whether there is a continuity within a single lineage or a succession of species partially overlapping in time.

(7) *Scaliognathus anchoralis* Datum. Corresponds to the development of a sub-equal length of all the three processes in **sp** elements of the *Scaliognathus dockali → S. praeanchoralis → S. anchoralis* lineage. The transition is relatively well known owing to American material described by Lane & Ziegler (1983; see also Belka & Groessens 1986) but, as in *Gnathodus*, it remains unclear whether all these three forms represent partially sympatric species or just morphotypes.

In the Viséan, perhaps the *Mestognathus* lineage evolution documented by Bełka (1983) and Bitter *et al.* (1986) and that of the robust *Lochriea* species (Nemirovskaya *et al.* 1994), may provide appropriate sets of events of some correlative value (Belka 1990 proposed some other events to be of use in correlation). The succession of *Mestognathus* species, as presented by Bitter *et al.* (1986), shows quite a continuous and gradual development and expansion of the parapet, suggestive that the lineage is monospecific in any time horizon with only one inconsistency in the pattern of distribution. This is the age of *M. groessensi* Bełka, 1983, which has been dated as being older than the ancestral species of the lineage, *M. harmalai* Bitter *et al.*, 1986.

M. groessensi occurs in an oolitic limestone immediately above the Famennian–Tournaisian discontinuity in the borehole WB-64 near Olkusz, together with some *Siphonodella* and *Gnathodus* species (Bełka 1985). The specimens of *Siphonodella* illustrated by Bełka (1985) do not differ from those occurring together with *Scaliognathus anchoralis* in the marls covering a similar discontinuity in Ostrówka. I suggest that in both cases they are reworked and that *M. groessensi* does not differ much in age from *M. praebeckmanni* Bitter *et al.*, 1986, of which it is a senior synonym.

Beginning from the latest early Viséan, the ammonoids become much more sensitive and reliable guide fossils (see Korn 1995) than the conodonts. It would be desirable to identify and define evolutionary events within the goniatitid and girtyoceratid lineages to supplement the conodont scheme.

Below, after some introductory comments on taxonomic methodology, provisional apparatus identifications of conodont species and comments on identifications of ammonoid species from Dzikowiec and Kowala are presented.

Taxonomic methodology

Population *versus* typologic species concept. — All the conodont species discussed below have been identified and defined populationally which in many cases has resulted in a rather apparent disagreement with the 'vertical' taxonomy of some conodont species. To be consistent, in this biological approach I also use descriptors to element sides based on their orientation in the apparatus, following Dzik (1991b) and Dzik *et al.* (1994). The conventional anterior end becomes thus the ventral one.

Character displacement *versus* transition zone. — It is a common feature among conodonts that, whenever a new branch develops, at the beginning of its evolution the population variability is so wide that it may cover the ranges of a few related species (when they occur sympatrically). This results in a lot of taxonomic and nomenclatorial problems which are usually attempted to be solved by applying the vertical definition of species, that is, to extend backward the ranges of variability typical for later members of an evolutionary branch. Among the Early Carboniferous conodonts this is well exemplified by the evolution of the Tournaisian *Gnathodus* lineage (Lane *et al.* 1980). As a result several sympatric species have been distinguished even if there is a complete morphologic gradation between them within samples. This feature is commonly referred to as a transition zone.

Identification of several species within the same sample requires a multimodal distribution of a diagnostic character. To do it in unimodal samples is hardly acceptable from a methodological point of view because this unavoidably leads to a destruction of any objective basis for taxonomy in palaeontology. If allowed in transition zones, why should subjective rules not be applied to any palaeontological sample? Such an approach is not unavoidable, as the difference between the transition zone and normal patterns of variability seems to result from a character displacement – an effect of competition between related sympatric species when they meet in the same environment after experiencing a period of allopatric evolution long enough to prevent interbreeding. Probably generally in the evolution of conodonts the width of niches occupied by particular species decreased, resulting in narrower and narrower ranges of population variability, even if similar number of sympatric species co-occurred. This is why differences in the apparatus organisation among, e.g., Middle Ordovician conodonts were much more apparent (even if the number of co-occurring species may range up to twenty) than among Late Carboniferous conodonts (with up to six sympatric species: see Boogaard & Bless 1985). Samples with few co-occurring closely related species are thus more variable populationally.

In the present paper, this biological interpretation of transition zones is preferred, which means that species identification is done in each sample separately, without applying any *a priori* standards for the range of population variability.

Taxonomy of the early Tournaisian conodonts

The species discussed below are arranged in order of their familial affiliation. The review will start with the prioniodinids, then the polygnathids with more and more complex apparatus structure will follow. Precise suprageneric affiliation of these forms requires additional confirmation of the proposed apparatus reconstruction which, with the limited material available to me, can be treated only as provisional. New and emended taxa are diagnosed at the end of the paper.

Prioniodina cf. *subrecta* **Huddle, 1934**. — Prioniodinid elements occur in all Dzikowiec samples but never in numbers large enough to enable apparatus restoration. They all show rather generalised morphology of the symmetry transition series but there are at least two morphologically rather distinct **ne** element types. The more advanced one, known from sample Dz-15, shows a rather short dorsal process with fan-like arrangement of wide denticles (Fig. 6F), which makes it somewhat similar to the homologous elements of *Pinacognathus*, although it remains largely albid. Attribution of this element type to the *Prioniodina* apparatus must remain tentative. An alternative attribution to associated *Cudotaxis* cannot be excluded. The second element type, more common in the section, is a generalised prioniodinid **ne** element.

In Kowala the prioniodinids occur throughout the section but in small number and poor preservation, precluding species indentification in most samples. The only sample large enough to enable this is Ko-138, taken from a loose block but almost certainly coming from about 3.3 m below the top of the section. The **sp** elements are there rather robust, the **ne** elements, having straight cusp and elongated base, are of a slightly *Lochriea*-like appearance. The processes of **hi** elements are strongly arched.

As the material is not sufficient to be sure of the apparatus reconstructions it is even more difficult to attribute names to it. Most probably the second of the species is a generalised member of the genus, probably conspecific with that occurring in the Stockum Limestone of the Rhenish area. The elements illustrated by Luppold *et al.* (1994: pl. 4: 2–3, 5–6, 9) under names *Spathognathodus* sp., *Plectospathodus* sp., *Prioniodina* sp., and *Lonchodina* sp. apparently represent a conspecific population. One of the available names is *Prioniodina subrecta* Huddle, 1934 with the type population in the late part of the New Albany Shale of Indiana (Huddle 1934).

Arisemotaxis? **sp.** — Another prioniodinid occurs less frequently both in Dzikowiec and in Kowala (Fig. 6I–Q); it differs from *P*. cf. *subrecta* in a more massive appearance of **sp** elements and short, strongly curved external processes in the symmetry transition series elements (Fig. 6G). Its **ne** elements are characteristic, in some cases being difficult to be separated from co-occurring *Falcodus*. Possibly, the species may belong to the same branch, related to the prioniodinids, from which several late Tournaisian and Viséan conodonts with this characteristic shape of the **ne** elements emerged, as included in restorations of their apparatuses by Chauff (1981). Otherwise its apparatus, the restoration of which is based on the Kowala material, seems to be closely similar to that of *Prioniodina* (see Fig. 21). The suggested generic affiliation is tentative, at best.

Falcodus **sp.** — Very characteristic elements of the symmetry transition series of this species, with strongly recurved ventral branches and short dorsal ones can be traced in virtually all Dzikowiec samples (Fig. 7E–J). There are some difficulties in matching them with other elements, but at least in the case of **oz** elements this can be done on the basis of some morphologic similarities. Quite numerous and very variable **oz** elements with strongly recurved ventral branches (Fig. 7B–D) are invariably associated with those of the symmetry transition series. Some **ne** element with wide

processes and long denticles may belong to the species. The crucial point is, however, the identity of the **sp** element. No platform element type can be correlated with this set of ramiforms on the basis of its distribution in the section. Among associated 'spathognathoduses' the only one that shows distribution along the sections and morphology consistent with that of the discussed ramiforms, is that with a gently arched blade.

The restored apparatus organisation resembles *Cudotaxis priceslingi* Chauff, 1981 from the late Tournaisian and earliest Viséan (Chauff 1981). In the Muhua section, above the range of occurrence of this species, another related form occurs that bears some similarity to later species of *Synprioniodina*. Perhaps all these genera belong to a single evolutionary branch.

***Protognathodus kockeli* (Bischoff, 1957).** — The platform elements of the *Protognathodus* apparatus change their ornamentation significantly during histogeny by adding some additional tubercles and making the base more and more robust. Practically all morphologies reported in literature under different species names within this genus can be identified in the Dzikowiec collection of *Protognathodus* (Fig. 8). I do not see any discontinuity in the morphologic variability within particular populations that would allow distinction of more than one species of the genus. There is also no apparent evolutionary change in platform morphology although the species continues for a significant time span in the area and those from the upper part of the Dzikowiec section (Fig. 8A–C) can be classified in *Gnathodus delicatus* Branson & Mehl, 1938.

The apparatus of *Protognathodus* (Fig. 22) is of a rather generalised polygnathid morphology. Only the relatively loosely distributed denticles and elongated processes of the **oz** element may allow its discrimination from similar apparatuses. Because of generalised morphology affinities of the species are difficult to trace.

As there seems to be no need to distinguish more than one species in the assemblage of *Protognathodus* from Dzikowiec and apparently also other European localities I attribute it to the name of the type species. Its type population comes from the *Gattendorfia* Limestone at Wocklum in the Rhenish Massif (Bischoff 1957) although it remains unclear from which bed. In the type section both the *Protognathodus* fauna and typical assemblages of the *Gattendorfia* Stufe are represented. Luppold *et al.* (1994: pl. 4: 1, 4, 7, 8) illustrated an almost complete set of ramiform elements of the *Protognathodus* apparatus from a low-diversity sample of the Stockum Limestone under conventional form taxonomic names.

It is remarkable that the most primitive species of the genus *Gnathodus*, *G. punctatus* (Cooper, 1939) does not show the characteristic feature for later species (and all the idiognathodontids) of its **hi** elements: the strong external curvature of the ventral process (see Chauff 1984). In this respect the **hi** element of *G. punctatus* resembles rather *Protognathodus kockeli*. *G. delicatus* Branson & Mehl, 1938, which in North America occurs in the upper portion of the range of *Siphonodella* (Thompson & Fellows 1970), being thus coeval with latest *Protognathodus* populations in Europe, differs from *P. kockeli* only in a more asymmetric distribution of tubercles on the conical part (cup) of the **sp** elements. Its apparatus remains unknown but one may suppose that this is a little more advanced member of the same *Protognathodus* lineage.

***Mehlina* sp.** — The species is represented only by uncommon **sp** elements that are not numerous enough to enable apparatus reconstruction (Fig. 8P). They are hardly distinguishable from their Devonian relatives so there seems to be no reason to expect any significant difference in the apparatus. Because of a high population variability it remains uncertain in many cases whether

Fig. 6. Tournaisian prioniodinids from Dzikowiec in the Sudetes (**A–H, R**) and Kowala (**I–Q**) in the Holy Cross Mts. **A–F**. *Prioniodina subrecta* Huddle, 1934 from sample Dz-15 of Dzikowiec; all × 66 except for **A**, which is × 80; elements **sp** (**A** juvenile, **B**), **oz** (**C**), **pl** (**E**), **ne** (**F**), and **tr** (**D** in medial and lateral views). Specimens ZPAL C XVI/90, 84–86, 88, and 479, respectively. **G–R**. *Arisemotaxis*? sp.: from sample Dz-15 (**G, H**) and Dz 14 (**R**) of Dzikowiec and Ko-21 of Kowala (**I–Q**); elements **oz** (**I**, × 100; probably **J**, × 100), **tr** (**K**, × 82), **hi** (**H**, × 112; **L, M**, both × 100), **pl** (**N**, × 100), and **ne** (**O, P**, × 100; **Q** juvenile, × 133; **R** juvenile, × 66; some may belong to *Falcodus*); specimens ZPAL C XVI/89, 184, 263–264, 266–267, 272, 265, 270–271, 269, and 380, respectively.
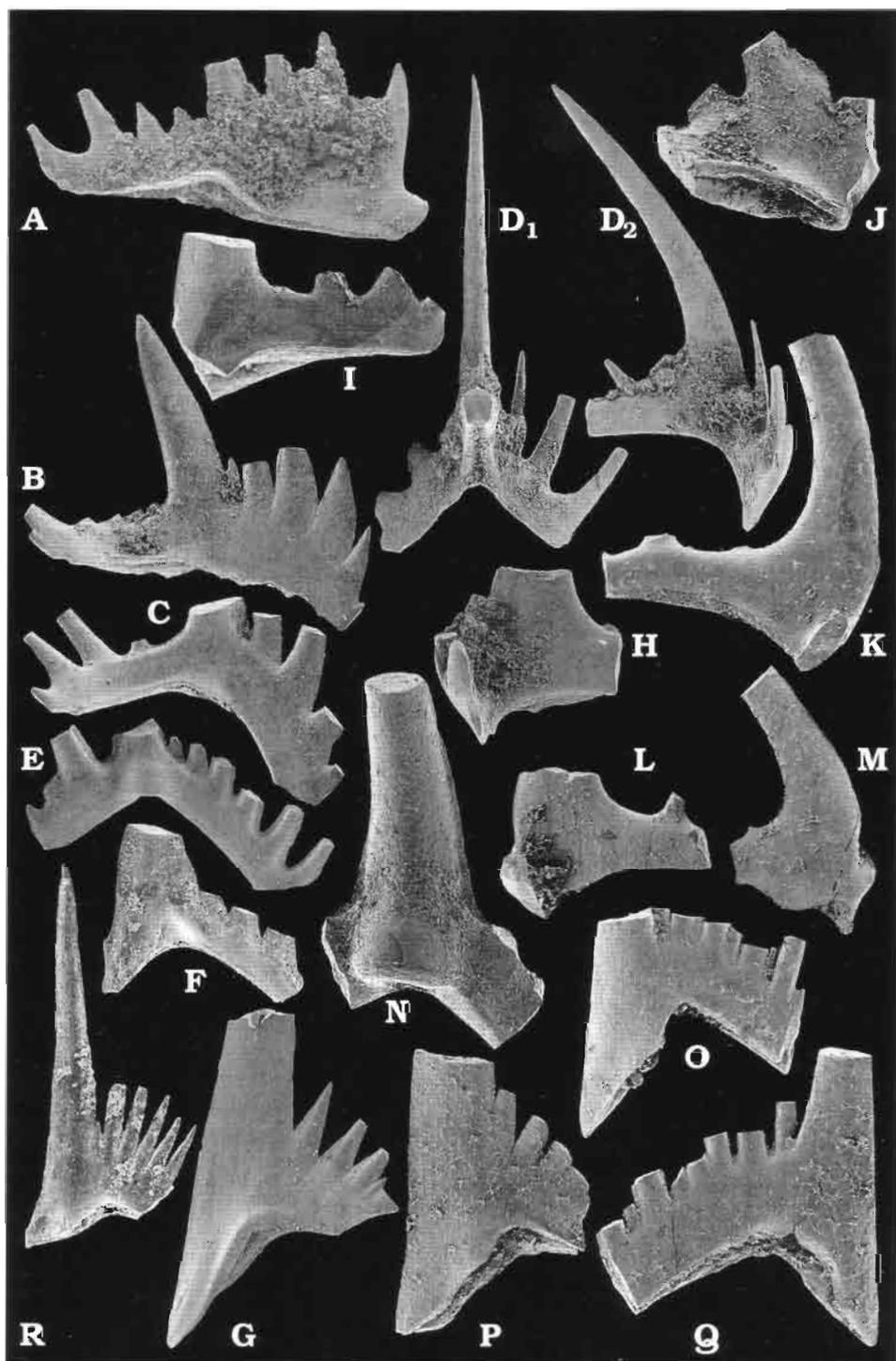
a separate species of *Mehlina* is represented in the Polish sections or just that extreme morphotypes of other simple polygnathids mimic it.

'Pandorinellina'laterigranosa (Gedik, 1969). — The **sp** elements of this species show extremely elongated processes with an incipient platform continuing along at least the dorsal process (Fig. 8K). The true platform never develops, instead, in an adult specimen (there is only one identified, in sample Dz-46) two strong denticles develop on both sides of the cusp. In younger samples from Dzikowiec, juveniles hardly distinguishable from those of sample Dz-46 frequently occur but they do not reach the size at which lateral denticles develop. Whether they are conspecific or just represent the generalised *'Bispathodus' stabilis* stock is hard to decide. I am not able to trace the ancestry of this species.

The associated **oz**, symmetry transition series, and **ne** elements, well identifiable also in the Muhua samples, are of a very generalised polygnathid type (Fig. 21). Morphologic distinctions between **oz** elements of *Weyerognathus, Pseudopolygnathus, Mehlina,* and *Falcodus* are difficult to specify and it seems that their population variabilities overlap. Those elements with strongly arched contours and relatively short external process most probably represent *Falcodus*, as their frequencies correlate with other elements attributed here to this genus. The elements **oz** with basal margins of processes merging angularly can be attributed to *Weyerognathus.* Those with an almost straight profile of the base may represent *Pseudopolygnathus.* The most difficult to separate are elements of *Mehlina* and *Pandorinellina* which are the most generalised and this can be safely done only in samples with a large number of elements of these genera.

The type population of *Spathognathodus (Pandorinellina) laterigranosus* Gedik, 1969 is from sample 3623 of Plöckenpaß in the Carnic Alps, the holotype being an adult specimen with well developed lateral denticles on the basal cup. There are also juveniles without this feature in the same sample.

Pseudopolygnathus primus Branson & Mehl, 1934. — The **sp** elements of this species are characterised by an occlusal area ornamentation of the icrion type (Fig. 9), with lateral denticles of the same height as those of the main row of the blade and connected with them by transverse ribs. In Kowala the oldest sample with elements of this type, having denticulation on both sides of the blade at adult stages, is Ko-53 collected 15.2 m below the top of the section. Juvenile specimens are present of *P. ('Bispathodus') costatus* morphology, and adults are still narrow, with a long smooth furrow separating the posterior row of denticles (there is rather a platform than icrion at this side of the element). The sample Ko-56, 0.6 m below, contains only elements with the icrion developing on one side of the blade even in large specimens. In samples taken higher above, the **sp** elements are more robust at comparable histogenetic stages and more triangular in appearance. This may reflect some evolutionary change but the great population variability and relatively small sample sizes do not allow one to document it biometrically.

The populations of the species strongly differ in **sp** elements morphology from those of the lineage of *W. inaequalis* which co-occur with them beginning from the horizon of sample Dz-66. No intermediate between them has been identified despite a high population variability. The younger populations of *Pseudopolygnathus* show much lower population variability and have generally a more primitive appearance. This may result from a species distinctness or from character displacement, an influence of the related *Weyerognathus* lineage.

This is the type species of *Pseudopolygnathus* and its type population comes from the Bushberg sandstone at Brickeys, Missouri (Branson & Mehl 1934: pl. 24: 24, 25), probably significantly younger than the Dzikowiec populations.

Fig. 7. *Falcodus* from the Tournaisian Wapnica beds of Dzikowiec. **A–K**. *Falcodus* sp. from samples Dz-15 (**A, D, E, G–J, K**), Dz-50 (**B, F, L**); elements **sp** (**A**, × 80), **oz** (**B–D**, × 66), **tr** (**E**, × 100), **lo** (**F, G**, × 80; **H**, × 66), **pl** (**I**, × 66; **J**, × 80), and **ne** (**K**, × 66), **hi** (**L**, × 66); specimens ZPAL C XVI/211, 105, 379, 190–191, 106, 197, 194, 196, 193, 459, and 114, respectively. **M–Q**. Possible *Siphonodella* or Gen. et sp. indet. from sample Dz-15 (**M**), Dz-14 (**N, O, Q**), and Dz-31 (**P**); all × 66; elements **hi** (**M, N**), **ne** (**O, P**), and **tr** (**Q**); specimens ZPAL C475, 384, 365, 385, and 386, respectively.
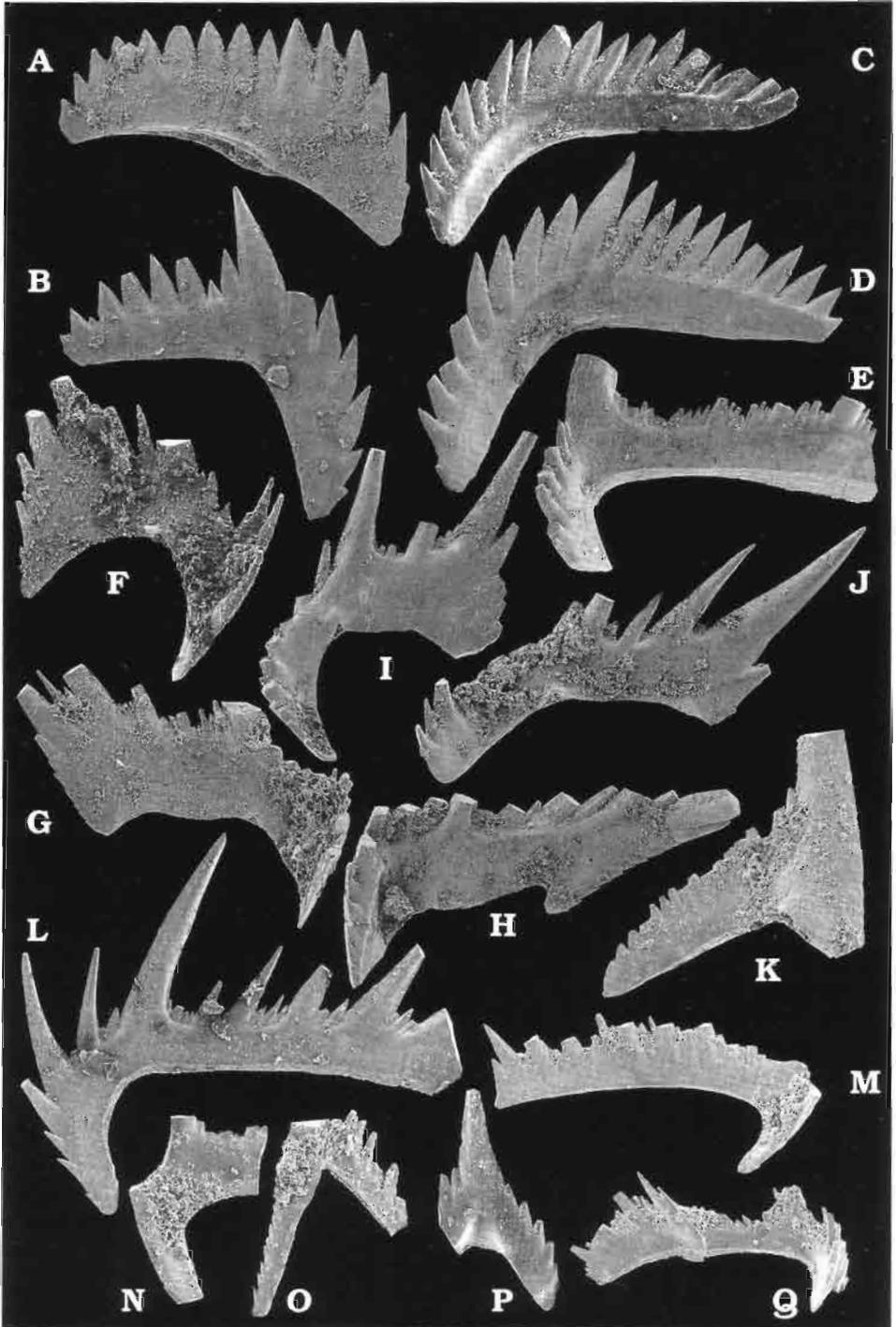
Weyerognathus inaequalis **(Voges, 1959)**. — The elements **sp** are here generally robust but highly variable, some having prominent high ribs at the occlusal surface that look almost like denticles, others have a relatively thin platform ornamented with rather low sharp ribs (Fig. 10). Juvenile specimens develop a platform much above the base but still below the main row of denticles, which makes this population distinct from the co-occurring *P. primus* which still preserves an ancestral icrion-type arrangement of denticles, with only an incipient platform. As commented above, the **sp** elements in populations of *P. primus* co-occurring sympatrically with *W. inaequalis* show a low population variability, with their occlusal surface invariably developed as an icrion. By contrast, the population variability of *P. primus* preceding stratigraphically the first *Weyerognathus* in the Muhua and Dzikowiec sections is so wide that both the icrion and platform morphologies can be recognised among specimens of various histogenetic age. Thus either an allopatric speciation event alone was connected with divergent specialisation of the oral surface morphology, or it occurred after the already separated species met again sympatrically. No complete record of the phyletic transition is available now, but a dense sampling of the Muhua section may provide it (see Fig. 4).

The largest series of elements of the species come from samples Dz-66 and Dz-6. In the Kowala section the first representatives of this lineage, probably *W. inaequalis*, have been found in sample Ko-46, the presence of the species being better documented by sample Ko-42.

The type population of *W. inaequalis* comes from the sample taken 82–97 cm below the top of the Hangenberg Limestone at the railroad cut at Hönnetal near Oberrödinghausen in the Rhenish Slate Mountains (Voges 1959: pl. 34: 51, 52; see also Paproth *et al.* 1986: fig. 14).

Weyerognathus triangulus **(Voges, 1959)**. — Unlike the preceding species, the platform of **sp** elements is here always low, with sharp but low ridges (Fig. 11G). The width of the basal cavity (pit) is also significantly smaller than in the older species of the lineage (Fig. 4). Identification of the species requires a sample of at least a dozen **sp** elements because of a rather wide population variability.

The rest of the apparatus also seems to be less robust than in the ancestral *P. inaequalis* (Fig. 22). It is a matter of convention whether to apply to these two forms species or chrono-subspecies rank.

The widening of the platform, making it more symmetrical, and the reduction in size of the basal cavity took place between the deposition of beds represented by samples Dz-46 (Dz-23) and Dz-45 (Dz-22). In the Kowala section the number of specimens of *Weyerognathus* is too low to provide a good record of evolution. Only in the Muhua section does there seem to be a gradual change in the basal cavity of the **sp** elements size that makes discrimination of the chronospecies quite arbitrary (Fig. 4). This character reaches a status comparable with that in Kowala sample Ko-30 (where *W. triangulus* appears for the first time) or with Dzikowiec samples Dz-14 close to the top of the limestone Wangyou Formation.

The type population of the species comes from the sample taken 0–10 cm below the top of the Hangenberg Limestone at Hönnetal (Voges 1959: pl. 35: 7, 8). The transition from the ancestral *W. inaequalis* took place before the sedimentation of bed Ha 10 in this locality.

Weyerognathus **aff.** *pinnatus* **(Voges, 1959)**. — The topmost sample Dz-15 in the Dzikowiec section, instead of providing evidence for further reduction of the basal cavity in the *Weyerognathus* lineage, has yielded *Weyerognathus* **sp** elements with the basal cavity of size ranges comparable to the much older *W. inaequalis* (Fig. 4). The platform is also not as wide as in *W. triangulus* but rather triangular with a tendency in adult specimens to develop an extension at one corner (Fig. 10F–I). In this respect this population seems to show, in an incipient form, the features diagnostic of the late

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Fig. 8. Non-platform polygnathids from the Tournaisian Wapnica beds of Dzikowiec. **A–I**. *Protognathodus kockeli* (Bischoff, 1957) from sample Dz-24, all × 66, except for **H** which is × 60; elements **sp** (**A–C**), **oz** (**D**), **tr** (**E**), **lo** (**F**), **pl** (**G**), **hi** (**H**), and **ne** (**I**); specimens ZPAL C XVI/334–341, respectively. **J–O**. '*Pandorinellina laterigranosa* (Gedik, 1969), from samples Dz-15 (**J, M–O**) and Dz-14 (**K, L**); elements **sp** (**J**, × 95; **K**, × 66), **oz** (**L**, × 66), **pl** (**M**, × 83), **hi** (**N**, × 83), and **ne** (**O**, × 83), specimens ZPAL C XVI/212, 377–378, 216, 214, 215, respectively. **P**. *Mehlina* sp. from sample Dz-23, element **sp** ZPAL C XVI/330; × 66.
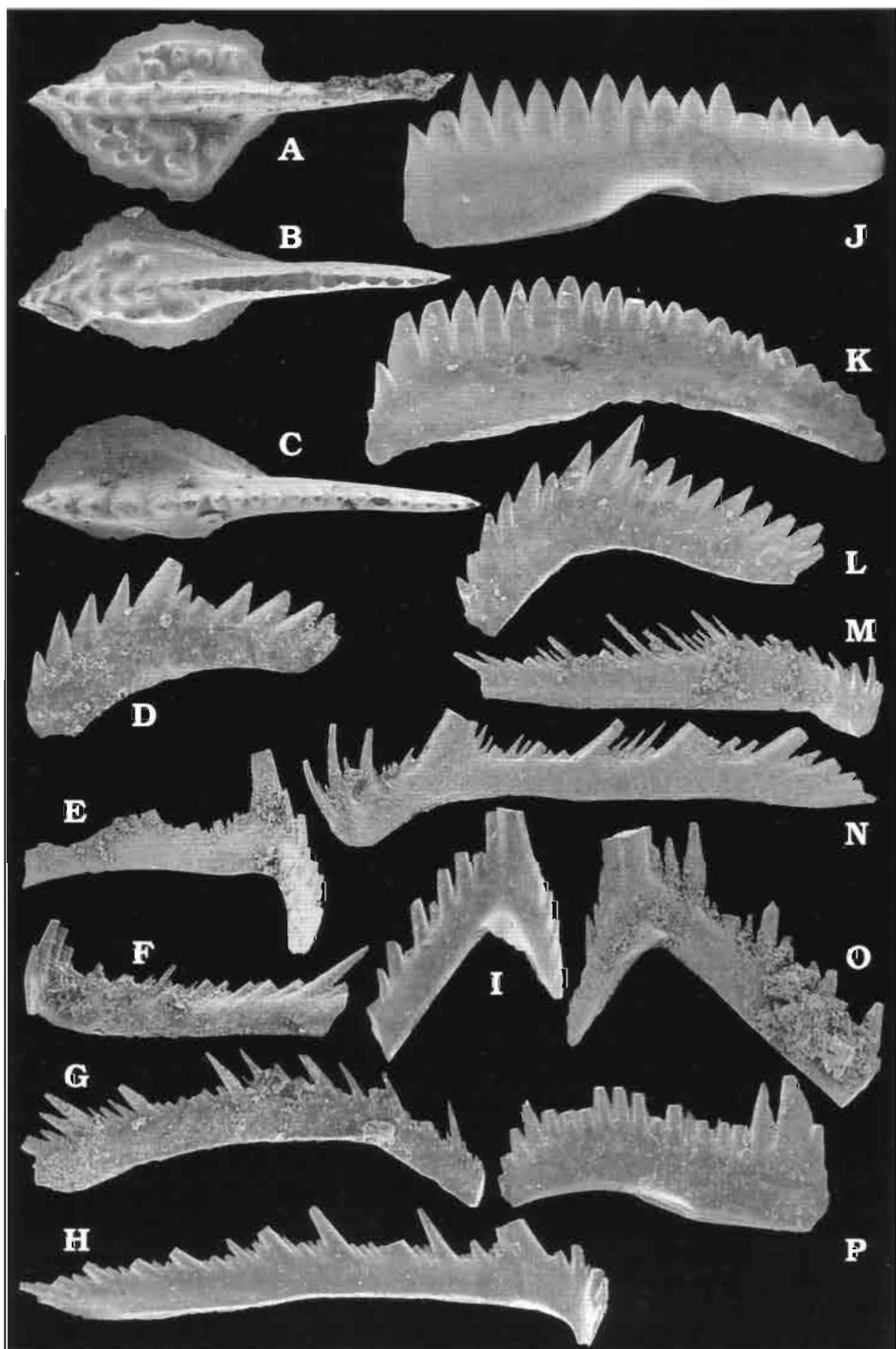
Tournaisian *W. pinnatus* and most probably represents its lineage that immigrated to the area at the beginning of the sea deepening.

Neopolygnathus communis (**Branson & Mehl, 1934**). — Four related species that occur in large numbers in sample Dz-46 do not show any morphological transitions and thus are obviously biologically distinct: *N. communis*, *N. purus*, *N. vogesi*, and *N. biconstrictus*. Of them, *N. communis* shows the most generalised morphology of its **sp** elements. They can be distinguished from those of other species by the almost parallel and strongly bent platform margins and by the depression in the lower surface immediately dorsal (posterior) of the pit. The platform is smooth except for singular knobs constricting the central concave area of the platform from both sides (Fig. 12I).

The species occurs commonly in the Tournaisian part of the section in Kowala, its abundant occurrence alone starting from the shale bed above the *Wocklumeria* limestone. In Dzikowiec it follows *N. purus*, being always a subordinate and rather irregularly distributed component of the fauna. Its distribution in the upper part of the Chinese Muhua section is similar (Figs 4, 5) but, unlike the European occurrences, after being replaced by *N. subplanus* at the beginning of the Tournaisian (sample Mu-24), it did not reappear until the latter species changes into *N. purus*.

The apparatus of *N. communis* (Fig. 23) can be reconstructed owing to sample Dz-24, where **sp** elements of this species dominate numerically over few elements of *N. purus* and *N. vogesi*. The **oz** elements of *N. communis* are distinct from the related species and easily distinguishable on the basis of a clearly separated cusp, much larger than other denticles. In this respect the species is less derived than the other two.

The type population of the species comes from the outcrop of Bushberg sandstone at Brickeys, Missouri (Branson & Mehl 1934: pl. 24: 1–4). This is an extremely long ranging species (Klapper 1966) from which all the remaining forms of the group are derived.

Neopolygnathus vogesi (**Ziegler, 1962**). — Two oblique ridges on the platform bordering the blade in its ventral part and very distinct histogeny make this species easily identifiable in Tournaisian samples (Fig. 12E). At the earliest recognisable histogenetic stages the platform is already fully developed as very thin asymmetrical lobes, strongly bent and with crenulated margins (Fig. 12F). Ridges develop much later.

The apparatus reconstruction is possible owing to sample Dz-46, where the species is very numerous (Fig. 23). It is followed by almost as numerous *N. purus* but in several other samples where *N. purus* is common, *N. vogesi* is lacking. This means that element types missing in these samples but associated with **sp** elements of *N. vogesi* in sample Dz-46 can be connected with it. On this basis I also attribute here rather robust **oz** elements with numerous sharp denticles on both processes. The whole element has a distinctly triangular shape, like that of *N. purus*, being generally larger, more elongated and bearing more numerous denticles. In the Chinese Muhua section *N. vogesi* is missing.

Neopolygnathus biconstrictus (**Gedik, 1969**). — This seem to be an extremely variable species in respect to its **sp** elements, as already shown by Gedik (1974). Some specimens are strongly elongated with very narrow platform even at relatively late ontogenetic stages, the others show rounded and strongly ornamented platform (Fig. 12D). The richest samples Dz-15 and Dz-46 are not large enough, however, to be sure that only one species is represented.

Fig. 9. Pseudopolygnathids with icrion and gnathodid from the Tournaisian Wapnica beds of Dzikowiec (**A–F, I–P**) and Kowala (**G, H**). **A–F**. *Pseudopolygnathus primus* (Branson & Mehl, 1934) early form from sample Dz-28; all × 66; elements **sp** (**A–C**, the latter in occlusal and lateral views), **pl** (**D**, possibly **E**), and **hi** (**F**), specimens ZPAL C XVI/357–358, 356, 361, 360, 359, respectively. **G–M**. *Pseudopolygnathus primus* (Branson & Mehl, 1934) late form from samples Ko-45 (**G**), Ko-53 (**H**), Dz-50 (**I**), Dz-31 (**J–M**) and Dz-15 (**O, P**); all × 66 except for **K** which is × 76; elements **sp** (**G–I**, the latter in occlusal and lateral views), **oz** (**J, O, P**), **lo** (**K**), **pl** (**L**), and **hi** (**M**), specimens ZPAL C XVI/299, 306, 97, 366, 369, 368, 367 and 480–481, respectively. **N**. *Protognathodus kockeli* (Bischoff, 1957) from sample Dz-31, element **ne** possibly representing the species, ZPAL C XVI/367; × 66.
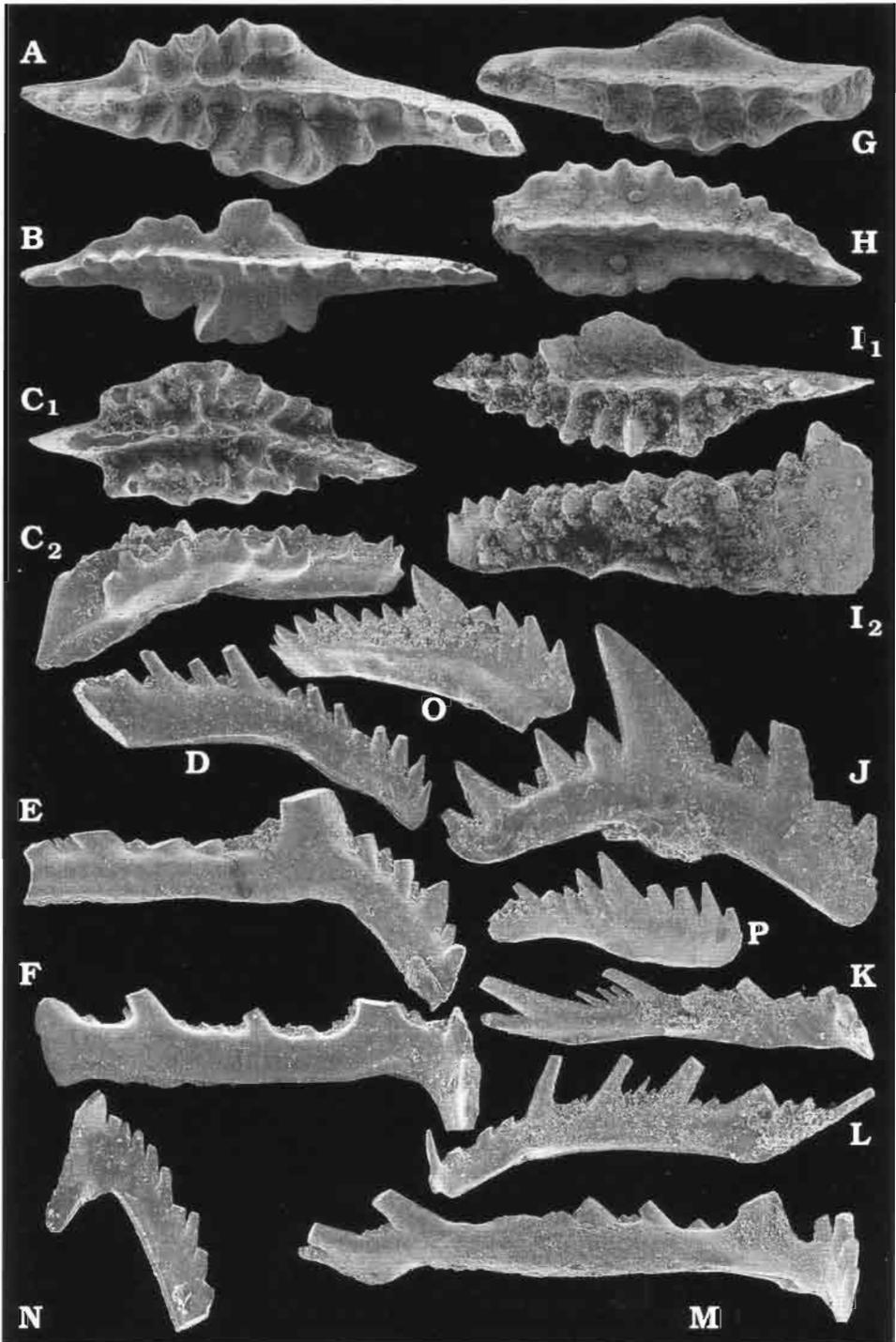
The type population of the species comes from the sample 3623 of Plöckenpaß in the Carnic Alps (Gedik 1974: pl. 4: 1, 2, 4–7), the holotype (his pl. 4: 7) being an **sp** element with a more than usually elongated platform.

Neopolygnathus subplanus (**Voges, 1959**). — In the population from sample Dz-65 virtually all elements have their platform margin bent upward. Only a few per cent of them, those with a thin, wide platform, have them almost flat. The most robust mature elements develop tuberculation that in extreme cases consists of oblique rounded ridges, resembling those in *N. vogesi* but not elevated above the tubercles following them externally. Sometimes these are incipient transverse ridges but the low tubercles constricting the furrows of the platform, so typical for *N. communis*, do not develop in clearly identifiable form (Fig. 13J).

In some populations of the species (for instance Dz-66) numerous **sp** elements have margins of the platform strongly curved to reach almost the morphology of *N. communis*. There is, however, no morphologic discontinuity in the morphologic variation of the elements that would suggest a real presence of separate species.

The type population of the subspecies comes from 82–97 cm below the top of the Hangenberg Limestone at Hönnetal.

Neopolygnathus purus (**Voges, 1959**). — Unlike associated elements attributed to *N. vogesi*, the platform in this species develops gradually in the histogeny, initially as a narrow crest on both sides of the blade base (Fig. 13A). Even if slightly concave occlusally in some specimens, it does not grade into morphologies typical for associated elements attributed to *N. communis*. It also never develops crenulation typical of associated elements of *N. vogesi* and *N. biconstrictus*.

Samples Dz-15 and Dz-23 provide most complete information on the apparatus structure. The elements **oz** are characteristic owing to their short processes and distinctly triangular outline with the denticle tips of the dorsal process arranged along a steeply dipping line. The symmetry transition series elements are of rather generalised morphology and it is rather difficult to distinguish them from associated juvenile elements of other polygnathid genera. The **tr** elements T-shaped in occlusal view seem to belong here, as opposed to those Y-shaped, which probably belong to *Pandorinellina*. Associated **tr** elements tentatively attributed to *Siphonodella* have a much shorter medial process.

In the Chinese Muhua section the record of the *N. communis* → *N. purus* lineage evolution seems to be continuous (Fig. 5). The first *N. subplanus* population appears there at the base of the Wangyou Formation, and up to about 1.0 m higher, the platform in **sp** elements becomes completely flat in most specimens (a feature of *N. purus*) and then increases in width. The widest **sp** elements characterise the level of about 1.5 m but higher above they became again narrower, which is also followed by an increase in size of the largest elements in samples. This looks like a reversal of their evolution, but the **sp** elements from the top of Wangyou Formation, although as narrow as at its base, do not show platform convexity typical of their ancestors.

The type population of *N. purus* comes from the sample taken 68–75 cm below the top of the Hangenberg Limestone at the railroad cut at Hönnetal near Oberrödinghausen in the Rhenish Slate Mountains (Voges 1959: pl. 33: 21, 22).

Neopolygnathus sudeticus **sp. n.** — The **sp** elements of *N. purus* lineage population in sample Dz-50 of Dzikowiec show bimodal distribution of platform relative width (Fig. 4). There seems to be, together with a member of the main lineage, another species represented. This species with a narrower platform shows variability resembling much older populations of *N. purus*. This may reflect a general reversal in the evolution of the platform, shown well in the succession of *N. purus*

Fig. 10. Pseudopolygnathids with platform from the Tournaisian Wapnica beds of Dzikowiec. **A–E, J.** *Weyerognathus inaequalis* (Voges, 1959) from sample Dz-6; elements **sp** (**A** juvenile, × 66; **B, C,** × 66), finely denticulated **oz** (**D,** × 59) and **pl** (**E,** × 50), and extremely robust **hi** (**J,** × 57); specimens ZPAL C XVI/243, 241–242, 244, 246, and 245, respectively. **F–L.** *Weyerognathus* aff. *pinnatus* (Voges, 1959) from sample Dz-15; elements **sp** (**F** of atavistic morphology, × 66; **G** in occlusal and lateral views, × 63; **H** juvenile, × 66; **I,** × 66), **oz** (**K,** × 66), and extremely robust **lo** (**L** in occlusal and lateral views, × 66); specimens ZPAL C XVI/200, 202, 201, 203, and 199, respectively.
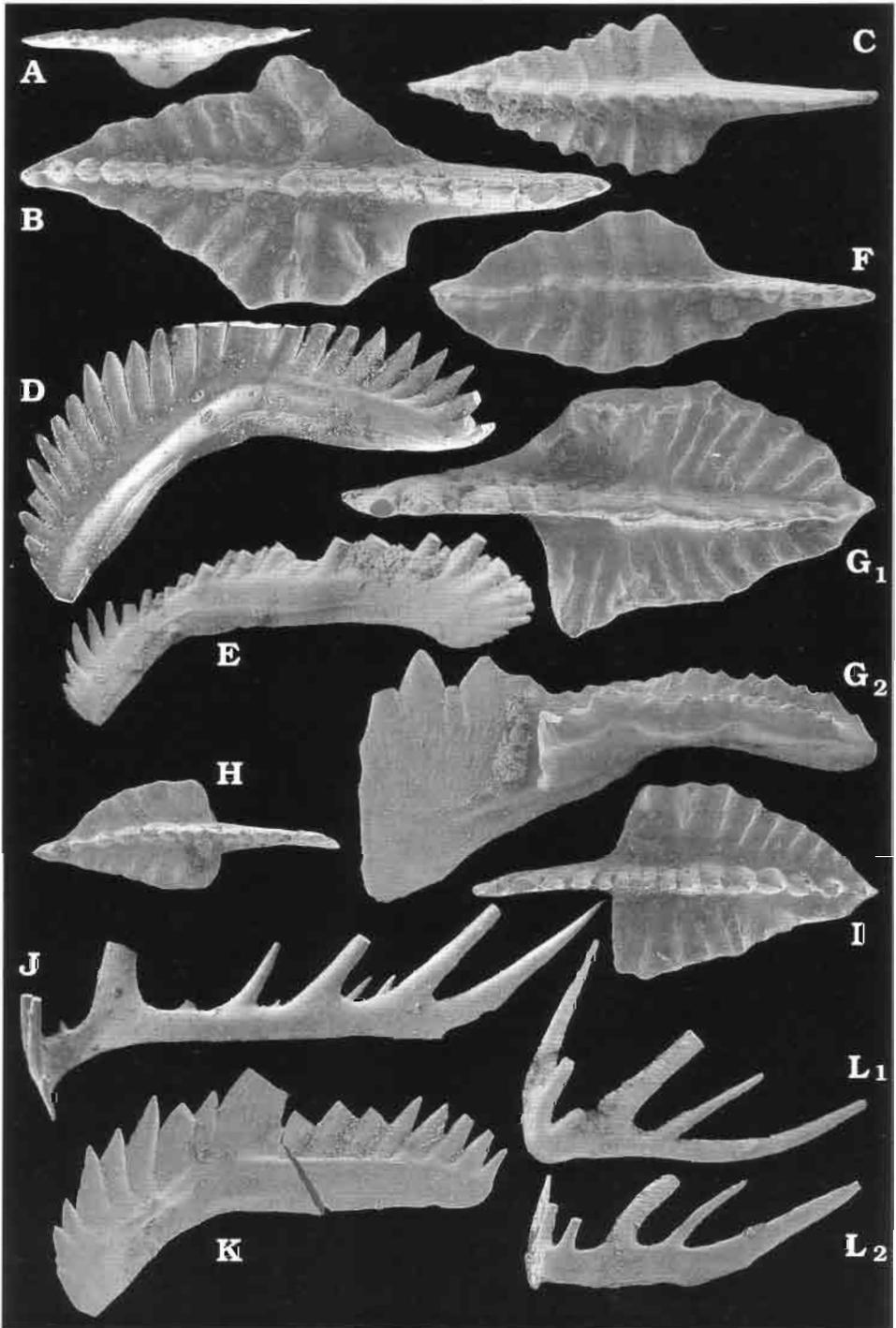
in the Muhua section (Fig. 4) or perhaps another example of the character displacement effect. The latter seems more probable, as the wide-platform form (Fig. 13H) does not seem to continue above or below in this or other sections and perhaps represents rather an exotic element that invaded the area after some period of isolation enabling allopatric evolution from some early population of *N. purus*. The morphologic difference is clear enough to allow easy discrimination of the Dzikowiec population and it deserves separation as a species (see p. 153) but is not sufficient to attribute intermediate specimens to particular species. This is why they are counted together in the data matrix (Table 1) and their percentage proportions are estimated (Figs 5, 23).

Pinacognathus? *praesulcatus* **(Sandberg, 1972).** — According to the current definition of the Devonian–Carboniferous boundary, all the populations of *P.*? *praesulcatus* (= *Siphonodella praesulcata*) that occur below the appearance of its successor in the lineage, *P. sulcatus*, are Famennian in age. The validity of the evolutionary transition from *P. praesulcatus* to *P. sulcatus* at the systemic boundary defined in La Serre stratotype has been questioned by Ji Quiang *et al.* (1989: p. 71) and, because of high population variability, this lineage does not seem to be especially useful in precise time correlation.

