Evolution and migration of conodonts and ammonoids near the end of Devonian recorded in distant localities

Jerzy Dzik[1,2*], **Nguyen Duc Phong**[3], **Nguyen Thi Thuy**[3] **and Przemysław Świś**[1]
[1]*Institute of Evolutionary Biology, Faculty of Biology, Biological and Chemical Research Centre (CNBCh UW), University of Warsaw, Warsaw, 02-089 Żwirki i Wigury 101, Poland*
[2]*Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warszawa, Poland*
[3]*Vietnamese Institute of Geosciences and Mineral Resources, 67 Chien Thang, Van Quan, Ha Dong, Hanoi, Vietnam*
email: dzik@twarda.pan.pl

ABSTRACT: The Devonian-Carboniferous boundary is allegedly marked by one of the most catastrophic global extinctions associated with sedimentation of the Hangenberg black shale. A dense sampling of the Kowala section in the Holy Cross Mountains, Poland, challenges this view, showing that the faunal dynamics across the Hangenberg black shale was not more dramatic than that across the preceding Kowala black shale. Quantitative analysis and biologically meaningful conodont apparatus study of the Kowala material offer probably the most complete record of faunal change in the latest Famennian and earliest Tournaisian among those sampled bed-by-bed for ammonoids and conodonts. It appears that the faunal dynamics of both cephalopods and conodonts was controlled by environmental changes that resulted in numerous immigrations and disappearances of particular lineages. Only a small fraction of lineages persisted long enough at the place, and transformed their morphology fast enough, to leave a record of their evolution. Most of the evolution apparently took place elsewhere. Locations of remote refugia where these lineages evolved in the time span bracketed by the Kowala and Hangenberg black shale events remain to be identified. Conodont apparatus study on geographically distant Vietnamese locality Cát Bà provides evidence that at least in the latest Famennian some conodont species unknown from Poland were present in Vietnam. Moreover, the contribution of species known from both localities to Polish and Vietnamese fossil assemblages was dramatically different.

Keywords: Devonian-Carboniferous boundary, Hangenberg Event, Evolution, Paleobiogeography, Poland, Vietnam