The material from Kowala and Dzikowiec is not rich enough to enable apparatus reconstruction. Both in the Polish material and in samples taken from the *Wocklumeria* Zone at Mal Paso in the Carnic Alps, only generalised polygnathid elements of apparatuses co-occur with **sp** elements of *P.*? *praesulcatus*. Its generic attribution is thus based solely on the assumed relationship with *P. sulcatus*.

The type population of *Siphonodella praesulcata* Sandberg, 1972 comes from the top 60 cm of the Sappington Member of Three Forks Formation at Lick Creek Road, Little Belt Mountains, Montana.

Pinacognathus sulcatus **(Huddle, 1934).** — In Kowala the largest sample of its **sp** elements has been collected 15.2 m below the top of the section. It shows significant variation in the diagnostic curvature, most elements being laterally bent (Fig. 14N). The basal cavity is also variable in adult specimens being slightly swollen and *Pseudopolygnathus*-like. Dzikowiec samples Dz-65 and Dz-31 provide the most numerous elements of the species (Fig. 14A–D). They show much variation in the curvature of the **sp** elements, symmetrical elements not being rare. Generally the basal cavity shows the morphology typical of *Siphonodella*, that is fusiform in shape, but a few very mature specimens are in this respect somewhat transitional to *Pseudopolygnathus*. The only co-occurring **oz** elements that could belong to the same apparatus are rather robust and variable in morphology. They tend to develop a narrow platform along the dorsal process that gives them a slightly 'notognathella' appearance (Fig. 14B). Singular recognised elements of the symmetry transition series show some resemblance to elements of the younger *Pinacognathus* sp. although they are not so specialised morphologically. More numerous **oz** and symmetry transition series elements (included in the reconstruction in Fig. 24) belonging to the species have been encountered in samples from the Muhua section. In sample Mu-24, just above the marls with concretions marking the top of the Devonian rocks, **oz** elements are rather variable in morphology, only some develop a platform at the robust inner process. Morphologies somewhat similar to those associated with *S. duplicata* occur there, too. In sample Mu-25, immediately above in the section, only robust **oz** elements occur, associated with the symmetry transition series elements closely similar to those of *Pinacognathus*.

Polygnathus gediki Luppold, 1994, co-occurring with *P. sulcatus* at Hangenberg in the Rhenish Massif (Luppold *et al.* 1994), seems to be based on adult **sp** elements of this species.

The type population of *Polygnathus sulcata* Huddle, 1934 comes from the upper New Albany Shale near its top just above gray-green shale containing Devonian brachiopods near Rockford, Indiana (Huddle 1934; Sandberg *et al.* 1972).

Pinacognathus sp. — This is a common species in older horizons represented by samples Dz-66 and Dz-6 in Dzikowiec which can be characterised by the mode of development of its platform in **sp** elements. Unlike associated platform elements of other polygnathids, juveniles of *P.* sp. show a widely gaping basal cavity that uniformly narrows towards the dorsal ('anterior') end of the element and a relatively robust platform develops at some distance above the element base. All this gives to the **sp** elements of this species an appearance resembling Devonian '*Siphonodella*' *praesulcata*, to
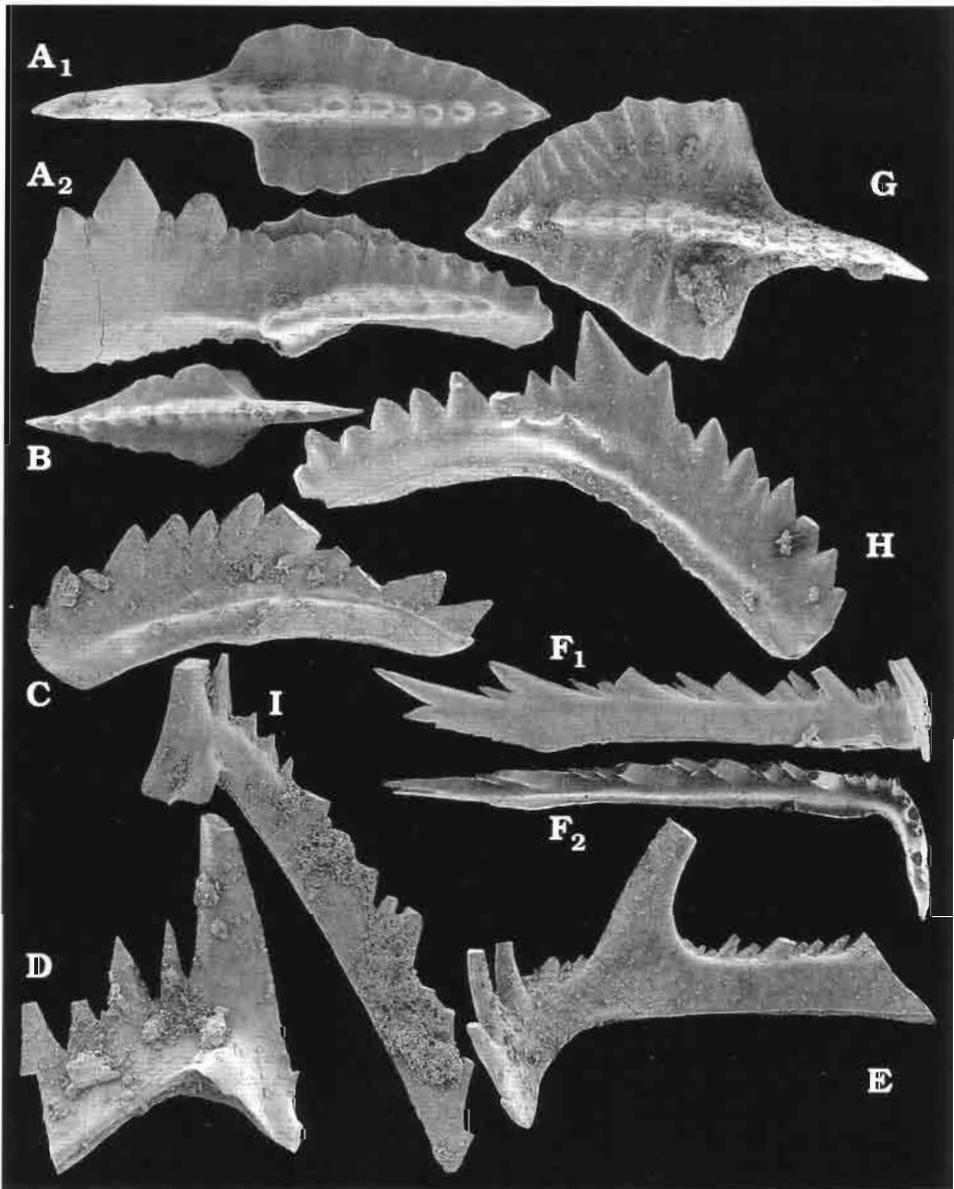
Fig. 11. Advanced platform pseudopolygnathids from the Tournaisian Wapnica beds of Dzikowiec. **A–F.** *Weyerognathus inaequalis* (Voges, 1959) from sample Dz-50; elements **sp** (**A** in occlusal and lateral views, × 66; **B** juvenile, × 66), **oz** (**C**, × 100), **ne** (**D, G,** × 66), **hi** (**E,** × 100) and **lo** (**F** in lateral and occlusal views, × 74); specimens ZPAL C XVI/98–100, 104, 103, 101, respectively. **G, H.** *Weyerognathus triangulus* (Voges, 1959) from sample Dz-14; × 66, elements **sp** (**G**) and **oz** (**H**), ZPAL C XVI/120 and 376. **I**. *Weyerognathus* aff. *pinnatus* (Voges, 1959) from sample Dz-15; element **ne**, ZPAL C XVI/195, × 80.

which it seems to be, in fact, related. The morphology of **sp** elements of this species (Fig. 15A) is more robust and less variable than in closely related populations occurring higher up in the section.

In the lower part of the *Gattendorfia* limestone in Dzikowiec **oz** elements with glossy surface, and a strong tendency to conceal denticles developed at earlier histogenetic stages, co-occur which most probably represent the same apparatus. They are very variable within each sample but most specimens have their denticulation rather well developed (Fig. 15C–D).

In younger samples Dz-15 and Dz-46, **sp** elements are rather variable. The platform in some specimens is very low with respect to the base and remains very thin and relatively flat, which makes them transitional to associated elements classified as *Polygnathus fornicatus.* The only difference between transitional elements of these species thus remains the shape of the basal cavity (pit). However clearly different in typical elements, the basal cavity varies considerably both in *P. fornicatus* and *P.* sp. and in many cases the decision to which of the species a specimen has to be attributed remains arbitrary.

In Dzikowiec sample Dz-15 some **sp** elements occur closely resemble the elements from the Muhua locality identified as *Polygnathus pupus* Wang & Wang, 1978 (juveniles) and *Polygnathus inornatus rostratus* Rhodes, Austin, & Druce, 1969 (mature) by Ji *et al.* (1989). The horizon with *P. dapoushanensis* (Ji *et al.*, 1989) , where they occur, is significantly older than that in Dzikowiec and the similarity in platform element morphology may be just a result of homeomorphy. Data on the whole apparatus structure are necessary to solve the problem.

The **oz** elements (Fig. 15L, R) that seem to be invariably associated with **sp** elements of this kind, have a glossy surface and poorly recognisable boundaries between denticles on the element sides even at early stages of histogeny (Fig. 15R). They tend to have a rather high and robust blade, which makes them different from **oz** elements of older populations of *Pinacognathus.* The evolution in the symmetry transition and **ne** elements of the apparatus is not so apparent. The apparatus shows some resemblance to that of *Dinodus* and this refers especially to **pl, hi,** and **ne** elements, which tend to develop strong ribs along processes below their denticles (Fig. 15E–R).

Two Muhua section samples taken 0.6 and 2.3 m above the base of the Wangyou Formation contain **sp** elements of morphologies approaching rather *P. inornatus,* associated with other elements of the apparatus almost identical with those co-occurring with *P.* sp. in sample Dz-6 of Dzikowiec. These two Muhua populations of different age seem to differ mostly in the morphology of **oz** elements, with a very high triangular profile ('*P. profundus*' morphology) in the older sample and more robust and elongated in the younger, more similar to those of the typical *P. inornatus.* Because of the derived morphology of ramiform elements some uncertainty remains regarding homology of particular element types. The most characteristic, both in Dzikowiec and Muhua samples, are elements with a long, undenticulated external process, possibly corresponding to the **hi** location. Such elements have not been found higher in the Dzikowiec section where typical *P. inornatus* occurs. *P. dapoushanensis* is a succesor of *P. sulcatus* in the Muhua section, perhaps developing there allopatrically in respect to *P.* sp.

The holotype of *Pinacognathus nodomarginatus* (E.R. Branson, 1934), the type locality of which is the Hannibal of Formation of Palmyra in Missouri (Klapper 1981: p. 379), shows the morphology of the platform much more advanced than that typical for the Dzikowiec specimens, with a tendency to develop additional ridges characterising rather *P. inornatus.* The **oz** elements attributed here to the Dzikowiec species are morphologically indistinguishable from the holotype of *Pinacognathus*

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Fig. 12. Polygnathids from the Tournaisian Wapnica beds of Dzikowiec (**A, B, E–P**) and Kowala (**C, D**). **A–C.** *Pinacognathus inornatus* (E.R. Branson, 1934) from samples Dz-14 (**A,** × 50), Dz-23 (**B** juvenile specimen, × 66), and Ko-30 (**C,** × 66); elements **sp,** specimens ZPAL C XVI/371, 326, and 279. **D.** *Neopolygnathus biconstrictus* (Gedik, 1969) from sample Ko-45; element **sp,** specimen ZPAL C XVI/298; × 66. **E–G, K.** *Neopolygnathus vogesi* (Ziegler, 1962) from sample Dz-6 (**E, G**), Dz-22 (**F**) and Dz-24 (**K**); elements **sp** (**E,** × 60; **F** juvenile, × 66), **oz** (**G,** × 66), and **hi** (**K,** × 66); specimens ZPAL C XVI/250, 316, 227, and 352, respectively. **H–J, L–P.** *Neopolygnathus purus* (Voges, 1959) from sample Dz-24; elements **sp** (**H** juvenile, × 66, surface reticulation × 267; **I,** × 66, surface reticulation × 267), **oz** (**J,** × 66), **tr** (**L** in lateral and dorsal views, × 73), **lo** (**M** in lateral and occlusal views, × 73), **pl** (**N,** × 64), **hi** (**O,** × 64), and **ne** (**P,** × 73); specimens ZPAL C XVI/344, 343, 345, 346–347, 349–350, and 348, respectively.
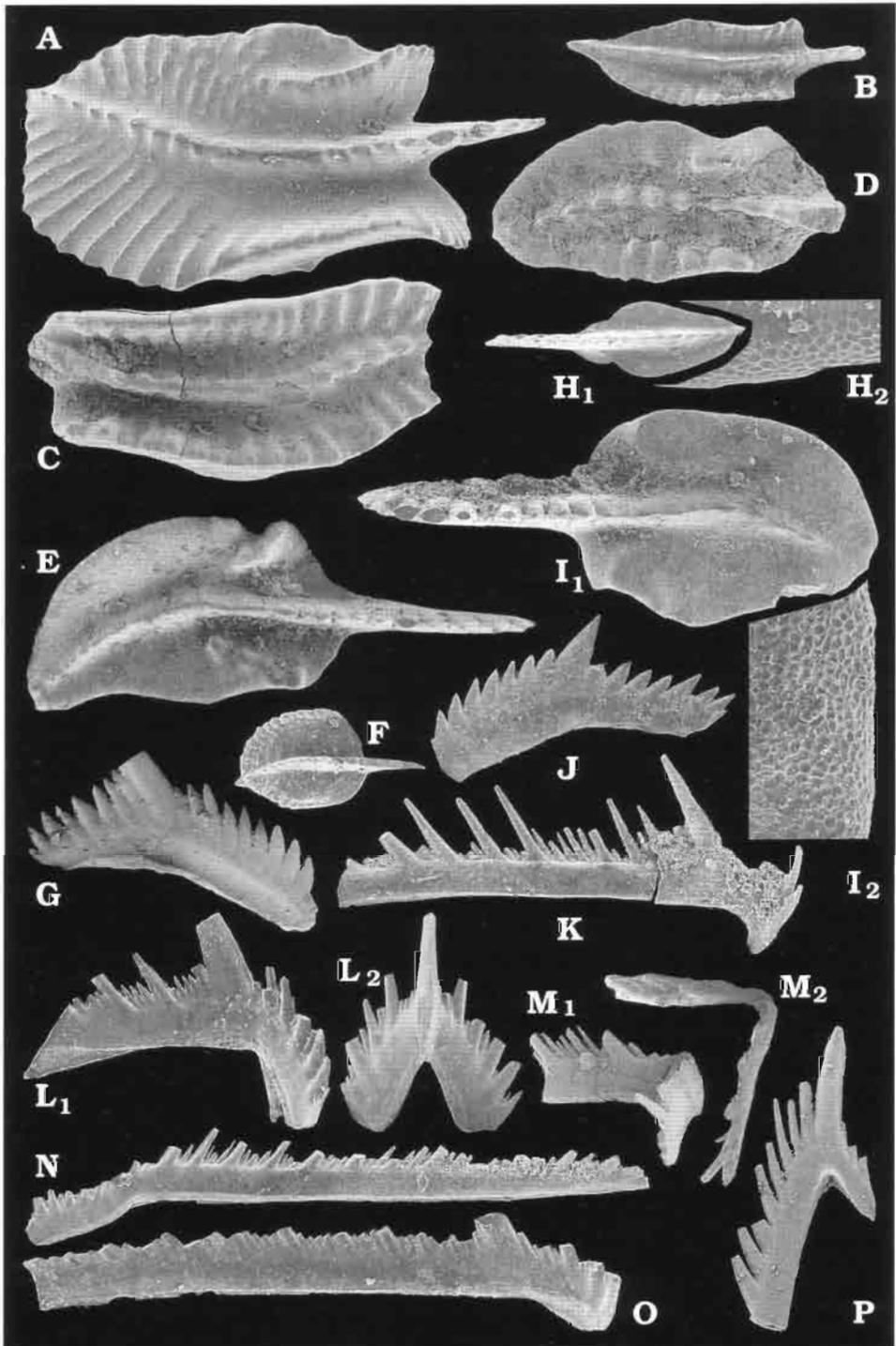
profundus (Branson & Mehl, 1934) from the Bushberg sandstone. The holotypes of *Prioniodus barbatus* Branson & Mehl, 1934, *Palmatodella ultima* Branson & Mehl, 1934, and *Synprioniodina delicatula* Branson & Mehl, 1934 from the same locality seem to belong to the same species but no platform element of comparable morphology to that from Dzikowiec is represented among specimens described by Branson & Mehl (1934). They may represent another species of the same genus.

Pinacognathus inornatus (E.R. Branson, 1934). — Morphologically, this is a rather generalised and variable species (Fig. 12A–C). It differs from associated *Pinacognathus* species in the strongly concave platform of **sp** elements, giving them a half-cylindrical shape, ornamented with transverse ribs. *P. inornatus, P.* sp., and *P. fornicatus* represent a morphocline in this respect, the occlusal surface of the platform (especially in its ventral = anterior part) ranging from a strongly convex to flat. The youngest identified juveniles from sample Dz-15 are elongated, with a thin semicylindrical appearance of the platform and relatively large and fusiform basal cavity (pit). The largest element, found in sample Dz-14, shows the first stages in development of an extended platform on both sides of the vertical ridges parallel to the blade. This is a process analogous to that so typical for *Siphonodella*, but the distance between parallel ridges is more than two times larger than in *Siphonodella* species.

Pinacognathus sp. and *P. inornatus* co-occur sympatrically in Dzikowiec, which makes apparatus distinction difficult. Most probably, their apparatuses were very similar to each other and there is no way to say to which of the three sympatric species of the genus the best preserved specimens from sample Dz-15 belong (Fig. 15F–I, L–R; an alternative attribution: Fig. 24).

In the Kowala section, together with advanced *Siphonodella*, populations similar to *P. inornatus* occur that are different from those from Dzikowiec in some respects. These are usually robust but rather narrow **sp** elements (Fig. 12C). The extensions of the platform outside the ridges, so typical for large **sp** elements of this species, develop also in the Kowala specimens but the distance between the main row of denticles and ridges seems here significantly smaller. This parallels the differences between some populations of *Siphonodella* but the taxonomic value of this feature requires additional studies on more numerous and better-preserved material. The basal cavity of the Kowala populations is also more variable in size and shape than those from Dzikowiec. In some cases (for instance sample Ko-30, 2.6 m below the top of the section) I have difficulties with distinguishing specimens of *P. inornatus* from those of *P.* sp. If criteria of discrimination of *P. inornatus* from related *Polygnathus distortus* Branson & Mehl, 1934 proposed by Klapper (1975) are used, at least some of Polish specimens would fall into the range of the latter species.

In the Muhua section *P. inornatus* replaces *P. dapoushanensis* in the upper part of the section, having an apparatus of a similar morphology.

The type population of the species is represented by sample C199-3 from the Hannibal Formation near Monroe City in Missouri (Branson 1934: pl. 25: 8).

Pinacognathus fornicatus (Ji, Xiong, & Wu, 1985) (?) — This is another species of the genus with very variable and difficult to determine **sp** elements and other elements of the apparatus probably similar to other species of *Pinacognathus* (Fig. 20J, K). Being best represented in the sample Dz-28 it may represent a stage, or just an oscillation, in the evolution of the *Pinacognathus* lineage. Generally, the platform of **sp** elements is wide, flat and relatively thin, with a strong occlusal ornamentation of the ribs. The margin in some elements is crenulated but in others remains smooth. There is a remarkable variability in element shapes, some being close to juveniles of *Dinodus lobatus*. Most of the **sp** elements attributed to this species are strongly angular and bent at the cusp so their basal surface is concave. Some juvenile specimens from sample Dz-14 have their platform linear in profile and may represent yet another related or convergently similar species. The well separated,

Fig. 13. Polygnathids and *Falcodus* from the Tournaisian Wapnica beds of Dzikowiec. **A–G**. *Neopolygnathus purus* (Voges, 1959) from samples Dz-15 (**A–E**), Dz-14 (**E**), and Dz-22 (**G**); × 100 except for **A** and **E** which are × 66; elements **sp** (**A** juvenile in lateral view; **B**), **oz** (**C**), **tr** (**D**), **lo** (**E** in lateral and basal views), **hi** (**F**), and **ne** (**G**); specimens ZPAL C XVI/205–207, 176, 387, and 322, respectively. **H, I**. *Neopolygnathus sudeticus* sp. n. from sample Dz-50; × 100; elements **sp** (**H**, holotype) and **oz** (**I**), ZPAL C XVI/94 and 108.
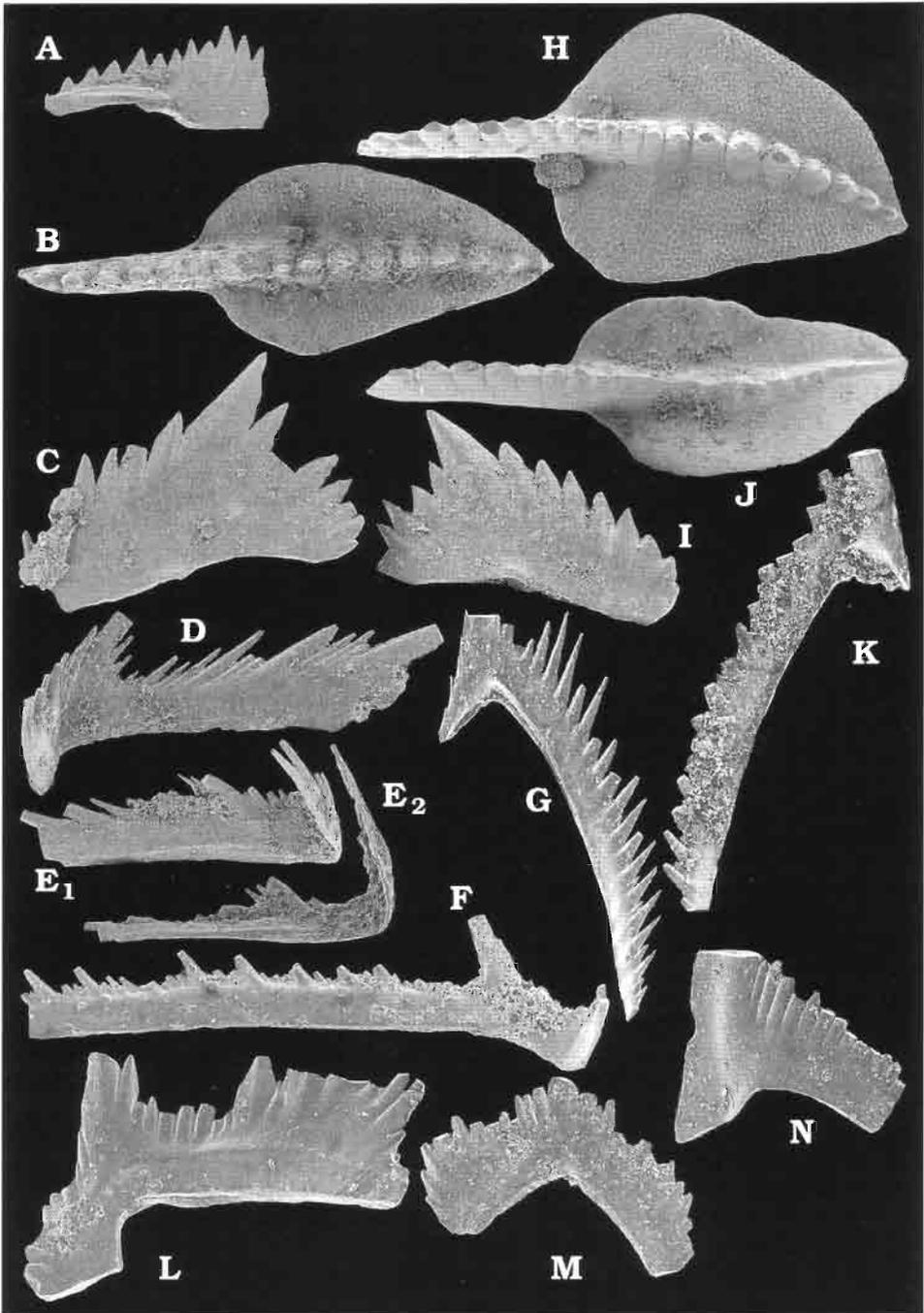
J, K. *Neopolygnathus subplanus* (Voges, 1959) from sample Dz-6; elements **sp** (**J**, × 60) and **ne** (**K**, × 66); specimens ZPAL C XVI/251 and 252. **L–N**. *Falcodus* sp. from sample Dz-22; all × 66; elements **hi** (**L**), **pl** (**M**), and **ne** (**N**), specimens ZPAL C XVI/318, 317, and 319, respectively.

typically polygnathid pit (Fig. 20J) may, however, gape also in the more dorsal part of the element, which may make distinction from the associated *Pinacognathus* sp. problematical. In fact, the apparatuses of these two species may appear identical (Figs 15D, E, 24). Unfortunately, as in the case of *P. inornatus*, no Dzikowiec sample contains elements of this species in larger number without being associated with *P.* sp. This makes separation of their apparatuses practically impossible. Most probably they are closely similar.

The type populations of *Polygnathus fornicatus* Ji, Xiong, & Wu, 1985 co-occurs with *S. carinthiaca* at Muhua. Its relationship to *P. flabellum* Branson & Mehl, 1938 remains to be clarified – specimens identified by Voges (1959) as similar to this North American species are apparently conspecific with those from Dzikowiec. The Polish populations attributed here to *P. fornicatus* may appear conspecific with *Siphonodella uralica* Zhuravlev, 1994, which may be based on juveniles of *D. lobatus,* as suggested by small size of the **sp** elements figured by Zhuravlev (1994).

Siphonodella duplicata (Branson & Mehl, 1934) *sensu auctorum.* — Samples Dz-6 and Dz-66 have yielded a small number of elements of this species (Fig. 14E–G; the former sample was taken from a breccia and both may have actually originated from the same bed).

Small sizes of available samples make apparatus reconstruction difficult and it can only be considered as tentative. In sample Dz-6, a few elements of the *Dinodus* symmetry transition series have been found but the set of elements attributed to this genus shows no correlation with *Siphonodella* **sp** elements in its distribution in Dzikowiec and in Muhua. Perhaps the symmetry transition series of *S. duplicata* is represented by rare elements of morphologies similar to associated elements of *Neopolygnathus purus* but more gracile and with shorter processes in the **lo** and **pl** elements. The minute **oz** elements that may be potentially attributed to *S. duplicata* in this and other samples grade morphologically into juvenile **oz** elements of *N. purus* or *N. vogesi.* They seem to differ in a triangular gaping of the basal cavity. If their attribution to *S. duplicata* is correct (Fig. 25), the non-platform part of the apparatus in this species would be very gracile and small-sized. This resembles in some respects the apparatus of *Vogelgnathus* (see Purnell & Bitter 1992); perhaps in both cases a primitive appearance is related to small element size.

Yet another possibility of restoring the apparatus of *S. duplicata* is suggested by the material from a sample taken from 2.3 m above the base of the Wangyou Formation in Muhua. Some **sp** elements of morphology typical for this species co-occur there with **oz** elements showing a characteristically oblique profile of the external margin of the base (resembling in shape short *Mehlina* **sp** elements) and symmetry transition series elements with very robust processes and reclined cusps. This Muhua population represents an unusually late return of the species, after being for a long time replaced by much more advanced members of the lineage. Virtually identical elements occur in the sample Dz-6 associated there with typical *S. duplicata* and robust asymmetrical **sp** elements identified here as *S.* sp. [aff. *S. crenulata* (Cooper, 1939)] (Fig. 25). Only because of the robust appearance shared by these **sp** and symmetry transition series elements I place them in the same apparatus. The outcome of this decision is that the Chinese second *S. duplicata* represents the same lineage.

The lectotype of *Siphonognathus duplicata* Branson & Mehl, 1934, as chosen by Klapper (1975), was collected from the Bushberg sandstone at the same locality as the type series of *S. lobata, S. quadruplicata,* and *S. sexplicata.* This is not a natural co-occurrence of these species as usually understood and the lectotype is hardly conspecific with what is now considered *Siphonodella duplicata.* Unless it is reworked from older strata, it corresponds rather to the Chinese return of the *S. duplicata* morphology or even to an aberrant specimen of a more advanced *Siphonodella.* Perhaps the name *S. duplicata,* as applied to the earliest species of *Siphonodella* s.s., should rather be abandoned in favour of *Polygnathus plana* Huddle, 1934, with its type population coming from the

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Fig. 14. *Pinacognathus–Siphonodella* transition forms from the Tournaisian Wapnica beds of Dzikowiec (**A–M, O**) and Kowala (**N, P, Q**). **A–D, N–Q.** *Pinacognathus sulcatus* (Huddle, 1934). **A, B**. Elements **sp** and **oz** from sample Dz-31, specimens ZPAL C XVI/362 and 363; × 66. **C–, D, N–Q**. Elements **sp** from samples Dz-28 (**C, D**), Ko-53 (**N**), and Ko-48 (**P, Q**); × 66, specimens ZPAL C XVI/353–354, 307, 302,
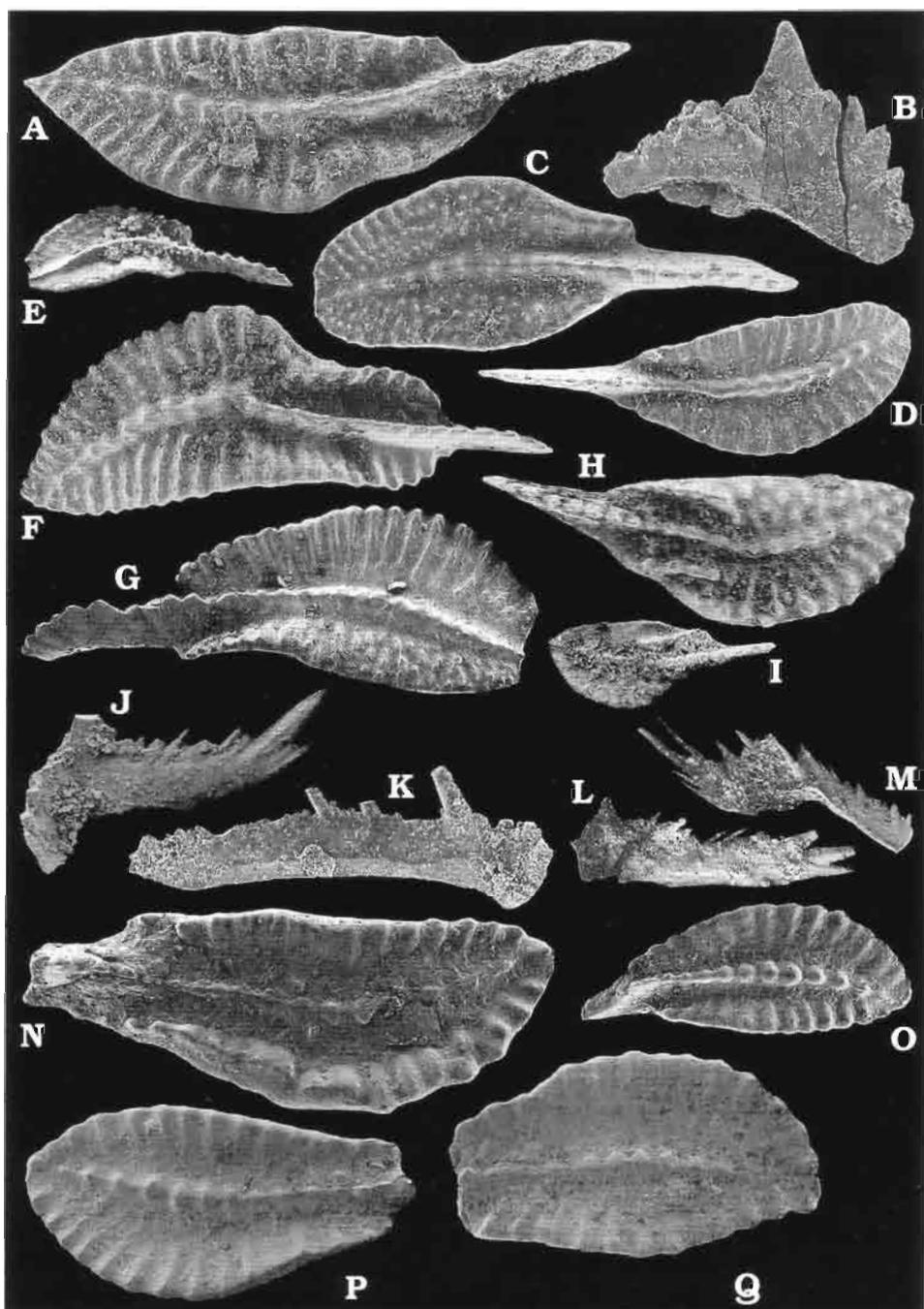
300, and 301, respectively. **E–G, J–M**. *Siphonodella duplicata* (Branson & Mehl, 1934) early form from sample Dz-6, elements **sp** (**E** juvenile, × 66; **F**, × 65; **G**, × 66), **tr** (**J**, × 100), **hi** (**K**, × 66), **lo** (**L**, × 66), and **pl** (**M**, × 66) specimens ZPAL C XVI/226, 225, 224, 236, 351, 229, and 228, respectively. **H, I**. *Dinodus* early form? from sample Dz-6; elements **sp**; specimens ZPAL C XVI/222–223.

upper New Albany shale of Indiana and undoubtedly conspecific with the early Tournaisian popula-
tions under discussion.

Siphonodella **sp. [aff.** *S. crenulata* **(Cooper, 1939)].** — The extremely asymmetrical, robust **sp**
elements from samples Dz-6 and Dz-66 (Fig. 14H, I) do not seem to represent end-members of the
population variability of *S. duplicata*. They are either angularly bent, with resulting triangular shape
of the platform or with the vertical platform margins continuing into ridges that point towards the
cusp. In the latter character and widely extended posterior lobe of the platform they resemble much
later *S. crenulata* and may appear ancestral to it. As mentioned above, they are arbitrarily proposed
to be matched in the apparatus with co-occurring robust symmetry transition elements (Fig. 25).
Another interpretation of this species, which occurs also in the Muhua section, has been offered by
Ji *et al.* (1989: p. 99, pl. 14: 5–8). According to them, this is a connecting link between *S. duplicata*
and '*S.' lobata*. In fact, there are associated symmetry transition series elements of *Dinodus* (to which
the latter species is here transferred) in the Dzikowiec samples and, if their evolutionary interpretation is
correct, quite another restoration than that proposed here of these species apparatuses would be necessary.

Siphonodella carinthiaca Schönlaub, 1969. — Adult **sp** elements of *Siphonodella* abundantly
occurring in samples Dz-23 and Dz-46 (Fig. 16), which probably come from the same bed at opposite
ends of the Dzikowiec quarry, usually show widened denticle tips of their blade (carina) in the region
dorsal of the cusp. The tubercles covering the anterior half of the platform are then arranged in
a fingerprint pattern that merges with the denticles of the blade. This is not so well visible, if present
at all, in juvenile specimens and there is generally quite a wide variation in the platform ornamenta-
tion. All the elements of typical *Siphonodella* from these samples (except for the aberrant *S. belkai*
sp. n.) show generally the same platform shape and none of them develops additional crests. It thus
seems that the population is homogeneous and that the platform ornamentation variation is a matter
of intraspecific variability. Less numerous elements of the same species encountered in higher parts
of the section show similar ranges of the platform ornamentation.

The type population of this species comes from sample 436 of the locality Kronhofgraben in the
Carnic Alps where it is the dominant species, only some specimens attributed to *S. duplicata*
co-occurring with it (Schönlaub 1969). This is the oldest bed containing *Siphonodella* in this section.
The **sp** elements of *S. carinthiaca* (*Siphonodella* cf. *duplicata* of Gedik, 1974) are associated in
sample 3623 from Plöckenpaß in the Carnic Alps with the type series of *Pinacognathus valdecavatus*
Gedik, 1969, which seems to represent the **oz** element of the same species. It co-occurs with other
morphologies of **sp** elements in the more complete section of Kronhofgraben in the same region
(Schönlaub 1969). Below, it is proposed to restrict the meaning of the genus *Siphonodella* to species
having **oz** elements of this type and **sp** elements with well developed ridges, other species transferring
to *Pinacognathus* and *Dinodus*.

In the Muhua section the oldest occurrence of **oz** elements resembling those attributed here to
Siphonodella s.s. is 0.6 m above the base of the Carboniferous rocks (sample Mu-28), where **sp**
elements are at best transitional from *P. sulcatus* to *S. duplicata*.

Siphonodella belkai **sp. n.** — (Fig. 19A–F; see description on p. 154).

Fig. 15. *Pinacognathus* from the Tournaisian Wapnica beds of Dzikowiec. **A–E.** *Pinacognathus* sp. early
form. Samples Dz-6 (**A, B**), Dz-28 (**C**), Dz-23, (**D, E**); elements **sp** (**A,** × 50; **B** juvenile, × 66) **oz** (**D**
juvenile, × 80; **C**, × 66) and **lo** (**E**, × 66); specimens ZPAL C XVI/232–233, 325, and 327 (elements other
than **sp** may as well belong to *Pinacognathus fornicatus* (Ji, Xiong, & Wu, 1985); see Fig. 20J–K) elements
sp (**I** juvenile, × 66; **J**, × 66), **oz** (early form, **K** typical form, **Q** juvenile, all × 66), **tr** (**I, P,** both × 66); **pl**
(**F, H,** both × 66), **lo** (**M,** × 80), **hi** (**G,** × 66), and **ne** (**L, O,** both × 66; **N,** × 80); specimens ZPAL C
XVI/232–233, 355, 463, 462, 482, 467, 185, 183, 219, 169, 465–466, 217, and 460, respectively. **F–R.**
Pinacognathus sp. late form. Sample Dz-15; elements **sp** (**K,** × 66; **J** juvenile, × 66), **oz** (**L, R** juvenile, both
× 66), **tr** (**I, Q,** both × 66); **pl** (**F, H,** both × 66); **hi** (**G,** × 66); and **ne** (**N, O,** both × 66; **M, O,** both × 80);
specimens ZPAL C XVI/355, 463, 462, 482, 467, 185, 183, 219, 169, 465–466, 217, and 460, respectively.
Note that elements of the symmetry transition series from sample Dz-15 may appear either indistinguish-
able from, or belonging to, co-occurring *P. inornatus*, as alternatively shown on Fig. 24.
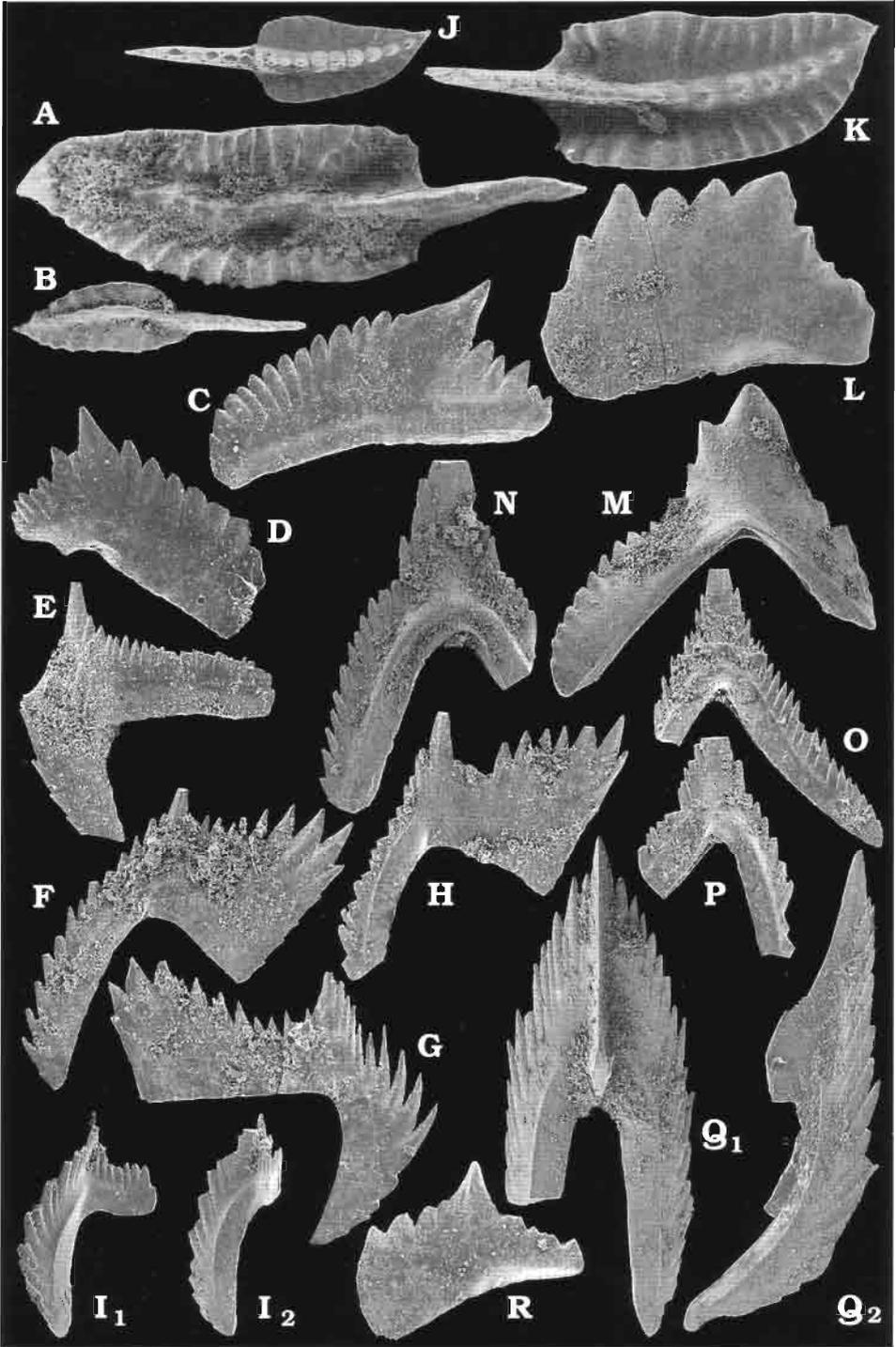
***Siphonodella* cf. *quadruplicata* (Branson & Mehl, 1934)**. — Immediately above *S. belkai* in the Kowala section yet another, unrelated species of *Siphonodella* appears that seems to be the oldest Polish member of the main branch of *Siphonodella* with a transversely ribbed platform and a tendency to develop several ridges in the **sp** elements (Fig. 18N–S). Samples Ko-40 and Ko-39 taken at 8.2 m and 7.6 m below the top of the Kowala section contain **sp** elements of *Siphonodella* with one or two ridges developing at the posterior lobe of the platform. They run at a large angle to the element axis, ending approximately at the cusp level, either at the platform margin or in the middle of the platform lobe. The Kowala populations are characteristic in having the whole surface of its platform elements well ornamented. The ridges usually terminate at the level of the cusp, but in some specimens the posterior ridge continues further and approaches gently the platform margin. The tuberculation of the anterior lobe is irregular, which makes this population different from those below and above. In specimens from sample Ko-41, taken at 8.6 m, tubercles tend to be arranged in transverse rows, otherwise the element is of similar morphology to those attributed here tentatively to *S. quadruplicata*. In younger samples, starting from Ko-38, at 7.2 m, the tubercles are arranged in longitudinal rows and ridges at the posterior part of the platform are parallel to its margin. This is probably *S. sandbergi* that replaced Kowala populations of *S.* cf. *quadruplicata* without any intermediates.

A single specimen of the same morphology as those from Kowala has been found in Dzikowiec sample Dz-24, located below the first appearance of *S. carinthiaca*.

Perhaps the form under discussion is conspecific with *Siphonodella quadruplicata* (Branson & Mehl, 1934) (Branson & Mehl 1934: pl. 24: 18–20, the lectotype selected by Klapper (1966: p. 17) and *S. sexplicata* (Branson & Mehl, 1934) from the Bushberg Sandstone at Brickeys in St. Genevieve County of Missouri.

***Siphonodella sandbergi* Klapper, 1966**. — Populations of *Siphonodella* from sample Ko-38 upwards in the Kowala section are distinct from those below in having tubercles arranged in more or less regular longitudinal rows. The inner area of the platform remains ribbed (Fig. 19H) which makes these populations different from later *Siphonodella* with a smooth corresponding part of the platform, where only irregular tubercles may develop. In this respect they are similar to apparently much younger American *S. obsoleta* and *S. isosticha*.

The holotype of *S. sandbergi* Klapper, 1966 comes from the sample taken from the basal 6 inches of a dark shale unit at South Fork Rock Creek in Big Horn Mountains, Wyoming. Four other species of *Siphonodella* have been identified in this sample by Klapper (1966), namely *S. cooperi, S. obsoleta, S. quadruplicata,* and *S. sexplicata*. This makes either homogeneity of the sample or taxonomic identifications of those species unlikely (perhaps both). The meaning of *S. sandbergi* thus remains to be clarified.

According to the original description (Klapper 1966: p. 19), the type series shows an extremely short free blade. Although only a few specimens in the Kowala samples have the free blade partially preserved, it does not seem very short (judging from the thickness of its broken base) and the dorsal part of the element is narrow, as in the type specimen of *S. obsoleta*. More completely preserved specimens are small in size and there may be an ontogenetic difference in proportions between the free blade length and size of the platform. A relatively short free blade characterises also adult specimens of *S. belkai* sp. n., that appears in Polish sections surprisingly low and must have been derived from an ancestor with *S. sandbergi* morphology. Perhaps *S. sandbergi* developed allopatri-

Fig. 16. Early *Siphonodella* from the Tournaisian Wapnica beds of Dzikowiec (**A–K**) and Kowala (**L–Q**). **A–G, L, M**. *Siphonodella carinthiaca* Schönlaub, 1970 from sample Dz-22 (**A–G**) and Ko-40 (**L, M**); elements **sp**, all × 66 (**B** in lateral and occlusal views); **B, C**, and **M** being juveniles morphologically indistinguishable from *S. duplicata*, **oz** (**D**, × 100), **ne** (**E**, × 66; **F**, × 100), **pl** (**G**, × 80) and **hi** (**H**, × 66); specimens ZPAL C XVI/313, 312, 310, 314, 323, 321, 320, 315, and 288–289, respectively. **I–K, N–Q**. *Siphonodella duplicata* (Branson & Mehl, 1934) late form from samples Dz-23 (**I–K**), Ko 45 (**N–O**) and Ko-44 (**P, Q**); all × 66 (**K** in lateral and occlusal views); elements **sp**; specimens ZPAL C XVI/333, 332, 331, 296–297, 295, and 294, respectively.
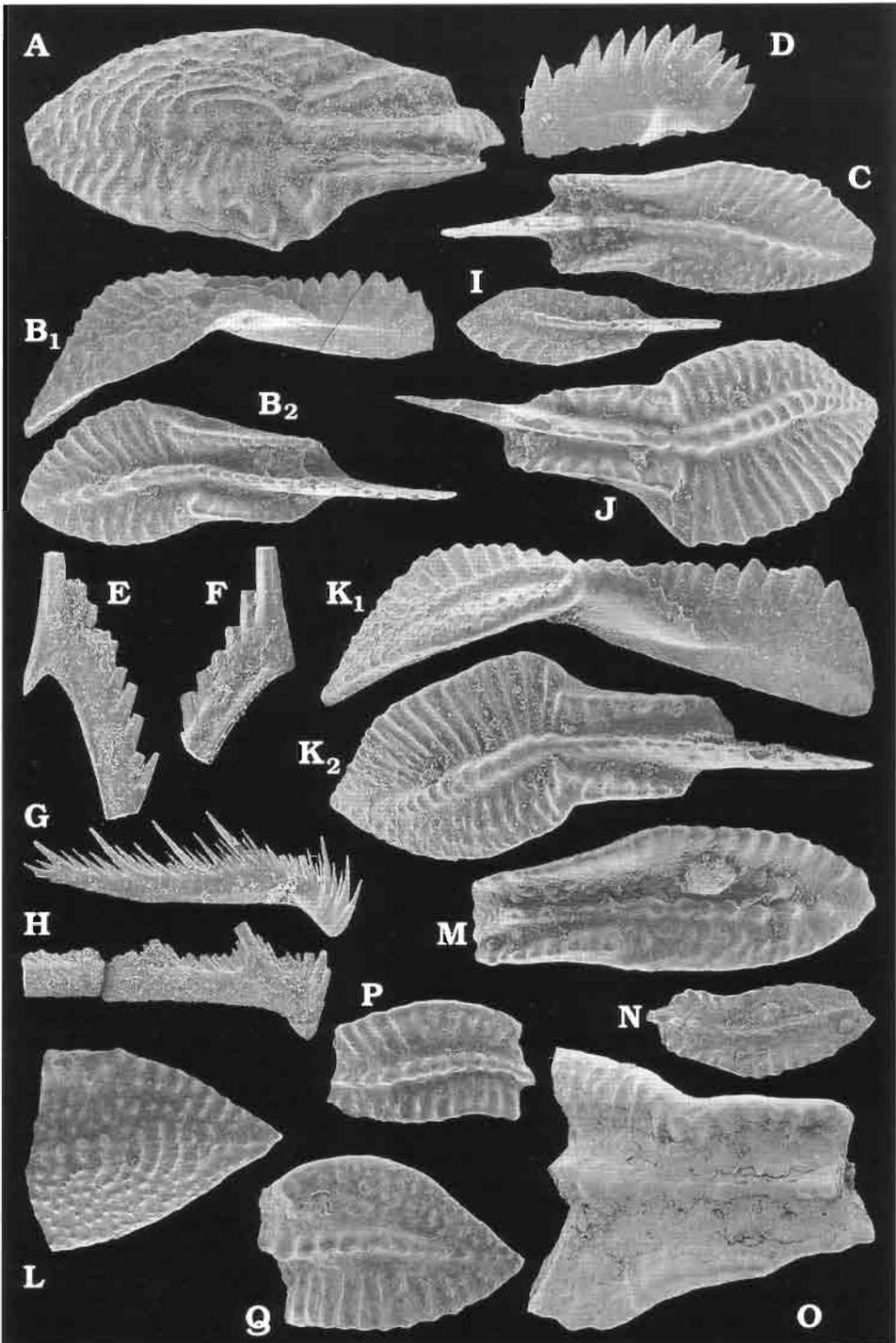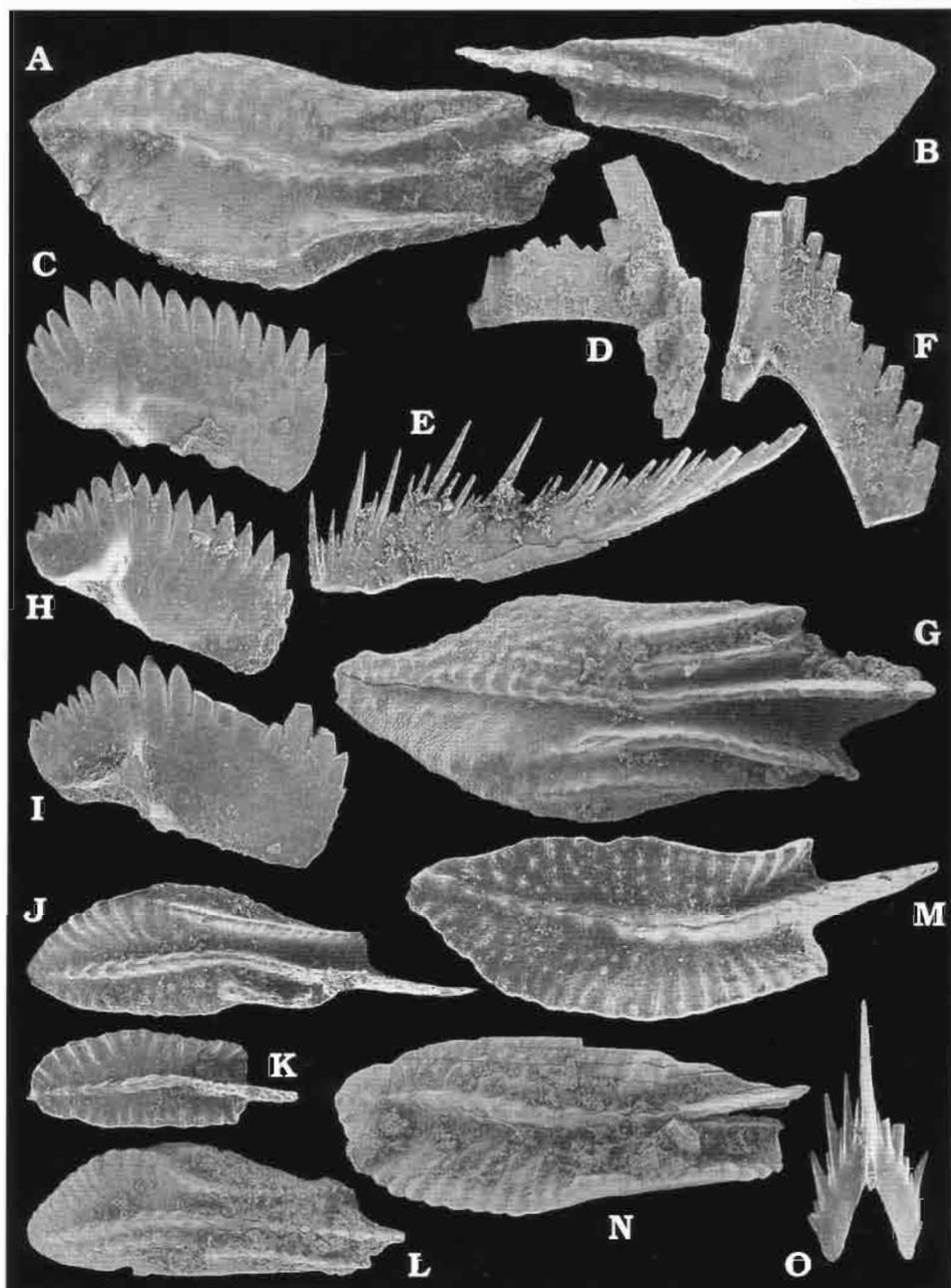
Fig. 17. Morphologically advanced *Siphonodella* from the Tournaisian Wapnica beds of Dzikowiec. **A–F.** *Siphonodella* sp. cf. *S. isosticha* (Cooper, 1939) from sample Dz-50; elements **sp** (**A**, **B**, × 66), **oz** (**C**, × 100), **tr** (**D**, × 115), **pl** (**E**, × 101), and **ne** (**F**, × 101); specimens ZPAL C XVI/91–92, 113, 119, and 116–117. **G–O.** *Siphonodella* sp. cf. *S. obsoleta* Hass, 1959 from sample Dz-14; elements **sp**, all × 66 (**G**, **J**, **K** juvenile, **L** and **M** juvenile and larger specimen of *P. sulcatus* morphology, may belong to *Pinaco-* →
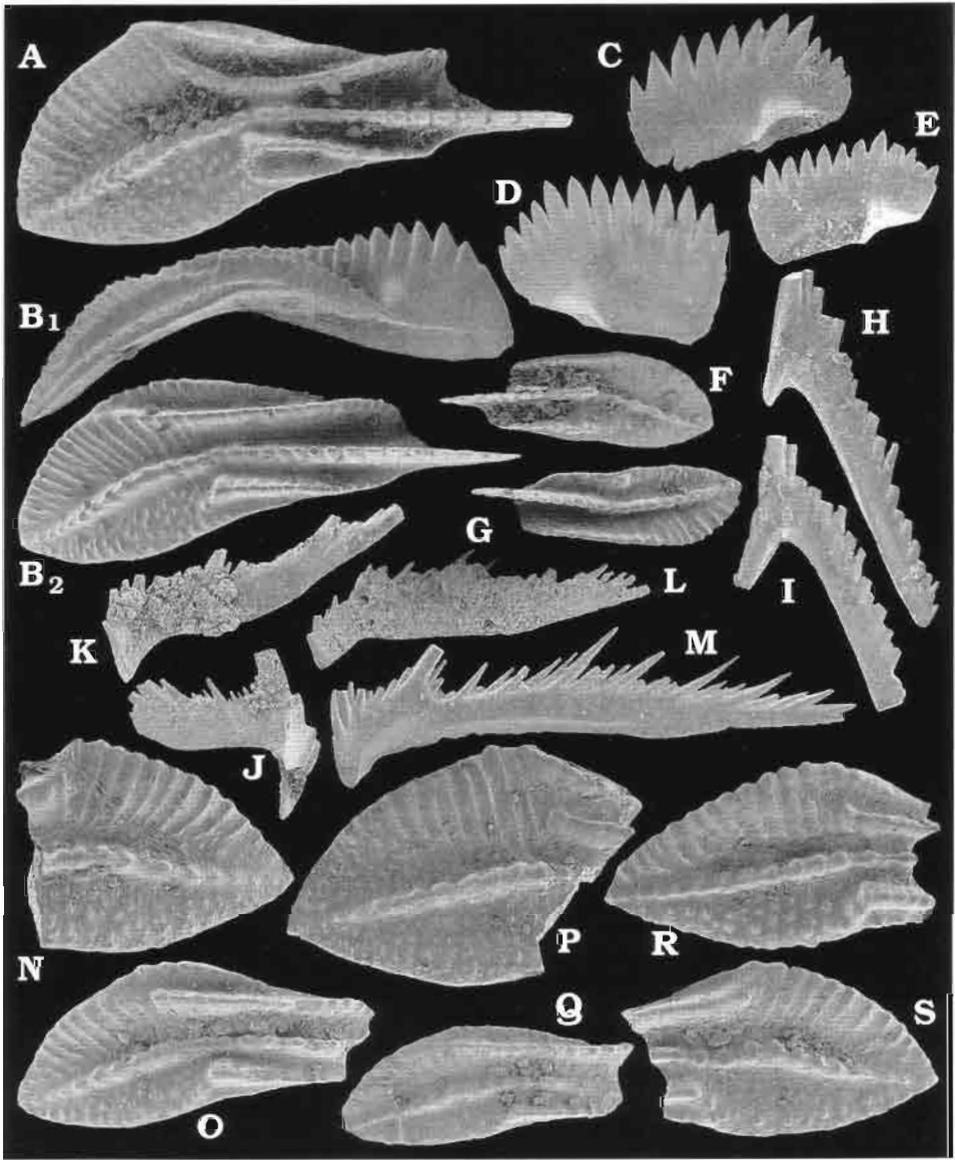
Fig. 18. The last *Siphonodella* from the Tournaisian Wapnica beds of Dzikowiec (**A–K**) and first advanced *Siphonodella* from Kowala (**N–S**). **A–M**. *S*. cf. *cooperi* Hass, 1959 from sample Dz-15; elements **sp** (**A**, × 50; **B** in lateral and occlusal views, × 66; **F** and **G** juveniles, × 66), **oz** (**C**, **D**, × 100; **E**, × 66), **ne** (**H**, **I**, × 98), **tr** (**J**, × 66), lo (**K**, × 66), **pl** (**L**, × 66) and **hi** (**M**, × 66, **J**, × 100, **K**, × 80); specimens ZPAL C XVI/171–172, 220–221, 477, 173–174, 474, 468, 472, 471, 470, and 469, respectively. **N–S**. *S*. cf. *quadruplicata* Branson & Mehl, 1934, elements **sp** from samples Ko-39 (**N**, **O**) and Ko-40 (**Q–S**); all × 66; specimens ZPAL C XVI/287, 283, 286, 284–285, and 282, respectively.

gnathus, **N** of *S. duplicata* morphology), **oz** (**H**, **I**, × 100), and **tr** (**O**, × 80); specimens ZPAL C XVI/373, 375, 123, 374, 125, 124, 382, 122, and 383, respectively.

cally to the European lineages of ridged *Siphonodella*, and much earlier. In Muhua, specimens of *S. sandbergi* with a short free blade occur high in the section (sample Mu-41; see also Ji *et al.* 1989).

The species identity of the Kowala series of those *Siphonodella* populations remains obscure. If the longitudinal ridges are homologous to those in *S. sandbergi,* the Kowala population would represent a morphology ancestral for *S. sandbergi.* Being unable to find a better affiliation for it I will apply the name *S. sandbergi* until its relationships are clarified.

Siphonodella sp. cf. S. isosticha (Cooper, 1939). — The populations of *Siphonodella* represented in samples Dz-44 and Dz-45 from the southern end of the Dzikowiec quarry and samples Dz-22 and Dz-50 (the last from a loose block) seem to not differ significantly. In all of them the **sp** elements are highly variable, but almost all mature specimens show characteristic features that make this form different from the populations above and below in the section. This refers to the second posterior rostral ridge which runs parallel to the margin (unlike the first one that is directed almost transversely to the platform margin), usually forming only a ramp in the dorsal part of the element. Some odd elements in the largest sample Dz-44 show either reversed relations between posterior ridges (the inner one being parallel to the platform margin), or do not develop the second crest despite attaining appropriate size. Those latter may, in fact, represent an extreme member of associated *S. carinthiaca,* closely similar elements of which occur below in the section (as well as in the Carnic Alps type population; see Schönlaub 1969).

Virtually all the Dzikowiec specimens of the species discussed show a smooth and wide central concave area of the platform. This makes them similar to rare specimens occurring in sample Ko-28 in Kowala (Fig. 19K) which may be conspecific.

Some associated ramiform elements similar to those attributed provisionally to other *Siphonodella* species have also been encountered (Table 1). Their apparatus attribution remains highly tentative. The gracile **hi** elements co-occurring in samples with *Siphonodella* **sp** elements vary mostly in the length of their processes and the angularity of the external process. In most of them the external process is relatively long and only slightly reclined; relatively robust examples probably represent species of *Pandorinellina*; smaller ones may as well belong to *Neopolygnathus*. There is no easily discernible morphologic gap in their variability. The more gracile morphs with reclined external process seem to represent two morphologic classes, also with a clear overlap in variability. Some of them have the external process bent almost strictly in the same plane as the short internal (dorsal) process, others show the external process curved both externally and posteriorly and a relatively long dorsal process. I am not able to exclude the possibility that this difference refers to different locations in the apparatus (**hi** and **ke**) but the concurrence of small **pl, lo,** and **tr** elements showing unusually short processes with the short morph of **hi** elements is suggestive of their being members of the same apparatus, most probably of *Siphonodella,* **sp** elements of which are there of high frequency (for instance in sample Dz-15).

In the American succession **sp** elements without transverse ribs, characteristic for *S. cooperi hassi* Thompson & Fellows, 1970 (representing *S. isosticha* according to Klapper 1971, 1973), succeed those with prominent ribbing, classified as typical subspecies of *S. cooperi* by Thompson & Fellows (1970). The same was most probably the succession of morphologies in Poland as the populations with ribbed platform (identified here as *S.* cf. *quadruplicata)* precede in time the species with a smooth centre to the platform. The real meaning of this parallelism, which is of high importance for the time correlation between Europe and America, remains unclear. At present the proposed provisional taxonomic identifications seem to be the most parsimonious solution.

Fig. 19. Advanced *Siphonodella* from Kowala (**A, D–P**), and Dzikowiec (**B, C**) elements **sp**; all × 66 except for **N** which is × 133. **A–F.** *S. belkai* sp. n. from sample Ko-42 (**A, D–F**) and Dz-46 (**B, C**); specimens ZPAL C XVI/293, 391–392, 309, 308 (holotype, **E**), and 292, respectively. **H, J, M.** *S. sandbergi* Klapper, 1966 from sample Ko-30; elements ZPAL C XVI/278, 276, and 277, respectively. **G, L, K.** *Siphonodella* sp. cf. *S. isosticha* (Cooper, 1939) from sample Ko-28; elements ZPAL C XVI/273, 274, and 275, respectively. **I, N–P.** *Siphonodella* sp. cf. *S. obsoleta* Hass, 1959 from sample Ko-21, the youngest *Siphonodella* in Kowala section; specimens ZPAL C XVI/261–262, 259, and 260, respectively.
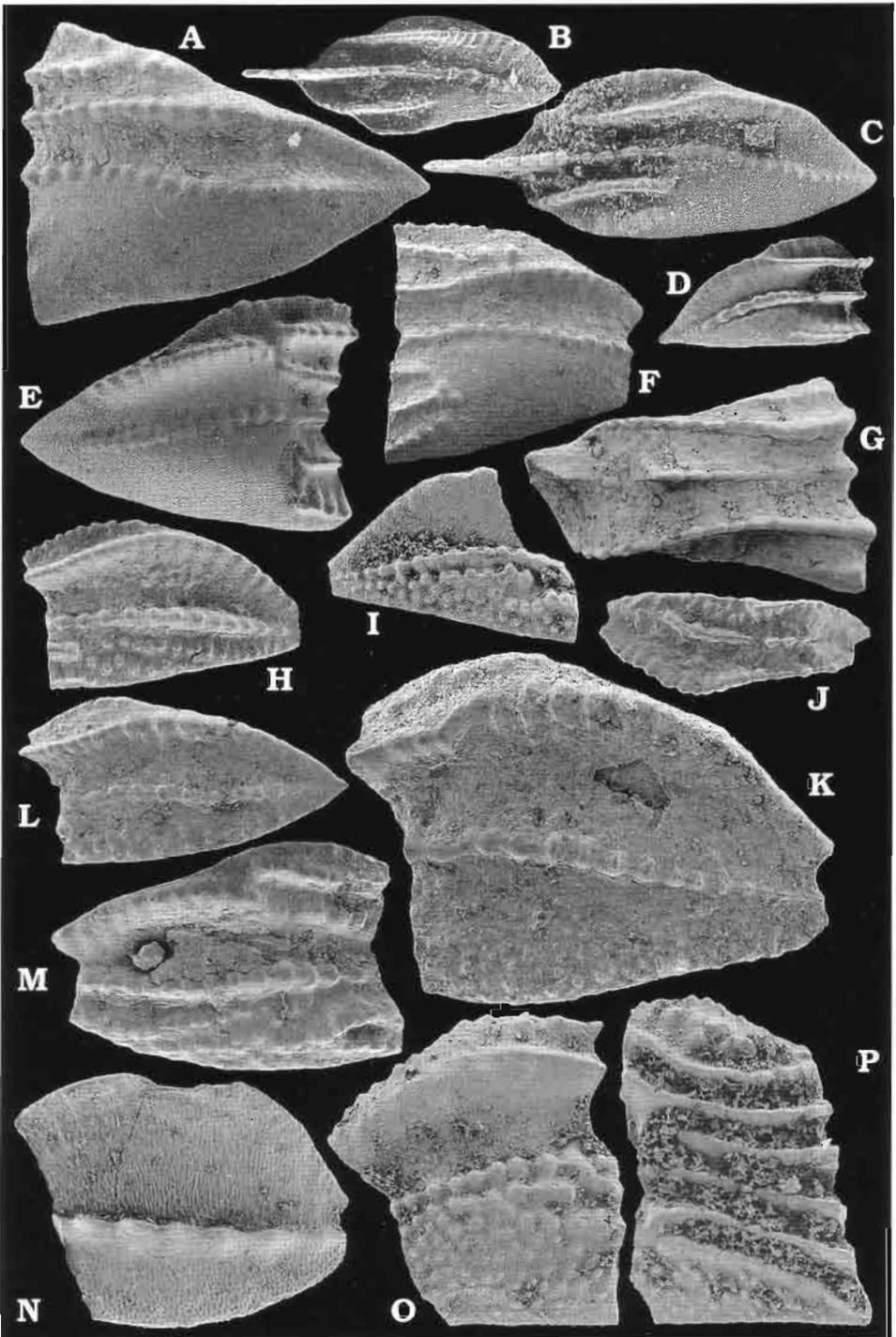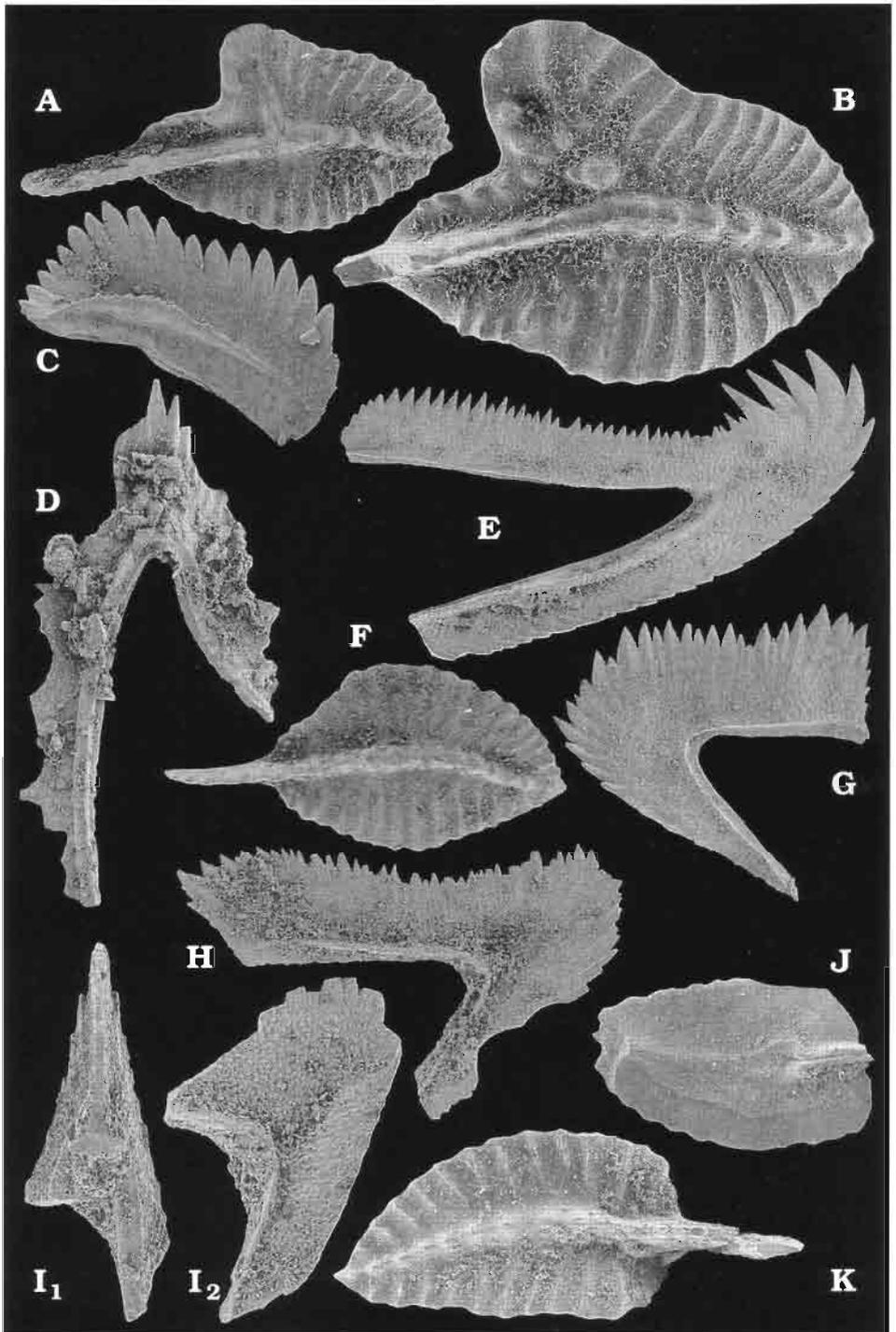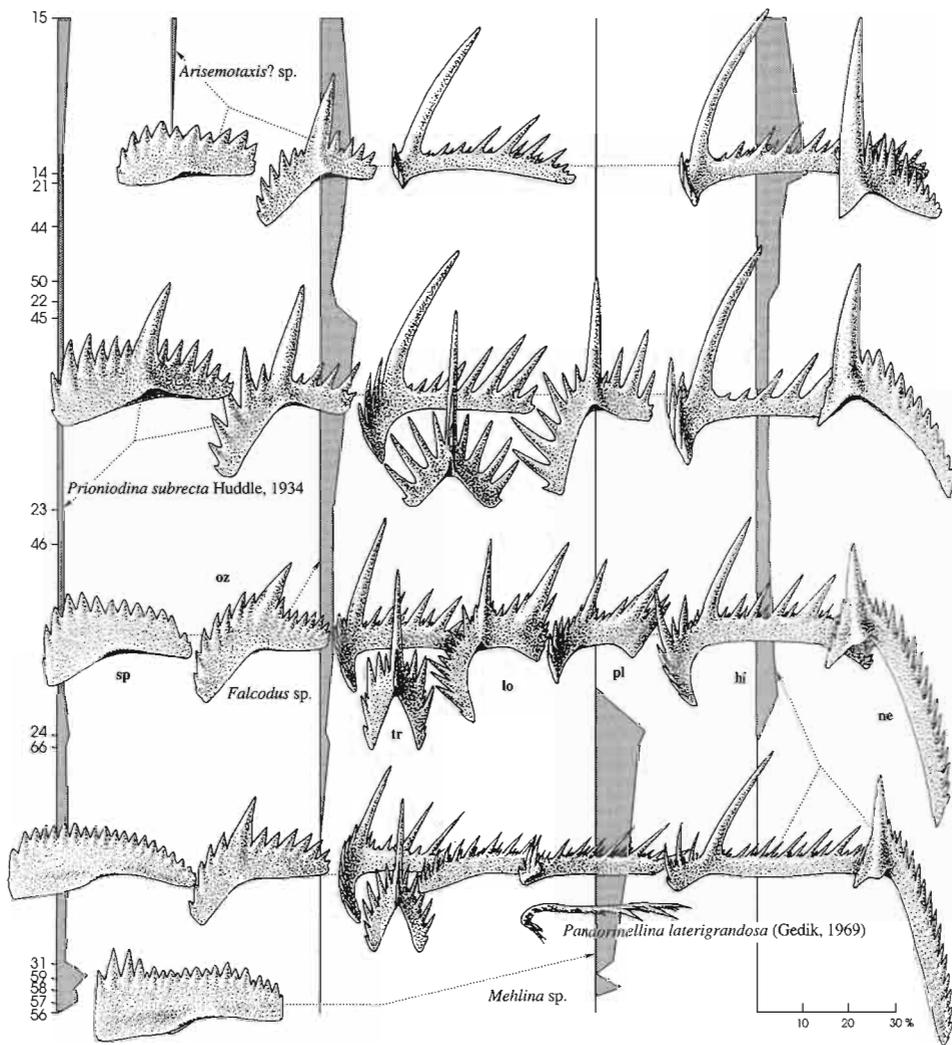
Fig. 21. Succession of prioniodinid and non-platform polygnathid conodont apparatuses in the early Tournaisian of Dzikowiec and percentage contribution of particular lineages to the whole conodont fauna in samples; distances between samples standardised based on correlation with the Kowala section to give a better approximation to time.

Fig. 20. *Dinodus* and possibly related forms from the Tournaisian Wapnica beds of Dzikowiec. **A–I**. *Dinodus lobatus* (Branson & Mehl, 1934) from samples Dz-15 (**A, C, E, F, H, I**), Dz-14 (**B**) and Dz-50 (**D, G**); elements **sp** (**A, B**, ×66; **F** juvenile, ×66), **oz** (**C**, ×80), **hi** (**E**, ×60), **pl** (**G, H**, ×66), and **tr** (**I** in medial and lateral views, ×100); specimens ZPAL C XVI/182, 372, 175, 110, 82, 180, 111, 81, and 80, respectively. **J, K**. *Pinacognathus fornicatus* (Ji, Xiong, & Wu, 1985) (?) from sample Dz-23, elements **sp**; × 66, specimens ZPAL C XVI/329 and 328.
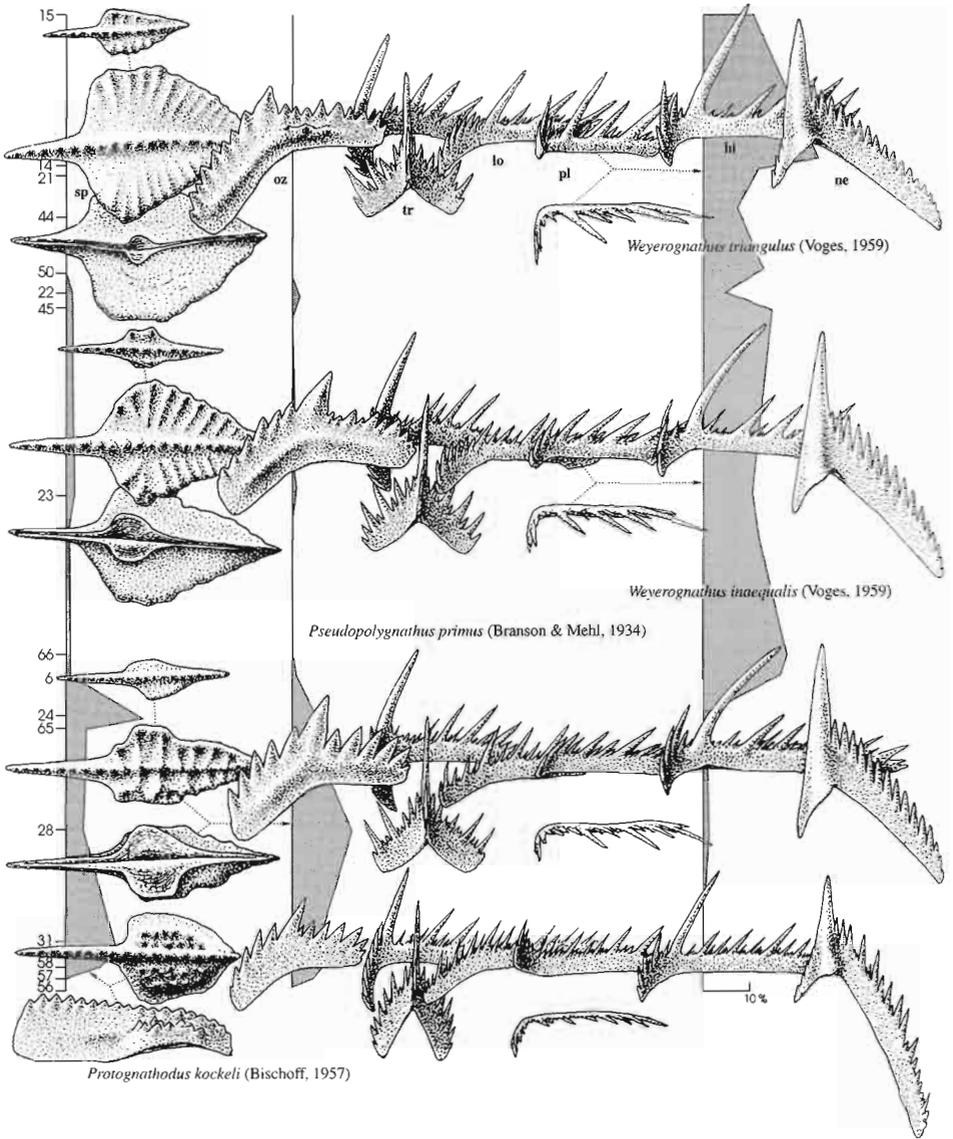
Fig. 22. Succession of polygnathids with wide basal cavities of **sp** elements in Dzikowiec.

The holotype of *Siphonodella isosticha* Cooper, 1939 from the 'pre-Welden' shale of the Arbuckle Mountains in Oklahoma (younger than *Siphonodella obsoleta* according to Over 1992: p. 297) is a juvenile specimen.

Siphonodella **sp. cf. *S. obsoleta* Hass, 1959**. — The platform elements in the population represented by samples Dz-14 (S end of the quarry in Dzikowiec) and Dz-21 (N end) are rather variable in ornamentation of their occlusal surfaces. In specimens mature enough to be determinable, the posterior rostral ridges continue much above the level of the cusp (basal pit), almost half of them being sinusoidally curved and reaching the posterior margin asymptotically. In numerous specimens, however, the ridge curves posteriorly meeting the platform margin at a high angle: the pattern typical
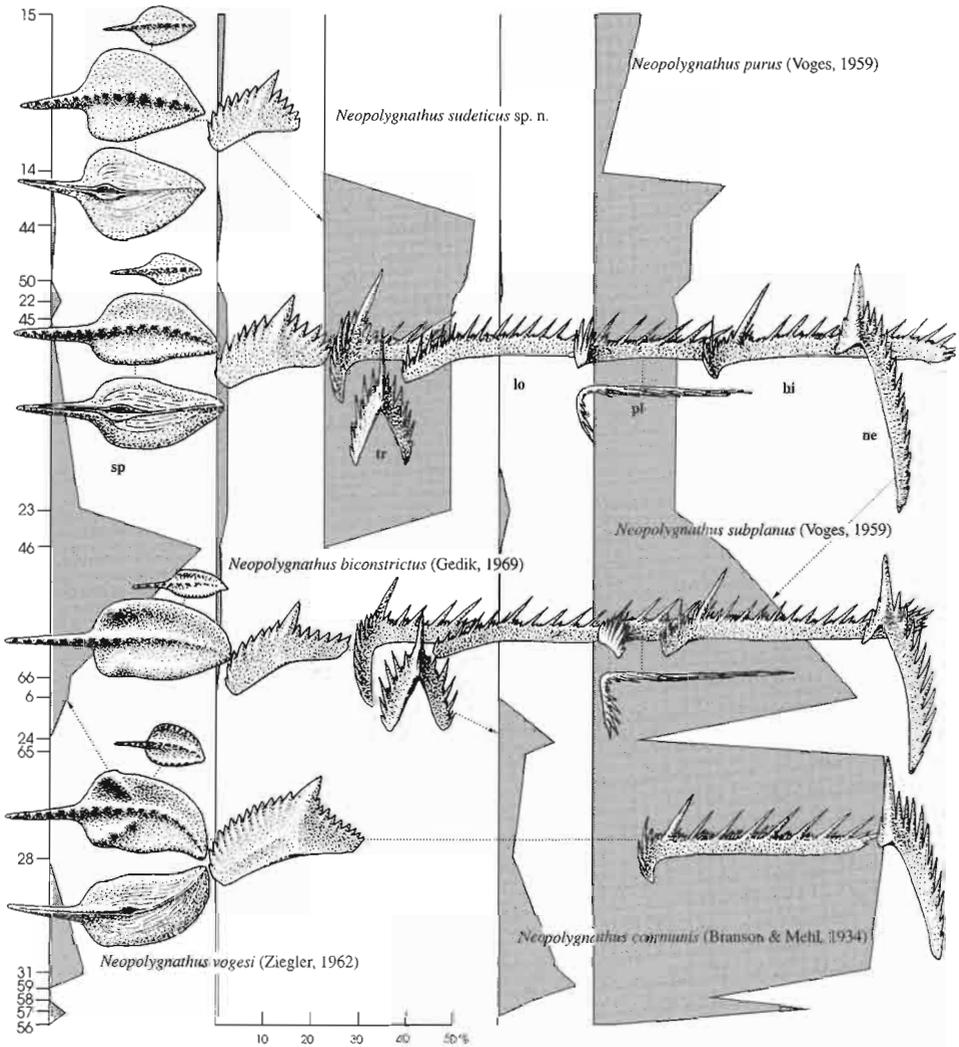
Fig. 23. Succession of *Neopolygnathus* in Dzikowiec.

of populations occurring below and above in the Dzikowiec section. Unlike the older populations, the concave central part of the platform is ornamented by at least weakly developed transverse ridges or, rarely, by tubercles. It remains possible that the observed differences between the Dz-50 and Dz-14 populations are just a result of an intraspecific variability, which is very wide in both cases. I am not able to prove it biometrically because of problems with quantifying the diagnostic characters, which are also not easily discernible using light microscopy.

Specimens with a narrow unribbed central part of the platform occur in the youngest productive sample of the Kowala section, Ko-21 (Fig. 19O), and may be conspecific with these Dzikowiec populations.

Only a few ramiform elements that can be matched with these platform elements have been found. The **oz** elements are of morphology similar to those occurring below in the section except for
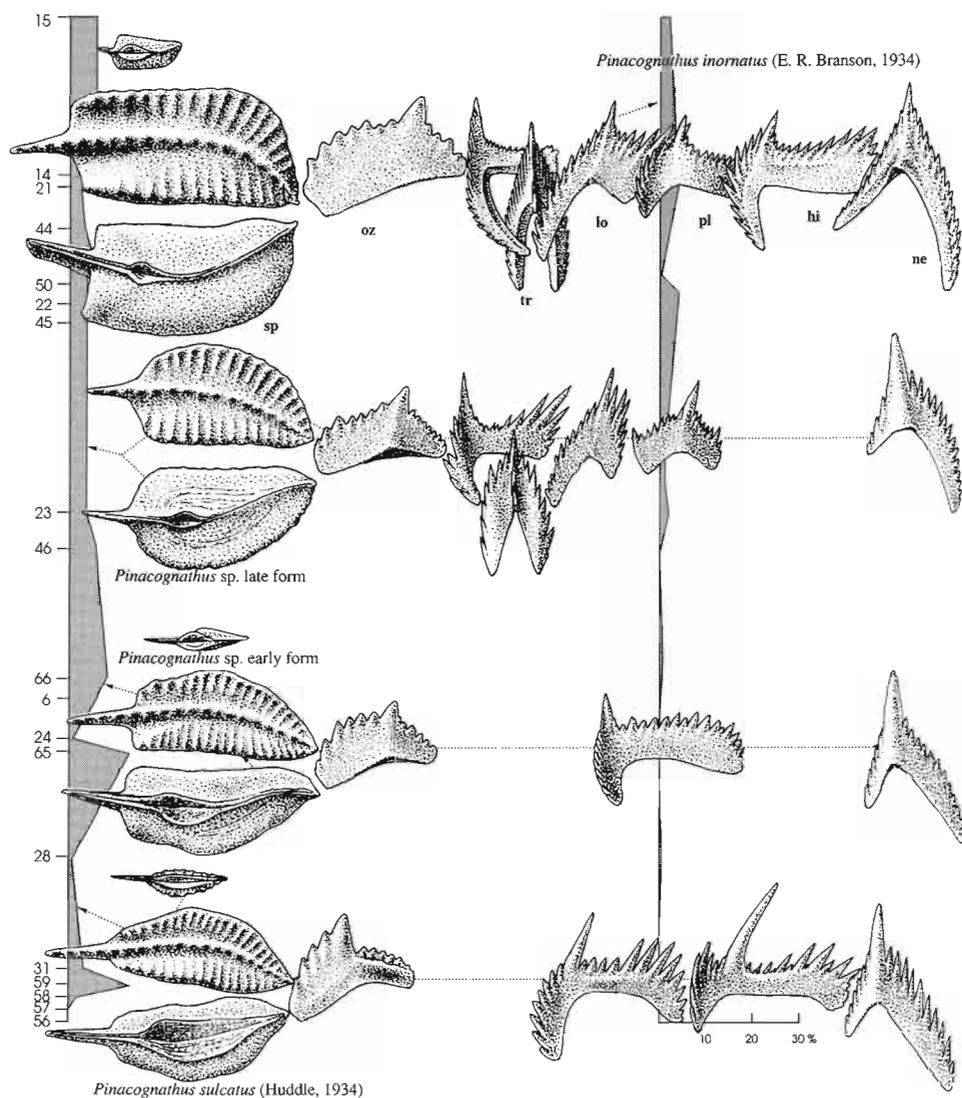
Fig. 24. Succession of *Pinacognathus* in Dzikowiec (apparatus reconstruction of *P. sulcatus* based mostly on the Muhua material; symmetry transition series of sympatrically occurring species have been attributed to them arbitrarily).

much stronger transverse ridges at the basal cavity, giving the element a cruciform appearance when seen occlusally. The **hi** elements (if correctly identified) do not differ significantly from those attributed to other species of the genus.

Exactly the same element morphology that dominates among mature elements in the Dzikowiec population seem to characterise the type population of *Siphonodella obsoleta* from sample 9301 taken 2.5–3.0 m below the top of the Chappel Limestone at the Barton Ranch section in Mason County, Texas. The holotype (Hass 1959: pl. 47: 2) seems to be a typical member of its population represented by 52 specimens co-occurring in a low diversity assemblage with much more numerous *Gnathodus*
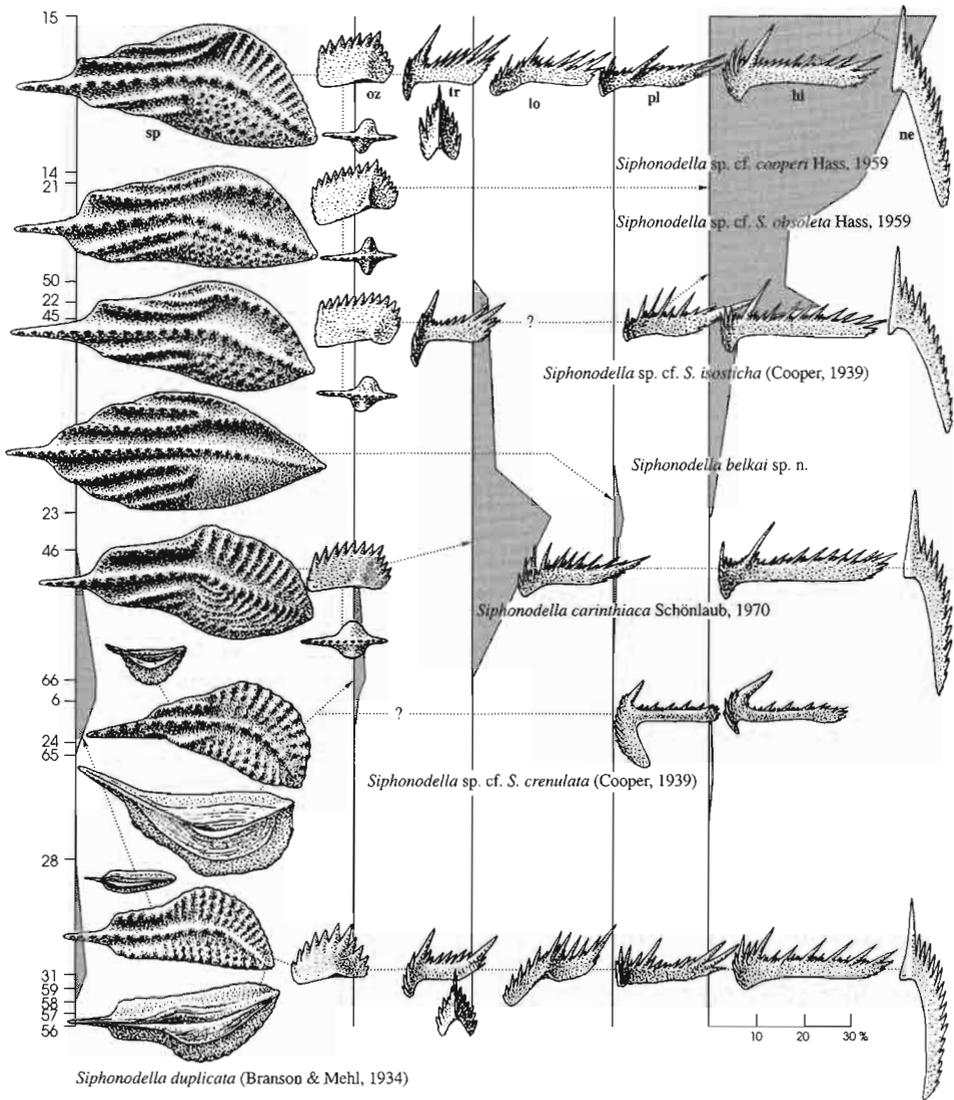
Fig. 25. Succession of *Siphonodella* in Dzikowiec (attribution of symmetry transition series in apparatus reconstructions is highly tentative).

punctatus Cooper, 1939. However, the currently accepted time correlation between American and European sections makes this taxonomic identification unacceptable, as was also the case with the preceding species.

Siphonodella cf. cooperi Hass, 1959. — Conodonts of the genus *Siphonodella* are the most common in the sample Dz-15 taken from the topmost bed of the Dzikowiec section. The sample is strongly unbalanced and the species is mostly represented by the most massive platform **sp** elements. There seems to be enough other elements, however, to enable apparatus study. Most fortunate for the restoration of the *Siphonodella* apparatus is the relative rarity of *Neopolygnathus purus* elements.
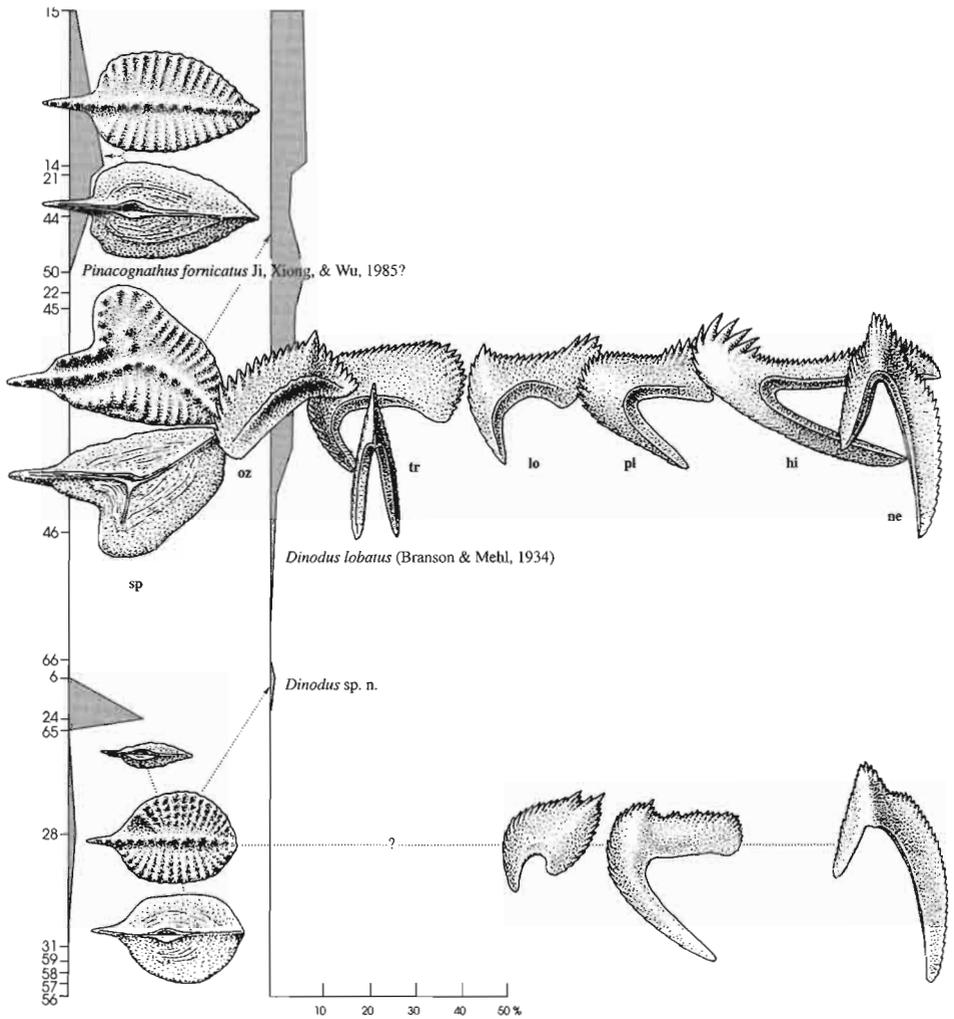
Fig. 26. Succession of *Dinodus* and related forms in Dzikowiec. The apparatus of *P. fornicatus* may be identical with, or closely similar to, that attributed here to *P. inornatus* (Fig. 24).

Their abundance in other samples containing late species of *Siphonodella* makes difficult separation of the symmetry transition series elements to each of the apparatuses that in this respect seem similar (note that the virtual lack of *Dinodus* ramiform elements in samples Dz-6 and Dz-30 is used to exclude them as possible members of the *Siphonodella* apparatus). Although still conjectural, the apparatus of late *Siphonodella* is thus reconstructed here as typically polygnathid.

The most typical, and attributed there with the highest probability, are elements in the **oz** position. They are minute, short-bladed, and sharply denticulated. Much more problematic is the identification of the symmetry transition series elements. There are some in the samples with **sp** and **oz** elements of the species that seem to differ from associated *Neopolygnathus purus* elements in their shorter processes. Such a morphology is to be expected in *Siphonodella* if it was really derived from *Pinacognathus*. A very small adult size of the non-platform elements in the *Siphonodella* apparatuses would differentiate these genera if the attribution is correct. The **hi** elements are very similar to juveniles of associated *Neopolygnathus*, but seem to be separated from them, apart from short ventral

processes, in a fan-like arrangement of denticles, usually with the base of the process projecting externally. The **ne** elements tentatively classified here have undenticulated and sometimes almost completely reduced ventral processes.

In the large sample of **sp** elements of this species different histogenetic stages are well represented. The smallest identified elements have their platform gently bent orally, resembling in morphology simple polygnathids. Because of lanceolate shape of the platform, its margins in the part of element ventral (posterior) of the cusp (identifiable only on the basis of basal pit position) reach almost vertical orientation. In subsequent growth, a new platform margin develops at the level of the element base that grows in the same way as the initial platform until vertical position of the margin is reached. In the dorsal ('posterior') part of the element growth continues in the previous direction. This pattern is repeated several times, the largest elements found have three parallel (rostral) ridges on each side of the blade (carina). The distance between ridges is stable, approximately 120 μm. Apparently there was a morphogenetic field along the blade and ridges inhibiting their origination in shorter distances. The ability to form ridges suddenly disappears dorsally of the cusp but during growth of the element the boundary between ridge-bearing and ridge free areas expands somewhat dorsally which result in its obliquely angular course. At least the end of the two first originating anterior ('inner') ridges is underlined by a development of transverse junction. This is the most characteristic feature of the Dz-15 population. To be identified taxonomically, elements adult enough to have two ridges on both sides of the blade are thus required.