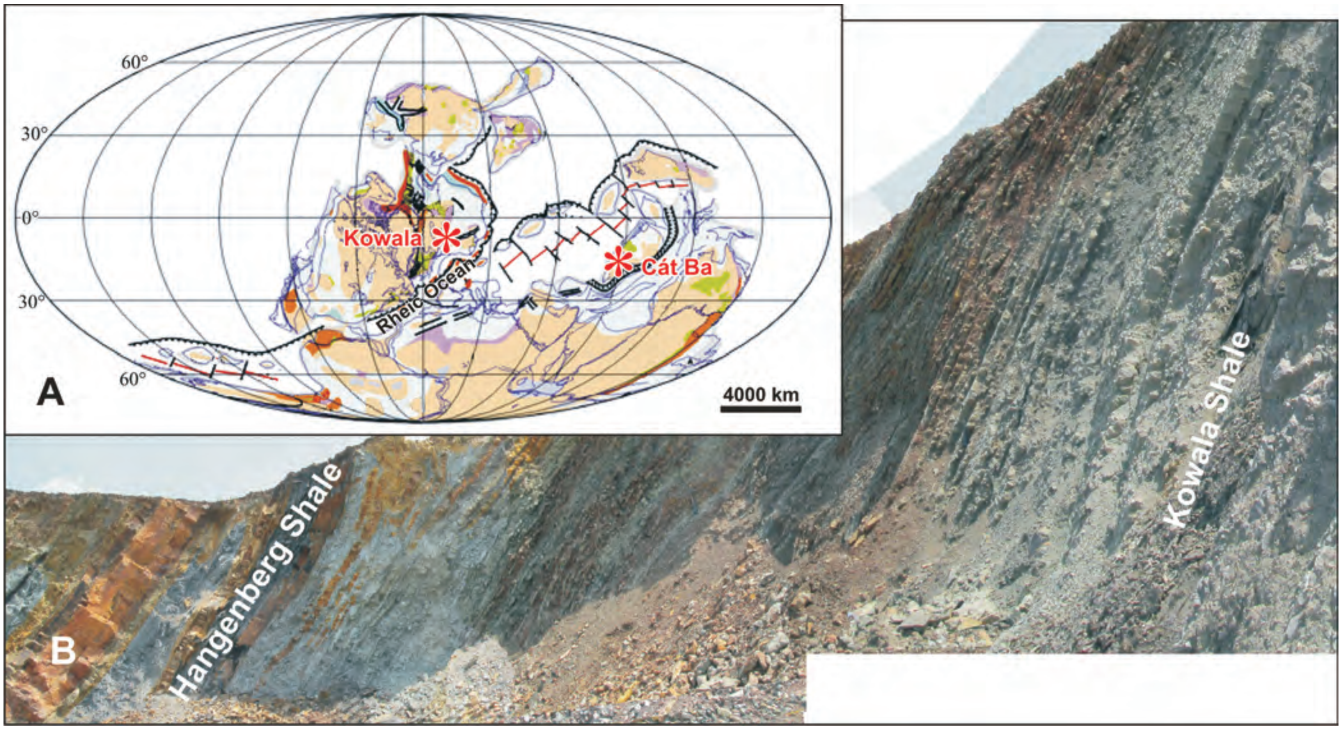
INTRODUCTION

One of the most enigmatic aspects of the Late Devonian seems to be the astonishing uniformity of open-sea conodont and ammonoid faunas over the world. The same species are encountered in geographically very distant localities, which strongly contrasts with the present-day, Ordovician or Jurassic paleobiogeography. At least two factors may contribute to this apparently non-actualistic picture of paleobiogeography. First, it is a result of the near-(paleo)equatorial location of main carbonate platforms (text-fig. 1A) with high diversity and abundant fossils of originally aragonitic shells of ammonoids preserved in rocks that enable also easy extraction of conodont elements. There are sparse data on the Famennian faunas outside Europe, North America, or Australia (e.g., Flessa and Hardy 1988). The second aspect of the alleged uniformity of the Late Devonian faunas is the imprecise taxonomic discrimination of species obscuring real faunal differences, especially in the case of conodonts. Most researchers on Late Devonian conodonts rely for species determination exclusively on the robust P elements neglecting the composition of the whole apparatus. This unavoidably results in distortion of faunal diversity, as species lacking platform elements in their apparatuses dominate in many fossil assemblages and in some species non-platform-bearing elements are the most taxonomically diagnostic (e.g., Dzik 2006). To avoid such bias, in this paper we apply apparatus taxonomy to the studied latest Devonian conodont material.

Despite apparent similarity of conodont faunas near the Devonian-Carboniferous boundary, some evidence to the contrary already has been reported for the Tournaisian. The succession of species in Europe, as exemplified by the Dzikowiec locality in the Sudetes, was much more chaotic than that from the South Chinese Muhua locality (Dzik 1997). An opportunity to check whether this difference refers also to the latest Devonian has emerged with exposures of strata immediately below the Hangenberg black shale newly accessible for sampling in the Holy Cross Mountains in Poland (text-figs 1B, 2) and on the Cát Bà Island in Vietnam (Komatsu et al. 2014). These two localities, representative of the East European Platform and the South China Plate (text-fig. 1A), were not less distant from each other in the Devonian than today, which enables us to supplement extensive evidence already assembled on the subject, summarized in Kaiser et al. (2016) and Becker et al. (2021). As we show herein, despite a superficial identity of the latest Devonian faunas over the world, more in-depth approach to their study, at least with respect to conodonts, exposes significant regional differences. It appears that global scale migrations of allopatrically originating species overshadow their evolution. Although the succession of co-occurring ammonoids is more difficult to trace because of shortage of a well-preserved fossil material, they seem to expose some regional differences as well, at least within the Rheic Ocean.

GEOLOGICAL SETTING

Among the Devonian-Carboniferous transition strata within the Rheic Realm, those cropping out near the Kowala Village in the Holy Cross Mountains, southern Poland, are probably the least diagenetically altered and are very fossiliferous (e.g., Szulczewski 1971; Bond and Zatoń 2003; Filipiak and Racki 2005; Marynowski and Filipiak 2007; De Vleeschouwer et al. 2013;