A few **sp** elements of *Siphonodella* found in sample Dz-15 do not show clear dorsal boundaries in the range of ridges. They do not show any apparent signs of reworking; it remains thus unknown whether they are end-members of population variability or rather came from the underlying strata.

Several populations of *Siphonodella* are known that show dominance of the character most typical for the latest Dzikowiec species, that is, the transverse connection between two anterior ridges in the **sp** element. Cooper (1939) illustrated several specimens of this morphology from the pre-Welden shale of the Arbuckle Mountains in Oklahoma, which is younger than *Siphonodella obsoleta* in age (see Over 1992: p. 297). Several new names were proposed by Cooper (1939), but to recognise their exact biological meaning a more detailed study of material from the type locality is necessary.

The type population of the species comes from the sample 9300 taken about 6 meters below the top of the Chappel Limestone at the Barnett Trench section in Mason County, Texas (Hass 1959: pl. 48: 36). It remains unclear whether the American population has anything to do with the European one, but it seems unreasonable to separate them until more data on the population variability and vertical distribution in the type section are provided.

The same variety of element morphologies as in sample Dz-15 seems to characterise sample 438 of the Kronhafensgraben in the Carnic Alps, where they have been identified as representing several species of *Siphonodella*, namely *S. crenulata*, *S. cooperi*, *S. obsoleta*, *S. isosticha*, and *S. quadruplicata* by Schönlaub (1969). The elements were extracted by him from the last, thin bed of the limestone sequence in the area, exactly as in Dzikowiec. Above, there are black shales with limestone concretions. *Siphonodella* platform elements that agree in ornamentation with those from the youngest Dzikowiec population occur also in the middle and upper part of the Limushan Formation in the Muhua section in Guizhou (Ji *et al.* 1989: pl. 15: 1–6, 16: 3–9).

***Dinodus* sp. n.** — The oldest *Dinodus* symmetry transition series elements in the Dzikowiec section occur in sample Dz-6 and in the Muhua section 0.6 m above the base of the Tournaisian limestone. They differ from later elements of the same genus in not having any platform-like ridges at their bases; they thus probably belong to a new species. In samples Dz-6 and Dz-66 they are associated with strongly asymmetric **sp** elements that were proposed by Ji *et al.* (1989) to represent a transition between *S. duplicata* and '*S.*' *lobata*. These two species differ rather profoundly in the morphology of the basal surface of the **sp** elements but, if both really have the same apparatus composition, the idea of their evolutionary relationship would receive additional strength. This problem cannot be solved with the available data, so I have to take a rather arbitrary choice of matching the robust symmetry transition elements from sample Dz-6 with the robust *Siphonodella* **sp** elements co-occurring there, which are another kind of **sp** element included in this early *Dinodus*

apparatus (Fig. 26). These are similar morphologicallly to homologous elements of later *P. fornicatus* but with an even wider platform. Only a few specimens have been found and this apparatus reconstruction is, in fact, very weakly substantiated.

The issue is even more complicated by the presence of yet another candidate among **sp** elements to be matched with *Dinodus* in the low diversity Muhua sample Mu-28. These are elements resembling *S. duplicata* morphology but much more primitive than those from the Dzikowiec sample, which are transitional to *S. sulcata* in the platform appearance. There are some problems with the **oz** location in this case as, along with a single large element of morphology fitting very well *Dinodus*, there are several minute elements transitional in shape between elements attributed here to *S. carinthiaca* and those interpreted above as belonging to *S. duplicata* in the Muhua section. It is unlikely that these are juvenile elements that would later in their histogeny have developed the morphology of the *Dinodus* **sp** elements. Perhaps at this stage of evolution the lineages of *Dinodus* and *Siphonodella*, although having developed different apparatuses, did not differ in **sp** element morphology.

***Dinodus lobatus* (Branson & Mehl, 1934).** — The **sp** element of this species is very characteristic and there is no problem with its distinction from associated conodont elements (Fig. 20A, B). The basal cavity is distinctly polygnathid, similar to associated and stratigraphically lower *P. fornicatus* but not like any species of *Siphonodella*. No **sp** specimens with transitional morphology between these two species have been found in Dzikowiec, but juveniles of *D. lobatus* are of the same morphology as some specimens of *P. fornicatus*.

The **oz** elements of *Elictognathus lacerata* Branson & Mehl, 1934 type and the symmetry transition series (including also the **ne** elements) of *Dinodus* occur consistently together with **sp** elements of this species. This set of elements had been considered as possibly representing the *Siphonodella* apparatus by Sandberg *et al.* (1978), but this is contradicted by virtual lack of such elements in the richest samples of *Siphonodella* **sp** elements in Dzikowiec (for instance Dz-15, but also Dz-46). Instead, their distribution fits that of the **sp** elements that are here proposed to form the same apparatus but not being related to true *Siphonodella*.

The type population of *Siphonodella lobata* comes from the Bushberg sandstone at Brickeys in Missouri, the holotype being an adult specimen (Branson & Mehl 1934: pl. 24: 14, 15).

Latest Famennian and early Tournaisian ammonoids from Poland

The Polish part of the Variscan belt belongs to the same province as the Rhenish Massif, not only tectonically, but also faunally. The differences, if observed, are due mostly to different time horizons being represented by ammonoid assemblages in the Dzikowiec section and in the Rhenish localities. The unusually low diversity of the Kowala *Acutimitoceras* fauna is probably real, but the low number of species identified in Dzikowiec almost certainly results from still superficial knowledge of the locality, as shown also by finds of unexpected protoconch morphologies in conodont samples. The topmost beds of the Dzikowiec section contain ammonoid assemblages unknown from the Rhenish Massif, but definitely related to them and they apparently represent the next step in the evolution of the fauna (Fig. 3). There is no reason to expect that in Dzikowiec the ammonoid succession was different from that in Thuringia and the Rhenish Massif. In all these areas, the beginning of the *Gattendorfia* Stufe carbonate sedimentation is marked by an immigration of a new exotic fauna with quite advanced forms like discoidal sharp-edged *Acutimitoceras acutum* (Schindewolf, 1923) and

evolute *Eocanites*. Such a fauna occurring immediately above that with *A. prorsum* in Thuringia has been dated by Weyer (1977) as *S. duplicata* Zone.

The review below is based on a small new collection of ammonoids from the area studied and it has been attempted to match the new evidence with that provided by German authors, mostly Vöhringer (1960), Weyer (1965), and Korn (1994). Probably only a small fraction of the real faunal diversity of the Dzikowiec ammonoids is known, as suggested by several specimens that can not be easily identified specifically with those known from other areas.

Acutimitoceras prorsum **(H. Schmidt, 1925) (?)**— As mentioned above, the bedding plane of a tuffite 1.2 m above the top of the *Wocklumeria* limestone in the Kowala trench is covered with numerous specimens of ammonoids probably conspecific with, or at least closely related to, Rhenish *Acutimitoceras prorsum*. When compared with the type population from Stockum in the Rhenish Massif (Korn 1994; see also House 1992), the Kowala specimens seem to differ slightly in having a less prominent ventral sinus of the aperture and more regular distribution of growth lines. However, this may be partially a result of differences in preservation (Fig. 27A–G). More importantly, the Kowala assemblage seems to be monospecific as more than a hundred fragmentarily preserved specimens seem to represent the same conch morphology. The same species occurs also in the laminated limestone 1.5 m above (Fig. 27H) but there it is very rare. Some other coiled mollusc conchs have been found there (Fig. 27I) but these seem to be pelagic? bellerophontid monoplacophorans.

cf. *Prionoceras (Mimitoceras) hoennense* **(Korn, 1993)**. — The oldest identifiable ammonoids in the Dzikowiec section have been found in sample Dz-28 with *Pinacognathus sulcatus*, thus of earliest Tournaisian age. Only one side of a juvenile, relatively compressed conch is preserved (Fig. 28A) which fits, in general shape and surface ornamentation, *M. hoennense*. Its type horizon, Oberrödinghausen Bed 2, is much younger than the Dzikowiec stratum.

cf. *Acutimitoceras convexum* **(Vöhringer, 1960)**. — The next younger Dzikowiec ammonoids come from sample Dz-24 with *S. duplicata* and the first *S.* cf. *quadruplicatai* (Fig. 28B). These are four more completely preserved juveniles that seem not unlike *A. convexum* from Oberrödinghausen Bed 5, thus presumably being older that the type population of the species.

cf. *Acutimitoceras sphaeroidale* **(Vöhringer, 1960)**. — Two large specimens, the larger being adult, as evidenced by sutural crowding, but deformed (Fig. 28C, D). They come from old museum collections and their exact source remains unknown.

cf. *Nicimitoceras trochiforme* **(Vöhringer, 1960)**. — Perhaps the poorly preserved, strongly compressed specimen ZPAL Am VII/764 (Fig. 28E) belongs here. The species has already been reported by Weyer (1965), who attributed another specimen from an old museum collection to the related *N. heterolobatum* (Vöhringer, 1960), which seems to have, however, a more subacute venter (see Korn 1994).

Acutimitoceras subbilobatum **(Münster, 1839)**. — The species has been identified on the basis of museum specimens of unknown exact origin by Weyer (1965).

Acutimitoceras simile **(Vöhringer, 1960)**. — Weyer (1965) described specimens of this species from an old collection. A fragmentary specimen that shows well developed constrictions typical of the species has been encountered in the sample Dz-46.

Gattendorfia crassa **H. Schmidt, 1924**. — The well preserved specimen of unknown origin (Fig. 28G) fits morphologically into the range of variability proposed for the species by Korn (1994). A larger, more widely umbilicate specimen has been placed here by Weyer (1965). The species occurs in Bed 2 in Oberrhödinghausen.

Gattendorfia costata **Vöhringer, 1960**. — A large ammonoid with sharply edged wide umbilicus found in sample Dz-21, as well as others of unknown exact provenance (Fig. 28F) may represent this species, known from Oberrödinghausen Bed 1, thus approximately the same horizon.
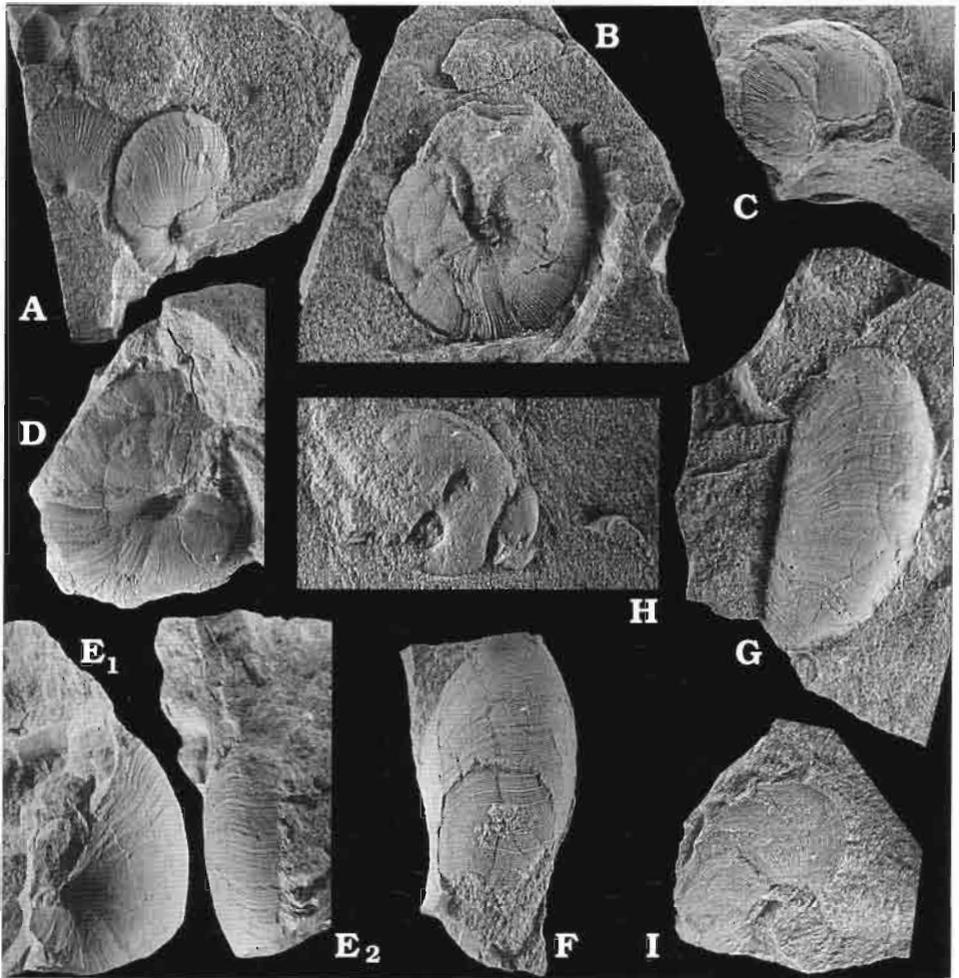
Fig. 27. Latest Famennian ammonoids and a possible bellerophontid gastropod (see Korn *et al.* 1994: p. 19) from the tuffite layer (sample Ko-52: **A–G**) and laminated limestone (Sample Ko-51: **H, I**) in the Kowala trench; all × 2. **A–H**. *Acutimitoceras prorsum* (H. Schmidt, 1925); specimens ZPAL Am VII/1659, 1658, 1660, 1708, 1707, 1661, 1657, and 1651, respectively. **I**. *Sinuitina*? sp.; ZPAL AmVII/1662.

Gattendorfia tenuis **Schindewolf, 1952**. — The horizon, from which the characteristically compressed specimen with distinct constrictions described by Weyer (1965) came, may be the same as that of *G. costata*; in Oberrödinghausen both species co-occur.

Eocanites nodosus (**H. Schmidt, 1925**). — Several juvenile specimens of this species have been found in sample Dz-46. Suture line, traced in the specimen ZPAL Am VII/1693 (Fig. 3) and well preserved growth lines, variable in density (Fig. 29B) do not show any significant differences with respect to the Rhenish population (see Korn 1994). The relationship of the juvenile specimen identified by Weyer (1965) with this species, as well as *E. tener* (Vöhringer, 1960) and *E. brevis* (Vöhringer, 1960), to those of sample Dz-46 remains unclear.

Eocanites **n. sp. A Weyer, 1965**. — The specimen described by Weyer (1965) comes from a museum collection. In conch ornamentation and suture line (Fig. 3) it does not resemble any other species of the genus.

Eocanites **sp. n. aff.** *E. rursiradiatus* **Ruan, 1981**. — A single large specimen from sample Dz-14 (Fig. 29A) is different from all other species of the genus in the strongly compressed whorl cross section and concave venter. The suture, perhaps in connection with the whorl shape and size, shows saddles wider than those in related species, the ventral lobe with gaping slopes slightly resembling those in *Merocanites*, and the latero-dorsal lobe a little better developed than typical for *Eocanites* (but somewhat resembling *E.* sp. n. A). The Chinese species of Ruan (1981) may appear transitional between *E. nodosus* (according to Vöhringer 1960 adults of this species have compressed whorl section) and this apparently new species.

Paprothites dorsoplanus **(H. Schmidt, 1924)**. — More or less fragmentary specimens with high conch expansion rate and flat venter typical of the species have been found in sample Dz-46 (Fig. 29C).

Pseudarietites silesiacus **Frech, 1902**. — This is probably a successor of the preceding species within the same lineage (Fig. 3), which is consistent with its occurrence in much higher position of sample Dz-15 (Fig. 29E, F). The type specimens of the species (Fig. 29D, G) may have came from this horizon, too.

Pseudarietites planissimus **Vöhringer, 1960**. — This species, identified in Dzikowiec by Weyer (1965) belongs to a parallel, rapidly evolving lineage within the genus that developed an acute venter with a medial keel (see Korn 1994). Juvenile specimens identified by Weyer as *Protocanites (Eocanites) carinatus* (Vöhringer, 1960) may belong to the same species or, as suggested by superposition in Oberrhödinghausen, come from another, older bed. In fact, there is not much choice in this respect in the highly condensed Dzikowiec section (Fig. 3).

Paralytoceras crispum **(Tietze, 1871)**. — Both the two specimens redescribed by Weyer (1965; herein Fig. 29H) are of unknown stratigraphic position. This is a highly advanced species and hardly could be expected below the horizon of sample Dz-14; perhaps it originated from the topmost bed, from which sample Dz-15 was taken (Fig. 3).

Qiannites? **sp**. — Fragments of juvenile ammonoid conchs commonly occur in samples processed for conodonts. In older samples from the Dzikowiec section they are mostly of rather generalised morphology and uniform size (Fig. 30C–E) that does not allow more precise identification, except that these are prionoceratids. In sample Dz-21, however, there is more diversity in protoconch morphologies and along with typical prionoceratid protoconchs of significantly smaller size, possibly representing *Eocanites* (Fig. 30B), as well as extremely large ones (Fig. 30A), occur. The latter protoconch type is virtually indistinguishable in size and shape from that attributed to a prodromitid from the Exshaw Shale of Alberta by Schindewolf (1959) and House (1992). Only two larval septa are represented in the Dzikowiec specimen, so it is unclear whether the prodromitid subdivision of the ventral lobe was developed there. Probably not yet, as the age of the Dzikowiec sample is significantly older than the Exshaw Shale ammonoids, but phylogenetic affinity to the prodromitids seems clear. I find it also unlikely that the protoconch belonged to a genus unknown from the European or southern Chinese Tournaisian. This means that the ancestry of this still enigmatic North American lineage has to be sought among oxyconic *Gattendorfia* Stufe ammonoids exhibiting a tendency to subdivide the ventral lobe. At least two such forms are known: *Voeringerites peracutus* (Vöhringer, 1960) from Bed 5 at Oberrhödinghausen (see Korn 1994), thus much older than the Dzikowiec species, and *Karagandoceras?* sp. n. I of Bartsch & Weyer (1988) from the *S. sandbergi* Zone of Thuringia, which is more or less coeval or a little older. Of similar age is also the most primitive Chinese prodromitid, *Qiannites acutus* Ruan, 1981. The Dzikowiec species may belong to the same lineage being somewhat older than *Eoprodromites* from the *S. crenulata* Zone of the Hannibal Shale in Missouri, the ancestor of *Prodromites* (Work *et al.* 1988).

Latest Devonian biotic events

The only place in Poland where the faunal transition between the Famennian and Tournaisian can be studied in a stratigraphically continuous section is Kowala. It fits well the general pattern documented in other areas of the world, being probably one of the least condensed and unmetamorphosed. Unfortunately, the ammonoids, abundant in the Famennian (including the *A. prorsum* fauna) are missing in the Tournaisian. The conodont record, however, is quite complete and their recovery is only a matter of time--consuming sample processing to obtain their elements in high quantities from almost unlithified clays and limestone concretions.

In Kowala, the clymeniid *Wocklumeria sphaeroides* occurred to the end of the Devonian carbonate sedimentation (*Parawocklumeria paradoxa* has also been found in the same part of the section, although not directly in the wall of the trench), together with the last palmatolepidid conodonts: *Tripodellus gracilis* and *T. sigmoidalis*. Only *Neopolygnathus communis*, associated with rare specimens of the latter species, *Branmehla? bohlenana, Mehlina*, and *Prioniodina*, thus a typically Devonian and rather diverse assemblage of very generalised species, continued to occur when only fine clastic sediment was deposited immediately later. There is no evidence of *Protognathodus* until carbonate sedimentation resumed (it was followed by *N. communis* and rare *T. sigmoidalis*, perhaps reworked). Presumably, *Protognathodus* was present already when the ammonoid *Acutimitoceras prorsum*, abundantly represented in the tuffite, invaded the area, and such is its pattern of occurrence in the Rhenish Massif (Korn *et al.* 1994). *Protognathodus* disappeared together with the carbonate facies and again the dominant species was *N. communis*, followed by *Pseudopolygnathus ('Bispathodus') costatus*. First members of the *Pinacognathus* lineage appeared soon and then a surprisingly advanced *Pseudopolygnathus*. From this point a typical succession of the *Gattendorfia* Stufe conodonts started (Fig. 5) with gradually increasing diversity and reduced contribution of generalised species of the *Neopolygnathus* lineage. This pattern is suggestive of a purely ecological control of appearances, with no contribution of local phyletic evolution and speciation. The physical cause for this faunal replacement remains unclear, but most probably climatic factors were more important than pure eustacy, which does not seem profound there. Even if the change from the carbonate to fine clastic sedimentation was connected with a transgression terminating the *Wocklumeria* limestone, sedimentation and tuffites are the result of inland erosion at the time of a regressive event.

Early Tournaisian conodonts are also known in the Holy Cross Mountains from sediments filling fissures within the late Devonian carbonate buildups (Szulczewski 1973), the phenomenon reported also from the Harz Mountains (Fuchs 1987).

Fig. 28. Prionoceratid and gattendorfiid ammonoids from the early Tournaisian Wapnica beds in Dzikowiec. **A.** cf. *Prionoceras (Mimimitoceras) hoennense* (Korn, 1993), a fragmentary specimen ZPAL Am VII/1681 from sample Dz-28; × 2. **B.** cf. *Acutimitoceras convexum* (Vöhringer, 1960), specimen ZPAL Am VII/1679 from sample Dz-24; × 2. **C, D.** cf. *Acutimitoceras sphaeroidale* (Vöhringer, 1960), specimens IG 139.II.79 and 70, horizon unknown; both × 1. **E.** cf. *Nicimitoceras trochiforme* (Vöhringer, 1960), specimen ZPAL Am VII/ 764, horizon unknown, possibly corresponding to Dz-46; × 1. **F.** *Gattendorfia costata* Vöhringer, 1960, specimen ZPAL Am VII/973, horizon unknown, possibly corresponding to Dz-22; × 1.5. **G.** *Gattendorfia crassa* H. Schmidt, 1924, specimen ZPAL Am VII/765, horizon unknown; × 1.
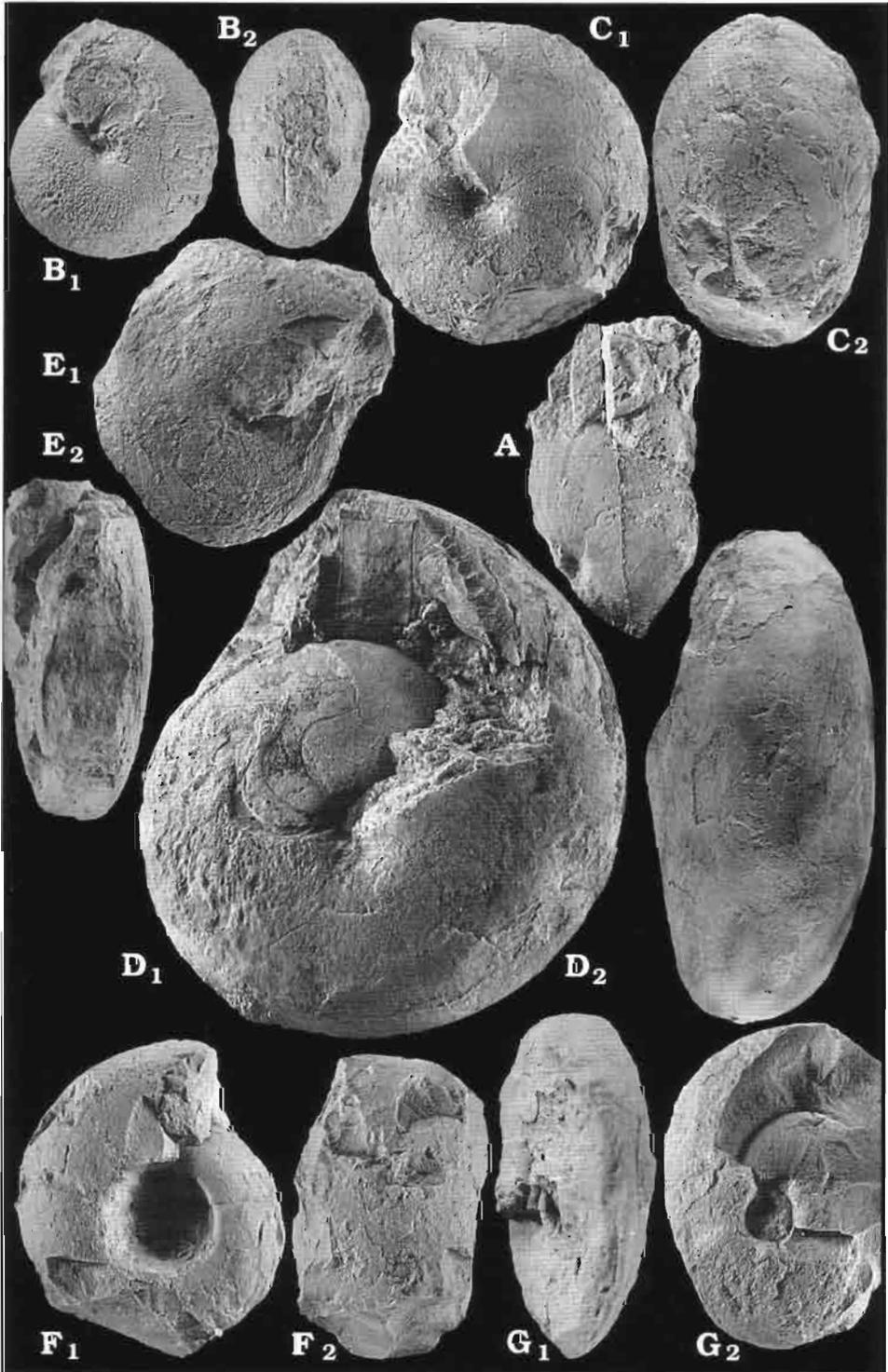
Corresponding bioevents in other sections. — The deepest-water facies section where the events at the Devonian–Carboniferous boundary are recorded by conodont assemblages has been described from the Arbuckle Mountains of Oklahoma by Over (1992). Both the Famennian and early Tournaisian are represented there by black, organic-rich shales of a relatively deep shelf sedimentary environment, the dominating conodonts being *Bispathodus stabilis* and *Branmehla inornata*. In most sections the boundary strata are missing and the non-deposition period is marked by a pelletal phosphorite intercalation (Over 1992). Phosphorites are generally common in the section. Wocklumeriid ammonoids are reported from 21 m below the top of the Devonian at the Ryan Shale Pit locality (Over 1992: p. 300) and both this finding, and the associated fauna with *'Pseudopolygnathus' trigonicus*, provide sufficient evidence that the black shale is an equivalent to the European *Wocklumeria* limestone. Only in a single locality, the Wapanucka Shale Pit, do the boundary events seem to be completely recorded and there the black shale sedimentation changes to paler shales together with the incursion of the *Protognathodus* fauna equivalent to that known from above the European black Hangenberg Shale. This may represent a shallowing event.

The Hangenberg Black Shale of the Rhenish Massif is interpreted as representing the maximum sea-level stand that culminated and ended the *Wocklumeria* Stufe transgression (Van Steenwinkel 1983; Girard 1994). No conodonts are known from it but from the Rhenish locality Drewer the last clymeniid ammonoids are reported from this horizon, which points to an ecological continuity with the preceding carbonates (Korn 1992).

The incursion of the *Protognathodus* fauna in the Puech de la Serre section in the Montagne Noire coincided with the re-establishing of carbonate sedimentation and apparent shallowing of the sea, expressed in a domination of *Neopolygnathus* throughout the early Tournaisian. *Protognathodus* is relatively numerous (almost 50 per cent) in the basal bed of the limestone, and contributes significantly to the assemblages only in two separated horizons, much less than 10 per cent of the platform elements (Girard 1994).

In the classic southern Midcontinent North American localities of Tournaisian rocks in central and southern Missouri, where most of the conodont species of this age have their type localities, the geological record of the Devonian–Carboniferous boundary is missing. The oldest Carboniferous is represented there by the single calcareous sandstone bed of the Bachelor Formation (Bushberg of Branson & Mehl 1934) containing a conodont assemblage dominated by a robust *Pseudopolygnathus*, with probably reworked or at least time-averaged *Siphonodella* showing quite a range of morphologic variability (Thompson & Fellows 1970). The co-occurrence of *Siphonodella duplicata* and *S. lobata* suggests reworking; before the *S. duplicata* Zone there was apparently a time of non-deposition. Presumably, continuous sedimentation was initiated there with the world-wide transgression of the *S. crenulata* Zone (e.g., Savoy & Harris 1993). Sections in northern Missouri are relatively complete (Ziegler & Sandberg 1984).

The best record of conodont faunal dynamics at the Devonian–Carboniferous boundary in shallow-water environments is provided by Australian sections of the Canning Basin (Nicoll & Druce 1979). The latest Famennian Hangenberg transgression seems to correspond there to sedimentation of the Gumhole Formation with
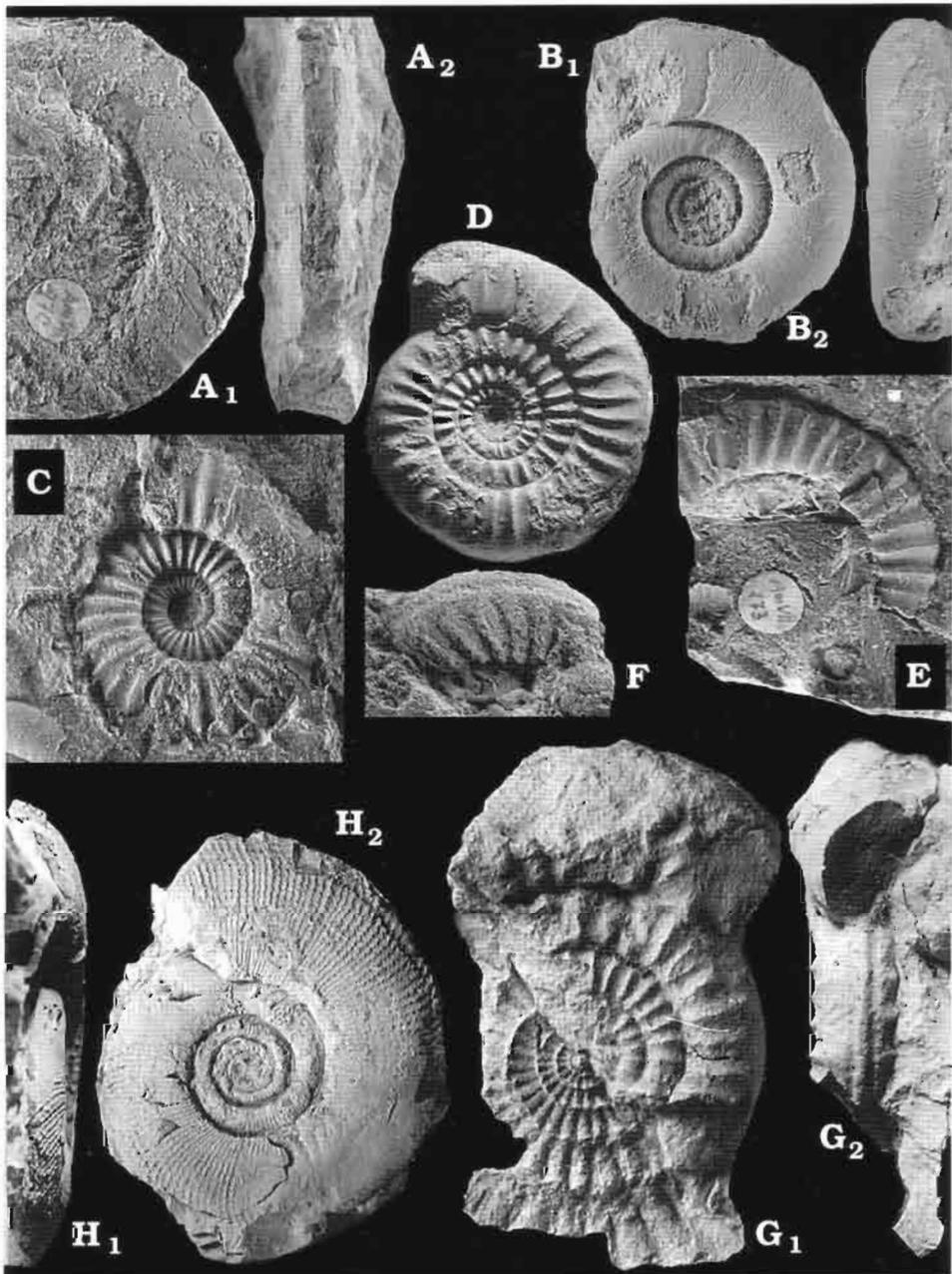
Fig. 29. Prolecanitids and pseudarietitines from Dzikowiec. **A**. *Eocanites* sp. n. aff. *E. rursiradiatus* Ruan, 1981, specimen ZPAL Am VII/770 from sample DZ-14; × 1.5. **B**. *Eocanites nodosus* (H. Schmidt, 1925), specimen ZPAL Am VII/1694, sample Dz-46; × 3. **C**. *Paprothites dorsoplanus* (H. Schmidt, 1924), specimen ZPAL Am VII/1711; × 2. **D–G**. *Pseudarietites silesiacus* Frech, 1902. **D**. Holotype UWR 1773s; × 2. **E**. Specimen ZPAL Am VII/773, sample Dz-14; × 1.5. **F**. Specimen ZPAL Am VII/771, sample Dz-14; × 1.5. **G**. Paratype UWR 2089; × 2. **H**. *Paralytoceras crispum* (Tietze, 1870), holotype MB (unnumbered); × 1.

Pelekysgnathus australis, *Vyaloviodus platys*, *Pandorinellina*, and *Neopolygnathus* dominating the low-diversity assemblage. The shallowing event of the Hangenberg Limestone seems to correspond to the Yellow Drum Sandstone, when *Neopolygnathus* is replaced in the assemblage by *Pseudopolygnathus*. At the beginning of the following eustatic rise of the Laurel Limestone, a *Syncladognathus* species (Apparatus A of Nicoll & Druce 1979) appears with single elements of *Siphonodella isosticha* (*S. obsoleta* according to G. Klapper, personal communication) and *Dinodus* (including '*Polygnathus*' *thomasi*?). After its disappearance, *Clydagnathus*, which occurred earlier, became the dominant element of the fauna.

In Ireland, an ammonoid assemblage with '*Imitoceras* cf. *prorsum*' appears in an episode of black shale sedimentation within an extremely thick coarse clastic sequence (Matthews 1983). In the Mugodžary area at the southern tip of the Urals, at the locality Berčogur, black clays cover the late Famennian algal limestones and underlie a thin bed with lenses of a cephalopod limestone containing a diverse assemblage of *Acutimitoceras* and *Mimimitoceras* ammonoids. The bed is dated as *S. sulcata* Zone, the conodont assemblage being dominated by an early *Pseudopolygnathus* (Barskov *et al.* 1987).

The order of events thus seems global. It starts from the cessation of warm-water carbonate sedimentation of equivalents to the *Wocklumeria* limestone. High-diversity pelagic faunas disappear with a deepening that resulted in sedimentation of anoxic black shale of Hangenberg Shale-type. Subsequent shallowing corresponds with the appearance of low-diversity, probably cold-water faunas. With the following deepening and climate warming these faunas were gradually enriched by successive immigration of numerous species of completely new high-diversity pelagic faunas of the *Gattendorfia* limestone. Their geographic provenance remains unknown.

Analogies with other major bioevents. — The changes recorded in the central European sections in proximity to the Devonian–Carboniferous boundary surprisingly closely parallel those associated with the Ordovician–Silurian transition in regions of temperate climate. Thus, some increase in diversity of pelagic assemblages and their sudden disappearance associated with the end of carbonate sedimentation can be compared with similar events at the end of the Caradoc in the Holy Cross Mountains and Thuringian sections (see Dzik 1990; Dzik *et al.* 1994). The conodont faunas that replaced the relatively warm-water assemblages of the latest Caradoc in these areas, as well as in the Carnic Alps and the Baltic area, were of relatively low diversity. The dominating conodont element morphology, instead of earlier massive platforms, is a thin crown with a deep basal cavity – apparently a way to use more efficiently a limited supply of calcium. Like the Late Ordovician suppression of *Amorphognathus*-like conodonts with elaborated platform in **sp** elements by thin-crowned *Sagittodontina* and other members of the *Hamarodus* fauna, in the latest Devonian the palmatolepidids and polygnathids with prominently ornamented platforms disappeared gradually, being replaced by *Protognathodus*. Carbonate sedimentation ended in most areas and instead fine clastics were deposited. Low-diversity faunas came with a reappearance of shallower water communities of the *Hirnantia* fauna or *Acutimitoceras prorsum* fauna. Then recovery comes, with limestone facies abounding in platform conodont elements but of species not related to those that disappeared earlier. In the Llandovery these were pterospathodontids, inconspicuous in the Ordovician.
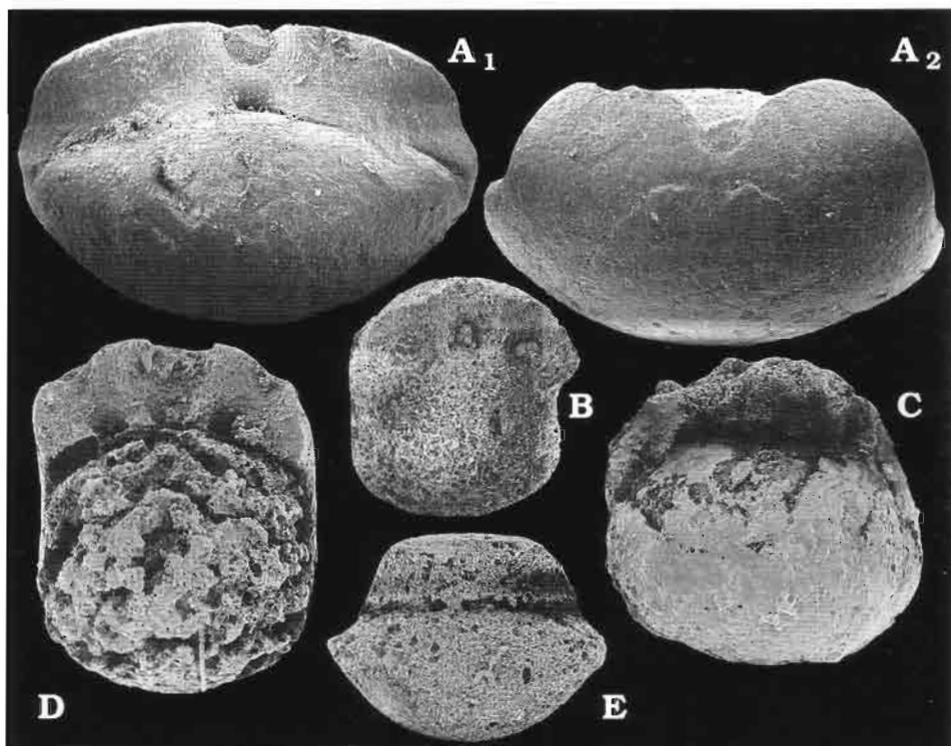
Fig. 30. Nuclei of initial conch parts from Dzikowiec; all × 50. **A**. Extremely large protoconch of prodromitid affinities, possibly *Qiannites* sp., ZPAL Am VII/1693 from sample Dz-21. **B**. Small size specimen ZPAL Am VII/1694 from the same sample. **C**, **D**. Prionoceratid ZPAL Am VII/1695 and 1696 from sample Dz-22. **E**. Closely similar ZPAL Am VII/1697 from sample Dz-23.

while in the Tournaisian the branch of *Siphonodella* speciated into at least three (perhaps five) lineages. No doubt that in both series of events climate and eustacy were the controlling factors. Most probably, the changes of both were driven by the glaciations of Gondwana.

Faunal dynamics of the *Gattendorfia* Stufe

All the three sections of the *Gattendorfia* Stufe studied quantitatively for conodonts show similar patterns in their successions (Fig. 2), despite the wide geographic distances separating them in the Tournaisian (Fig. 47). The most apparent common feature is a gradual rebuilding of the faunas at the beginning of carbonate sedimentation and relative stability throughout. The most stable in composition is the Muhua section (even if some of this is a result of a rather sparse sampling). Except for a gradual increase in the contribution of *Siphonodella* and decrease of *Neopolygnathus* up to complete disappearance of this relatively shallow water form, little has changed in the area. A significant part of the succession within particular evolution-

ary branches at the generic level was connected with phyletic evolution and was probably more significant than replacements by migration. The opposite end of the variation in faunal dynamics is shown by the Kowala succesion. There, the basal rebuilding is much more profound and a few horizons where ecological conditions were probably basically altered can be pointed out. Thus, the lower half of the section shows rather smooth and directional rebuilding of the assemblage. The first change is the disappearance of *Protognathodus* which may correspond to both deepening and warming of the sea. Then, in a long time span, *Neopolygnathus* reduces its importance at the cost of more robust *Pinacognathus* – this seems to be a continuation of the same trend in the environment. A sudden rebuilding of the assemblage in the middle of the *S. carinthiaca* Zone is still in the same direction. Despite some oscillations that are difficult to interpret, this newly established community continues up to the end of the section, with the only disturbance, but very prominent, occurring in the middle of *W. triangulus* Zone. A sudden dramatic increase in the contribution of *Neopolygnathus* and *Protognathodus* indicates a short reappearance of cold-water conditions at the beginning of the *Gattendorfia* Stufe.

Most interestingly, the sudden changes in composition of conodont faunas do not correspond to any sudden changes in sedimentation regime. They do not correspond either to any apparent evolutionary transformations within lineages. The environment of sedimentation changes gradually from purely fine clastic (with some minute levels of anoxic conditions and volcanic ash falls) to the rhythmic horizons with calcareous nodules in the middle of the section, and again domination of clay above. The regularity in distribution of nodules suggests control by a Milanković-driven cyclicity. Perhaps as a result of warming, more calcium carbonate was supplied to the water at that time, periodically approaching the level of purely carbonate sedimentation. This was hardly connected with shallowing as the conodont assemblage testifies to the opposite. With shallowing, indicated by conodonts, the carbonates disappear.

The Dzikowiec succesion is at first glance less dramatic, but on closer examination shows the same events as in Kowala. The end of significant contribution of *Protogna-thodus* seems to coincide more or less with the beginning of deepening in Kowala and in both sections *Siphonodella* then became more important. The prominent change in the upper part of the Kowala section seems to correspond to the discontinuity in record between samples Dz-14 and Dz-44 in Dzikowiec, probably caused by a brief shallow-ing of the sea and non-deposition or submarine erosion.

The occurrences of ammonoids in the Dzikowiec section are probably related to the environmental changes recorded by conodonts. In the lower part of the section, where *Protognathodus* co-occurs with *Neopolygnathus*, only rare generalised prionoceratids occur. The high-diversity ammonoid fauna comes together with abundant *Siphonodella*.

In all three sections the end of carbonate sedimentation is preceded by clear evidence of deepening (probably also climatic warming) provided by faunal changes. *Neopolygnathus* virtually disappears as *Siphonodella* became dominant, the assemb-lage diversity continuing to be high or even higher than before. The *Weyerognathus* population shows no close similarity to the stratigraphically preceding *W. triangulus* but, instead, seems transitional morphologically between much older *W. inaequalis* and the late Tournaisian *W. pinnatus*. This seems to indicate a basic rebuilding of the conodont faunas at the beginning of the *S. crenulata* transgression.

The pattern presented above seems to be typical for the whole Variscan province. With the incoming *S. crenulata* transgression, in all three sections marked by the change to black shales or radiolarites, the good record of conodont and ammonoid evolution ends. The shallow-water seas of the areas earlier exposed in Belgium and the North American Midcontinent are since that moment centres of evolution for pelagic organisms. In the Polish part of the Variscan sea the nearest opportunity to see the composition of conodont and ammonoid communities comes not earlier than close to the end of the Tournaisian.

Late Tournaisian conodonts

In Dzikowiec, the Gołogłowy Formation black shales are followed by gneissic sandstones of the Nowa Wieś Formation. Limestone pebbles found within the basal coarse clastic part of this formation have yielded *Dollymae bouckaerti*, *Scaliognathus ancho-ralis*, various gnathodontids, and *Mestognathus beckmanni*, hence limestone sedimentation and conodont faunas continued here throughout the late Tournaisian and early Viséan (Chorowska & Radlicz 1984, 1994). Some middle and late Tournaisian conodonts are known from the Sudetes from the shales above the Devonian limestones cropping out in Gołogłowy, not far from Dzikowiec (Haydukiewicz 1981), and from limestone blocks within shales from the Kaczawa region (Chorowska 1978). However, the only locality where fossiliferous late Tournaisian strata with ammonoids are exposed in Poland is the Ostrówka Quarry in the Holy Cross Mountains, where a few layers of pink or yellow-coloured marls within shales of the Radlin beds are exposed immediately above the condensed Famennian strata and below younger black shales and radiolarites of the Zaręby Beds (Szulczewski & Skompski 1995; Szulczewski *et al.* 1996). The fossil content of these strata, deposited above an extremely condensed Famennian at the top of a Frasnian carbonate platform, is the same as in the Erdbach Limestone, occurring in a similar palaeotopographic context in the Rhenish Massif (Schindewolf 1951; Krebs 1968), that is *Scaliognathus anchoralis* conodont and *Ammonellipsites kochi* ammonoid assemblages. The same or closely similar faunas are known as far from central Europe as in the Sahara (Pareyn 1961), Canada (Savoy & Harris 1993), and Australia where both conodonts (Jenkins 1974) and ammonoids (Campbell *et al.* 1983) are closely similar.

The Ostrówka conodonts are illustrated here and only briefly reviewed, as they provide little new palaeontologically important information. The samples Ost-6 and Ost-4 have been taken from two marly beds, 15 and 25 cm above the base of the Radlin beds, respectively (see Szulczewski *et al.* 1996). They yielded similar assemblages (Table 5), different mostly in a higher contribution of reworked elements and the presence of *Bactrognathus* in the upper sample Ost-4.

Eotaphrus burlingtonensis **Pierce & Langenheim, 1974**. — Groessens (1974) proposed the origin of *Eotaphrus* (Fig. 31L) either from the '*Spathognathodus*' *bultyncki* or *Dollymae hassi* lineages.

Scaliognathus anchoralis **Branson & Mehl, 1941**. — The Ostrówka population of the species (Fig. 33) contains **sp** elements with all three processes being of subequal length at mature stage and with well developed platform. There seems to be no difference between samples in this respect. All

the other elements of the apparatus are represented in the collection although the symmetry transition series elements are always fragmentary. Sinuous orientation of denticles in these elements is a very characteristic feature of the genus. Otherwise the apparatus shows much resemblance to that of later *Lochriea*, which is suggestive of having a common origin in an as yet unidentified Tournaisian lineage, possibly of prioniodinid affinities.

The type population of the species comes from the Pierson Limestone, Roaring River Park, Barry County in Missouri (holotype Branson & Mehl 1941: pl. 19: 22, 23). The type population of *Scaliognathus praeanchoralis* Lane *et al.*, 1980 comes from sample MDP-1 of the Deseret Limestone at Morgan, Utah. Together with typical morphotypes of the species (47 specimens) with a rudimentary anterior process, several specimens lacking such processes (20 in number, identified as *S. dockali* Chauff, 1981 by Lane & Ziegler 1983) and rare specimens with all three processes of almost equal length (2 in number, identified as *S. anchoralis*) occur there. The assemblage is thus completely distinct from the type population of *S. anchoralis* and little doubt remains that there is an ancestor-successor relationship between them. *S. dockali* Chauff, 1981, with its type population 32 m above the base of the Deseret Limestone at the Samak Section in the Uinta Mountains of Utah, is a even more primitive member of the lineage (Chauff 1981) having biramous **sp** elements. I am not able to determine the Ostrówka populations in terms of subspecies of *S. anchoralis* proposed by Lane & Ziegler (1983).

***Doliognathus latus* Branson & Mehl, 1941**. — Only a few specimens have been found in Ostrówka (Fig. 31F). Along with very characteristic platform **sp** elements there are some other elements of the apparatus that may belong to the same species. They are of rather robust external appearance and share relatively deep and wide basal cavities.

The type population of the species comes from the Pierson Limestone, Roaring River Park, Barry County in Missouri (holotype Branson & Mehl 1941: pl. 19: 31, 32). According to Chauff (1985), the species originated from *D. dubius* Branson & Mehl, 1941, which occurs in strata older than the *S. anchoralis* Zone.

***Gnathodus cuneiformis* Mehl & Thomas, 1947**. — As admitted by Lane *et al.* (1980), in early *Gnathodus* from their isosticha-Upper crenulata Zone there is a continuity in morphologic variability extending through all species recognised there. This applies as well to the populations from the *Scaliognathus anchoralis* Zone of Ostrówka, where all morphologies corresponding to species occurring in this horizon according to Lane *et al.* (1980) form a single continuum of morphologies (Fig. 34). I see no possibility at the present stage of knowledge to distinguish there any sympatric species of the genus. The variability is not only completely continuous but there is no apparent multimodality in the distribution of characters. The morphologies do not form any linear morphocline so I failed in quantifying the pattern of variability. Although the presence of several species cannot be excluded, as in any case of morphologically defined palaeontological species, I find it parsimonious not to subdivide the sample arbitrarily into more than one species, even if some future quantitative study of a better preserved and larger assemblage, or identification of the alleged 'species' in separate samples, may prove their biological validity.

All that remains in this situation is to apply a species name to this probably homogeneous series of populations in Ostrówka. No holotype of *Gnathodus* species comes strictly from this horizon but the closest in age seems to be that of *G. cuneiformis* Mehl & Thomas, 1947 from the Fern Glen Formation at Castlewood, Missouri. The specimen, reillustrated by Lane *et al.* (1980: pl. 10: 7) is a juvenile with no specific characters, but there is no reason to suspect that its population was different from that from Ostrówka, although the Fern Glen Formation is somewhat older than the Radlin beds. The same applies to the horizon 14.9 m above base of the Lake Valley Formation in Dog Canyon of New Mexico, from where the type series of *Protognathodus cordiformis* Lane, Sandberg, & Ziegler, 1980 comes. It is associated with specimens classified by Lane *et al.* (1980) as *Gnathodus cuneiformis* (early) and *G. delicatus*. *Scaliognathus praeanchoralis* dates the horizon.

Another possible name-bearer is the type of *G. pseudosemiglaber* Thompson & Fellows, 1970 from the Reeds Spring Formation at the Tahlequah North section of Oklahoma, where the conodont assemblage is clearly monospecific. Probably in populational terms these populations are conspe-
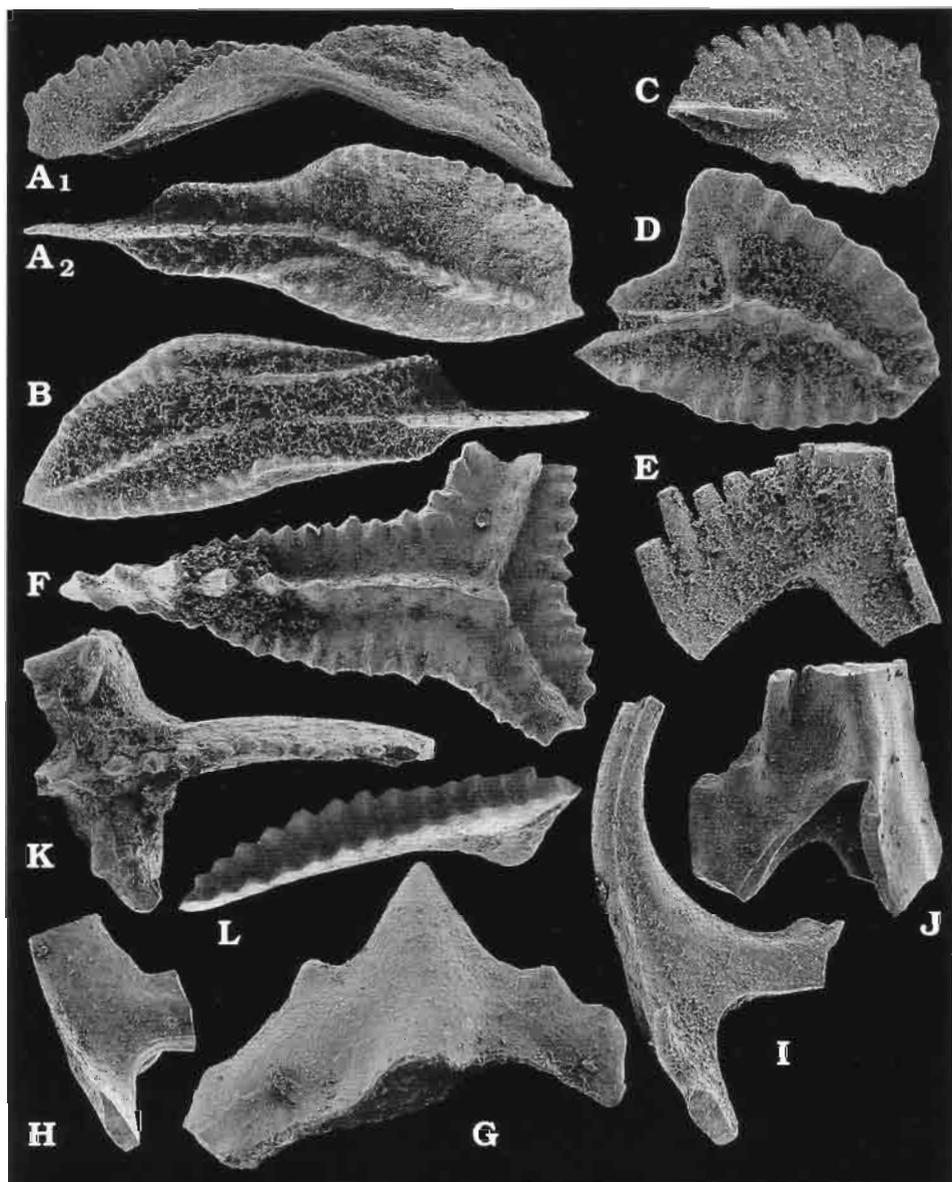
Fig. 31. Probably reworked early Tournaisian and indigenous late Tournaisian conodonts from the marly intercalations in shales of the Radlin beds of the Ostrówka quarry in the Holy Cross Mts; all from sample Ost-6, except for **L** which is from Ost-4. **A**, **B**. *Siphonodella crenulata* Cooper, 1939, elements **sp** (**A** in lateral and occlusal views, × 66; **B**, × 65), specimens ZPAL C XVI/37–38. **C**. Unidentified juvenile polygnathid, × 132; specimen ZPAL C XVI/25. **D**. *Dinodus lobatus* (Branson & Mehl, 1934), element **sp**, × 66, specimen ZPAL C XVI/32. **F–J**. *Doliognathus latus* Branson & Mehl, 1941, element **sp** (**F**, × 66), **oz** (**G**, × 100), **tr** (**H**, × 100), **hi** (**I**, × 100), and **ne** (**J**, × 66); specimens ZPAL C XVI/35, 39–42, respectively. **K**. *Dollymae bouckaerti* Groessens, 1977, element **sp**, × 66, specimen ZPAL C XVI/36. **L**. *Eotaphrus burlingtonensis* Pierce & Langenheim, 1974, element **sp**, specimen ZPAL C XVI/509.
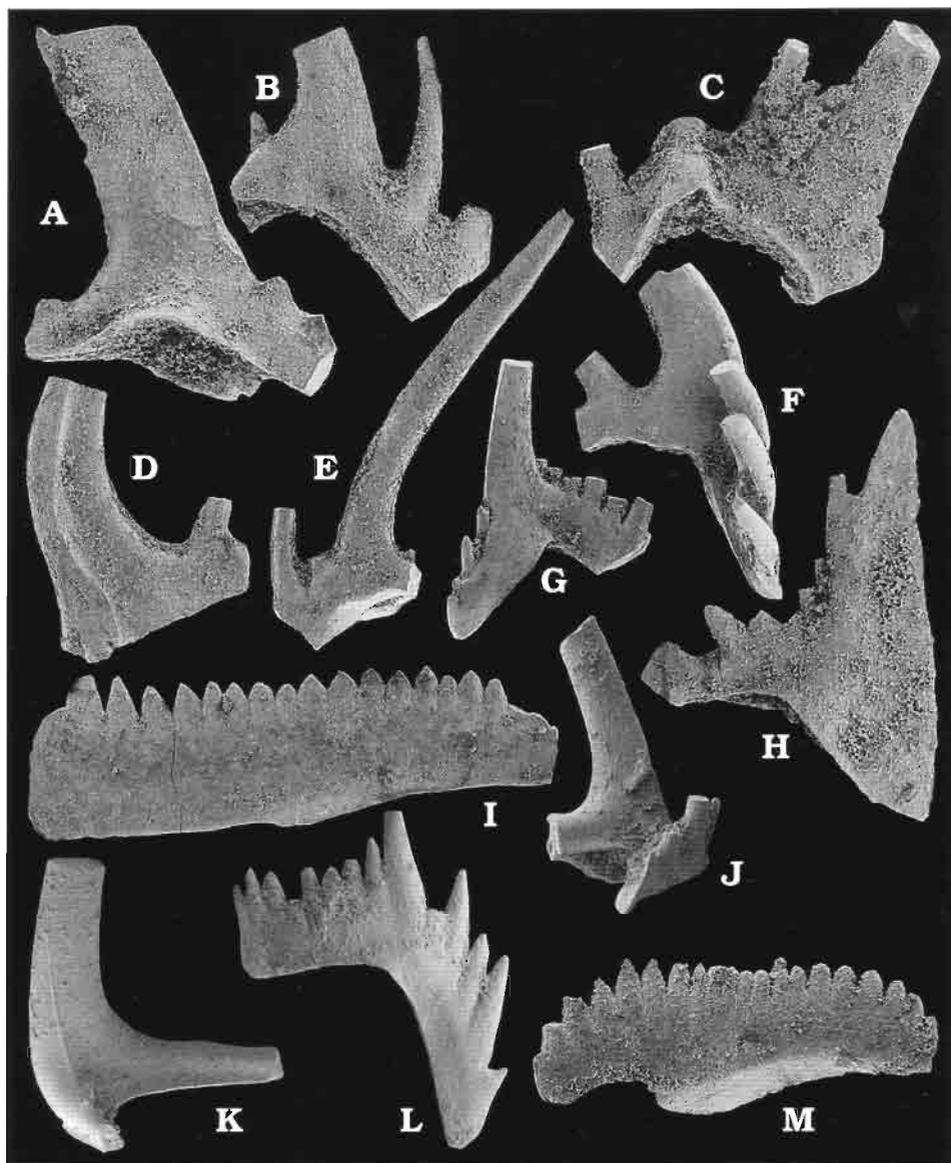
Fig. 32. Prioniodinids from the late Tournaisian of Ostrówka. **A–F, H.** *Idioprioniodus* sp. from sample Ost-6; elements **sp** (**A**, × 82), **oz**? (**B**, × 85), **pl** (**C**, × 100), **tr** (**D**, × 100), **hi** (**E**, × 50), **lo**? (**F**, × 66), and **ne** (**H**, × 66); specimens ZPAL C XVI/18, 21, 19, 22, 14, 45, and 16, respectively. **G, I–L.** *Bactrognathus* sp. from samples Ost-6 (**G, I**) and Ost-4 (**J–L**); elements **ne** (**G**, × 66), **sp** (**I**, × 73), **hi** (**J**, × 66), **tr** (**K**, × 50), and **oz** (**L**, × 50); specimens ZPAL C XVI/4, 12, 510 and 511, respectively. **M.** *Mehlina*? sp. from sample Ost-6; element **sp**, × 100, specimen ZPAL C XVI/24.

cific. The *Gnathodus typicus* Cooper, 1939 type series comes from the same stratum as *G. punctatus* Cooper, 1939 and both may be reworked from older strata of unspecified age. *G. semiglaber* Bischoff, 1939 comes from a horizon younger than that in Ostrówka.
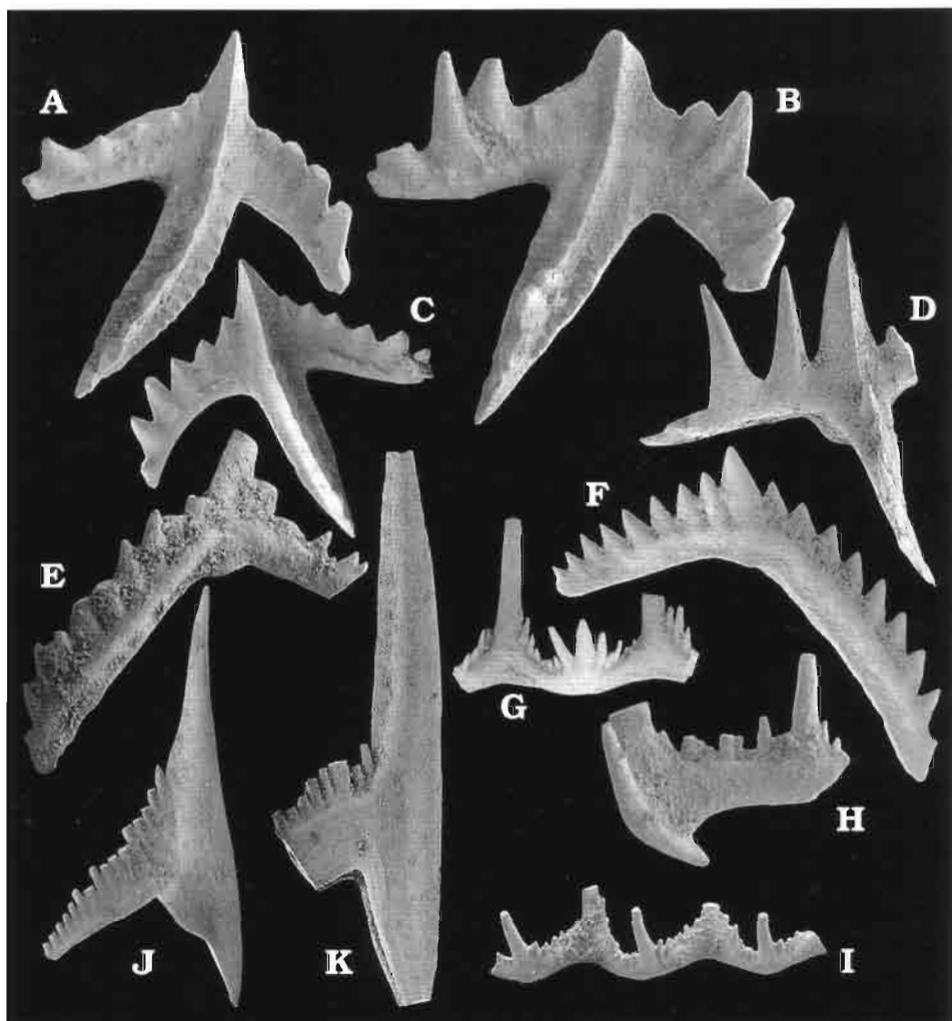
Fig. 33. *Scaliognathus anchoralis* Branson & Mehl, 1934 from the late Tournaisian of Ostrówka; samples Ost-4 (**A–C, E–J**) and Ost-6 (**D, K**); elements **sp** (**A, B**, × 50; **C**, × 40; **D** juvenile, × 66), **oz** (**E**, × 50; **F**, × 47), **hi** (**G–I**, × 50), **ne** (**J**, × 30; **K**, × 50); specimens ZPAL CXVI/5, 17, 20, 23, 26, 27, 30, 34, 512, 6, 33.

Weyerognathus pinnatus Voges, 1959. — In the Ostrówka samples the platform shapes of **sp** elements of *Weyerognathus* show a quite extensive variability, ranging from strongly asymmetrical, narrowly triangular to almost symmetrical and wide (Fig. 35). It remains unknown whether this is a real variability or rather a time averaging effect as a result of reworking of older Tournaisian specimens.

The type population of this species comes from the sample taken 7.5 m below the top of the limestone series at the old quarry in Osthang Burg near Referinghausen in the Rhenish Slate Mountains. It is associated there with *Scaliognathus anchoralis* and is thus of the same age as the Ostrówka samples.

Pinacognathus? bischoffi (Rhodes, Austin, & Druce, 1969). — The species is defined as being different from *P. inornatus* in having a less asymmetrical appearance of the platform in **sp** elements (Fig. 35G).
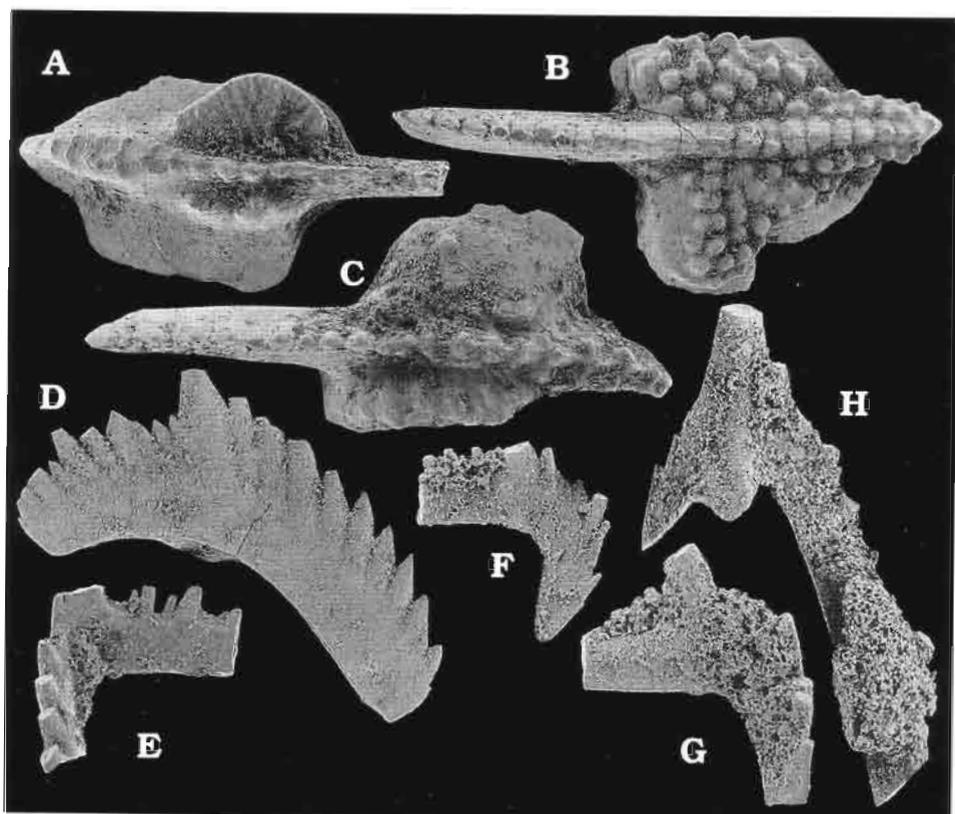
Fig. 34. *Gnathodus cuneiformis* Mehl & Thomas, 1947 from the late Tournaisian of Ostrówka, all from sample Ost-6; elements **sp** (**A** 'pseudosemiglaber' morphotype, × 66; **B** typical, × 60; **C** *'Protognathodus cordiformis'* morphotype, × 66; a continuous gradation between these morphotypes can be traced in Ostrówka, their possible species rank requires thus statistical verification), **oz** (**D**, × 82), **tr** (**E**, × 80), **hi** (**F**, **G**, both × 100), and **ne** (**H**, × 100); specimens ZPAL C XVI/29, 15, 28, 31, 2, 11, 13, and 10, respectively.

***Siphonodella crenulata* (Cooper, 1939)**. — Typical *S. crenulata* specimens occur in the sample Ost-4 in Ostrówka, together with the *Scaliognathus anchoralis* fauna. Most probably they are reworked although the elements in Ostrówka are very well preserved and relatively numerous and in both these aspects differ strongly from other undoubtedly reworked Famennian and early Tournaisian species in the samples. This may have resulted from a difference in matrix of reworked rocks – perhaps *S. crenulata* occurred originally in unconsolidated clays of the Alum Shale type, while older *Siphonodella* species come from eroded limestones.

Both Voges (1959) and Klapper (1966) defined the species on the basis of the characteristic outline of the platform. The holotype of the species comes from the same stratum as the type specimen of *S. isosticha*, that is from the pre-Welden shale of Oklahoma. These are an extremely small juvenile (*S. isosticha*) and an extremely mature **sp** element (*S. crenulata*).

***Dollymae bouckaerti* Groessens, 1977**. — The species (Fig. 31K) has been suggested by Groessens (1974) to be a homeomorph of unrelated older *Dollymae hassi* Voges, 1959 for which the generic name *Icriognathodus* Gedik, 1984 is available (Gedik 1984). Its distribution elsewhere suggests that it may be reworked from strata deposited immediately below the invasion of the *S. anchoralis* fauna.
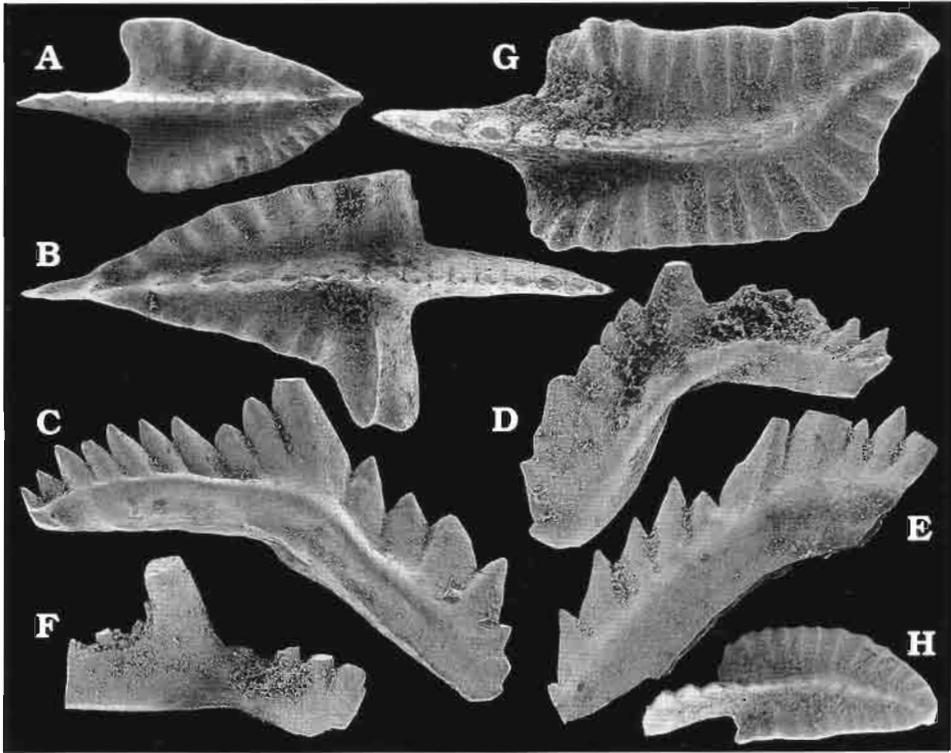
Fig. 35. Polygnathids from the late Tournaisian of Ostrówka. **A–F**. *Weyerognathus pinnatus* (Voges, 1959) from sample Ost-4 (**A**) and Ost-6 (**B–F**); elements **sp** (**A** juvenile, × 40; **B**, × 65), **oz** (**C**, × 50; **D** very robust, 'notognathella' type, × 66; **E**, × 66), and **hi** (**F**, × 66); specimens ZPAL C XVI/513, 7, 3, 37, 9, and 1, respectively. **G**, **H**. *Pinacognathus* aff. *inornatus* Branson & Mehl, 1934 from samples Ost-6 (**G**) and Ost-4 (**H**), elements **sp** (**G**, × 66; **H** juvenile, × 40); specimens ZPAL C XVI/8 and 514.

Late Tournaisian ammonoids

A collection of ammonoids from the late Tournaisian marls of the Radlin beds at Ostrówka has been assembled by Stanisław Czarniecki from the Institute of Geological Sciences of the Polish Academy of Sciences in Kraków. The specimens were collected in an area now completely destroyed by quarrying (Czarniecki 1992), and I was able to complement the sample only by a few specimens of *Merocanites applanatus* collected loose at the edge of the quarry wall. I had occasion to study the collection in the late eighties and the photographs done at that time are reproduced here (with kind permission of S. Czarniecki, who plans to publish a detailed description of the fauna; Figs 36–38). Pieces of the rock matrix obtained during preparation of some specimens, if productive, invariably yielded *Scaliognathus anchoralis*. Most of the ammonoid specimens are preserved in a pink marl and there is no reason to expect that they come from different horizons. The Radlin beds marls exposed in the quarry are pink or yellow but commonly also variegated.

The Ostrówka ammonoid assemblage is closely similar to that from the classical Erdbach locality in the Rhenish Massif. A preliminary review of them, based on a part of S. Czarniecki's collection, is presented below.

***Merocanites applanatus* (Frech, 1899)**. — In the type species of *Merocanites, M. compressus* (J. Sowerby, 1813), the generically diagnostic ventral lobe of the suture line (Riley 1996) appears to be basically the same as in *M. applanatus,* so there is no need for a separate generic name, *Erdbachites,* as proposed by Weyer (1972b). Its holotype comes from the latest Tournaisian *Ammonellipsites kochi* Zone of the Erdbach Limestone (see Kullmann 1963) and seems to be conspecific with the Ostrówka specimens (Fig. 36A, B). The suture line has been traced in three of them, representing different ontogenetic stages. No significant differences from other populations of the species have been discerned.

***Irinoceras ornatissimum* (de Koninck, 1881)?** — Only one crushed specimen with partially preserved septa has been collected in the yellow marl at Ostrówka (Fig. 36C). Its characteristic ornamentation points to identity with this species (see Pareyn 1961) although the specimen is too incomplete for confident identification.

***Ammonellipsites kochi* (Holzapfel, 1889)**. — The specimens from Ostrówka, although not showing sutures, are so characteristically ornamented (Fig. 36D–F) that at least most of them belong to this typical species of the Erdbach Limestone.

***Neopericyclus hauchecornei* (Holzapfel, 1889)**. — In the general shape of the conch, its ornamentation and course of constrictions, the specimens in hand (Fig. 37) fit quite well the Erdbach Limestone originals (see also Schindewolf 1951) and there is little doubt regarding their being conspecific even if the suture line remains unknown.

***Muensteroceras barroisi* (Holzapfel, 1889)?** — Large, relatively evolute conchs collected do not show any remnants of suture (Fig. 38). The shell surface is smooth. The smallest specimens are the most involute, whereas the largest specimen shows rather evolute coiling, but all of them may represent the same species which is, however, impossible to prove because of lack of data on suture morphology. Their identity with the Erdbach Limestone species is at least likely. The genus, characterised by parallel-sided ventral lobe, is not known below the Osagean (Gordon 1986). Thus, this is one of its oldest species.

The origin of the pelagic communities of the Polish late Tournaisian

The latest Tournaisian *Scaliognathus anchoralis* Zone limestones of the Radlin beds (Szulczewski *et al.* 1996) represent only a marginal facies episode within the generally black shale sedimentation that started with the *Siphonodella crenulata* Zone both in the Sudetes and the Holy Cross Mountains. In the Sudetes, in shales of the Gołogłowy Formation at the type locality Gołogłowy (Hollenau) near Dzikowiec, immediately above the *Wocklumeria* Stufe limestone both *Weyerognathus inaequalis* (documenting time equivalents of lower *Gattendorfia* limestone in clastic facies) and *Dollymae hassi* Voges, 1959, of middle Tournaisian age, occur (Haydukiewicz 1981). The presence of the latest Tournaisian *Scaliognathus anchoralis* strata in limestone facies is documented by pebbles from the late Viséan Nowa Wieś Formation (Chorowska & Radlicz 1994). *Dollymae hassi* and *Scaliognathus* are known also from allochthonous limestones in the Kaczawa region in the northern Sudetes (Chorowska 1978). The whole Tournaisian is represented by alternating shales and limestones in the marginal parts of the Moldanubicum immediately south
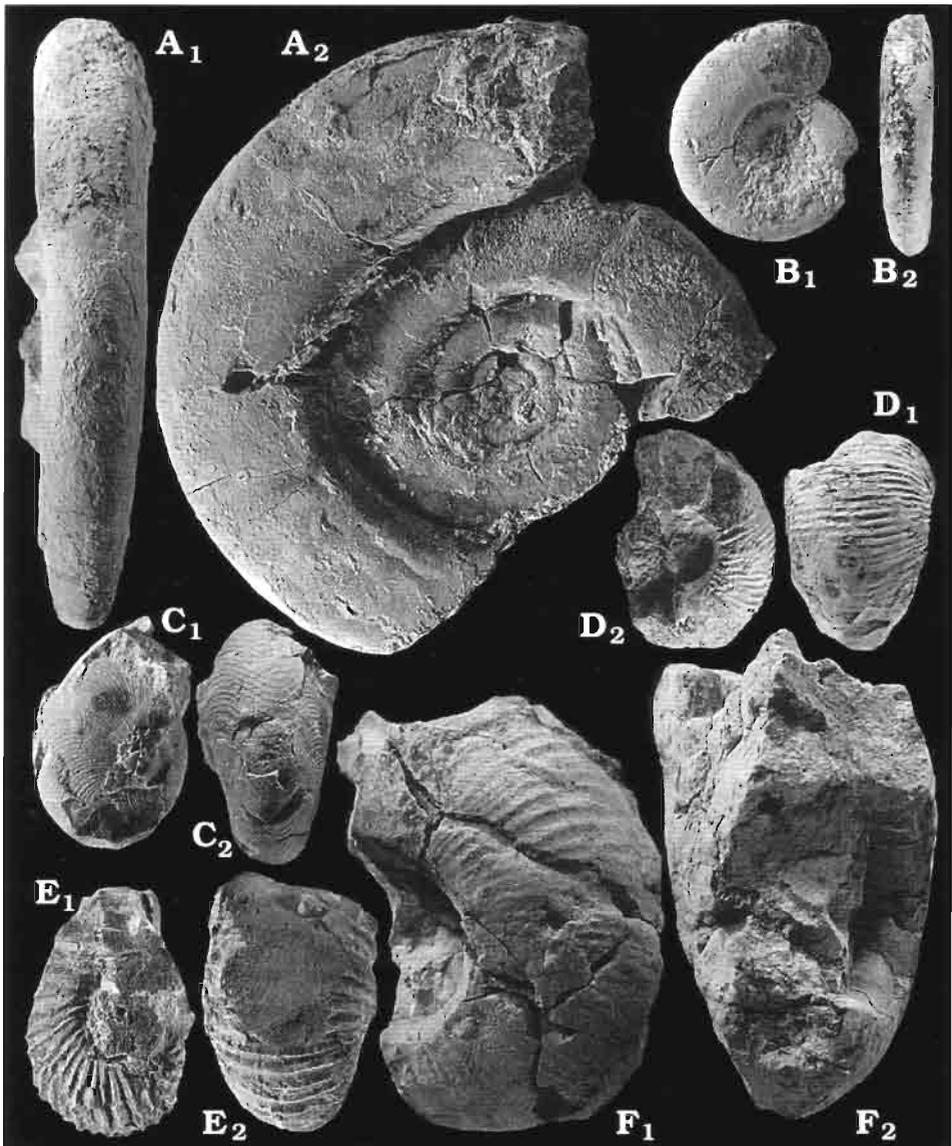
Fig. 36. Ammonoids from the late Tournaisian Radlin beds of Ostrówka (ZMS; collected and determined by Dr. Stanisław Czarniecki, Kraków), all × 1. **A, B.** *Merocanites applanatus* (Frech, 1899). **C.** *Irinoceras ornatissimum* (de Koninck, 1881). **D–F.** *Ammonellipsites kochi* (Holzapfel, 1889); note the variation in ornamentation, which may suggest that more than one species of the genus is here represented.

of the discussed area (Chlupač & Zikmundova 1976). There was thus a continuity in the evolution of pelagic ecosystems in the area but definitely a significant decrease in diversity was connected with the *S. crenulata* transgression and the high diversity communities were displaced to other areas. No good record of events in these environments is available from the eastern part of the Variscan orogenic belt, but the
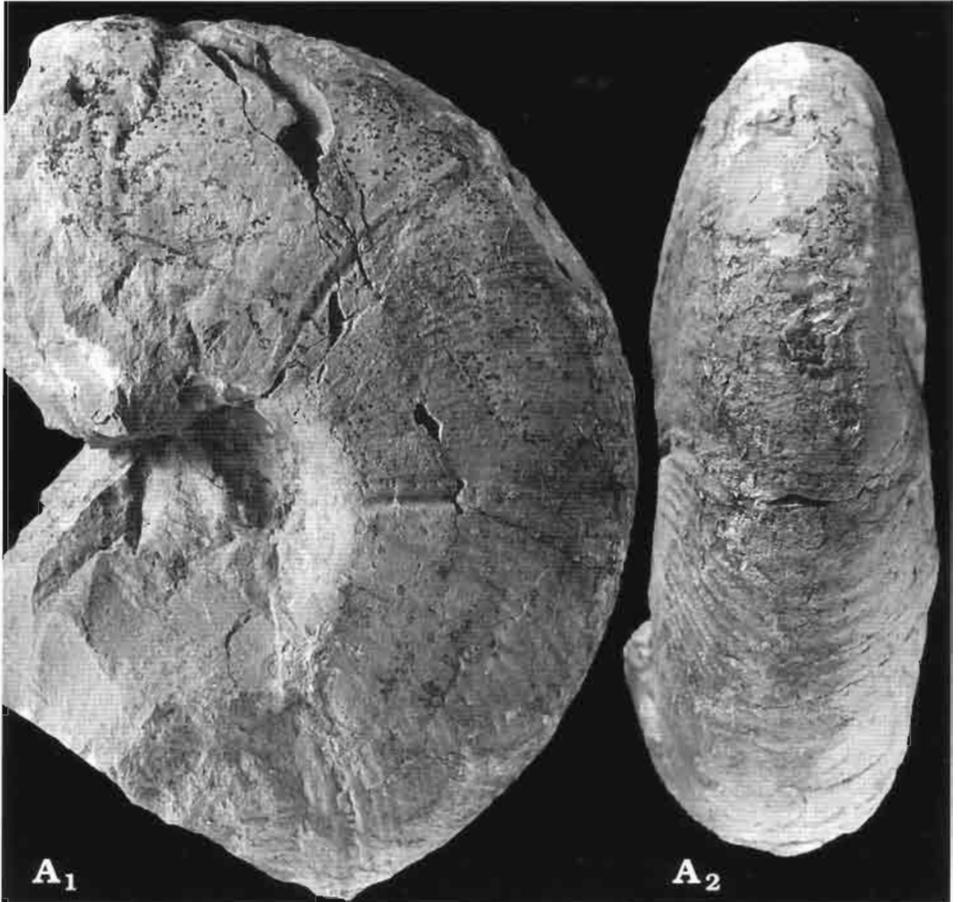
Fig. 37. *Neopericyclus hauchecornei* (Holzapfel, 1889) from the late Tournaisian Radlin beds of Ostrówka (collected and determined by Dr. Stanisław Czarniecki, Kraków), × 1.

American Midcontinent and the classical Belgium localities of that age provide some information on the evolution of the faunas.

The fossil record of the early Tournaisian pelagic communities is rather limited in North America. According to Manger (1975), the oldest Carboniferous ammonoids there are the poorly preserved imitoceratids from the Hannibal shale, possibly as old as *S. sulcata* Zone. Subsequent in age is the assemblage of the Exshaw Shale with crushed larger imitoceratids and juvenile pyritised specimens representing several genera (Schindewolf 1959; House 1994). A probable anaptychus has been described from this formation as an enigmatic organism, *Libodiscus ascitus* by Conway Morris *et al.* (1991), providing a valid name for a cephalopod. Its age is determined by the occurrence of *Siphonodella sandbergi* as being younger than the *S. duplicata* Zone.

Well preserved Carboniferous ammonoids do not occur in America below the middle Tournaisian Chouteau Limestone and its age equivalents, all marking the
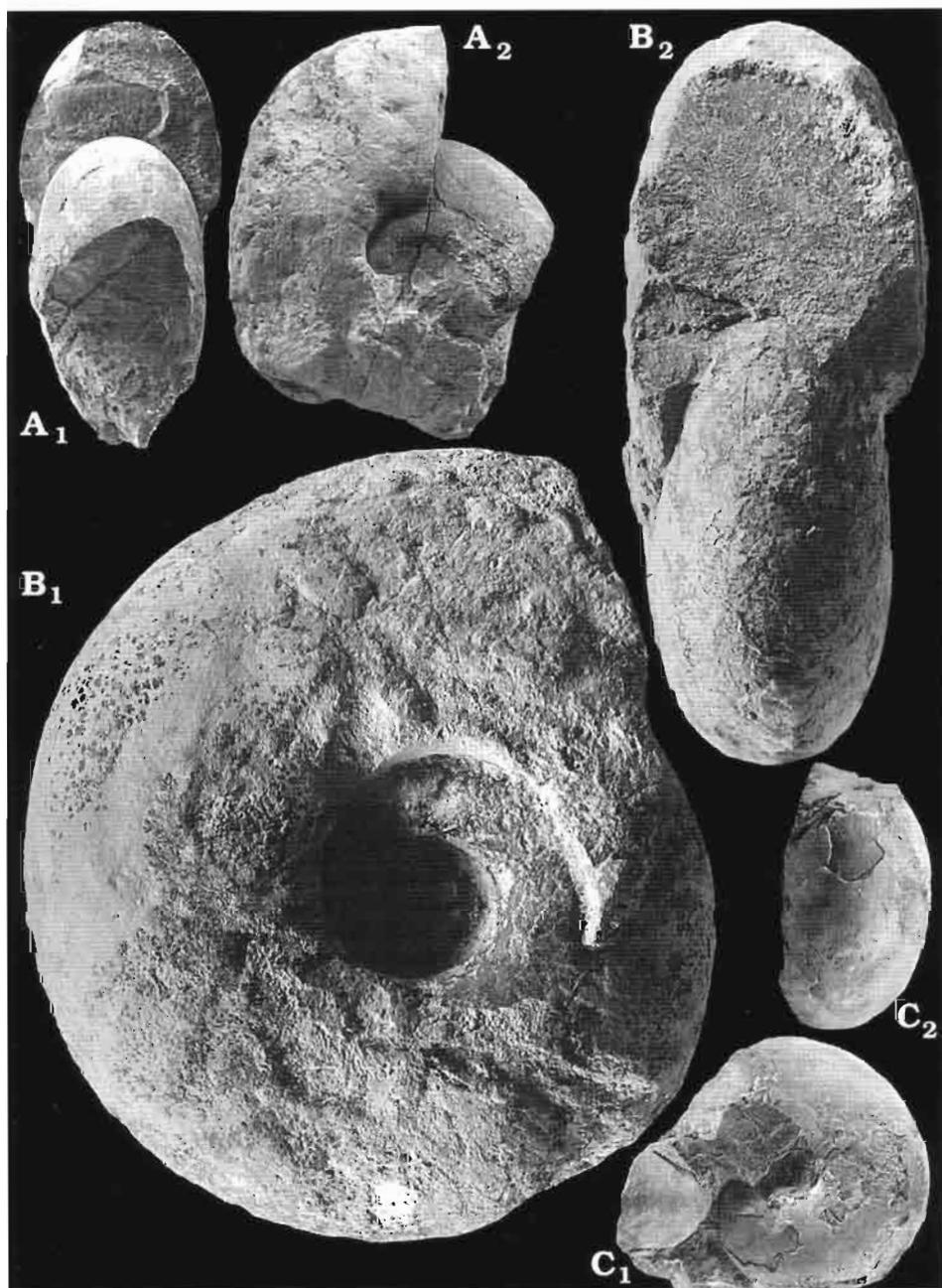
Fig. 38. A–C. *Muensteroceras barroisi* (Holzapfel, 1889) from the late Tournaisian Radlin beds of Ostrówka in the Holy Cross Mts (collected and determined by Dr. Stanisław Czarniecki, Kraków), all × 1.

transgression coeval with the end of sedimentation of the *Gattendorfia* limestone (Manger 1975; Savoy & Harris 1993). The American ammonoid faunas thus fill the

gap between the European assemblages of the *Gattendorfia* Stufe and the Erdbacher Kalk, as shown by Matthews (1970) and Gordon (1986). Evolutionary roots of most of the ammonoids represented in the European late Tournaisian can be identified within these Midcontinent faunas and the same is the case with the *Scaliognathus anchoralis* assemblage of conodonts. Little doubt remains that the appearance of the very characteristic late Tournaisian pelagic community in the Variscan area of central Europe was a result of expansion of these faunas to regions previously dominated by deeper water black clay sedimentation. Carbonate sedimentation was re-established in the late Tournaisian in areas roughly corresponding to those where earlier *Wocklumeria* and *Gattendorfia* limestones were deposited, that is in relatively shallower regions, frequently, as in Ostrówka, at the top of Devonian carbonate buildups. The *Ammonellipsites kochi* ammonoid and *Scaliognathus anchoralis* conodont communities reached that time almost a world-wide distribution.

This ended with the new transgression of the sea, in the Holy Cross Mountains represented by the black clays and radiolarites of the Zaręby Beds. All the elaborated-platform-element conodont species disappeared again and the ammonoid record of that epoch in the whole Variscan area is virtually missing. They emerge again close to the end of the early Viséan.

Viséan conodonts

Viséan conodonts occurrences have been reported from the Kaczawa and Bardo regions of the Sudetes (Chorowska 1978; Haydukiewicz 1986; Chorowska & Radlicz 1994), Kraków region (Gromczakiewicz-Łomnicka 1974; Bełka 1982), Miechów (Chorowska 1972) and Olkusz areas of the subsurface (Matyja & Narkiewicz 1979; Bełka 1985), the Holy Cross Mountains (Bełka & Skompski 1988; Szulczewski *et al.* 1996), and the Lublin Coal Field (Skompski & Soboń-Podgórska 1980).

In the most eastward located Lublin region, boreholes Rudno and Podedworze 2 yielded conodonts from four limestone series above the clastic Viséan rocks with coal seams and separated by clastic intercalations, some of them with coal seams (Skompski & Soboń-Podgórska 1980). The conodont assemblages, unfortunately not described separately from each unit, are of standard composition, with *Lochriea*, *Gnathodus bilineatus*, and *G. girtyi*. In the little more offshore Rudno core also *Cavusgnathus* and *Mestognathus* have been identified. The presence of *G. girtyi collinsoni* in the uppermost sample of the Rudno borehole was taken as the evidence of the latest Viséan age of this stratum.

The latest Viséan algal limestone intercalation in dark shales of Orlej near Kraków contains a low diversity assemblage with *Gnathodus girtyi* (four 'subspecies' identified there by Bełka 1982 are probably morphotypes), *Lochriea*, and a prioniodinid. Nearby located coeval assemblages from limestones of Czerna are much more diverse (Gromczakiewicz-Łomnicka 1974), yielding also two more idiognathodid species, *Syncladognathus*, common *Mestognathus* and rare *Cavusgnathus*. This, and the thin cephalopod limestone bed 2 close to the top of the Carboniferous limestone section at Todowa Grząba section XXI described by Bełka & Skompski (1988; see also Szul-
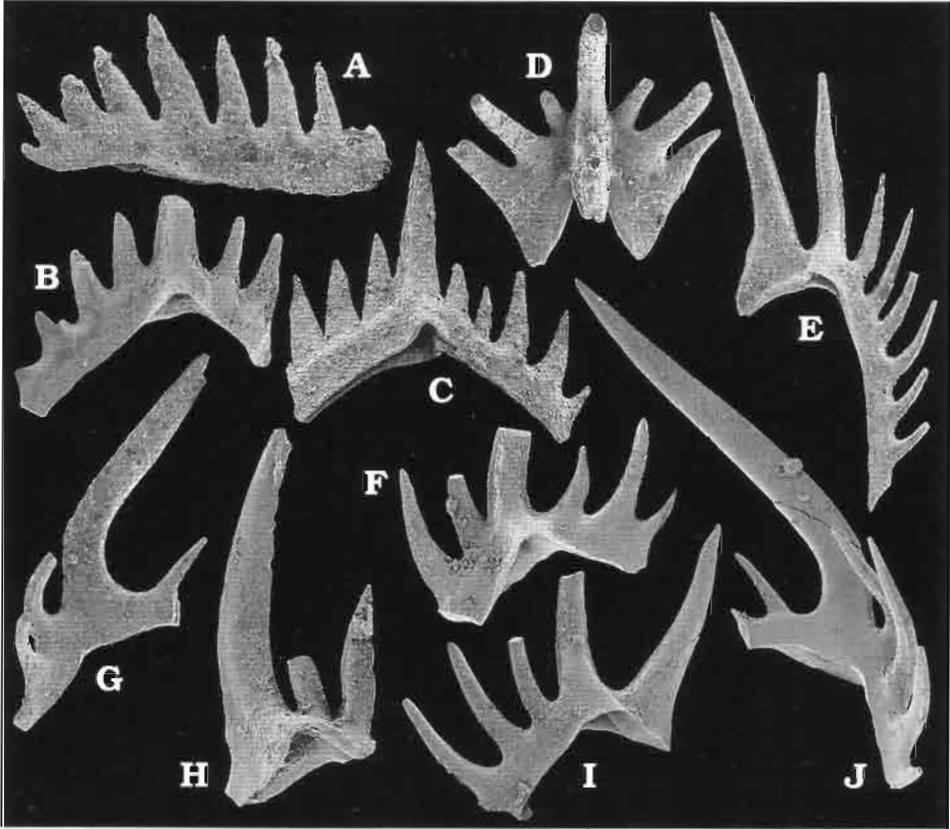
Fig. 39. *Idioprioniodus* from the late Viséan of Czerna near Kraków (**A, C–E, G**) and Todowa Grząba in the Holy Cross Mts. (**B, F, H–J**); elements **sp** (**A**, × 100), **oz** (**B, C**, both × 66), **tr** (**D**, × 82), **pl** (**E, I**, both × 66), **lo** (**F**, × 66), **hi** (**G**, × 72; **J**, × 60), and **ne** (**H**, × 66); specimens ZPAL C XVI/60, 160, 61–63, 162, 64, 164, 161, and 163, respectively.

czewski *et al.* 1996) are the only easily accessible outcrops of Viséan limestones with conodonts abundant enough to enable their apparatus studies.

I sampled for conodonts in both these localities (Table 5) and below I review the conodont apparatus species occurring there.

Idioprioniodus **sp.** — Populations from Czerna and Todowa Grząba are probably conspecific, although these highly generalised morphologically and variable elements hardly provide any firm basis for species-level taxonomic identification (Fig. 39). The apparatus structure is closely similar to that proposed by Chauff (1984) for *Idioprioniodus? conleyharpi* Chauff, 1984 from the Chappel Limestone.

Kladognathus **sp.** — The apparatus of the Namurian *Kladognathus* is well known owing to statistical studies by Horowitz & Rexroad (1982) and analysis of natural assemblages by Purnell (1993). The genus is well represented both in Todowa Grząba and Czerna (Fig. 40) by populations that differ in general appearance of elements but preserve the same apparatus structure. In Todowa Grząba, elements of *Kladognathus* show a well developed intercalary denticulation; both processes and the main denticles remain flattened even at late stages of histogeny. The Czerna specimens are robust, with intercalary denticulation weakly developed or missing and with strong and arched cusps

of the symmetry transition series. Whether this is a species rank distinction related to difference in age or only an influence of different environmental factors remains to be solved.

The very short third process in **sp** elements and its lack in **oz** elements indicates that the Polish species are not conspecific with any of the North American Chesterian species.

***Lochriea commutata* (Branson & Mehl, 1941)**. — The type population of *Spathognathodus commutatus* Branson & Mehl, 1941 comes from the Pitkin Limestone at Craig County in Oklahoma (Branson & Mehl 1941) which is of Chesterian (Namurian, *Eumorphoceras* E2) age, being thus much younger than the Polish occurrences of this lineage but almost coeval and perhaps conspecific with the type species of the genus, *Lochriea montanaensis* Scott, 1942. I am not able to find any significant differences between the apparatus structure of Polish populations from the late Viséan of Czerna (Fig. 41) and those from the Namurian of North America, as reconstructed by Rexroad & Horowitz (1990). *L. cracoviensis* (Bełka, 1985) seems to represent a population of the lineage. The robust appearance of the **sp** elements, with strongly widened tips of the denticles, may be a feature of advanced histogenetic stages and the difference in respect to other populations from Poland may be a matter of population dynamics. Adult specimens in American populations of *L. commutata* approach this morphology (see Rexroad & Horowitz 1990; von Bitter & Norby 1994).

***Lochriea mononodosa* (Rhodes, Austin, & Druce, 1969)**. — The population of *Lochriea* from Todowa Grząba contains rare specimens developing one or two tubercles at the basal cavity. Such a morphotype has been separated into *Lochriea mononodosa* (Rhodes, Austin, & Druce 1959). Its type population is represented by a sample collected from the topmost Viséan (*Gnathodus girtyi collinsoni* Zone) at the north of the South Wales Coalfield. As there is hardly a reason to consider denticulated specimens distinct specifically from the rest of the sample I use this name to distinguish them from the main lineage of the genus. In the latest Viséan of southern and eastern Europe even more elaborate platform of the **sp** element structures develop in this region (Nemirovskaya *et al.* 1994). Perhaps in the late Viséan *Lochriea* was split into two allopatrically evolving lineages, the more conservative American *L. commutata* and more progressive European *L. mononodosa* leading to prominently ornamented *Lochriea multinodosa* (Wirth, 1967). This trend to develop tuberculation on the basal cone has been traced also in the Viséan–Namurian succession of *Lochriea* populations in the Lublin area (Skompski 1996)

***Syncladognathus libratus* (Varker, 1967)**. — The apparatus of this highly characteristic species is known owing to the work of Rexroad & Varker (1992). It is well represented in Czerna (Fig. 42) and a complete set of elements can be assembled. Biramous **oz** elements and the characteristic profile of **sp** elements suggest a direct relationship with *Hindeodus* and the ancestry in primitive ozarkodinids. The similarity of the apparatus to that of Devonian *Apatognathus* is difficult to explain – perhaps all three genera have ancestry in an even older ozarkodinid.