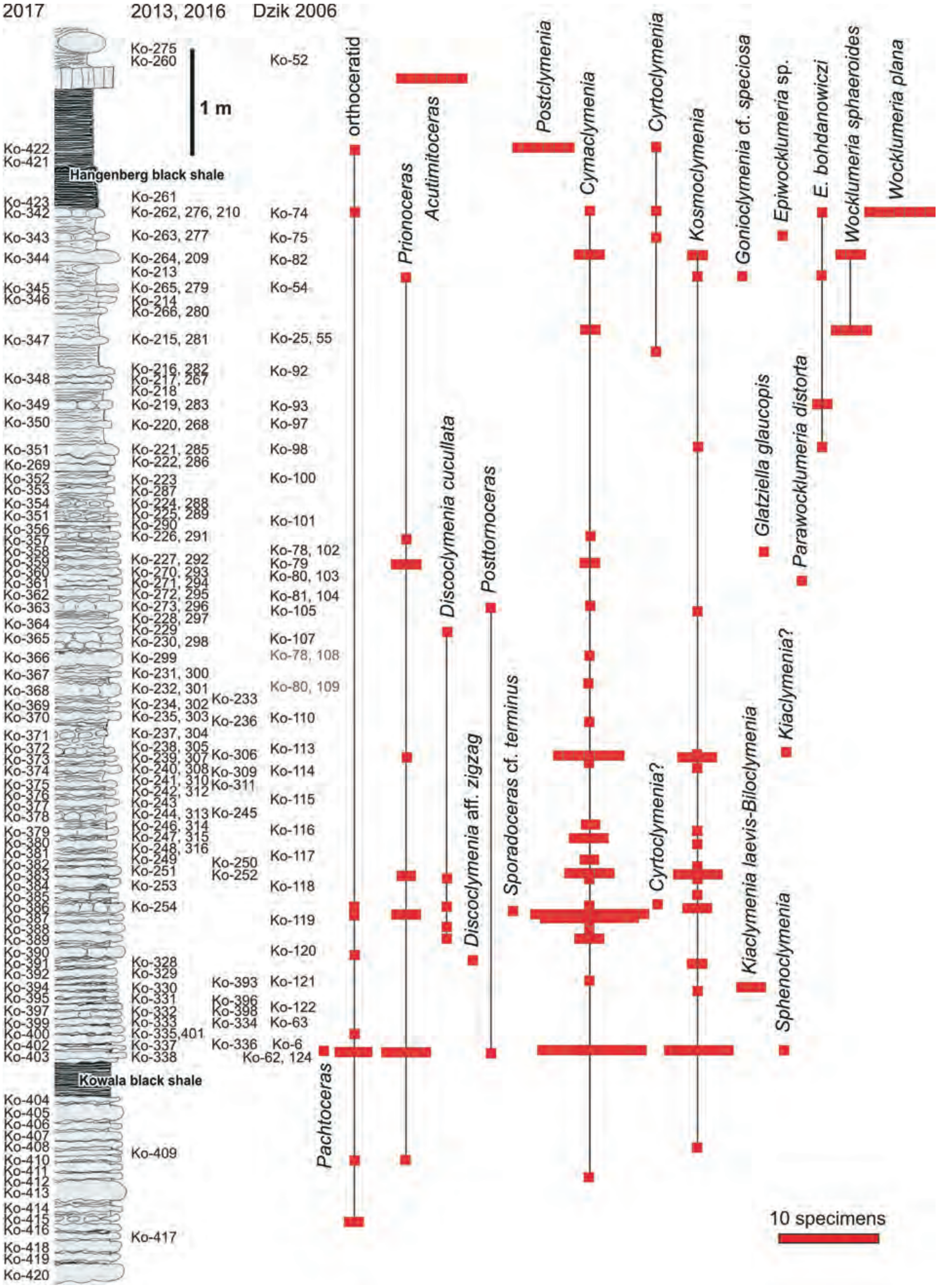
TEXT-FIGURE 1
A. Position of the Kowala and Cát Bà localities on the Late Devonian palaeogeographic world map (modified after Golonka 2020). B. The Kowala Quarry section of the topmost Famennian as exposed in 2017.

Myrow et al. 2014). They have yielded a relatively complete succession of well-preserved fossil assemblages of ammonoids and conodonts across the Devonian-Carboniferous boundary and there is an extensive literature on it (reviewed in Dzik 1997, 2006 and Woroncowa-Marcinowska 2006). Until recently, the ammonoids and conodonts from the Kowala have been known mostly from trenches dug in the field north of the Nowiny II Quarry (Czarnocki 1989; Malec 2014). Equivalents of the Hangenberg Shale and the Hangenberg Sandstone were represented in the trench material but the rock was apparently deeply weathered in the area where the trench was dug making the exact thickness of the strata difficult to measure. Fortunately, in the last decades the quarry expanded northward and both the topmost Famennian and basal Tournaisian strata became accessible in the quarry wall (text-fig. 1B; Marynowski et al. 2012). A rich Tournaisian conodont assemblage and a single but stratigraphically important ammonoid of this age was recently found (Świś and Dzik 2020). Also the topmost Famennian strata have appeared relatively productive, both in respect to conodonts and ammonoids.