***Protognathodus homopunctatus* (Ziegler, 1962)**. — Although the species is rather common in Todowa Grząba (Fig. 44A), I am not able to separate elements of the apparatus other than **sp** from associated species. The primitive morphology of the **sp** elements suggests that it is rather a direct successor of early Tournaisian *Protognathodus* than a relative of true idiognathodontids with their characteristically bent ventral processes of **hi** elements.

***Gnathodus girtyi* Hass, 1953**. — This is the most numerous species of the genus in both studied localities (Fig. 43A–N) and most of associated idiognathodontid ramiform elements must belong to it.

***Gnathodus bilineatus* (Roundy, 1926)**. — The apparatus of the species is known owing to the work of Schmidt & Müller (1964) on natural assemblages and Grayson *et al.* (1990) on isolated elements. The material from Polish localities (Fig. 43O–R) is not numerous enough to allow separation of non-platform elements from associated, more numerous species. The **sp** elements from Czerna show more regular arrangement of tubercles, that form clear concentric rows. This may be connected with the older geological age of the Czerna assemblage.

Fig. 40. *Kladognathus* from the late Viséan of Todowa Grząba (A–F) and Czerna (G–K). **A–F.** *Kladognathus* sp. from sample TG-1; elements **sp** (**A**, × 66), **oz** (**B**, × 66), **hi** (**C**, × 60), **pl** (**D**, × 82), **tr** (**E**, × 66), and
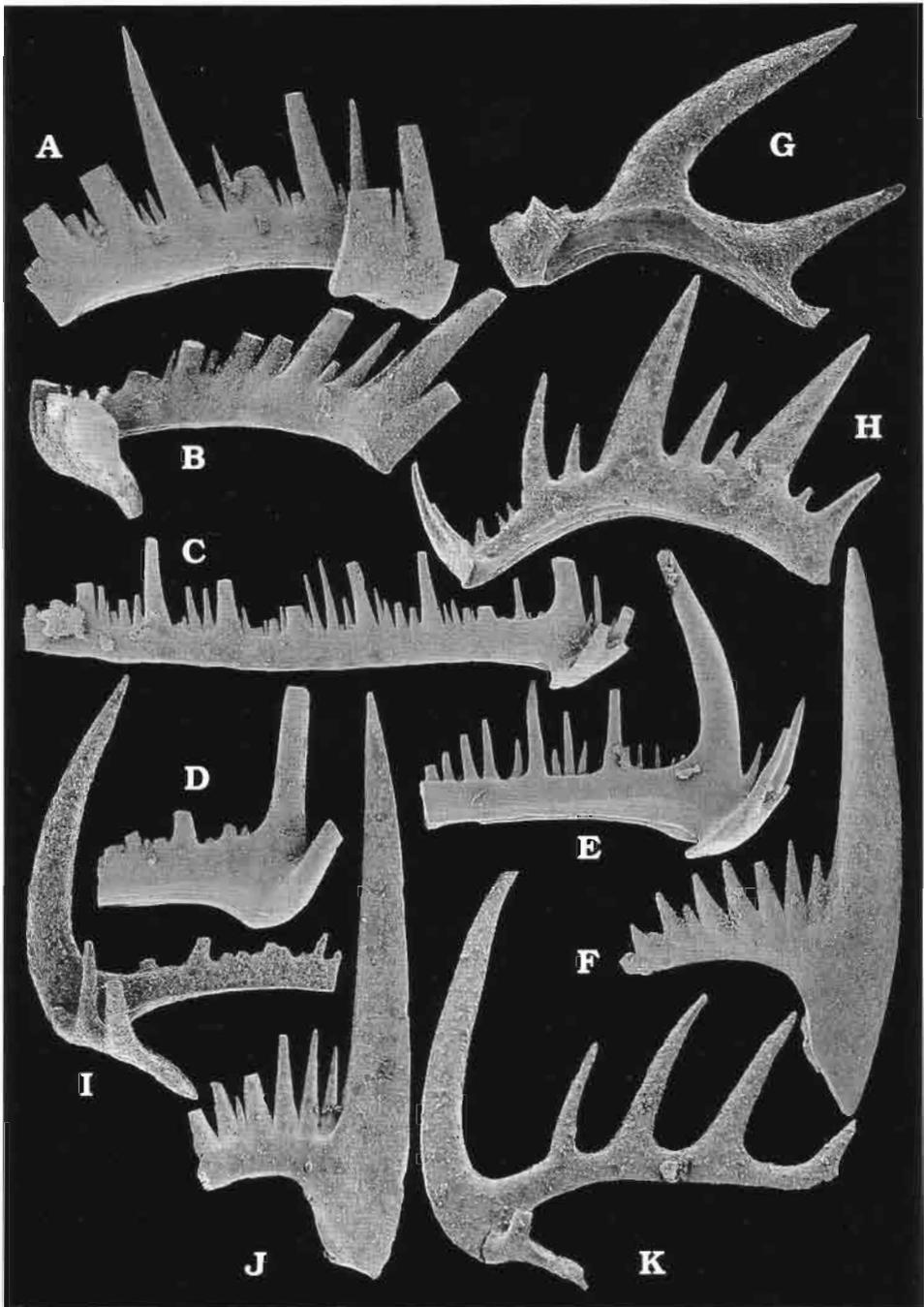
ne (**F**, × 66); specimens ZPAL C XVI/166, 155, 167, 158, 156, and 158, respectively. **G–K**. *Kladognathus* sp. from sample Cz-1; elements **sp** (**G**, × 74), **oz** (**H**, × 88), **tr** (**I**, × 80), **ne** (**J**, × 60), and **hi** (**K**, × 66); specimens ZPAL C XVI/56, 55, 57, 59, and 58, respectively.

Cavusgnathus **sp.** — These conodonts show, like coeval *Mestognathus*, axial symmetry of their **sp** elements being differentiated not only in the wider basal cavities but probably also in a more derived apparatus structure. This has been recognised in other species of *Cavusgnathus* by Von Bitter & Plint (1987), Rexroad & Horowitz (1990), and Purnell (1992). In the Polish species, which is probably related to *C. unicornis* Youngquist & Miller, 1949 despite having a much narrower platform (Fig. 44C, D), associated finely denticulated ramiform elements with short processes may represent the same apparatus.

Mestognathus bipluti **Higgins, 1961.** — The evolutionary position of this species has been discussed by Bełka (1983) and Bitter *et al.* (1986). According to them, this is the last member of the lineage, in which the tip of the parapet gradually develops denticulation. The Czerna specimens usually have two or three denticles (Fig. 44K, O). Purnell (1992) identified **oz** elements in *M. beckmanni* Bischoff, 1957. Similar, although not so robust, elements occur in Czerna being associated with symmetry transition series elements of generalised morphology. They may belong to *Mestognathus*, too.

The only published evidence on Namurian conodonts is that by Vašíček (1982) on the Gaebler marine horizon in the Czech part of the Upper Silesian Basin. Judging from identified and illustrated elements from relatively well balanced samples, the conodont fauna is represented by numerous *Gnathodus bilineatus* (Roundy, 1926), much less common *Lochriea nodosa* (Bischoff, 1957) with elements lacking tubercles at the base or with only one tubercle equally numerous as those with several tubercles, uncommon *Prioniodina* sp., and rare *Cavusgnathus naviculus* (Hinde, 1900). This is the typical association known also from coeval strata in western Europe and in the Lublin area (Skompski 1996), of low diversity and with species showing relatively slow evolutionary rates. The dating of late Viséan to earliest Westphalian strata in Poland relies mostly on ammonoids but Skompski (1996) has reported the presence *of Gnathodus bollandensis*, diagnostic of its own zone of early Namurian (Arnsbergian) age, in the Lublin area. In the late Namurian he has identified there an assemblage with *Idiognathodus, Idiognathoides, Neognathodus, Declinognathus*, and rare *Adetognathus*. The last marine horizon with *Dunbarella* contains conodonts indicative of the *Idiognathoides tuberculatus* Zone, of latest Westphalian A age.

Late Viséan to Westphalian ammonoid succession

Virtually all the material of the Viséan to Westphalian ammonoids from Poland comes from drill cores and I am not able to offer any new original data. A review of the literature data (Fig. 46) is given below with some comments and the taxonomic nomenclature which was made consistent with that in the GONIAT database (Kullmann *et al.* 1994).

As in the case of the middle Tournaisian, the early Viséan record of ammonoids in central Europe is very scarce (Weyer 1972a; Riley 1993). The black radiolarites and shales with phosphorite concretions of the Zaręby Beds, which overlie the latest Tournaisian marls of the Radlin Beds in the Holy Cross Mountains (Szulczewski & Skompski 1995; Szulczewski *et al.* 1996), do not contain any specifically identifiable ammonoids or conodonts.

→

Fig. 41. *Lochriea* from the late Viséan of Todowa Grząba and Czerna. **A–D, G, H, J, K, M.** *L. mononodosa* (Rhodes, Austin, & Druce, 1959) from Todowa Grząba; elements **sp** (**A** in occlusal and lateral views, × 66; **B** 'nodosa' morphotype, × 66; **C** juvenile, × 100; **D** 'mononodosa' morphotype, × 66, microornamentation of denticles, × 534), **oz** (**G, H**, both × 66), **tr** (**J** in lateral and oblique views, × 66), **hi** (**K**, × 56), and **ne** (**M**, × 66); specimens ZPAL C XVI/126, 128, 151, 129, 168, 130, 131, 133, and 132, respectively. **E, F, I, L, N.**
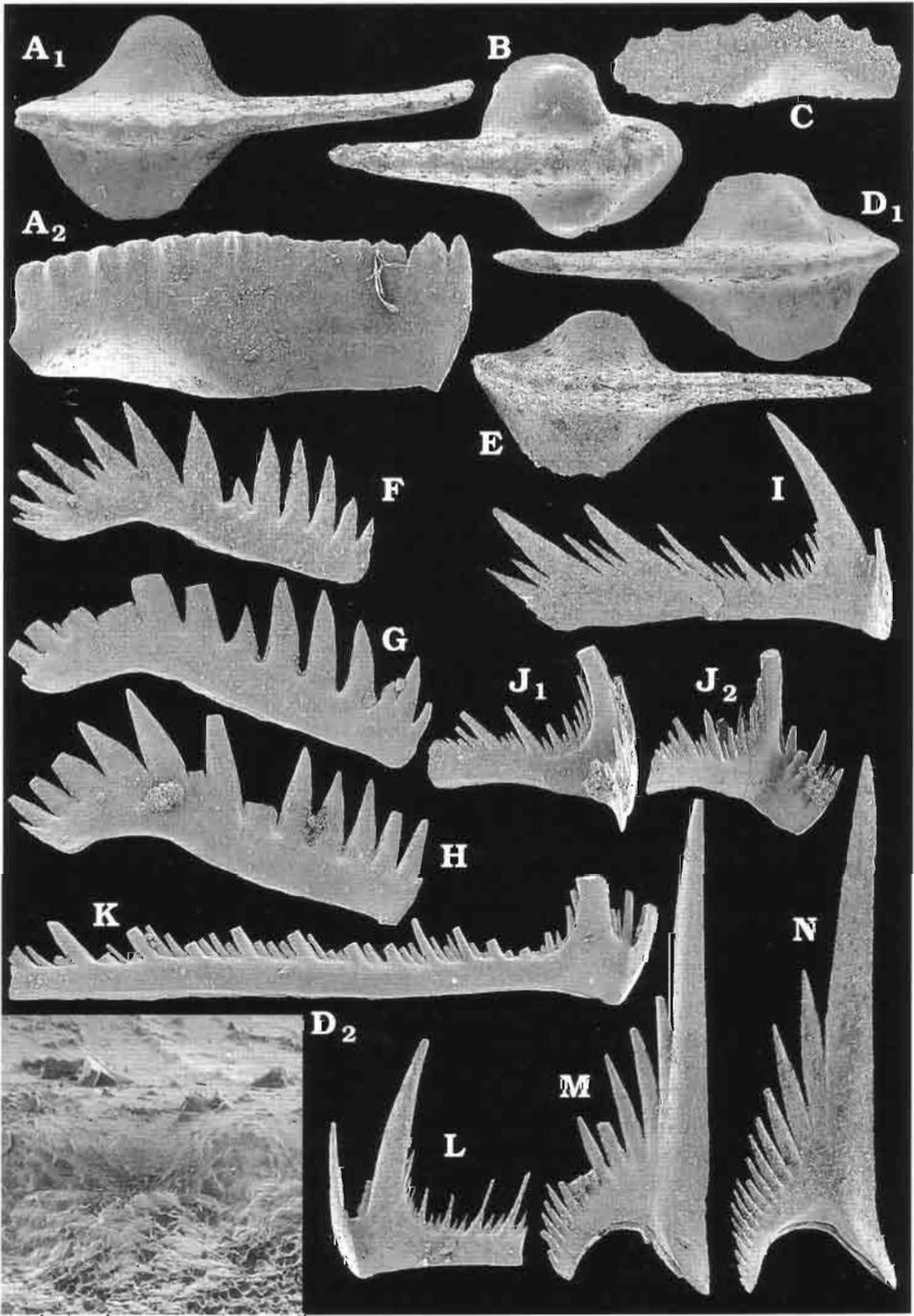
L. commutata (Branson & Mehl, 1941) from Czerna; elements **sp** (**E**), **oz** (**F**), **tr** (**I**), **hi** (**L**), and **ne** (**N**); specimens ZPAL C XVI/43–47, respectively; all × 66.

The only early Viséan ammonoid reported from Poland is *Entogonites nasutus* (Schmidt, 1941). Crushed conchs of this species have been identified by Bojkowski (1979) in the subsurface lower Malinowice beds of Upper Silesia and by Musiał (1993; Musiał *et al.* 1995) from the Olkusz area. It may be a derivative of the *Nomismoceras* lineage, perhaps *Nomismoceras frechi* Schmidt, 1925 from Sokolec (the locality Weitengrund) near Nowa Ruda in the Sudetes, tentatively dated as latest Tournaisian (see Schmidt 1925) and most probably found in a clast within the Nowa Wieś Formation (see Chorowska & Radlicz 1994). *E. nasutus* has a prominent ornamentation with riblets that follow in their course the appearance of the conch margin, being variably subdivided in the middle of the flanks – this furcation distinguishes it from its successor, *E. grimmeri* (Kittl, 1904) from the latest early Viséan (Korn 1988, 1996; Musiał *et al.* 1995). This evolutionary transition is an excellent late early Viséan datum. The lineage of *Nomismoceras,* possibly ancestral to *Entogonites*, does not reappear in the area until the late Viséan, when the smooth evolute conchs of *N. vittiger* (Phillips, 1836) become common in the Kulm facies in the Sudetes (Żakowa 1960a, b, 1966), Upper Silesia and the Olkusz area (Bojkowski 1979; Musiał *et al.* 1995), and the Holy Cross Mountains (Żakowa 1974, 1992). The adult conchs have compressed whorls with tabulate venter (Korn 1990b). There are several evolute ammonoids in the early Viséan that may be ancestral to *N. vittiger* (see Kusina 1980). Latest Viséan populations attributed to this species by Ruzhentsev & Bogoslovskaya (1971) are more involute than those from somewhat older strata of western Europe.

Only in the late Viséan strata of Poland are ammonoids common fossils. The late Viséan Kulm facies strata with crushed ammonoids are widespread in the Upper Silesian subsurface, where they yielded good palaeontological evidence for dating both in the Polish (Bojkowski 1979) and Czech (Kumpera 1977) parts of the coal basin. Even in the areas with a continuous sedimentation throughout the Viséan, ammonoids seem to be represented best in the *Goniatites crenistria* Zone, presumably owing to an increased supply of calcium carbonate to the basin enhancing their preservation. Rare three-dimensionally preserved ammonoids occur in the Carboniferous limestone in Ostrówka that contains mostly corals and brachiopods (Bełka & Skompski 1988; Belka *et al.* 1996), from where they have been described by Czarniecki (1973) and Żakowa (1974). Evolute conch morphologies are represented there, instead of *Nomismoceras*, by members of the prolecanitid lineage that revisited the area. The most widespread and known from different facies is *Prolecanites serpentinus* (Phillips, 1836) described from Ostrówka by Czarniecki (1973) and identified also by Schmidt (1925) and Żakowa (1966) in the *Goniatites crenistria* Zone of the Sudetes. The latter is the type stratum of *Prolecanites ceratitoides* (Buch, 1840), as pointed out by Weyer (1972b: p. 181). He did not indicate, however, any features that would contradict conspecificity of these two species. Well preserved specimens of *Pronorites cyclolobus* (Phillips, 1836), showing suture, occur also in Ostrówka (Czarniecki 1973). A poorly preserved crushed specimen without suture from the late Viséan of the fore-Sudetic Monocline has been illustrated as *Praedarelites* sp. by Korejwo & Teller (1967). Ruzhentsev & Bogoslovskaya (1971) synonymised the genus with *Epicanites* and, accordingly, transferred the Polish specimen to this genus.

Bollandites kielcensis Żakowa, 1992 from the *Goniatites fimbriatus* Zone of Kielce in the Holy Cross Mountains differs from *B. castletonensis* Bisat, 1924, only in bearing
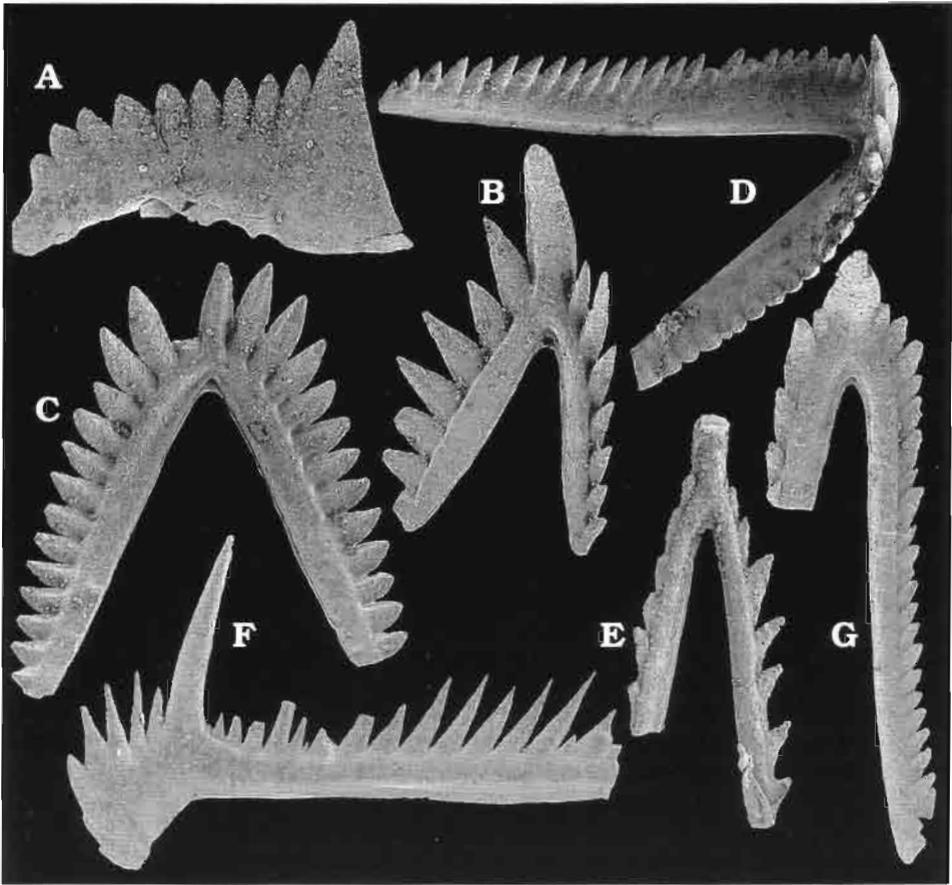
Fig. 42. *Syncladognathus libratus* (Varker, 1967) from the late Viséan of Czerna; all × 66 except for **F** that is × 60; elements **sp** (**A**), **oz** (**B**), **tr** (**C**), **lo** (**D**), **pl** (**E**), **hi** (**F**), and **ne** (**G**); specimens ZPAL C XVI/72, 68, 67, 65, 66, 74, and 69, respectively.

more frequent constrictions which makes species distinction rather problematic. In the latter species the umbilicus is relatively wide in specimens up to a diameter of 21 mm and then whorl height increases rapidly, adult specimens having relatively flat sides (Bisat 1924). Similar forms occur already in the early Viséan and the *Bollandites* lineage can be rooted in some Tournaisian *Muensteroceras* species (Kusina 1980). According to Riley (1996), *Bollandites* is the end-member of a series increasing involuteness and smoothening of adult conch stages, represented by the series of *Ammonellipsites* → *Hammatocyclus* → *Parahammatocyclus* → *Bollandites*.

The most useful for time correlation of the late Viséan rocks are ammonoids of the *Goniatites* lineage that appear in the fossil record at the beginning of this epoch. Like most other Viséan ammonoids, they provide few features in the conch morphology that could be used to define high-rank units. Perhaps the most typical for the branch is the zigzag appearance of the otherwise simple suture, and a tendency to develop prominent longitudinal (spiral) ornamentation. Both these characters developed also in other

lineages of Early Carboniferous ammonoids and stratophenetically oriented phylogenetic interpretations seem to be the main tool in establishing their classification. The most common species of the genus is *Goniatites crenistria* Phillips, 1836, known in the fore-Sudetic Monocline (Korejwo & Teller 1967), in the Holy Cross Mountains (Czarniecki 1973; Żakowa 1974, 1992), and in the Lublin Coal Basin (Korejwo 1986). Specimens were determined on the basis of conch surface ornamentation with crenulated growth lines and a suture with pointed ventrolateral saddles and V-shaped lobes – a feature of the whole (sub)genus. According to Korn (1988, 1990), the stratigraphically slightly older and possibly ancestral *G. hudsoni* Bisat, 1934 differs in having wider juvenile conchs, and oblique aperture with almost no separate ventral sinus at subadult stages. Adult *G. crenistria* conchs may reach 70 mm in diameter, at the last stage developing a little wider umbilicus.

Goniatites fimbriatus (Foord & Crick, 1897) is known, under the name *G. c. intermedius* Kobold, 1933, from the Sudetes, fore-Sudetic Monocline and the Holy Cross Mountains (Żakowa 1966, 1992; Korejwo & Teller 1967). It succeeds stratigraphically, and probably phylogenetically, *G. crenistria*. It differs from it, according to Korn (1988), in a more prominent crenulation of growth lines that in the umbonal part of the conch transforms into longitudinal striation, a wider umbilicus, and weak ventrolateral lobes of the aperture at subadult stages. Adults reached larger sizes than related species of *Goniatites*. This is probably the last member of the *G. hudsoni* lineage but the relationship to *G. crenistria* remains somewhat unclear.

Goniatites spirifer Roemer, 1850 is known, under the name *G. striatus* (Sowerby, 1814), from the Sudetes, Upper Silesia, and Holy Cross Mountains (Żakowa 1960a, 1992; Bojkowski 1979). Prominent longitudinal (spiral) striation extends over the whole conch (Korn 1988, 1990). This may be a continuation of the trend represented by *G. fimbriatus*. *G. spirifer* shows close similarities to *G. globostriatus* (Schmidt, 1925), occurring in the Rhenish Massif below *G. crenistria*, which may mean that they represent a lineage developing independently of *G. crenistria–G. fimbriatus*. Adults of *G. spirifer* may reach 70 mm in diameter developing numerous transverse furrows at the conch wall near the aperture (Hodson & Moore 1959; see also revision of data by Korn 1990a).

Densely distributed transverse furrows of the kind appearing close to the adult aperture of *G. spirifer* developed in *Goniatites falcatus* Roemer, 1850, already at late juvenile stages. Identifications of crushed specimens from the Sudetes, Upper Silesia, Olkusz area, Holy Cross Mountains, and Lublin region (Żakowa 1960a, 1992; Żelichowski 1972; Bojkowski 1979; Ł. Musiał, personal communication) are based on this feature. The main difference between this species and possibly ancestral *G. spirifer* is the evoluteness of the earliest ontogenetic stages, which was used by Korn (1988) as the basis for their separation at the generic level. Juveniles of *G. falcatus* develop

Fig. 43. *Gnathodus* from the late Viséan of Czerna (**A, F, I, J, M**) and Todowa Grząba (**B–E, G, H, K, L**). **A–N**. *Gnathodus girtyi* Hass, 1953 from samples Cz-1 (**A, F, I, J,** and **M**) and TG-1 (**B–E, G, H, K, L,** and **N**); elements **sp** (**A**, × 66; **B**, × 50; **C** juvenile, × 100), **oz** (**D–F**, all × 66), **tr** (**G**, × 66), **lo** (**H** in lateral and occlusal views, × 66), **pl** (**I** aberrant?, × 66; **J**, × 60), **hi** (**L**, × 54), and **ne** (**M, N,** both × 66); specimens ZPAL C XVI/49, 136–137, 140–141, 50, 145, 144, 52, 51, 143, 142, 53, and 146, respectively. **O–R**. *Gnathodus bilineatus* (Roundy, 1926) from samples Cz-1 (**O**) and TG-1 (**P–R**); elements **sp** (**O**, × 50; **P**, × 58; **Q**, × 60; **R** juvenile, × 66); specimens ZPAL C XVI/48, 134, 165, and 135, respectively.
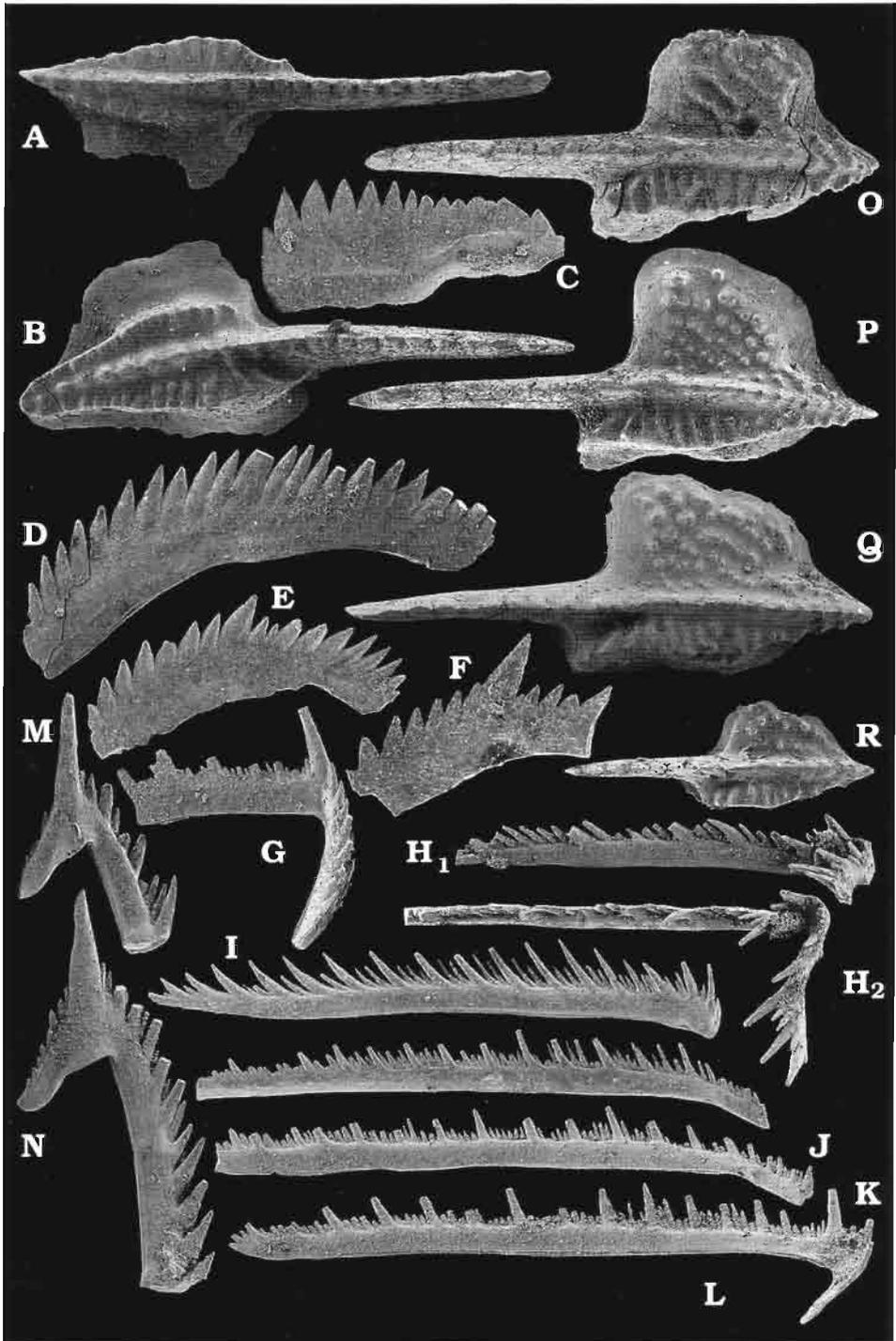
a prominent ventral lobe in the aperture, a feature that was inherited by later members of the lineage and was proposed to define the next generic level boundary by Korn (1988).

Perhaps specimens from the Holy Cross Mountains found in bed 1 of the trench XXI at Todowa Grząba in Gałęzice by Żakowa (1974; see also Bełka & Skompski 1988) belong to *Goniatites arnsbergensis* (Brüning, 1923), as suggested by the similarity in conch ornamentation and suture line (see Korn 1988). The Rhenish specimens have very wide juvenile conchs which, together with less robust ornamentation, makes them different from ancestral *G. falcatus*. The lineage seems to continue into *G. (Hibernicoceras) tumidum* (Moore & Hudson, 1958) with even lower whorls but shorter evolute stage. The specimen attributed to *Sudeticeras newtonense* Moore, 1950 by Bojkowski (1979: pl. 3: 4) shows a prominent spiral ornament close to the umbilicus and may belong to this species.

A zigzag shaped suture line suggests that the second of Żakowa's (1974) *Goniatites* species occurring in bed 1 of the trench XXI at Todowa Grząba is *G. (Arnsbergites) gracilis* (Korn, 1988), coeval with *G. arnsbergensis* but always allopatric to it (Korn 1988). This assemblage of longitudinally (spirally) striated goniatites occurs in close proximity to the two thin cephalopod limestone beds recognised in the outcrop at Todowa Grząba by Bełka & Skompski (1988) and from where the late Viséan conodonts illustrated here come. Even younger strata are represented in the Kulm facies of the Lechówek Beds above (Żakowa 1971, 1982, 1992).

Populations from the Lechówek Beds of the Holy Cross Mountains and subsurface fore-Sudetic Monocline attributed to *G. granosus* Portlock, 1843 by Korejwo & Teller (1967) and Żakowa (1971) are probably conspecific with *G. (Lusitanoceras) poststriatus* (Brüning, 1923) from the Rhenish Massif, identified as *Dombarites poststriatus* (Brüning, 1923) by Kullmann & Pitz (1980) and *Lusitanoceras poststriatum* (Brüning, 1923) by Korn (1988). The Namurian type species of *Dombarites* has a keeled adult living chamber but no sign of any tendency towards such a morphology is seen in adults of *G. poststriatus* reaching 70 mm in diameter (Korn 1988). *G. poststriatus* may be a descendant of *G. (Hibernicoceras) tumidum,* which shows already a tendency to develop very low coils at early stages of the ontogeny (see Korn 1988). Thus, though some of the species attributed to *Goniatites, Arnsbergites, Hibernicoceras,* and *Lusitanoceras* by Korn (1988, 1990) may constitute a monospecific lineage, I find it more practical to apply a conservative approach to generic-rank taxonomy of these taxa.

The narrow umbilicus connected with prominent longitudinal (spiral) ornamentation characterises the crushed specimen from the late Viséan of the Lublin area identified by Bojkowski (1979) with *Beyrichoceras* cf. *micronotum* (Phillips, 1836) which, like other species of its genus, does not show so prominent a spiral ornamenta-

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Fig. 44. Polygnathids from the late Viséan of Todowa Grząba (**A, B, D–J**) and Czerna (**C, K–O**). **A, B.** *Protognathodus homopunctatus* Ziegler, 1962 from sample TG-1; elements **sp** (**A,** × 83; **B** juvenile, × 100); specimens ZPAL C XVI/138–139). **C–J.** *Cavusgnathus* sp. from samples Cz-1 (**C**) and TG-1 (**D–J**); elements **sp** (**C, D** both in lateral and occlusal views, × 66), **oz** (**E,** × 100), **lo** (**F,** × 100), **hi** (**G,** × 101), **tr** (**H,** × 100), **ne** (**I,** × 100), and **pl** (**J,** × 100); specimens ZPAL C XVI/76, 147–148, 150, 152, 149, 153, and 151, respectively. **K–O.** *Mestognathus bipluti* Higgins, 1961 from sample Cz-1; elements **sp** (**K, O** juvenile, both in lateral and occlusal views, × 66) and tentatively attributed **oz** (**L,** × 83), **pl** (**M,** × 66), and **hi** (**N,** × 66); specimens ZPAL C XVI/70, 76–78, and 71, respectively.
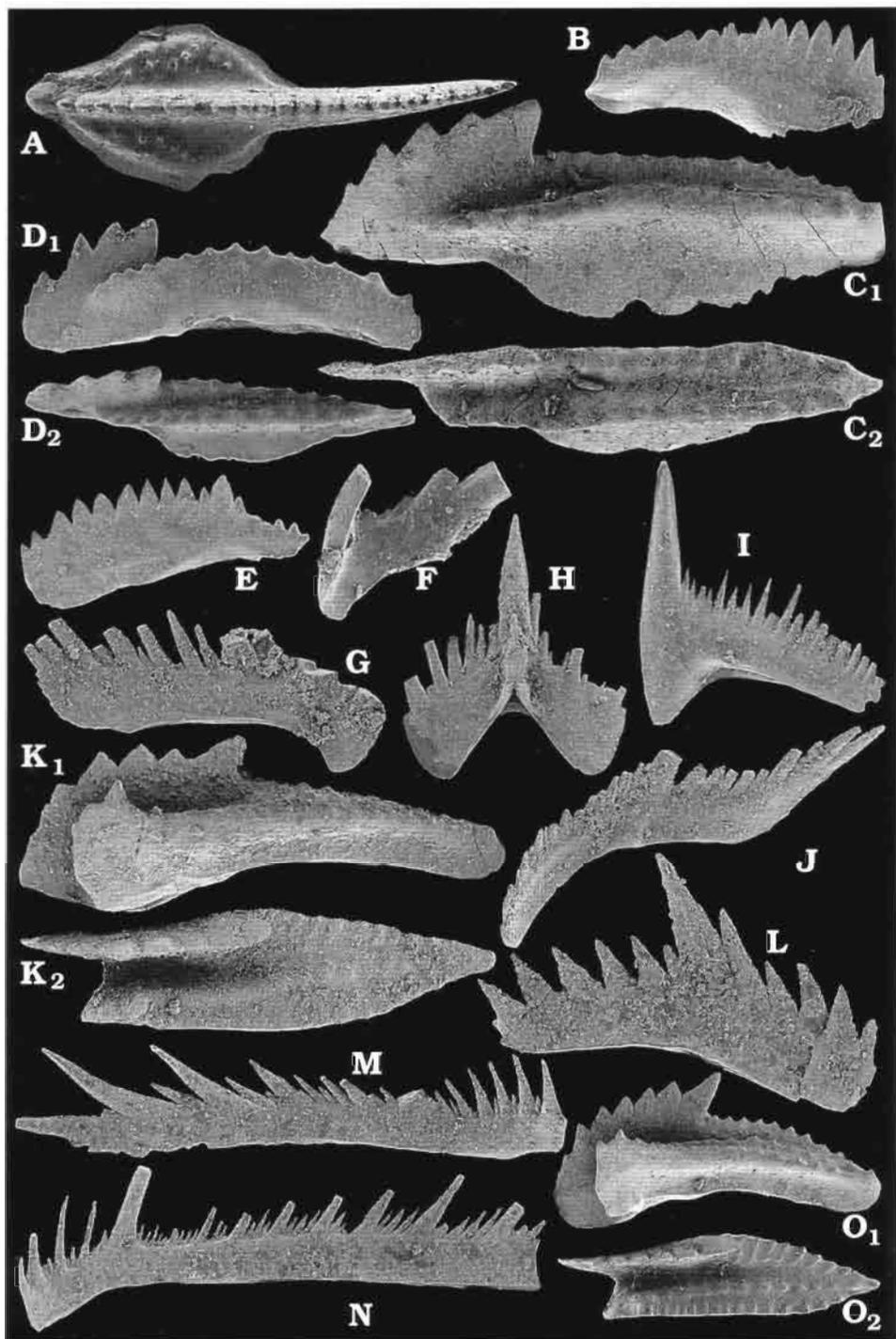
tion. This, and the narrow siphuncle, make the specimen similar to those of the Rhenish *G. (Goniatitella) agricola* Korn, 1988 which is known, however, only from much smaller specimens.

Characteristically evolute and prominently spirally ribbed specimens of *Neoglyphioceras spirale* (Phillips, 1841) have been described from the fore-Sudetic Monocline by Korejwo & Teller (1967) and from the Holy Cross Mountains by Żakowa (1971). In the Rhenish succession it is followed by even more robustly ornamented *N. sauerlandense* Korn, 1988. Relatively involute conchs of *Lusitanites circularis* Korn, 1988 from the Holy Cross Mountains have been attributed by Żakowa (1971) to the American *L. subcirculare* (Miller, 1889), which has much fewer spiral ribs. Both Rhenish and American species have laterally flattened whorls with constrictions and a narrow umbilicus. Evolute and robust conchs associated with the above discussed species in the Holy Cross Mountains were attributed by Żakowa (1971) to another American species, *L. newsomi* (Smith, 1903), but here relationships between Rhenish and American forms are of opposite nature, the latter being a little more densely ribbed (Gordon 1965; Sutherland & Manger 1977). These are rather specimens of *Lyragoniatites eisenbergensis* (Ruprecht, 1937).

Along with the *Goniatites* branch and related forms there were also even less derived ammonoids in the late Viséan, direct successors of the Tournaisian prionoceratids. Here can be attributed several species identified on the basis of juvenile specimens in the latest Viséan Lechówek Beds of the Holy Cross Mountains and coeval strata in the Upper Silesian and Lublin Coal Basins. Żakowa (1971) described several small pyritised specimens from several boreholes in Gałęzice (near Ostrówka) of an ammonoid showing a rather primitive appearance of the suture considering its late age, dated by associated *Lusitanoceras*. She compared them with Namurian *Cluthoceras* (type species *C. truemani* Currie, 1954), known only from juvenile specimens, which may be a successor of *Eoglyphioceras*. An attribution to the latter genus seems preferable. Similar-looking early ontogenetic stages are shown by a form from the late Viséan of the Upper Silesian Coal Basin*, attributed to *Cluthoceras* by Bojkowski (1979). Another species of *Eoglyphioceras*, identified by Żakowa (1974) in bed 1 of her already mentioned trench XXI in Gałęzice (together with *Goniatites arnsbergensis*) is very characteristic in showing prominent growth lines. It was compared with the poorly known *E. fournieri* (Delepine, 1940) which was probably more globose at the stage represented by the Polish specimen. *Eoglyphioceras truncatum* (Phillips, 1836) is a widespread species known from the *Goniatites crenistria* Zone of Kulm facies of the Upper Silesia and Lublin areas (Bojkowski 1979) and the Carboniferous limestone of the Holy Cross Mountains (Żakowa 1974). It can be characterised by its delicate growth lines showing distinct ventrolateral lappets and shallow lateral sinuses (Korn 1988). Adult specimens of diameters up to 75 mm have flat flanks and incipiently tabulate venter (Currie 1954).

Among the most phylogenetically important and widespread lineages of the latest Viséan and Namurian is that of *Sudeticeras*, ammonoids of rather generalised conch

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* Referred to also as 'Upper Silesia Coal Basin', in order to avoid confusion with Silesian (Upper Carboniferous series); see Gradziński R. & Porębski S.J. (eds) 1995. Carboniferous Upper Silesia Coal Basin: Case studies in sedimentology and basin evolution. — *Studia Geologica Polonica* **108**. (Editors)

morphology, relatively simple aperture developing ventrolateral lobes and a tendency to develop delicate spiral ornament. The lineage of *Sudeticeras* appears quite late, in the *Lusitanoceras poststriatum* Zone of the Viséan, its ancestry remaining unknown. Although its conch is similar to that of some *Goniatites* species, the suture is a little more primitive in that the ventrolateral saddle is not pointed. Korn (1988) suggested it originated from *Beyrichoceras*.

Sudeticeras newtonense Moore, 1950 has been identified by Żakowa (1974) in the Holy Cross Mountains and Korejwo (1969) in the Lublin area. It has a characteristic ornamentation of crenulated growth lamellae and represents the group of species within *Sudeticeras* with relatively weak apertural lappets. The conch has a rounded venter and a relatively large umbilicus (Currie 1954). Like the species just cited, *Sudeticeras crenistriatum* (Bisat, 1928) (Żelichowski 1972; Korejwo 1974; Żakowa 1971) has a relatively shallow sinus in the aperture but less regular growth lines and better developed spiral striation. It is different from all other species of the genus in its very narrow umbilicus (Korn 1988). *Sudeticeras splendens* (Bisat, 1928) (Korejwo & Teller 1967; Żakowa 1971; Bojkowski 1979; Korejwo 1986) is perhaps more advanced because of its prominent spiral ornament.

Well developed ventrolateral lappets of the aperture are associated with spiral striae in *Sudeticeras wilczeki* Patteisky, 1928. Its crushed shell fragments are known from the Holy Cross Mountains (Żakowa 1971, 1982) and the fore-Sudetic Monocline (Korejwo & Teller 1967). This is the type species of the genus, as it includes *S. hoeferi* (Patteisky in Folprecht, 1929) originally indicated as such (see Ruzhentsev & Bogoslovskaya 1971).

Early Namurian species of *Sudeticeras* are represented by poorly known *Sudeticeras? parvalingue* Patteisky, 1936, probably rather primitive within its genus, from the marine horizons VII, Barbora, Koks, Jindřich, and Gaebler of Upper Silesia (Schwarzbach 1937; Řehoř & Řehořova 1972; Bojkowski 1979). *Sudeticeras ostraviensis* Patteisky, 1930, from both the Upper Silesian (Řehoř & Řehořova 1972; Bojkowski 1979) and Lublin (Żelichowski 1972) Coal Basins, is probably closely related to the Viséan *S. wilczeki*. Another species of the same group based on crushed material is *Sudeticeras laevigatum* Ruprecht, 1937, known from the Lublin area (Bojkowski 1979).

Anthracoceras discus (Frech, 1899) is probably a successor of *Sudeticeras*. The type horizon of the species is the marine horizon 1b (Gaebler) of Upper Silesia. It is well represented by three-dimensionally preserved specimens (Schmidt 1925; Schwarzbach 1937; Miller & Furnish 1958; Bojkowski 1979; herein Fig. 45). Extremely well preserved and abundant material from the coeval Imo Formation of Arkansas allowed Saunders (1973) to establish a range of population variability in this species. He suggested that the morphologies usually separated into distinct species *A. paucilobum* (Phillips, 1836) are within the range of *A. discus*. This seems highly probable, at least in respect to the Upper Silesian specimens from the marine horizons 1b–d, but does not apply, however, to those from the horizon 1d Roemer classified as *A. paucilobum* by Bojkowski (1972: pl. 8: 8). These show a pattern in the growth lines rather suggestive of dimorphoceratid affinities. Both *A. paucilobum* and *A. discus* have been reported from several marine horizons of the Namurian in the Upper Silesian and Lublin Coal Basins (Czarniecki 1959, Řehoř & Řehořova 1972; Bojkowski 1972,

1979; Żelichowski 1972; Korejwo 1974; Musiał & Tabor 1988). Juvenile specimens of *Anthracoceras* from the Gaebler Horizon in the Czech part of the Upper Silesian Basin have been identified as *A. tenuispirale* Demanet, 1941 by Vašiček (1983), because of the presence of a spiral striation but, as shown by Saunders (1973), this is the feature of juveniles of *A. discus*.

The most characteristic ammonoids for the Namurian are those with oxyconic adult conchs. Their roots extend back to the middle Tournaisian, when in the American lineage of *Winchelloceras*, a derivative of open-umbilicate muensteroceratids, a discoidal conch shape developed. These were ammonoids of relatively large size for the Early Carboniferous. In the late Tournaisian, an acute venter developed in some members of the group, but the suture remained rather primitive. Sutural complication characterises only one small (but widespread) lineage of the dimorphoceratids that was probably derived from *Winchelloceras* (Riley 1996 suggests rather an affinity with *Dzhaprakoceras*).

The oldest Polish record of the lineage seems to be represented by three-dimensionally preserved juvenile specimens of *Glyphiolobus pseudodiscrepans* (Moore, 1939) with a rather simple suture found by Żakowa (1974) in the *Goniatites crenistria* Zone of the Holy Cross Mountains. Crushed specimen possibly belonging to this species occur, according to Bojkowski (1979), in coeval strata of Upper Silesia. *Glyphiolobus lunula* (Knopp, 1931) occurs in the late Viséan of the fore-Sudetic Monocline (Korejwo & Teller 1967), Upper Silesia (Bojkowski 1979; Musiał *et al.* 1995), and the Lechówek Beds of the Holy Cross Mountains (Żakowa 1982), in the latter area specimens being preserved three-dimensionally with sutures and growth lines showing deep lateral sinuses. According to Manger (1988), *Metadimorphoceras denticulatum* (Schmidt, 1925), identified as *M. varians* (Moore, 1939) by Żakowa (1971) in the Lechówek Beds, belongs to a lineage characterised by the increasing denticulation of the sutural lobes, in which it is preceded by *M. pseudodiscrepans* and *M. hodsoni* Moore, 1958, and succeeded by *Metadimorphoceras wiswellense* Moore, 1939, reported by Bojkowski (1979) from Upper Silesia. However, it was shown by Korn (1988) in a sample of *M. denticulatum* from the Rhenish Massif, coeval with *M. hudsoni*, that details of the suture are highly variable, which makes the very existence of separate lineages of *Metadimorphoceras* questionable. The same conclusion can be drawn from data of Manger (1988) who identified separate lineages in samples considered conspecific by earlier authors.

In the Namurian, only crushed specimens of the dimorphoceratids occur, easily recognisable owing to the characteristic pattern of the growth lines, but practically indeterminate at the species level. They are traditionally classified in the Namurian A (Korejwo 1969; Bojkowski 1979) and B (Musiał & Tabor 1988) of the Lublin Coal Basin as *Paradimorphoceras looneyi* (Phillips, 1839). Řehoř & Řehořova (1972) report *Dimorphoceras gilbertsoni* (Phillips, 1836) from marine horizons of Upper Silesia, Františka and Gaebler. Three-dimensionally preserved juveniles from the Gaebler horizon, described by Vašiček (1983) may belong to this species, too. This is the type species of the genus, the holotype of which is a subject of much controversy (see Ruzhentsev & Bogoslovskaya 1971; Manger 1988 questions even its attribution at the family level). Ruzhentsev & Bogoslovskaya (1971) were of the opinion that *Metadimorphoceras* should be included in *Paradimorphoceras*.
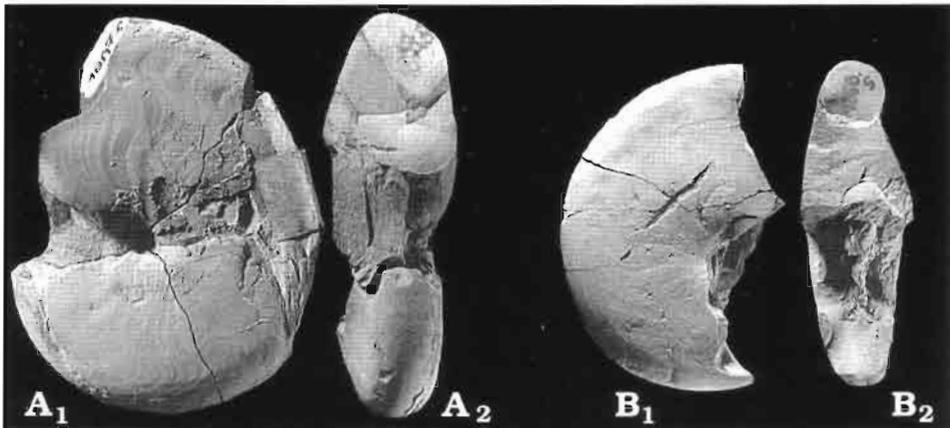
Fig. 45. *Anthracoceras discus* Frech, 1899, specimens UWR 1867s (**A**) and UWR 1866 (**B**) probably from the Frech's collection. No label has been preserved but nautiloids from the same collection preserved in identical way have labels indicating Carolina mine in Upper Silesia (see Dzik 1984: pl. 34: 6, 8, pl. 38: 2), so these are presumably topotypes from the Gaebler marine horizon 1b; both × 1.

Late Namurian dimorphoceratids from the Lublin area were attributed to *Anthracoceratites arcuatilobum* (Ludwig, 1863) by Korejwo (1969), those from the early Westphalian to *Anthracoceratites* cf. *vanderbeckei* (Ludwig, 1863) by Bojkowski (1979) and Musiał & Tabor (1988).

The only dimorphoceratid that is identifiable at species level in crushed material is *Kazakhoceras scaliger* (Schmidt, 1934), characteristically ornamented with sparse spiral striae and narrow lateral sinuses, known from the Namurian of the Lublin Basin and (Bojkowski 1979; Musiał & Tabor 1988) and the Czech part of the Upper Silesian Basin (Řehoř & Řehořova 1972). The latter authors identify with this species the fragmentary adult specimen described as *Eumorphoceras*? sp. by Schwarzbach (1937) from the marine horizon Nanetta, along with specimens from the Gaebler marine horizon. It does not show the complexity of aperture typical for the juveniles and the only basis for identification is the spiral striation. Ruzhentsev & Bogoslovskaya (1971) suggested that this species is synonymous with the Viséan *K. hawkinsi* (Moore, 1930). Although the conch aperture of *Kazakhoceras* is similar to that of the dimorphoceratids and it has also a complex suture, this complexity is a result of completely different evolutionary processes and on this basis Ruzhentsev & Bogoslovskaya (1971) proposed relationships of the lineage to the very different gonioloboceratids.

The most important lineage of discoidal ammonoids for dating of the Viséan–Namurian transition strata starts from *Girtyoceras*. Juvenile conchs in this lineage developed characteristic constrictions and furrows that allow easy identification. Specimens from the *Goniatites crenistria* Zone of the Holy Cross Mountains identified by Czarniecki (1973) as *G.* cf. *welleri* Gordon, 1965 are unlikely to be conspecific with this American form but may rather belong to *Girtyoceras moorei* Nicolaus, 1963, known from the level with *Goniatites hudsoni* and also (flattened) from the *E. grimmeri* level in the Rhenish Massif (Korn 1990b), although lack of data on shell ornamentation precludes specific

identification. Perhaps this is also true for specimens attributed to *G. premesleryanum* Moore, 1946 by Żakowa (1992) from the strata in the Holy Cross Mountains dated as *G. hudsoni* Zone. This is thus the oldest species of the *Girtyoceras* lineage, which has its roots in early Viséan *Beyrichoceras* or perhaps in the Tournaisian *Winchelloceras*. A relatively open umbilicus delimited by a ridge is characteristic of *G. moorei* (Korn 1990b). Its adult conchs had an acute venter, as in later *Girtyoceras* species and also in the early Viséan *Winchelloceras ruzhencevi* Kusina, 1971 (Kusina 1980).

Specimens from the latest Viséan of Upper Silesia attributed to *G. moorei* by Bojkowski (1979) have a too narrow an umbilicus for this species, and may rather belong to its possible successor, *G. brueningianum* (see Korn 1988). Specimens from the Lechówek Beds identified as *G. meslerianum* (Girty, 1909) by Żakowa (1971) differ from this American species, redescribed by Gordon (1965), in the much later development of a keeled venter in the ontogeny. This refers also to earlier identifications of *G. meslerianum* in the Rhenish Massif, for which the name *Girtyoceras goii* Korn, 1990 was proposed as a replacement.

Already in the latest Viséan, at least three independent lineages derived from *Girtyoceras* started to develop ventrolateral furrows in juvenile conchs. A dense distribution of constrictions and ribs at the conch flanks mark the beginning of the Namurian *Tumulites pseudobilingue* (Bisat, 1924), represented by crushed specimens in the earliest Namurian of the Upper Silesian and Lublin Coal Basins (Korejwo 1969; Bojkowski 1979; Musiał & Tabor 1988), had still rather widely spaced ribs at late juvenile stages and deep ventrolateral furrows separating the strongly convex and rounded ventral part of the conch. The furrows gradually disappear in ontogeny, and the adult conch is ornamented only with delicate growth lines. As presented by Korn (1988), the trend to develop such a conch form is expressed already in the late Viséan evolute *Sulcogirtyoceras burhennei* (Brünnig, 1923) from the *Neoglyphioceras rotundum* Zone, which had, however, very evolute early stages making its direct relationships with the *E. pseudobilingue* lineage unlikely. An incipient ventrolateral furrow developed independently in *E. postmeslerianum* (Brünnig, 1923) from the *Lusitanoceras granosus* Zone, which otherwise preserved constrictions typical for *Girtyoceras* (or rather depressions) at whorl flanks, a few per each whorl. In the earliest Namurian assemblage with *E. tornquisti* (Wolterstorff, 1899) and related forms, constrictions are at least as, or even more, numerous than in *S. burhennei*, being associated with irregularly developed ribs. Finally, in *E. pseudobilingue* a kind of ribbing developed at the conch flanks.

A specimen of *Eumorphoceras* cf. *rostratum* Yates, 1962 from the Lublin area illustrated in Musiał & Tabor (1988) represents one of the earliest species of the genus that differs from ancestral *Edmooroceras* in tabulate venter at late juvenile stages and from other species of *Eumorphoceras* in very long lappets and strong, sparse ribbing of the flanks. The American type population of *Eumorphoceras bisulcatum* (Girty, 1909) is characteristic in having densely distributed straight ribs on flanks of juvenile conchs (up to the diameter of about 30 mm) with tabulate venter and adult stages ornamented only with growth lines and with an acute venter (Gordon 1965; Saunders 1973). Most of the European populations, known only from crushed specimens, seem to represent earlier stages in the evolution of the lineage, with the venter still convex and ribs rather widely spaced. This refers also to specimens identified as such in the

Lublin Coal Basin by Żelichowski (1972), Bojkowski (1979), and Musiał & Tabor (1988). It has to be kept in mind that along with the main lineage of *Edmooroceras–Eumorphoceras*, characterised by an open umbilicus, at least one other lineage of *Cousteauoceras–Peytonoceras*, with closed umbilicus, occurs in the Namurian. Korn (1995) has proposed to define the base of the Namurian on the appearance of *Edmooroceras pseudocoronula* (Bisat, 1950).

Formally, the base of the Namurian is defined on the first appearance of *Emstites leion*, a species from quite another branch of the cravenoceratids, represented already in the latest Viséan by *Emstites schaelkensis* (Brünnig, 1923) (see Korn 1988). This lineage is rooted perhaps in the *Goniatites (Hibernicoceras)* lineage (Korn, personal communication) or in forms related to *Bollandites kielcensis* Żakowa, 1992 from the *Goniatites fimbriatus* Zone. The earliest Namurian *Emstites leion* (Bisat, 1930) have been identified as *Cravenoceras leion* Bisat, 1930 in the borehole Gołonóg IG-1 in Upper Silesia by Bojkowski (1979) on the basis of characteristic straight growth lines and longitudinal striation at the umbilicus. Another specimen, found in proximity to these fossils, that has bases of septa preserved at the ventral surface of the ornamented conch is the holotype and only specimen of *Paracravenoceras golonogensis* Bojkowski, 1979. The morphology of the dorsal part of the suture in the close relative of this species, *E. leionoides* Ruzhentsev & Bogoslovskaya, 1971, from the Namurian of the Urals (Ruzhentsev & Bogoslovskaya 1971), is not much different and there seems to be at present no reason to separate this specimen from the others either on the generic or specific level. Korn (1995) has questioned the alleged correlative value of *E. leion*, because it is frequently misidentified in crushed preservation.

Crushed specimens occurring above those identified as *Cravenoceras leion* in the same borehole have been attributed to *Emstites vetus* (Patteisky, 1937) by Bojkowski (1972, 1979). They have a narrow umbilicus with rounded margin, in this respect resembling latest Viséan *E. novalis* Korn, 1988. The type species of the related genus, *Cravenoceras* may occur in the Lublin area, being reported as *C. cf. malhamense* (Bisat, 1924) by Korejwo (1969). It differs from species of *Emstites* in evolute juvenile stages with wide whorls; adult conchs are discoidal in shape, with relatively narrow umbilicus. The *Cravenoceras roemeri* (Schmidt, 1929) type specimen comes from the marine horizon 1b in Upper Silesia where three-dimensionally preserved conchs occur. Its suture line remains unknown; from *C. malhamanse* it differs in a narrower umbilicus with a sharp ridge. Three-dimensionally preserved juvenile ammonoid conchs with such features occurring in the Gaebler marine horizon have been identified by Vašiček (1983) as a new subspecies *Anthracoceras tenuispirale patteiskyi*.

Cravenoceratoides edalensis (Bisat, 1928) has been identified on the basis of bifurcating transverse ribs and relatively open umbilicus in the early Namurian marine horizon VII of the Upper Silesia and the I *Posidonia* marine horizon of the Lublin area (Bojkowski 1979; Musiał & Tabor 1988). Straight and relatively robust transverse riblets characterise conchs of *Cravenoceratoides nitidus* (Phillips, 1836), known from the early Namurian of both the Upper Silesian (marine horizon 1d and 1b) and Lublin Coal Basins (Korejwo 1969, 1974; Bojkowski 1979). Rather delicate riblets of varying height and narrow umbilicus make crushed conchs of *Cravenoceratoides nititoides* (Bisat, 1932) characteristic. In the rather narrow umbilicus this species resembles *Nuculoceras* from which it differs in the lack of any spiral ornament, as pointed out by Vašiček (1983), who described

three-dimensionally preserved juveniles from the Gaebler marine horizon of the Czech part of the Upper Silesian Coal Basin. The species is also known from the Lublin area (Korejwo 1969; Bojkowski 1979; Musiał & Tabor 1988) where it occurs higher in the sequence than *C. edalensis*. The type horizon of *Cravenoceratoides simplex* Knopp, 1934 is the III marine horizon Henryk in the Polish part of the Upper Silesian Coal Basin. Juvenile stages from the Gaebler horizon were identified with this species by Vašiček (1983). Even narrower umbilicus and coarser ornament differentiate them from associated forms cited as *C. nititoides* (Vašiček 1983).

Ramosites macrocephalus (Frech, 1902) has its type horizon in the marine horizon 1b at Laura mine in Chorzów, Upper Silesia (Schmidt 1925). This is a derivative of the *Cravenoceratoides* lineage (Ruzhentsev & Bogoslovskaya 1971), having bifurcations of riblets similar to those in *C. edalensis* and narrow umbilicus as in late species of that genus and its attribution to either of these genera is arbitrary. *Ramosites divaricatus* (Hind, 1905), with riblets showing shallow lateral and ventral sinuses of the aperture, typical for the genus, is known from the Lublin area (Bojkowski 1979). According to Bisat (1924) this is a successor of his *Homoceratoides praedivaricatus*, characterised by a wider umbilicus.

A poorly preserved specimen from the II *Posidonia* marine horizon in the Lublin area was identified by Żelichowski (1972) as *Homoceras* cf. *diadema* (Beyrich, 1837), which is a synonym of *Isohomoceras striolatum* (Phillips, 1836), according to Ruzhentsev & Bogoslovskaya 1988). It is unlikely to occur at this level and may be conspecific with some of the related forms of Korejwo (1969). *Isohomoceras subglobosum* (Bisat, 1924) occurs in a marine horizon from the same area below that with *H. beyrichianum* (Korejwo 1969).

An edge-delimiting umbilicus is a feature of *Vallites* cf. *henkei* (Schmidt, 1925) represented by crushed specimens in a Namurian marine horizon above that with *H. beyrichianum*, being associated with the first *Reticuloceras adpressum* in the same region (Korejwo 1969). *Vallites* cf. *moorei* (Bouckaert, 1960) is another species of the genus reported by Korejwo (1969).

Evolute juvenile stages with sharp umbilical edges and oxyconic adults, which is hardly recognisable in crushed Namurian material from the Lublin area (Korejwo 1969; Bojkowski 1979), characterise *Homoceras beyrichianum* (de Koninck, 1843). *Homoceratoides* cf. *mutabilis* Bisat & Hudson, 1943 is a successor of *Homoceras* according to Ruzhentsev & Bogoslovskaya (1988). Its conch remains involute at all stages. Crushed material comes from a marine horizon in the Lublin area located above that with the first *H. beyrichianum* (Korejwo 1969). Even higher in the cores, shell fragments of *Homoceratoides varicatus* Schmidt, 1934 co-occur with *Reticuloceras* in the Lublin area (Korejwo 1969).

Unlike the preceding species, *Phillipsoceras* cf. *umbilicatum* (Bisat & Hudson, 1943) shows well developed lateral lappets at the aperture, which was the basis of its identification, in the same marine horizon as the above species, by Korejwo (1969). This is an early member of the *Reticuloceras* lineage characterised by a rather wide umbilicus at early stages (Ruzhentsev & Bogoslovskaya 1988). Prominent lappets are typical for *Reticuloceras adpressum* Bisat & Hudson, 1943 and *Reticuloceras todmordenense* Bisat & Hudson, 1943 known from two horizons in the western part of the Lublin area, but outside the coal basin (Korejwo 1969, 1986). In the course of evolution

of the *Reticuloceras* lineage, the sinus of the aperture and lappets develop earlier and earlier in ontogeny (see Ruzhentsev & Bogoslovskaya 1988).

The lappets are much narrower in *Bilinguites gracilis* (Bisat, 1924) from the *Carbonicola pseudacuta* horizon of the Namurian B of the same area (Żelichowski 1972; Musiał & Tabor 1988). *Bilinguites bilinguis* (Salter, 1864), with furrow-bordering lappets is known from a Namurian marine horizon above that with *Homoceratoides* and below another with *Bilinguites superbilinguis* (Bisat, 1924) of the Lublin area (Korejwo 1969, 1986). The lateral rims of the whorl are here delimited by furrows on both sides, which resembles the situation independently and much earlier achieved by *Eumorphoceras*.

Cancelloceras cf. *cancellatum* (Bisat, 1923) is characterised by the presence of a reticulate conch ornament with very strong longitudinal (spiral) striae. It is known from the Lublin area from crushed specimens co-occurring with *Agastrioceras* in a marine horizon of Namurian C (Korejwo 1969, 1986). In *Cancelloceras* cf. *cumbriense* (Bisat, 1924), lateral ribs are less densely distributed, becoming prominent at later stages of ontogeny, whereas spiral striae are weaker than dorsal transverse ribbing (Żelichowski 1972; Korejwo 1969, 1986; see also Nikolaeva & Kullmann 1995). The species occurs in western Europe in the last marine horizon, Schieferbank, of the Namurian C (Böger 1972).

Adult specimens of *Agastrioceras carinatum* (Frech, 1899) are oxyconic but only juvenile, relatively involute and crushed conchs of this species are known from the Namurian C of the Lublin Coal Basin (Korejwo 1969; Bojkowski 1979; Musiał & Tabor 1988).

Little crushed juvenile specimens of *Gastrioceras circumnodosum* Foord, 1903, which differs from ancestral *Cancelloceras* in the lack of spiral striation, originate from marine horizons of Westphalian A in the Lublin area (Bojkowski 1979; Musiał & Tabor 1988). *Gastrioceras listeri* (Sowerby, 1812) with tuberculated lateral edges of conch whorls already at juvenile stages is the guide fossil for the Westphalian A *Carbonicola pseudorobusta* marine horizon in the Lublin area (Bojkowski 1979). In the western European Carboniferous they both occur in the Finefrau horizon well above the base of the Westphalian A (Böger 1972). The last marine horizon in the Lublin area is the *Dunbarella* horizon, correlated by Musiał & Tabor (1980, 1988) with the Catharina horizon in the Ruhr Coal Basin. It has yielded *Anthracoceras vanderbeckei* (Ł. Musiał, personal communication). These are the last ammonoid species in the Polish Palaeozoic.

Viséan and Late Carboniferous pelagic communities in Poland

Until the end of the Viséan in most of the areas with preserved early Carboniferous rocks in Poland there was continuous marine sedimentation, generally fine clastics, with epochs of warm climate and low sea-level stands represented by changes to carbonates at least in elevated parts. In the Sudetes the early Viséan transgression is documented by the long-ranging *Mestognathus beckmanni* that occurs in a limestone bed covering the gneiss basement (Haydukiewicz 1986). The marine sedimentation ceased there after the early late Viséan *Goniatites fimbriatus* Zone (Żakowa 1963),

which is consistent also with the conodont evidence (Chorowska & Radlicz 1994). The Variscan orogeny started then, and in the Namurian the Lower Silesian Coal Basin formed in the area, supplied with clastics from a NE located new orogen (Bossowski & Ihnatowicz 1994).

In the Holy Cross Mountains the youngest palaeontologically documented Carboniferous marine strata of the Lechówek Beds represent the late late Viséan *Lusitanoceras poststriatum* Zone (see Żakowa 1982). The top of the Early Carboniferous is erosional there, so the exact end of marine sedimentation cannot be precisely dated.

Only in the Upper Silesian Coal Basin is the whole Viséan represented by virtually continuous fine clastic sedimentation, bordered eastward by shallow-water carbonates of the Kraków area (Bełka 1987).

Beginning from the end of the Viséan the distribution of ammonoids (and presumably conodonts) in Poland is completely connected with periodic brief transgression of relatively deep-water marine environments into the predominantly continental sedimentary basins. These marine horizons, being numerous in Namurian A, are sparse and geographically restricted later, the last being of Westphalian A age (Fig. 46). Both global eustasy and local tectonics control their distribution.

There are three Late Carboniferous coal basins in southern Poland that back from three sides the closing Variscan ocean. The Lower Silesian Coal Basin in the Sudetes developed near the previously and extensively discussed Dzikowiec locality – there are no marine incursions there within the continental deposits (see Bossowski & Ihnatowicz 1994). In contrast to the Sudetes, in the Upper Silesian Coal Basin numerous marine incursions took place during the Namurian, represented by about sixty horizons with a marine fauna, grouped into a series of marine bands (Kotas 1972; Bojkowski 1979).

An even more significant contribution of marine deposits characterises the sedimentation regime of the most eastward located Lublin Coal Basin. Above Famennian limestones, a variegated series of unknown age is developed there with erosional lower and upper boundaries. A continuous sedimentation started there probably with the latest Viséan transgression, at least this age is documented by both conodonts and ammonoids. Already in the Viséan the first coal beds developed. Always the coal immediately precedes marine sedimentation events (as is the case in Kentucky, see Chesnut 1994). This may reflect expansions of rain forests soon after each glacial period, similar to that in the Quaternary (see Walker & Chen 1987). Till the end of the Namurian A, 23 such cycles have been counted (Porzycki 1988: p. 44). They probably correspond to the same eustatic events that resulted in marine incursions to the Upper Silesian Coal Basin. Unlike Upper Silesia and despite the much more coarse terrigenous sediment supply in Namurian B, in the Lublin area marine horizons continue to occur throughout the entire Namurian and even the early Westphalian. Several limestone beds connected with these horizons are of correlative value and have been indicated with letter symbols (Fig. 46).

Similar marine horizons occur also in the Carboniferous sedimentary basins of western Europe. They usually contain distinct ammonoid faunas allowing identification and correlation. Ramsbottom (1977: fig. 12) proposed on this basis a series of eustatic events in the Craven Basin of northern England and his scheme has been successfully applied to the Carboniferous of the American Midcontinent (Saunders *et al.* 1979). In deeper-water environments of the Viséan and Namurian, periodic incur-

Fig. 46. Stratigraphic distribution of ammonoid species in the Lublin (left column) and Upper Silesian (right column) Coal Basins of Poland. Marine bands indicated with black lines, letters refer to marker limestone beds; data compiled from Korejwo (1969), Żelichowski (1972), Bojkowski (1979), Musiał & Tabor (1988), unpublished data of Dr. Łucja Musiał (Polish Geological Institute, Sosnowiec), and other sources, attribution to particular horizons in the Lublin area is mostly tentative — except for the *Posidonia* and few other horizons, for which exact lists of fossils have been provided, positions of particular findings have been interpolated from diagrammatic presentations of ranges.

sions of *Vogelgnathus* were proposed by Boogaard (1992) to express eustatic rises of sea level corresponding to the eustatic cycles of Ramsbottom (1977). It is tempting to match the British scheme with the record of eustatic transgressive events in the Polish Namurian, and such an attempt was done already by Ramsbottom (1977). Unfortunately, in the area between England and Poland this work has been only preliminary (Hodson 1957; Hodson & Leckwijck 1958), which makes use of faunal data difficult.

A compilation of the available data on ammonoids (Fig. 46) shows that in many cases the appearances of particular faunas in the Polish coal basins coincided with similar pelagic marine faunal incursions to those of the marginal parts of the Craven Basin, although not always. Thus, the earliest Namurian ammonoid assemblages are well represented in marine bands in both the Upper Silesian and Lublin basins, which agrees well with a long-lasting transgressive period in England. However, in both Polish basins the fauna with *Cravenoceratoides edalensis* is well represented in the upper Enna and I *Posidonia* bands, respectively, although it corresponds to a strong regression in the Craven Basin. *Nuculoceras* is missing in Poland, but *Homoceras beyrichianum* is represented in the Lublin Basin, as could be predicted. Early *Reticuloceras* faunas occur in the eastern part of the Lublin area, but did not reach the coal basin. In the Craven Basin there is a significant transgression at this horizon. Associated *Vallites henkei* occurs in similar position also in Germany (Hodson 1957). A good record of the succession within the *Bilinguites* lineage in the same part of the Lublin area corresponds to a long regression in England, although some record of this cycle has been identified in Arkansas. The following two ammonoid incursions to the Lublin area, those with *Cancelloceras cumbriense* and *Gastrioceras listeri*, well fit the transgressive events in the Craven Basin and Germany (see Nikolaeva & Kullman 1995 for review).

Environmental control of Carboniferous biotic events

The main factor controlling the environment of the latest Devonian and Carboniferous was the glaciation of Gondwana. A melting of continental ice cover of Gondwana was apparently the main cause of the sea level rises, not only those represented by the Late Carboniferous marine bands, when glaciers were widely developed, but also the earlier global marine transgression at the end of the *Wocklumeria* Stufe (Hangenberg Black Shale), *S. crenulata* transgression, and the early Viséan transgression. The first extensive glaciation of this ice epoch is of Famennian age, being separated by an interglacial interval from the second glaciations in the Tournaisian (Caputo 1985). The lower tillite contains an assemblage of land plant spores closely similar to that occurring in Europe in the latest Famennian (Loboziak *et al.* 1993) and it has been apparently assumed by these authors that during that glaciation the same plant species ranged from the tropics to the Southern Pole. On this basis the income of the Famennian glaciation has been dated as strictly corresponding to the disappearance of Devonian type ammonoids and conodonts and the change from carbonate sedimentation of the *Wocklumeria* limestone to dark clays of the Hangenberg event in the equatorial part of Laurasia. An alternative interpretation would be that the eustatic sea level rise and incursion of relatively cold waters to the Variscan sea corresponds rather to a deglaciation episode and temporal

disappearance of climatic gradients. The higher glacigenic strata in Brazil are of middle to late Tournaisian age according to Loboziak *et al.* (1992). The South American margin of Gondwana reached the South Pole at that time (Veevers & Powell 1987). After a period of retreat in the Tournaisian, the glaciers expanded again in the Viséan and, again after a warmer period, in the early Namurian. From this point, an almost continuous glaciation characterises the geological history of Gondwana, until gradual retreat of the continental ice in the Permian (Crowell 1995) when Gondwana migrated outside the South Pole. The direct dating of glacial deposits cannot be precise but this can be overcome by studying effects of the glacial events in more remote areas, where more complete biostratigraphic control is possible (Veevers & Powell 1987). The fossil record of the evolution of conodont and ammonoid faunas in the Variscan belt can also be used for this purpose.

The periods of relatively low sea level stands connected with carbonate sedimentation and warm-water high-diversity assemblages in this area may correspond to glacial epochs, when climatic zonality was stronger and the areas close to the Equator (including the Variscan belt) experienced higher mean annual temperatures. Of such nature was probably the cold episode of incursion of the *Acutimitoceras prorsum-Protognathodus* fauna to tropical regions, followed by the warmer *Gattendorfia* epoch with somewhat higher sea stand, the Erdbach limestone epoch with expansion of the *Ammonellipsites kochi–Scaliognathus anchoralis* fauna and the late Viséan flourishing of pelagic communities. Retreats of the ice cover and unification of the global climate resulted in black shale sedimentation of the Hangenberg Black Shale, as well as the *S. crenulata* Zone and early Viséan Alum Shales, with relatively low bottom temperatures and marine incursions to the continental basins.

Conditions changed with the beginning of the Namurian, perhaps in connection with more extensive glaciation and migration of the Variscan orogenic belt to a strictly equatorial position. Prominent climatic gradients and high precipitation resulted in disappearance of limestone sedimentation in the area and increase of terrigenous sedimentation rate. Melting of glaciers and following transgressions reduced erosion at the continents resulting in the development of coal swamps, subsequently flooded with the sea. The terminology of marine bands, whenever they reflect really global events, may thus be used to denote directly warm periods in Gondwana.

A tectonic evolution of the Variscan orogen was superimposed on this global pattern which resulted in a gradual ceasing of the marine influences. The first folded region were apparently the Sudetes, then Upper Silesia and finally the whole Variscan ocean was closed and the massifs south of it merged with the Laurasian continent.

Diagnoses of new and emended taxa

Pseudopolygnathus Branson & Mehl, 1934

Type species: *P. prima* Branson & Mehl, 1934.

Emended diagnosis. — Elements **sp** with more or less elaborated icrion (transverse ribs and tubercles of the same height as the main row of denticles), other elements of the apparatus of generalised polygnathid morphology, robust **oz** elements may develop a narrow platform.

Remarks. — The type species of *Pseudopolygnathus* is closely similar and undoubtedly represents the same low-rank evolutionary branch as the type species of *Bispathodus* Müller, 1962 – *Spathodus spinulicostatus* Branson, 1934. These somewhat unfortunate choices of type species that are not typical for the widely accepted concepts of their own genera make distinction between them quite unclear. There seems to be no way to formulate really useful diagnoses for these genera if *Pseudopolygnathus* encloses species either with icrion or platform and *Bispathodus* species without any modifications of the oral surface, with additional tubercles at the base or with a wide icrion. In such a situation the most reasonable solution would be to synonymize the two genera and restrict the use of redefined *Pseudopolygnathus* to species with a well developed icrion in the **sp** elements. Those with a platform or lacking any modifications of the occlusal surface of the **sp** elements should then be placed under other generic names.

Weyerognathus gen. n.

Type species: *Pseudopolygnathus triangulus* Voges, 1959

Derivation of the name: In recognition of works on the conodont stratigraphy of the Dzikowiec section by Dr. Dieter Weyer.

Diagnosis. — Elements **sp** with wide platform that in early species may range into a icrion. Other elements of the apparatus of generalised polygnathid morphology, robust, adult **oz** elements with platform of variable width.

Neopolygnathus Vorontsova in Barskov *et al.*, 1991

Type species: *Polygnathus communis* Branson & Mehl, 1934.

Emended diagnosis. — Elements **sp** with relatively thin and wide, generally smooth or weakly tuberculated platform and small pit; **oz** elements regularly triangular in profile, with densely distributed denticles; apparatus of generalised polygnathid morphology, all elements of rather small size and gracile appearance.

Remarks. — The generic name *Polygnathus* Hinde, 1879 is now a typical taxonomic 'waste basket' encompassing hundreds of remotely related species and it is now not possible to provide any sensible diagnosis for it. The Late Devonian type species of the genus, *P. dubius* Hinde, 1879, as currently understood, is an unspecialised member of evolutionary branch with a platform of **sp** elements strongly ornamented with transverse ridges and the rest of the apparatus of rather generalised morphology. I follow Barskov *et al.* (1991) in removing from this genus the advanced latest Devonian–Early Carboniferous branch of derived polygnathids, characterised by well developed but a morphologically simple platform of **sp** elements and compact, regularly denticulated **oz** elements. To encompass the limits of the genus requires more data on apparatus structure. At present at least derivatives of *N. communis* that differ from each other mostly in the pattern of early histogeny of the platform can be classified here.

Neopolygnathus sudeticus sp. n.

Fig. 13H–I.

Holotype: ZPAL C XVI/94; Fig. 9H.

Type horizon and locality: Wapnica beds in Dzikowiec, the Sudetes, sample Dz-50, *S. carinthiaca* Zone.

Diagnosis. — The width of platform in **sp** elements, which is of rounded triangular shape, reaches almost 80% of its length. Otherwise similar to *N. purus*.

Pinacognathus Branson & Mehl, 1944

Type species: *Pinacodus profundus* Branson & Mehl, 1934.

Emended diagnosis. — Aparatuses with **sp** elements characterised by lanceolate shape of the basal cavity with an almost flat surface and simple platform with transverse ribs and robust **oz** elements with smooth surface and blunt, obliterated denticles. Elements of the symmetry transition series with relatively short processes.

Remarks. — In Polish sections there is a continuity in distribution and apparatus morphology of the lineage of *Pinacognathus*. There seems thus to be little reason to separate these species in different genera and certainly there is no relationships between the late species of the lineage, whatever is its proper specific name, and species of *Pseudopolygnathus*. As they all seem to share closely similar and characteristic morphology of the **oz** elements, which is distinct from that in *Siphonodella*, they are here defined on this basis. With *Siphonodella* they share shape of the basal cavity and also some similarity in the apparatus structure.

Siphonodella Branson & Mehl, 1944

Type species: *Siphonognathus duplicatus* Branson & Mehl, 1934.

Siphonodella belkai sp. n.

Fig. 19A–F.

Siphonodella sp. indet.; Matyja 1976: p. 531, pl. 24: 5.

Holotype: Incomplete specimen ZPAL C XVI/308; Fig. 19E.

Type horizon and locality: *Siphonodella carinthiaca* Zone, sample Ko-42 taken from 9.0 m below the radiolarites in the Kowala trench, Holy Cross Mountains, Poland.

Derivation of the name: In recognition of the work on Carboniferous conodont stratigraphy by Zdzisław Bełka.

Diagnosis. — The dorsal ('posterior') part of the platform of **sp** elements completely smooth and convex, covered only with cell pits. The parallel arranged ridges end at the level of the cusp, the furrow between the blade and the posterior ridge continues to the tip of the platform. Free blade short.

Description. — The only identified part of the apparatus are **sp** elements. They are very unusual, as for *Siphonodella*, in having smooth (except for fine reticulation produced by epithelial cells) and gently convex, anterodorsal field of the platform. In juvenile specimens the first two ridges, that run strictly parallel to the carina, terminate abruptly at the level of the cusp and only immediately after the development of the ridges they merge with the platform margin (Fig. 19D). When additional ridges develop they tend to merge at their ends into pairs. Up to six ridges have been observed.

Relationships. — In a rather sudden narrowing of the platform at its ventral end, the elements resemble those of the type series of *S. sandbergi*, which may suggest common origin of these two species or even derivation of *S. belkai* from American *S. sandbergi*,

but in Polish sections no *S. sandbergi* has been found below the range of *S. belkai*. Moreover a population possibly corresponding morphologically to early *S. sandbergi* replaces *S. belkai* in the Kowala section.

Remark on the type series. — This is one of the most characteristic species of *Siphonodella* and its discrimination is extremely easy on the basis of large **sp** elements. Although several complete **sp** elements of this species are available from the condensed section of Dzikowiec, they are invariably juvenile (Fig. 19B, C). There is a possibility that in the suggested course of evolution from *S. sandbergi* to *S. belkai* different ontogenetic stages behaved in different way and more than one species may have developed similar juvenile stages. The specimens from Kowala come mostly from unconsolidated clays and, despite very good preservation, are usually fragmented as a result of rock compaction. It is of more importance to have the type population clearly recognisable than to select one nicely looking specimen from it. As there is little chance to collect a complete specimen form Kowala samples in predictable future I decide to make an incomplete specimen (but showing all the diagnostic features of the species) the holotype.

Occurrence. — Kowala in the Holy Cross Mountains, Dzikowiec in the Sudetes, Rzeczenice 1 borehole in West Pomerania (Matyja 1976); above *S. duplicata*, below or partially together with *S. carinthiaca*.

Conclusions

No apparent difference in the evolution of pelagic faunas between the eastern and western parts of the central European Variscan sea has been detected. If there are some peculiarities in local faunal successions, a control by bathymetric and sedimentary factors at particular localities seems to be involved rather than a more general biogeography.

In most general terms the succession of pelagic faunas in the Variscan sea throughout the Early and early Late Carboniferous can be traced in time and space, although several important questions remain to be answered, especially regarding faunal relationship with other biogeographic provinces. This is, however, beyond the scope of this review.

Perhaps the most enigmatic biotic event in the evolution of conodonts and ammonoids was the sudden replacement of the *Wocklumeria* limestone high-diversity faunas by those of the *Gattendorfia* limestone. The role of the *Acutimitoceras* ammonoid fauna, which is morphologically uniform, although rich in sympatric species, and low diversity *Protognathodus* conodont fauna, that invariably occur in between, remains also unclear.

The very characteristic pelagic community of the *Gattendorfia* limestone must have had time to develop so it is unlikely that its emergence was an effect of evolution in the area. Yet its geographic origin remains a mystery. It is tempting to interpret any appearance of a high diversity fauna as a result of an increased rate of evolution but also this case does not provide any evidence for such an assumption. In all well documented successions, faunal changes are effects of immigration of earlier diversified faunas. This lack of correspondence between the rate of evolution and rate of speciation has been
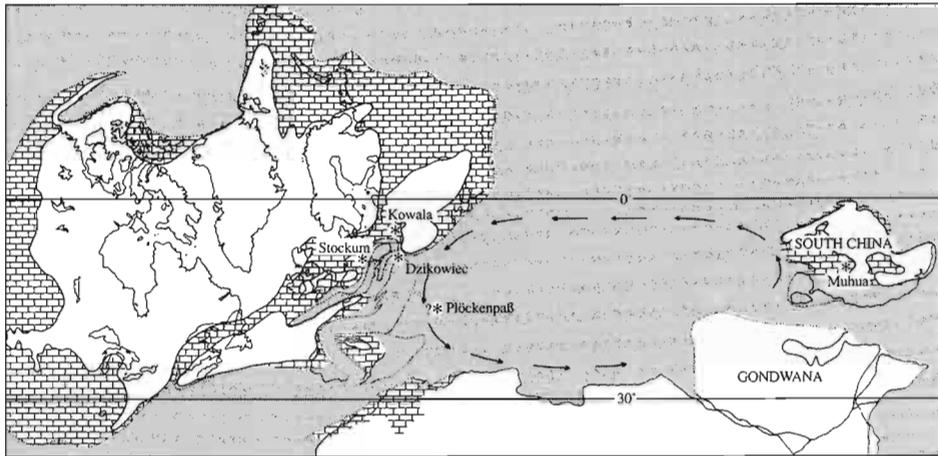
Fig. 47. Palaeogeographic position of the discussed localities in the Tournaisian, with boundaries of lands and marine shelf sedimentation (brick pattern) given (based on Ziegler 1990 and Liu & Xu 1994). Note that Dalziel *et al.* 1994 proposed drastically different position of main land masses, inconsistent with the location of Famennian–Tournaisian tillites in South America and carbonates in North Africa; Scotese *et al.* 1990 reconstruction for the Devonian–Carboniferous boundary places South China in northern tropical latitudes; according to Hsü *et al.* (1990) there is a suture between Yangtze and Huanan regions, corresponding to Palaeozoic Nanpanjiang Sea, that has not been closed until the end of the Triassic – South China represents thus two separate microcontinents of Palaeozoic age. Directions of oceanic currents inferred from this arrangement of land masses shown by arrows; note that the Muhua area was under influence of relatively colder water masses even though its latitudinal position was similar to that of central Europe.

already proven by stratophenetic studies on complete sections representative of other epochs in the evolution of pelagic faunas (see Dzik 1991a, 1995).

The end of the high diversity *Gattendorfia* limestone ecosystem in central Europe coincides with the establishing of its continuation in the newly flooded area of Belgium nearby and of the North American Midcontinent (see Fig. 47). Most lineages continued their rather slow evolution but some, like the ammonoid Prodromitidae, perhaps owing to the earlier developed advanced discoidal conch form and complex septal morphology, were able to reach a very sophisticated design. When a warm-water environment was re-established in Europe in the late Tournaisian, the American lineages invaded the area. While the conodonts of this time show quite an impressive range of morphologies, and the ammonoids represent conch shapes from completely involute (*Irinoceras*) to *Clymenia*-like (*Merocanites*, *Nomismoceras*), their diversity is hardly comparable with that of the *Wocklumeria* and *Gattendorfia* epochs. Even less impressive is the range of morphologies at the next return of warm-water conditions to central Europe, in the late Viséan, after another epoch of alum shale deposition. The same refers to the morphologic diversity and number of species of conodonts (see Table 4). It seems that with the climate becoming more and more unstable during the Late Carboniferous glacial epoch, short warm intervals alternating with cold ones, there was not enough time for evolution to re-establish high-diversity shallow-water assemblages. In effect, however, destructions caused by climatic changes were also less and less severe.

Acknowledgements

References

Alekseev, A.S., Barskov, & Kononova, L.I. 1987. Berčogur section. *In:* V.A. Maslov (ed.), *Fauna and biostratigraphy of Devonian/Carboniferous boundary sediments in Berčogur (Mugodžary)* [in Russian], 38–48. Nauka, Moskva.

Avchimovitch, V.I. & Turnau, E. 1994. The Lower Carboniferous *Polycospora claytonii* Zone of Western Pomerania and its equivalents in Belorussia and northeastern Europe. — *Annales Societatis Geologorum Poloniae* **63**, 249–263.

Barskov, I.S., Vorontsova, T.N. (Voroncova, T.N.), Kononova, L.I., & Kuzmin, A.V. 1991. *Identification key to Devonian and Lower Carboniferous conodonts* [in Russian], 1–184. Izdatielstvo Moskovskovo Universiteta, Moskva.

Bartsch, K. & Weyer, D. 1988. Die unterkarbonische Ammonoidea-Subfamilia Karagandoceratinae. — *Freiberger Forschungsheft C* **419**, 130–142.

Becker, R.T. 1993. Anoxia, eustatic changes, and Upper Devonian to lowermost Carboniferous global ammonoid diversity. *In:* M.R. House (ed.), The Ammonoidea: Environment, Ecology, and Evolutionary Change. — *Systematic Association Special Volume* **47**, 115–163.

Bełka, Z. 1982. Upper Viséan conodonts from Orlej in the Cracow Upland: stratigraphical and paleothermal implications. — *Acta Geologica Polonica* **32**, 57–67.

Bełka, Z. 1983. Evolution of the Lower Carboniferous conodont genus *Mestognathus.* — *Acta Geologica Polonica* **33**, 73–84.

Bełka, Z. 1985. Lower Carboniferous conodont biostratigraphy in the northeastern part of the Moravo-Silesian Basin. — *Acta Geologica Polonica* **35**, 33–60.

Bełka, Z. 1987. The development and decline of a Dinantian carbonate platform: an example from the Moravia-Silesia Basin, Poland. *In:* J. Miller, A.F. Adams, & V.P. Wright (eds), *European Dinantian Environments,* 177–188. John Wiley & Sons, London.

Belka, Z. 1990. Potential conodont levels for intercontinental division of the Lower Carboniferous. — *Courier Forschungsinstitut Senckenberg* **130**, 11–14.

Belka, Z. & Groessens, E. 1986. Conodont succession across the Tournaisian–Visean boundary beds at Salet, Belgium. — *Bulletin de la Société belge de Géologie* **95**, 257–280.

Bełka, Z. & Skompski, S. 1988. Mechanizm sedymentacji i pozycja facjalna wapienia węglowego w południowo-zachodniej części Gór Świętokrzyskich. — *Przegląd Geologiczny* **36**, 442–449.

Bełka, Z., Skompski, S. & Soboń-Podgórska, J. 1996. Reconstruction of a lost carbonate platform on the shelf of Fennosarmatia: evidence from the Viséan polymictitic debrite, Holy Cross Mts., Poland. *In:* P. Strogen, I.D. Sommerville, & G.L. Jones (eds), Recent Advances in Carboniferous Geology. *Journal of the Geological Society London Special Publication 107,* 315–329. Bath.

Bisat, W.S. 1924. The Carboniferous goniatites of the north of England and their zones. — *Proceedings of the Yorkshire Geological Society* **20**, 40–124.

Bischoff, G. 1957. Die Conodonten-Stratigraphie des rheno-herzynischen Unterkarbons mit Berücksichtigung der *Wocklumeria* Stufe und der Devon/Karbon-Grenze. — *Abhandlungen der hessische Landesamt Bodenforschung* **19**, 1–64.

Bitter, P.von & Plint, H.A. 1987. Conodonts of the Windsor Group (Lower Carboniferous), Magdalen Islands, Quebec, Canada. — *Journal of Paleontology* **61**, 346–362.

Bitter, P.H. von, Sandberg, C.A., & Orchard, M.J. 1986. Phylogeny, speciation, and palaeoecology of the Early Carboniferous (Mississippian) conodont genus *Mestognathus*. — *Royal Ontario Museum Life Sciences Contributions* **143**, 1–115.

Böger, H. 1972. Die Grenze Namur/Westfal (Silesium) in Westeuropa (Ein Diskussionsbeitrag zur stratigraphischen Metodik im paralischen Karbon). — *Newsletter on Stratigraphy* **2**, 55–76.

Bojkowski, K. 1979. Goniatyty z karbonu Górnośląskiego i Lubelskiego Zagłębia Węglowego. — *Biuletyn Instytutu Geologicznego* **311**, 5–68.

Boogaard, M. van den, 1992. The recurrence of *Vogelgnathus campbelli*-dominated conodont faunas of the Cantabrian Mts (Spain): a reflection of sea-level fluctuations? — *Scripta Geologica* **99**, 1–33.

Boogaard, M. van den & Bless, M.J.M. 1985. Some conodonts from the Aegiranum Marine Band. — *Proceedings of the Koninglijnke Nederlandse Akademie van Wetenschappen B* **88**, 133–154.

Bossowski, A. & Ihnatowicz, A. 1994. Palaeogeography of the Upper Carboniferous coal bearing deposits in NE part of the Intra-Sudetic Depression. — *Kwartalnik Geologiczny* **38**, 231–248.

Branson, E.R. 1934. Conodonts from the Hannibal Formation of Missouri. — *University of Missouri Studies* **8**, 301–334.

Branson, E.B. & Mehl, M.G. 1934. Conodonts from the Bushberg sandstone and equivalent formations of Missouri. — *University of Missouri Studies* **8**, 265–300.

Branson, E.B. & Mehl, M.G. 1941. New and little known Carboniferous conodont genera. — *Journal of Paleontology* **15**, 97–106.

Campbell, K.S.W., Brown, D.A., & Coleman, A.R. 1983. Ammonoids and the correlation of the Lower Carboniferous rocks of eastern Australia. — *Alcheringa* **7**, 75–123.

Caputo, M.V. 1985. Late Devonian glaciation in South America. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **51**, 291–317.

Chauff, K.M. 1981. Multielement conodont species from the Osagean (Lower Carboniferous) in Midcontinent North America and Texas. — *Palaeontographica A* **175**, 1–46.

Chauff, K.M. 1984. Multielement conodont species and an ecological interpretation of the Lower Osagean (Lower Carboniferous) conodont zonation from Midcontinent North America. — *Micropaleontology* **29**, 404–429.

Chauff, K.M. 1985. Phylogeny of the multielement conodont genera *Bactrognathus*, *Doliognathus* and *Staurognathus*. — *Journal of Paleontology* **59**, 299–309.

Chesnut, D.R., Jr. 1994. Eustatic and tectonic control of deposition of the Lower and Middle Pennsylvanian strata of the Central Appalachian Basin. *In:* J.M. Dennison & F.R. Ettersohn (eds), Tectonic and Eustatic Controls of Sedimentary Cycles. *SEPM Concepts in Sedimentology and Paleontology 4*, 51–64.

Chlupač, I. & Zikmundova, J. 1976. The Devonian and Lower Carboniferous in the Nepasice bore in East Bohemia. — *Věstnik Ustředniho ústavu geologickeho* **51**, 269–278.

Chorowska, M. 1972. Conodonts of the Upper Devonian and the Lower Carboniferous in the Węgrzynów IG-1 column (Miechów Trough). — *Biuletyn Instytutu Geologicznego* **6**, 161–208.

Chorowska, M. 1974. Dewon górny okolic Kłodzka w świetle badań konodontowych. — *Kwartalnik Geologiczny* **18**, 900–901.

Chorowska, M. 1978. Wizeńskie wapienie w epimetamorficznym kompleksie Gór Kaczawskich. — *Rocznik Polskiego Towarzystwa Geologicznego* **48**, 241–261.

Chorowska, M. & Radlicz, K. 1984. Karbońskie wapienie i zlepieńce zachodniej części struktury bardzkiej. — *Kwartalnik Geologiczny* **28**, 251–290.

Chorowska, M. & Radlicz, K. 1994. Revision of the age of the Lower Carboniferous deposits in the northern part of the Góry Bardzkie (Sudetes). — *Kwartalnik Geologiczny* **38**, 249–288.

Clausen, C.-D., Korn, D., Feist, R., Leuschner, K., Gross-Uffenorde, H., Luppold, F.W., Stoppel, D., Higgs, K., & Streel, M. 1994. Die Devon/Karbon-Grenze bei Stockum (Rheinisches Schiefergebirge). — *Geologie und Paläontologie in Westfalen* **29**, 71–95.

Collinson, C., Rexroad, C.B., & Thompson, T.L. 1971. Conodont zonation of the North American Mississippian. — *Geological Society of America Memoir* **127**, 353–394.

Cooper, C.L. 1939. Conodonts from a Bushberg-Hannibal horizon in Oklahoma. — *Journal of Paleontology* **13**, 379–422.

Conway Morris, S., Savoy, L.E., & Harris, A. 1991. An enigmatic organism from the 'Exshaw' Formation (Devonian–Carboniferous), Alberta, Canada. — *Lethaia* **24**, 139–152.

Crowell, J.C. 1995. The ending of the late Paleozoic ice age during the Permian period. *In:* P.A. Scholle, T.M. Peryt, & D.S. Ulmer-Scholle (eds), *The Permian of Northern Pangea. Vol. 1. Paleogeography, Palaeoclimates, Stratigraphy*, 62–73. Springer Verlag, Berlin.

Currie, E.D. 1954. Scottish Carboniferous goniatites. — *Transactions of the Royal Society of Edinburgh* **62**, 527–602.

Czarniecki, S. 1959. *Anthracoceras discus* Frech z piaskowców w Gołonogu i pozycja stratygraficzna tych warstw. — *Acta Geologica Polonica* **9**, 433–443.

Czarniecki, S. 1973. Goniatyty wapienia węglowego z Gałęzic. — *Rocznik Polskiego Towarzystwa Geologicznego* **43**, 227–248.

Czarniecki, S. 1992. Warunki sedymentacji karbonu Gałęzic. — *Przegląd Geologiczny* **40**, 604.

Dalziel, I.W.D., DallaSalda, L.H., & Gahagan, L.M. 1994. Paleozoic Laurentia-Gondwana interaction and the origin of the Appalachian-Andean mountain system. — *Geological Society of America Bulletin* **106**, 243–252.

Dzik, J. 1985. Phylogeny of the Nautiloidea. — *Palaeontologia Polonica* **45**, 1–219.

Dzik, J. 1990. Conodont evolution in high latitudes of the Ordovician. — *Courier Forschungsinstitut Senckenberg* **117**, 1–28.

Dzik, J. 1991a. Features of the fossil record of evolution. — *Acta Palaeontologica Polonica* **36**, 91–113.

Dzik, J. 1991b. Evolution of oral apparatuses in the conodont chordates. — *Acta Palaeontologica Polonica* **36**, 265–323.

Dzik, J., Olempska, E., & Pisera, A. 1994. Ordovician carbonate platform ecosystem of the Holy Cross Mountains. — *Palaeontologia Polonica* **53**, 5–41.

Dzik. J. 1995. Range-based biostratigraphy and evolutionary geochronology. — *Palaeopelagos Special Publication* **1**, 121–128.

Flajs, G. & Feist, R. 1988. Index conodonts, trilobites and environment of the Devonian/Carboniferous boundary beds La Serre (Montagne Noire, France). — *Courier Forschungsinstitut Senckenberg* **100**, 53–101.

Frech, F. 1902. Über devonische Ammoneen. — *Beiträge zur Paläontologie und Geologie des Österreich-Ungarns und des Orients* **14**, 27–112.

Freyer, G. & Żakowa, H. 1957. Famennian conodonts from borehole Bolechowice 1 (in the Holy Cross Mts.). — *Acta Geologica Polonica* **17**, 105–137.

Fuchs, A. 1987. Conodont biostratigraphy of the Elbingerode Reef Complex, Harz Mountains. — *Acta Geologica Polonica* **37**, 33–50.

Gedik, I. 1974. Conodonten aus dem Unterkarbon der Karnischen Alpen. — *Abhandlungen der Geologischen Bundesanstalt* **31**, 1–29.

Gedik, I. 1984. Adapazari-karasu Yoresinden alt karboniferé ait yeni bir conodont cinsi: *Icriognathodus kayai* n. gen. n. sp. — *Karadeniz Universitezi Dergisi, Jeoloji* **3**, 47–52.

Girard, C. 1994. Conodont biofacies and event stratigraphy across the D/C Boundary in the stratotype area (Montagne Noire, France). — *Courier Forschungsinstitut Senckenberg* **168**, 299–309.

Głuszak, A. & Tomaś, A. 1993. Age of the Nowa Wieś Formation (Bardzkie Mts., Middle Sudetes, SW Poland). — *Annales Societatis Geologorum Poloniae* **62**, 293–308.

Gordon, M., Jr. 1986. Late Kinderhookian (Early Mississippian) ammonoids of the western United States. — *The Paleontological Society Memoir* **19**, 1–36.

Grayson, R.C., Jr., Merrill, G.K., & Lambert, L.L. 1990. Carboniferous gnathodontid conodont apparatuses: evidence for a dual origin for Pennsylvanian taxa. — *Courier Forschungsinstitut Senckenberg* **118**, 353–396.

Groessens, E. 1974. Hypothéses concernant l'évolution de conodontes utiles à la biostratigraphie du Dinantien. *In:* J. Bouckaert & M. Streel (eds), *International Symposium on Namur, Belgian Micropaleontological Limits from Emsian to Viséan – September 1st to 10th, 1974, Publication 16*, 1–16. Geological Survey of Belgium, Brussels.

Gromczakiewicz-Łomnicka, A. 1974. Upper Viséan conodont fauna from the Carboniferous limestone north of Krzeszowice (environs of Cracow, Poland). — *Rocznik Polskiego Towarzystwa Geologicznego* **44**, 478–482.

Gromczakiewicz-Łomnicka, A. 1979. Conodont stratigraphy of the Uppermost Devonian and Lower Carboniferous rocks in the Racławka and Szklarka valleys west of Cracow. — *Acta Geologica Polonica* **29**, 489–487.

Haydukiewicz, J. 1981. Pelagiczne utwory turneju w południowo-zachodniej części Gór Bardzkich. — *Geologia Sudetica* **16**, 219–225.

Haydukiewicz, J. 1986. Stratigraphy of the Carboniferous deposits in northern part of the Góry Bardzkie, Sudetes. — *Geologia Sudetica* **21**, 143–147.

Hodson, F. 1957. Marker horizons in the Namurian of Britain, Ireland, Belgium and Western Germany. — *Publications de la Association pour l'Étude de la Paléontologie et de la Stratigraphie Houilleres* **24**, 1–26.

Hodson, F. & Leckwijck, W. van 1958. A Namurian marker-horizon at Büsbach near Aachen, Western Germany. — *Publications de la Association pour l'Étude de la Paléontologie et de la Stratigraphie Houilleres* **35**, 1–13.

Hodson, F. & Moore, E.W.J. 1959. *Goniatites striatus* and related forms from the Viséan of Ireland. — *Palaeontology* **3**, 384–396.

Horowitz, A.S. & Rexroad, C.B. 1982. An evaluation of statistical reconstructions of multielement conodont taxa from Middle Chesterian rocks (Carboniferous) in southern Indiana. — *Journal of Paleontology* **56**, 959–969.

Hou Hongfei, Ji Qiang, Wu Xianghe, Xiong Jianfei, Wang Shitao, Gao Lianda, Sheng Huaibin, Wei Jiayong, & Turner, S. 1985. *Muhua Sections of Devonian–Carboniferous Boundary Beds.* 226 pp. Geological Publishing House, Beijing.

House, M.R. 1992. Earliest Carboniferous goniatite recovery after the Hangenberg Event. — *Annales de la Société géologique de Belgique* **115**, 559–579.

Hsü, K.J., Li Jiliang, Chen Haihong, Wang Quinchen, Sun Shu, & Sengör, A.M.C. 1990. Tectonics of South China: key to understanding West Pacific geology. — *Tectonophysics* **183**, 9–39.

Jenkins, T.B.H. 1974. Lower Carboniferous conodont biostratigraphy of New South Wales. — *Palaeontology* **17**, 909–924.

Ji Qiang, Wang Zengji, Sheng Huaibin, Hou Jingpeng, Feng Rulin, Wei Jiayong, Wang Shitao, Wang Hongdi, Xiang Liwen, & Fu Guomin. 1989. *The Dapoushang Section. An Excellent Section for the Devonian–Carboniferous Boundary Stratotype in China.* 165 pp. Science Press, Beijing.

Klapper, G. 1966. Upper Devonian and Lower Mississippian conodont zones in Montana, Wyoming, and South Dakota. — *The University of Kansas Paleontological Contributions, Paper* **3**, 1–43.

Klapper, G. 1971. *Patrognathus* and *Siphonodella* (conodonts) from the Kinderhookian (Lower Mississippian) of western Kansas and southestern Nebrasca. — *Kansas Geological Survey Bulletin* **202**, 3, 1–14.

Klapper, G. 1973. Genus *Pseudopolygnathus* Barnes & Mehl, 1934b. *In:* W. Ziegler (ed.), *Catalogue of Conodonts, Vol. IV*, 355–408. Schweizerbartsche Verlagsbuchhandlung, Stuttgart.

Klapper, G. 1975. Genus *Siphonodella* Branson & Mehl,1944. *In:* W. Ziegler (ed.), *Catalogue of Conodonts, Vol. IV*, 451–470. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Korejwo, K. 1969. Stratigraphy and paleogeography of the Namurian in the Polish Lowland. — *Acta Geologica Polonica* **19**, 609–709.

Korejwo, K. 1974. Karbon struktury Abramowa. — *Acta Geologica Polonica* **24**, 631–661.

Korejwo, K. & Teller, L. 1967. Stratygrafia dolnego karbonu (wizen górny) z wierceń Sułów 1 i Lamki 1. — *Acta Geologica Polonica* **17**, 299–313.

Korejwo, K. 1986. Biostratigraphy of the Carboniferous deposits of the Świdnik blocks (Lublin Coal Basin). — *Acta Geologica Polonica* **36**, 337–346.

Korn, D. 1984. Die Goniatiten der Stockumer *Imitoceras*-Kalklinsen (Ammonoidea; Devon/Karbon-Grenze). — *Courier Forschungsinstitut Senckenberg* **67**, 71–89

Korn, D. 1986. Ammonoid evolution in late Famennian and early Tournaisian. — *Annales de la Société géologique de Belgique* **109**, 49–54.

Korn, D. 1988. Goniatites from the *Gattendorfia* Stufe of Hoppecke (Lower Carboniferous, Northeastern Rhenish Massif). — *Courier Forschungsinstitut Senckenberg* **100**, 217–218.

Korn, D. 1988. Die Goniatiten des Kulmplattenkalkes (Cephalopoda, Ammonoidea; Unterkarbon; Rheinisches Schiefergebirge). — *Geologie und Paläontologie in Westfalen* **11**, 1–293.

Korn, D. 1989. *Cymaclymenia* aus der *Acutimitoceras*-Fauna (prorsum-Zone) vom Müssenberg (Devon/Karbon-Grenze; Rheinisches Schiefergebirge). — *Bulletin de la Société belge de Géologie* **98**, 371–372.

Korn, D. 1990a. On the Upper Viséan P1b goniatite succesion in north Leitrim. — *Irish Journal of Earth Sciences* **10**, 109–114.

Korn, D. 1990b. Weitere Goniatiten aus dem Ober-Vise des Sauerlandes (Cephalopoda, Ammonoidea; Unterkarbon; Rheinisches Schiefergebirge). — *Geologie und Paläontologie in Westfalen* **15**, 11–69.

Korn, D. 1991. Threedimensionally preserved clymeniiids from the Hangenberg Black Shale of Drewer (Cephalopoda, Ammonoidea; Devonian/Carboniferous boundary; Rhenish Massif). — *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1991**, 553–563.

Korn, D. 1992. Ammonoideen aus dem Devon/Karbon-Grenzprofil an der Grünen Schneid (Karnische Alpen, Österreich). — *Jahrbuch der Geologische Bundesanstalt* **135**, 7–19.

Korn, D. 1993. The ammonoid faunal change near the Devonian–Carboniferous boundary. — *Annales de la Société Géologique de Belgique* **115**, 581–593.

Korn, D. 1995. Revision of the Rhenish Late Viséan goniatite stratigraphy. — *Annales de la Société Géologique de Belgique* **117**, 205–212.

Korn, D., Clausen, C.-D., & Luppold, F.W. (eds) 1994. Die Devon/Karbon-Grenze im Rheinischen Schiefergebirge. — *Geologie und Paläontologie in Westfalen* **29**, 1–221.

Kotas, A. 1972. Osady morskie karbonu górnego i ich przejście w utwory produktywne Górnośląskiego Zagłębia Węglowego. — *Prace Instytutu Geologicznego* **61**, 279–328.

Kotas, A. & Malczyk, W. 1972. Seria paraliczna piętra namuru dolnego Górnośląskiego Zagłębia Węglowego. — *Prace Instytutu Geologicznego* **61**, 329–426.

Krebs, W. 1968. Die Lagerungsverhältnisse des Erdbacher Kalkes (Unterkarbon II) bei Laugenbach-Breitschneid (Rheinische Schiefergebirge). — *Geotektonische Forschung* **28**, 72–103.

Kullmann, J. 1963. Die Goniatiten des Unterkarbons im Kantabrischen Gebirge (Nordspanien). II. Paläontologie der U.O. Prolecanitina Miller & Furnish. Die Alterstellung der Faunen. — *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **116**, 269–324.

Kullmann, J., Korn, D., & Petersen, M.S. 1994. *GONIAT v. 2.41. Paleozoic Ammonoids Database.* Universität Tübingen.

Kullmann, J. & Pitz, T. 1980. *Dombarites* (Goniatitida, Cephal.) aus dem Ober-Vise des Rheinischen Schiefergebirges. — *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **159**, 297–323.

Kumpera, O. 1977. A review of the fauna of the Moravo-Silesian Kulm. *In:* V.M Holub & R.H. Wagner (eds), *Symposium on Carboniferous Stratigraphy*, 235–260. Geological Survey, Prague.

Kusina, L.F. 1980. Saurian Ammonoidei [in Russian]. — *Trudy Paleontologičeskogo Instituta AN SSSR* **181**, 1–108.

Lane, H.R., Sandberg, C.A., & Ziegler, W. 1980. Taxonomy and phylogeny of some lower Carboniferous conodonts and preliminary standard post-*Siphonodella* zonation. — *Geologica et Palaeontologica* **14**, 117–164.

Lane, H.R. & Ziegler, W. 1983. Taxonomy and phylogeny of *Scaliognathus* Branson & Mehl 1941 (Conodonta, Lower Carboniferous). — *Senckenbergiana lethaea* **64**, 199–225.

Liu Baojun & Xu Xiaosong (eds) 1994. — *Atlas of the Lithofacies and Paleogeography of South China (Sinian–Triassic).* 192 pp. Science Press, Beijing.

Loboziak, S., Streel, M., Caputo, M.V., & de Melo, J.H.G. 1992. Middle Devonian to Lower Carboniferous miospore stratigraphy in the central Parnaiba Basin (Brasil). — *Annales de la Société Géologique de Belgique* **115**, 215–226.

Loboziak, S., Streel, M., Caputo, M.V., & de Melo, J.H.G. 1993. Middle Devonian to Lower Carboniferous miospores from selected boreholes in Amazonas and Parnaiba Basins (Brasil): Additional data, synthesis, and correlation. — *Documents de Laboratoire Géologique Lyon* **125**, 277–289.

Luppold, F.W., Clausen, C.-D., Korn, D., & Stoppel, D. 1994. Devon/Karbon-Grenzprofile im Bereich von Remscheid-Altenaer Sattel, Warsteiner Sattel, Briloner Sattel und Attendorn-Elsper Doppelmulde (Rheinisches Schiefergebirge). — *Geologie und Paläontologie in Westfalen* **29**, 7–69.

Malec, J. 1995. Devonian/Carboniferous boundary. *In:* M. Szulczewski & J. Dvorak (eds), *XIII International Congress on Carboniferous–Permian, August 28–September 2, Guide to Excursion B4: Evolution*

of the Polish-Moravian carbonate platform in the Late Devonian and Early Carboniferous: Holy Cross Mts., Kraków Upland, Moravian Karst, 15–16. Państwowy Instytut Geologiczny, Warszawa.

Manger, W.L. 1975. Lower Carboniferous ammonoid assemblages from North America. *Huitiéme Congres International de Stratigraphie et de Géologie Carbonifère, Moscou, Septembre 8–13, 1975, Compte Rendu Volume 3*, 211–221. Nauka, Moskva.

Matthews, S.C. 1970. A new cephalopod fauna from the Lower Carboniferous of east Cornwall. — *Palaeontology* **13**, 112–131.

Matthews, S.C. 1983. An occurrence of Lower Carboniferous (*Gattendorfia*-Stufe) ammonoids in southwest Ireland. — *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1983**, 293–299.

Manger, W.L. 1988. Phylogeny of the Carboniferous ammonoid family Dimorphoceratidae. *In:* J. Wiedmann & J. Kullmann (eds), *Cephalopods: Present and Past. O.H. Schindewolf Symposium, Tübingen 1985*, 29–42. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Matyja, H. 1976. Biostratigraphy of the Devonian–Carboniferous passage beds from some selected profiles of NW Poland. — *Acta Geologica Polonica* **26**, 489–539.

Matyja, H. & Narkiewicz, M. 1979. Lithofacies and conodonts in Viséan profile, Olkusz area, southern Poland. — *Acta Geologica Polonica* **29**, 475–488.

Mazur, S. 1987. Tektonika utworów górnego dewonu i dolnego karbonu w kamieniołomie w Dzikowcu (Góry Bardzkie). — *Przegląd Geologiczny* **35**, 327–332.

Miller, A.K. & Furnish, W.M. 1958. The goniatite genus *Anthracoceras*. — *Journal of Paleontology* **32**, 684–686.

Musiał, Ł. 1993. Makrofauna karbońska z profilu Pomorzany 2 koło Olkusza. *Materiały 16. Sympozjum – Geologia Formacji Węglonośnych Polski.* Kraków.

Musiał, Ł. & Tabor, M. 1980. The Carboniferous zoostratigraphy of the Lublin Coal Basin and its correlation with lithostratigraphic members. — *Biuletyn Instytutu Geologicznego* **328**, 75–94

Musiał, Ł. & Tabor, M. 1988. Stratygrafia karbonu na podstawie makrofauny. *In:* Z. Dembowski & J. Porzycki (eds), Karbon Lubelskiego Zagłębia Węglowego. — *Prace Instytutu Geologicznego* **122**, 88–111.

Musiał, Ł., Tabor, M., & Żakowa, H. 1995. Makrofauna. — *Prace Państwowego Instytutu Geologicznego* **148**, 23–43.

Nemirovskaya, T., Perret, M.F., & Meischner, D. 1994. *Lochriea ziegleri* and *Lochriea senckenbergica* – new conodont species from the latest Viséan and Serpukhovian in Europe. — *Courier Forschungsinstitut Senckenberg* **168**, 311–317.

Nicoll, R.S. & Druce, E.C. 1979. Conodonts from the Fairfield Group, Canning Basin, Western Australia. — *BMR Bulletin* **190**, 1–134.

Nikolaeva, S.V. & Kullmann, K. 1995. The Late Namurian genus *Cancelloceras* (Carboniferous Ammonoidea) and its distribution. — *Paläontologische Zeitschrift* **69**, 353–376.

Olempska, E. (in press) Faunal change in benthic ostracods across the Devonian–Carboniferous boundary in the Holy Cross Mountains. — *Acta Palaeontologica Polonica* **42**.

Over, D.J. 1992. Conodonts and the Devonian–Carboniferous boundary in the Upper Woodford Shale, Arbuckle Mountains, south-central Oklahoma. — *Journal of Paleontology* **66**, 293–311.

Paproth, E., Becker, T., Clausen, C.D., Kompa, R., Korn, D., & Stoppel, D. 1986. *Field Trip to the Late Devonian Outcrops in the Northern Rheinisches Schiefergebirge (Federal Republic of Germany).* 19 pp. Rheinisch-Westfälische Technische Hochschule, Aachen.

Pareyn, C. 1961. Les Massifs Carboniféres du Sahara Sud-Oranais. Tome II. Paléontologie Stratigraphique. — *Publications du Centre de Récherches Sahariennes, Série Géologie* **1**, 1–244.

Paszkowski, M., Jachowicz, M., Michalik, M., Teller, L., Uchmański, A., & Urbanek, A. 1995. Composition, age and provenance of gravel-sized clasts from the Upper Carboniferous of the Upper Silesia Coal Basin (Poland). — *Studia Geologica Polonica* **108**, 45–127.

Porzycki, J. 1988. Charakterystyka litologiczno-sedymentologiczna karbonu. *In:* Z. Dembowski & J. Porzycki (eds), Karbon Lubelskiego Zagłębia Węglowego. — *Prace Instytutu Geologicznego* **122**, 40–76.

Purnell, M.A. 1992. Conodonts of the Lower Border Group and equivalent strata (Lower Carboniferous) in northern Cumbria and the Scottish borders, U.K. — *Royal Ontario Museum Life Sciences Contributions* **156**, 1–79.

Purnell, M.A. 1993. The *Kladognathus* apparatus (Conodonta, Carboniferous): homologies with ozarkodinids, and the prioniodinid Bauplan. — *Journal of Paleontology* **67**, 875–882.

Purnell, M.A. & Bitter, P.H. von 1992. *Vogelgnathus* Norbz and Rexroad (Conodonta): new species from the Lower Carboniferous of Atlantic Canada and northern England. — *Journal of Paleontology* **66**, 311–332.

Ramsbottom, W.H.C. 1977. Major cycles of transgression and regression (mesothems) in the Namurian. — *Proceedings of the Yorkshire Geological Society* **41**, 261–291.

Řehoř, F. & Řehořova, M. 1972. *Makrofauna uhlonosného karbonu československe části Hornoslezské pánve*, 1–137. Profil, Ostrava.

Rexroad, C.B. & Varker, W.J. 1992. The new Mississippian conodont genus *Syncladognathus*. — *Journal of Paleontology* **66**, 165–10.

Riley, N.J. 1990. A global review of mid-Dinantian ammonoid biostratigraphy. — *Courier Forschungsinstitut Senckenberg* **130**, 133–143.

Riley, N.J. 1993. Dinantian (Lower Carboniferous) biostratigraphy and chronostratigraphy in the British Isles. — *Journal of Geological Society, London* **150**, 427–446.

Riley, N.J. 1996. Mid-Dinantian ammonoids from the Craven Basin, north-west England. — *Special Papers in Palaeontology* **53**, 1–87.

Ruan Yiping 1981. Devonian and earliest Carboniferous ammonoids from Guangxi and Guizhou. — *Memoirs of Nanjing Institute of Geology and Palaeontology, Academia Sinica* **15**, 1–140.

Ruzhentsev, V.E. & Bogoslovskaya, M.F. (Ružencev, V.E., Bogoslovskaâ, M.F.) 1971. Namurian stage in the evolution of Ammonoidei. Early Namurian Ammonoidei [in Russian]. — *Trudy Paleontologičeskogo Instituta AN SSSR* **133**, 1–376.

Ruzhentsev, V.E. & Bogoslovskaya, M.F. (Ružencev, V.E., Bogoslovskaâ, M.F.) 1978. Namurian stage in the evolution of Ammonoidei. Late Namurian Ammonoidei [in Russian]. — *Trudy Paleontologičeskogo Instituta AN SSSR* **167**, 1–335.

Sandberg, C.A., Ziegler, W., Leuteritz, K., & Brill, S.M. 1978. Phylogeny, speciation and zonation of *Siphonodella* (Conodonta, Upper Devonian and Lower Carboniferous). — *Newsletter on Stratigraphy* **7**, 102–120.

Saunders, W.B., Ramsbottom, W.H.C., & Manger, W.L. 1979. Mesothemic cyclicity in the mid-Carboniferous of the Ozark shelf region? — *Geology* **7**, 293–296.

Savoy, L.E. & Harris, A. 1993. Conodont biofacies and taphonomy along a carbonate ramp to black shale basin (latest Devonian and Earliest Carboniferous), southernmost Canadian Cordillera and adjacent Montana. — *Canadian Journal of Earth Sciences* **30**, 2404–2422.

Schindewolf, O. 1959. Adolescent cephalopods from the Exshaw Formation of Alberta. — *Journal of Paleontology* **33**, 971–976.

Schindewolf, O. 1920. Neue Beiträge zur Kenntnis der Stratigraphie und Paläontologie des deutschen Oberdevons. — *Senckenbergiana* **2**, 114–129.

Schindewolf, O.H. 1951. Über ein neues Vorkommen unterkarbonischer *Pericyclus*-Schichten in Oberharz. — *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **93**, 23–116.

Schmidt, H. 1925. Die carbonischen Goniatiten Deutschlands. — *Jahrbuch der preußische geologische Landesanstalt* **45**, 489–609.

Schönlaub, H. P. 1969. Conodonten aus dem Oberdevon und Unterkarbon des Kronhofsgrabens (Karnische Alpen, Österreich). — *Jahrbuch der Geologischen Bundesanstalt* **112**, 321–354.

Scott, H.W. 1942. Conodont assemblages from the Heath Formation, Montana. — *Journal of Paleontology* **16**, 293–301.

Schmidt, H. & Müller, K.J. 1964. Weitere Funde von Conodonten-Gruppen aus dem oberen Karbon des Sauerlandes. — *Paläontologische Zeitschrift* **38**, 105–135.

Skompski, S. 1996. Conodont stratigraphy of the Carboniferous in the Lublin Basin (E Poland). *VI International Conodont Symposium (ECOS VI), Abstracts*, 54. Warszawa.

Skompski, S. & Soboń-Podgórska, J. 1980. Foraminifers and conodonts in the Viséan deposits of the Lublin Upland. — *Acta Geologica Polonica* **30**, 87–96.

Stone, J.J. 1991. Arundian (Lower Carboniferous) conodonts from South Wales. — *Special Papers in Palaeontology* **46**, 1–63.

Sutherland, P.K. & Manger, W.L. 1977. Upper Chesterian-Morrowan stratigraphy and the Mississippian-Pennsylvanian boundary in northeastern Oklahoma and northwestern Arkansas. — *Oklahoma Geological Survey Guidebook* **18**, 117–137.

Szulczewski, M. 1973. Famennian–Tournaisian neptunian dykes and their conodont fauna from Dalnia in the Holy Cross Mts. — *Acta Geologica Polonica* **23**, 15–59.

Szulczewski, M. 1978. The nature of unconformities in the Upper Devonian–Lower Carboniferous condensed sequence in the Holy Cross Mts. — *Acta Geologica Polonica* **28**, 283–298.

Szulczewski, M., Bełka, Z., & Skompski, S. 1996. Chronicle of the drowning carbonate platform: the Devonian–Carboniferous example from the south-western Holy Cross Mountains (Poland). — *Sedimentology* **106**, 21–49.

Szulczewski, M. & Skompski, S. 1995. Ostrówka quarry. *In:* M. Szulczewski & J. Dvorak (eds), *XIII International Congress on Carboniferous–Permian, August 28–September 2, Guide to Excursion B4: Evolution of the Polish-Moravian carbonate platform in the Late Devonian and Early Carboniferous: Holy Cross Mts., Kraków Upland, Moravian Karst*, 20–23. Państwowy Instytut Geologiczny, Warszawa.

Thompson, T.L. & Fellows, L.D. 1970. Stratigraphy and conodont biostratigraphy of Kinderhookian and Osagean Rocks of southwestern Missouri and adjacent areas. — *Missouri Geological Survey & Water Resources Report of Investigations* **45**, 1–263.

Tietze, E. 1871. Über die devonischen Schichten von Ebersdorf unweit Neurode in der Grafschaft Glatz, eine geognostisch-paläontologische Monographie. — *Palaeontographica* **19**, 103–158.

Van Steenwinkel, M. 1993. The Devonian–Carboniferous boundary: comparison of the Dinant Synclinorium and the northern border of the Rhenish Slate Mountains, a sequence-stratigraphic view. —*Annales de la Société géologique de Belgique* **115**, 665–681.

Vašiček, Z. 1982. Konodonti Gaeblerova mořského horizontu karvinské části OKR (Namur A). — *Ostravské Muzeum, Přírodovědecký Sborník* **26**, 167–288.

Vašiček, Z. 1983. Beitrag zu den Juvenilen Goniatiten des marinen Gaebler-horizonts (Tschechoslowakischer Teil des Oberschlesischen Beckens, Namur A). — *Časopis Moravského Musea, Vědy přirodni* **68**, 29–56.

Veevers & Powell 1987. Late Paleozoic glacial episodes in Gondwanaland reflected in transgression-regression depositional sequences in Euramerica. — *Geological Society of America Bulletin* **98**, 475–487.

Voges, A. 1959. Conodonten aus dem Unterkarbon I und II (*Gattendorfia*- und *Pericyclus*-Stufe) des Sauerlandes. — *Paläontologische Zeitschrift* **33**, 266–314.

Vöhringer, E. 1960. Die Goniatiten der unterkarbonischen Gattendorfia–Stufe im Hönnetal (Sauerland). — *Fortschrifte der Geologie Rheinlands-Westfalen* **3**, 107–196.

Von Bitter, P.H. & Norby, R.D. 1994. Ontogenetic development of Pa element cup microsculpture in *Lochriea commutata* (Branson and Mehl, 1941)(Conodonta, Carboniferous): Taxonomic implications. — *Journal of Paleontology* **68**, 861–869.

Walker, D. & Chen, Y. 1987. Palynological light on rainforest dynamics. — *Quaternary Science Review* **6**, 77–92.

Weyer, D. 1965. Zur Ammonoideen-Fauna der *Gattendorfia*-Stufe von Dzikowiec (Ebersdorf) in Dolny Śląsk (Niederschlesien), Polen. — *Berichte der geologischen Gesellschaft der DDR* **10**, 443–464.

Weyer, D. 1972a. Trilobiten und Ammonoideen aus der *Entogonites nasutus*-Zone (Unterkarbon) des Büchenberg-Sattels (Elbingeröder Komplex, Harz). Teil 1. — *Geologie* **21**, 166–184.

Weyer, D. 1972b. Trilobiten und Ammonoideen aus der *Entogonites nasutus*-Zone (Unterkarbon) des Büchenberg-Sattels (Elbingeröder Komplex, Harz). Teil 2. — *Geologie* **21**, 318–349.

Weyer, D. 1977. Ammonoideen aus dem Untertournai von Schleiz (Ostthüringisches Schiefergebirge). — *Zeitschrift der geologische Wissenschaften* **5**, 167–185.

Work, D.M., Mapes, R.H., & Thompson, T.L. 1988. A new prodromitid ammonoid genus from the Hannibal Shale (Lower Mississippian) of Missouri. — *Journal of Paleontology* **62**, 772–778.

Zając, R. 1984. Stratigrafia i rozwój facjalny dewonu i dolnego karbonu południowej części podłoża Zapadliska Przedkarpackiego. — *Kwartalnik Geologiczny* **28**, 251–290.

Żakowa, H. 1960a. Górny wizen z Konradowa koło Wałbrzycha. — *Kwartalnik Geologiczny* **4**, 331–347.

Żakowa, H. 1960b. Poziom *Goniatites crenistria* z Glinna (Góry Sowie). — *Kwartalnik Geologiczny* **4**, 349–366.

Żakowa, H. 1963. Stratygrafia i zasięgi facjalne karbonu dolnego w Sudetach. — *Kwartalnik Geologiczny* **7**, 73–94.

Żakowa, H. 1966. Poziom *Goniatites crenistria* Phill. w okolicy Sokolca i Jugowa u podnóży Gór Sowich (Sudety Środkowe). — *Prace Instytutu Geologicznego* **93**, 1–197.

Żakowa, H. 1971. Poziom *Goniatites granosus* w synklinie gałęzickiej (Góry Świętokrzyskie). — *Prace Instytutu Geologicznego* **60**, 1–137.

Żakowa, H. 1974. Goniatitina from the Upper Viséan (Gałęzice Syncline, Holy Cross Mts). — *Rocznik Polskiego Towarzystwa Geologicznego* **44**, 3–30.

Żakowa, H. 1982. Poziom *Goniatites granosus* (wizen górny) w zachodniej części Gór Świętokrzyskich. — *Kwartalnik Geologiczny* **26**, 297–326.

Żakowa, H. 1992. Goniatites from the Upper Viséan (Kielce Syncline, of the Holy Cross Mts, Poland). — *Kwartalnik Geologiczny* **36**, 327–344.

Żakowa, H. & Chlebowski, R. 1984. Nowe dane o karbonie w okolicy Bolechowic i Kowali (Góry Świętokrzyskie). — *Kwartalnik Geologiczny* **28**, 317–340.

Żelichowski, A.M. 1972. Występowanie goniatytów w osadach karbonu na obszarze hrubieszowsko-to-maszowskim (SE Polska). — *Kwartalnik Geologiczny* **16**, 587–596.

Zhuravlev, A.V. (Žuravlev, A.V.) 1994. New species of siphonodellids (conodonts) from the Lower Carboniferous of northern Urals [in Russian]. — *Paleontologičeskij žurnal* **1994**, 138–139.

Ziegler, P.A. 1990. *Geological Atlas of Western and Central Europe*. 239 + 56 pp. Shell, Avon.

Ziegler, W. 1988. Stop B 4; Hönnetal, Railway Cut near Oberrödinghausen. — *Courier Forschungsinstitut Senckenberg* **102**, 173–175.

Ziegler, W. & Sandberg, C.A. 1984. Important candidate for stratotype of conodont based Devonian–Carboniferous boundary. — *Courier Forschungsinstitut Senckenberg* **67**, 231–239.

Powstanie i następstwo karbońskich zbiorowisk konodontów i amonitów w polskiej części oceanu waryscyjskiego

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Streszczenie

Koniec sedymentacji fameńskiego wapienia z *Wocklumeria* w Górach Świętokrzyskich i Sudetach oznaczał też zanik całego ciepłowodnego zespołu amonitów i konodontów o wysokim zróżnicowaniu taksonomicznym. Wśród ostatnich amonitów typowych dla dewonu dominowały bardzo różnorodne klimenie, zaś wśród konodontów palmatolepididy o najwyższym w ewolucyjnej historii dewońskich konodontów zróżnicowaniu aparatu. Zespoły, które pojawiły się później, były zupełnie odmiennej natury, o małym zróżnicowaniu taksonomicznym i rzucającej się w oczy prostocie anatomicznej. Zespół amonitowy składał się praktycznie z jednego gatunku *Acutimitoceras prorsum*, pokrewnego najprostszym goniatytom wcześniejszej części famenu. Podobnie mało zróżnicowane i proste anatomicznie były konodonty, zdominowane przez jeden, bardzo zmienny gatunek *Protognathodus*, cechujący się cienką ścianą korony elementów ostatniej pary. Konodonty o takich cechach w innych przedziałach czasu geologicznego są szczególnie typowe dla środowisk zimnowodnych.

Po pewnym czasie, odpowiadającym epizodowi sedymentacji ilastej (w Niemczech powstawały wówczas łupki Hangenberg), jeszcze przed końcem dewonu w arbitralnie dziś przyjętym jego znaczeniu, powróciły warunki sedymentacji wapiennej wapieni z *Gattendorfia*, a wraz z nimi wysoce zróżnicowane zespoły amonitów (udokumen-

towane w Sudetach) i konodontów. Reprezentowane wśród nich były wszystkie podstawowe typy morfologii znane z wapiennego famenu. Odpowiednikami klimenii stały się wtórnie rozwinięte amonity *Eocanites*, *Pseudarietites* i *Paralytoceras*, współwystępujące z prostszymi prionoceratidami. Miejsce wcześniejszych palmatolepididów i polygnathidów zajęły konodonty z grupy *Siphonodella*. Był to efekt imigracji z nieznanych źródłowych obszarów, z niewielkim udziałem ewolucji na miejscu.

Bardzo charakterystyczny i szeroko rozprzestrzeniony zespół amonitów i konodontów wapieni z *Gattendorfia* został zastąpiony przez kolejne zespoły o niskim zróżnicowaniu wraz z nawrotem sedymentacji czarnych łupków zony *Siphonodella crenulata*, prawdopodobnie odpowiadającym podniesieniu poziomu wód w oceanach w środkowym turneju. Mniej więcej w tym samym czasie transgresja morza na kontynencie północnoamerykańskim przyniosła tam konodonty i rzadkie amonity, stanowiące chyba kontynuację rozwoju zespołów środkowoeuropejskich.

Kolejny krótkotrwały nawrót wysoce zróżnicowanych zespołów do waryscyjskiego rejonu środkowej Europy przypadł na koniec turneju – z egzotyczną fauną konodontów *Scaliognathus anchoralis* i amonitów. Jeszcze raz zdarzyło się to w późnym wizenie, ale za każdym razem zróżnicowanie taksonomiczne i anatomiczne stawało się mniejsze. Najprawdopodobniej nie wystarczało czasu na ewolucyjne odtworzenie stosunków ekologicznych niszczonych przez kolejne zaburzenia klimatyczne. Dalsze przemiany zespołów konodontowych i amonitowych w poszczególnych obszarach polskiej części oceanu waryscyjskiego można interpretować jako skutek jego stopniowego zamykania oraz wpływu zlodowaceń Gondwany na klimat i eustatykę.

Artykuł ten zawiera przegląd fauny konodontowej i amonitowej polskiego karbonu. Wśród różnorodnych aparatów konodontów, prowizorycznie zrekonstruowanych w oparciu o dostępne dane, są dwa reprezentujące nowe gatunki, *Neopolygnathus sudeticus* i *Siphonodella belkai*; zaproponowany też został nowy rodzaj *Weyerognathus*.

Table 1. Conodont frequencies in the Wapnica beds at Dzikowiec (Dz), the Sudetes; samples (in vertical rows) arranged according to stratigraphic order, the oldest to right; element types (Jeppson's notation) that cannot be attributed unequivocally to particular species are listed jointly for all the species of a genus; reworked elements represent numerous Devonian species and are not separated here. For full taxonomic names see the text.

Sample nos	Dz	15	14	21	44	50	22	45	23	46	66	6	24	65	28	31	59	58	57	56
Prioniodina	sp	16	2		2						2	5		3	1	1				
	oz	17	1	3	1	1	1	1	1	3	2	2	6	1		1		2	2	
	tr	12		1						1	3	1	1	2		3		1		
	lo	?1							1	3	8			1						
	pl	15		1			1	1		3	4	2	6	4	1	1		1		
	hi	21			1		1	1		1	5	4	12	10		1	7		1	2
	ne	7	1	1			1				2	1	2			2	2	1		
Arisemotaxis?	hi	5																		
	ne	10																		
Falcodus	sp	154	10	9	6	1	2	7	9	30	19	21	2							
	oz	209	10	6	6	1	3	8		30	7	8		6						
	tr	10					1			1										
	lo	8				1	1													
	pl	51		1	5	3	2	1	3	4	3	2	1					1		
	hi	59		1	3	3	1		2	5	4	3	1	1						
	ne	41	1	1	3	1					9	5				2				
Mehlina	sp	3		3							11			38	19	33		8	1	
Pandorinellina	sp	339	27	22	9	7	4	3	8	60	44	71	10							
	oz	101	4	8	7	8	2		8	12	21	10	6	5	3	8				
	tr	16	1						2			5								
	lo	23	1									5								
	pl	71	2		3							19		3	1					
	hi	141	2	1	2	4					5	23		3	3					
	ne	62	2		6	3			5	16	5	19		4	3	2				
Protognathodus	sp					1	2	1	6	11	13	31	74	22	17	60	4	4		
	oz								3			12	20		6	3				
	tr											4			2					
	lo											10			2					
	pl											12			7					
	hi										1	14			12	1				
	ne								2		6	12			6					
Pseudopolygnathus	sp	41				1	8		2	7	8		36	19	36	36	2	6	5	
Weyerognathus	sp	739	92	39	31	32	13	20	53	260	228	390		6						
Pseud.-Weyer.	oz	201	10	7	8	8		7	13	80	55	120	10	2	10	1	1	1		
	tr	9						1			1	2			7					
	lo	14				1						2			1					
	pl	8		2	1	5					1	3			2					
	hi	22		1	2	4		2		11	9	6		2			1			
	ne	42				1			5	8	6	16		2	2	7				
P. fornicatus	sp	160	26	18	29								137		5	1				
P. inornatus	sp	127	12	13	13		11	3	12		3	1			5			1		12
P. sulcatus-sp.	so	459	16	9	10	18	5	8	18	118	127	159	3	62	5	23	5	2	3	1
Pinacognathus	oz	75	3	2	2	2	1		6	24	8	12		2	1	5				
	tr	3								1										
	lo	3																		
	pl	9			1		1		1	3		1		1						1
	hi	13	2								1	3		1		1				
	ne	5																		
S. aff. crenulata	sp									34		37								
	hi									7										
S. duplicata	sp									58		91	2		6	12				
S. carinthiaca	sp		2		5		6	11	96	313										
S. belkai	sp								10	25										
S. quadruplicata	sp	4085	92	119	81	33	43	14						1						
Siphonodella	oz	295	42	4	9	7	7		6	11	3				1	4				
	tr	3			1	1				1										
	lo	5			1						1	2								
	pl	4				1	2		2	2	1									
	hi	47	1	5	2	10	4			21		15								
	ne	76	2	1	7	11	4			14	3	26			3	1				
Dinodus	sp	453	30	11	9	16	10	1	6			5								
	oz	306	1	3	5	2	4	1	2			2								
	tr	9																		
	lo	30																		
	pl	9		1	2		1	2				1								
	hi	55	1	1	3	3	1	5				2								
	ne	7	1	1	1	3	1					4								
N. communis	sp				1	3			20	53		120	27	13	110	6	8			1
N. biconstrictus	sp	35			6		2	4	2	25	12									
N. purus	sp	1065	5	88	247	179	91	84	208	683	694	1377	7	266	187	370	11	15	36	3
Neopolygnathus	oz	95	1	11	42	22	16	8	51	65	94	132	26	23	38	76	3	8	9	1
	tr	5	1	2						2		7	6			3				1
	lo	3			3			1	1	3	1	5	4		1					1
	pl	7		2	2	3	1			5		10	11		1	1			1	1
	hi	43		8	3	4	2		21	12	28	79	14			16		5	1	1
	ne	75	1	4	5	5		2	14	17	24	55	17		4	32		2		
N. vogesi	sp				1		4		43	902	78	138	7	15	2	6			4	
reworked					4											3	3	27	40	440

Table 2. Conodont frequencies in the Tournaisian marly unit at Kowala (Ko), Holy Cross Mts; samples arranged according to stratigraphic order; elements of *Tripodellus gracilis, T. sigmoidalis* and following species are reworked.

Sample nos	Ko	21	27	28	30	31	32	33	34	35	22	36	23	37	138	38	39	40	41
Prioniodina	sp	1													3				
	oz												1	2					
	tr	3												1					
	lo													1					
	hi	10	1		12												9		
	ne	6	1		7				1								11		
Falcodus	sp												1						
	oz	1											1						
	tr																	1	
	ne											1					1		
Mehlina	sp												2						
Pandorinellina	sp	9		2	7		1	1		1			2		8		10	1	1
	oz	7											2		4			1	
	tr																		
	lo																		
	pl																		
	hi	3													2				
	ne	6													2				
Protognathodus	sp					38													
	oz					10													
	tr					1													
	pl					1													
	hi					10													
	ne					6													
Pseudopolygnathus	sp		1	9		12													
Weyerognathus	sp				17	1			3	2	1	4		2	11		10		1
Pseud.-Weyer.	oz	2			33								1				2		
	pl		1										1		1				
	lo		1																
	hi				8	8							1						
	ne												1						
P. inornatus	sp	40	7		225	2	4	9	2	6	1	9	10	2	28	17	13	11	4
P. flabellum	sp															4			
P. sulcatus-sp.	sp	17	3	22	181	4	2	13	3	1	1	2			2	4	1	2	4
Pinacognathus	oz	4		1	1										1				
	ne																1		
S. aff. crenulata	sp	20	2		1		5												
Siphonodella	hi	18	1		12														
S. carinthiaca	sp																	1	4
S. quadruplicata	sp	21	2	128	186	7		11	15	9	1	19	2	16	5	9	89	32	
Dinodus	sp	22			15								1	1	3		3	1	
	oz	1												1					
	pl	1															1		
	hi	1			1										1				
	ne	1																	
N. communis	sp				2	2											8		
N. purus	sp	1		2	2	435											1		
Neopolygnathus	oz					72											1		
	tr					2													
	hi					9													
	ne					32													
T. gracilis	sp																	9	
T. sigmoidalis	sp					2													
	hi					1													
P. acuta	sp	1				1													
P. pectinata	sp	1																	
P. trigonicus	sp					2													
	oz					1													
Icriodus	sp					1										5			
	oz					1													

Table 3. Conodont frequencies in the Tournaisian marly unit at Kowala, Holy Cross Mts (continued from Table 2).

Sample nos	Ko	42	43	44	45	46	48	49	50	53	56	57	58	24	51	71	72	73	74	75
Prioniodina	sp													1	1					
	oz	2																		
	pl																			1
	hi	2															1		1		1
	ne	2								1										
Mehlina	sp	2	1					2		2								2		3	1
Pandorinellina	sp	2																		2	
Protognathodus	sp											1			8	17					
	oz												4	3							
	pl												1								
	hi													1	3						
P. aculeatus	sp																		5		
Pseudopolygnathus	sp	19	2	1	10	2	13	12	7	9	4	5	2	2						20
Weyerognathus	sp	34	3	1		1														
Pseud.-Weyer.	oz	12				1				1										2
	lo	1																		1
	hi	2								1			1							1
	ne	1																		1
P. inornatus	sp	2	4		1														3	
P. sulcatus-sp.	sp	38	2	1	39	19	29	10	6	21	4	1							5	2
	ne				1															
S. carinthiaca	sp		3																	
S. belkai	sp	35		1																
S. quadruplicata	sp			3	9															
N. communis	sp	52			10	2	17	15	2	29	1	8	15	3	4	4				
N. purus	sp	2		1	8		5		14	6										
Neopolygnathus	oz	2			3					2		3		1	1					
	tr				2															
	pl	2			1															
	hi	3		6																
	ne			2			1	2												
N. vogesi	sp				2															
T. sigmoidalis	sp															1		2	1	11
	oz																			2
	hi																			1
B. bohlenana	sp															1	2	1	1	11
Pelekysgnathus?	oz																			2
B. stabilis	sp																		2	

Table 4. Conodont frequencies in the Wangyou Formation at Muhua (Mu), Guizhou province (see Fig. 2); samples arranged according to stratigraphic order, their numbers do not correspond to those in Hou *et al.* (1985).

Sample nos	Mu	23	24	25	28	34	35	38	39	40	41
Prioniodina	sp			4	4						
	oz	2	3	2	1	1	1	1	1		
	tr			1	1			1			
	lo			1	1	1		1			
	pl	1		1	1	1	2	1			1
	hi		1	3	1	1	4	2	3		5
	ne			1				2			1
Prioniodina	sp								8		
	oz								1		
	pl								2		
	hi								5		
Falcodus	sp				4		10	3	11	1	1
	oz				2				1	2	
	lo						3				
	pl						10	1	2	1	1
	hi						12	1	6		1
	ne						4		5	3	1
Mehlina	sp	7	11	11	2	3	12				6
Pandorinellina	sp	1			52	18	42	99	30	40	
	oz				11	18	40	45	9	11	
	tr				3	2	9	8	1		
	lo				2		10	13	2		
	pl				3	3	17	7	5		
	hi				10	6	46	29	8		
	ne				13	11	29	19	6		
P. costatus	sp					11	2		5		
Pseudopolygnathus	sp	3	4	6	29		1				
Metapolygnathus	sp									24	12
Weyerognathus	sp					32	55	48	45	24	20
Pseud.-Weyer.	oz	4	9	6	9	14	29	24	31	2	4
	tr		6			2		1	1	2	
	lo			1		2		2			
	pl					1		2	2		
	hi	1	10	7		3	4	11	7	6	4
	ne	1	8	5		2	15	13	7	3	1
P. inornatus	sp				6	9	46	92	56	8	17
P. nodomarginatus	sp		50	25							
P. dapoushanensis	sp					93	112				
Pinacognathus	oz		10	7	6	3	21	2	5	5	3
	tr				1				2		
	lo				2	1					
	pl		1	1	1		2		3	1	
	hi		1	2	14	5	2	1	6		
	ne		2	3	2	5	2		2		3
S. crenulata	sp								1		20
S. sandbergi	sp										15
S. sp.	sp									1	
S. quadruplicata	sp				50	30	54	114	76	138	91
Siphonodella	oz				11	3	8	24	2	7	8
Siphonodella?	tr						3				1
	lo					2	3			2	1
	pl					2	6		3	4	1
	hi					5	10		2	4	1
	ne							7		2	1
Dinodus	sp					39		14		36	30
	oz				1			9		3	2
	tr					1				2	
	lo				2					2	
	pl				2			1		4	
	hi							8		16	1
	ne				2			4		10	1
N. communis	sp				1	12		10	3		
N. sp	sp							13			
N. purus	sp	55	117	129	670	225	638	919	626	87	15
Neopolygnathus	oz	14	27	34	241	66	117	277	110	5	3
	tr	3	3	3	10	7	8	15	8	4	
	lo	1	4	5	12	10	5	23	6	1	
	pl	3	12	4	12	15	29	41	9	4	
	hi	18	20	20	71	56	51	103	40	6	
	ne	3	15	11	72	50	57	114	36	6	
P. delicatula	sp									54	80
	oz									11	10
	tr										4
	lo										10
	pl										12
	hi										27
	ne									7	12
Gen. indet.	sp									2	

Table 5. Conodont frequencies in the Radlin beds of Ostrówka (Ost) and the Carboniferous limestone of Todowa Grząba (TG) near Ostrówka in the Holy Cross Mts, and Czerna (Cz) near Kraków.

Sample nos	Ost	4	6
Idioprioniodus	sp	14	3
	oz	10	6
	tr	7	3
	lo	8	
	pl	3	2
	hi	18	15
	ne	4	3
Gen. n. sp. n. B	oz	45	28
	hi		5
	ne	7	28
Bactrognathus	sp	61	
	oz		
Arisemotaxis	tr	5	
	lo	2	
	pl		
	hi	27	7
	ne	6	3
Doliognathus	sp	3	2
	oz	2	2
	tr	2	
	ne	3	
Scaliognathus	sp	405	191
	oz	46	26
	tr	4	3
	hi	30	33
	ne	86	53
Dollymae	sp	1	3
Eotaphrus	sp	2	
Gnathodus	sp	307	169
	oz	24	18
	hi	2	1
	ne	6	
Weyerognathus	sp	235	71
	oz	48	10
	tr	2	
	lo	1	
	pl	5	
	hi	11	4
	ne	6	1
P. inornatus	sp	111	25
S. crenulata	sp	2	1
S. sandbergi	sp	5	20
Dinodus	sp	2	
	hi		2
P. communis	sp	10	25
	oz	3	
	ne	2	
Palm. trachytera	sp	1	1
	oz	1	
Tripodellus grac.	sp		1
Pander. acuta	sp	1	
	hi	2	
P. aculeatus	sp	2	
Pandorinellina	sp	19	8
	oz	1	
	ne	1	
Kladognathus	oz	1	

Sample nos		TG	Cz
Idioprioniodus	sp	2	1
	oz	9	2
	tr	1	2
	lo	7	
	pl	6	2
	hi	13	5
	ne	7	1
Kladognathus	sp	2	1
	oz	16	12
	tr	8	2
	lo	19	
	pl	23	
	hi	25	12
	ne	54	14
Lochriea	sp	807	87
	oz	122	42
	tr	8	3
	hi	123	21
	ne	238	3
Syncladognathus	sp		10
	oz		11
	tr		1
	lo		26
	pl		5
	hi		1
	ne		9
Protognathodus	sp	145	
Gnathodus girtyi	sp	343	88
	oz	69	7
	tr	5	
	lo	37	9
	pl	21	7
	hi	18	80
	ne	9	5
G. bilineatus	sp	69	3
	oz	2	
Clydagnathus	sp	1	3
	oz	7	
	tr	1	
	lo	1	
	pl	1	
	hi	2	4
	ne	2	1