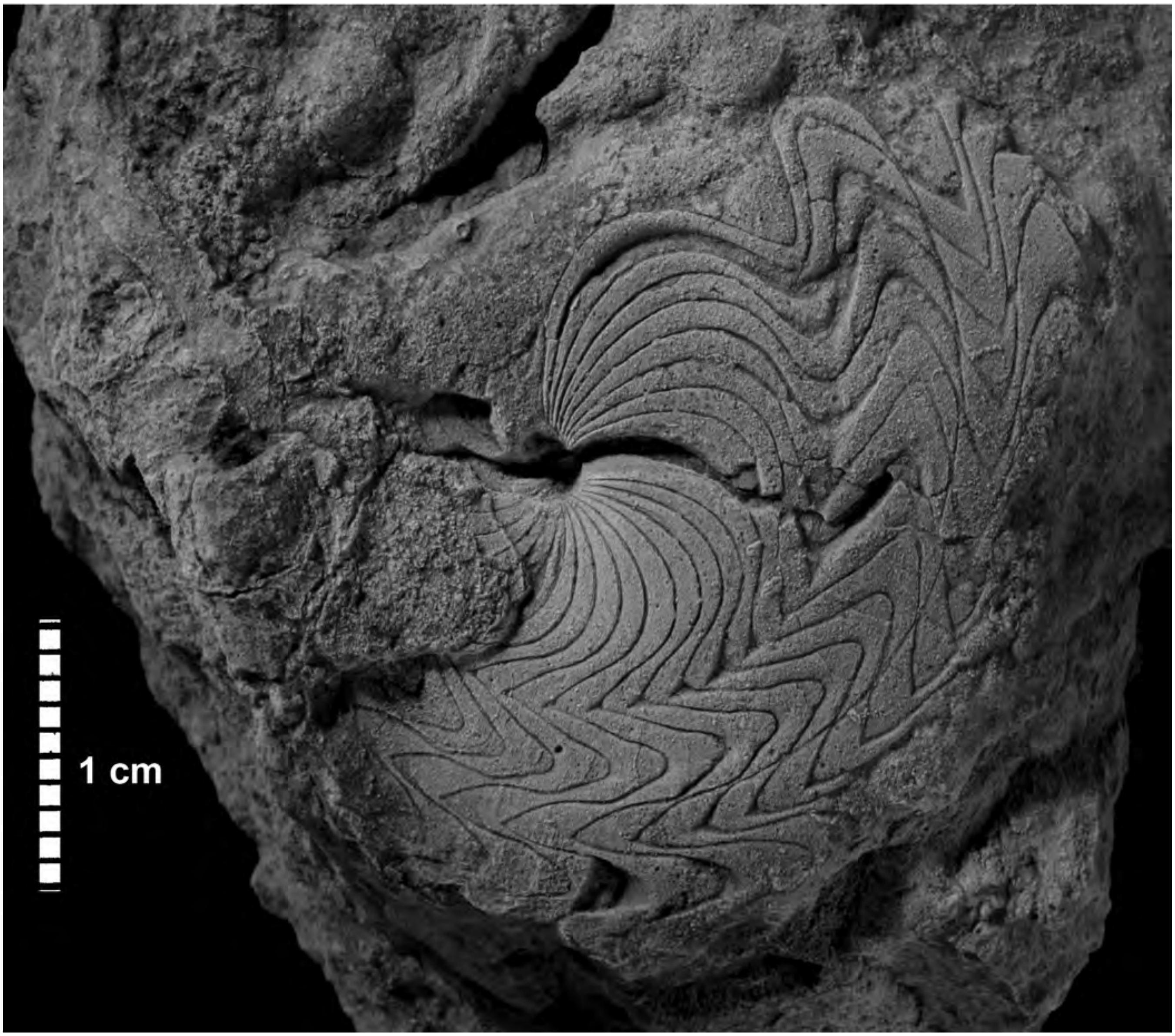
The part of the newly exposed section in the Kowala Quarry sampled for the purpose of this study covers the upper Famennian unit of nodular limestone beds intercalated with shale representing the conodont *Dasbergina trigonica* Zone (Dzik 2006). It is bracketed by two black shale horizons: the probable Hangenberg Shale equivalent near the top of the Devonian (Marynowski and Filipiak 2007) and the Kowala black shale eight meters below (text-figs 1B, 2; de Vleeschouwer et al. 2013) that may or may not be an equivalent of the transgressive Epinette Event in Belgium (Hartenfels and Becker 2016). The nodular limestone beds near their bases and tops are dark grey. The variegated and red-colored strata at the base gradually change into the olive-colored upper half of the unit between the dark grey ones. Specimens of *Wocklumeria sphaeroides* and *Parawocklumeria paradoxa* identified but not attributed to any specific bed by Czarnocki (1989) and found in the scree by the senior author (Dzik 2006) indicate the *Wocklumeria* Stufe age of this unit.

The upper 1.1 m thick black shale was first reported by Czarnocki (1933) from his trench and now is well exposed in the quarry (Filipiak and Racki 2005; Marynowski and Filipiak 2007; Marynowski et al. 2012). It has its equivalents in many other localities around the world (e.g., Racki 2005; Carmichael et al. 2015; Becker et al. 2016; Kaiser et al. 2016; Myrow et al. 2014). The approximately 20 cm thick tuffite layer that overlies the shale (Marynowski et al. 2012) is probably equivalent of the Hangenberg Sandstone. This stratum has yielded abundant crushed specimens of single putative *Acutimitoceras* species (Dzik 2006). Similarly a species-poor conodont *Protognathodus* assemblage (with *Prioniodina* sp., *Pseudopolygnathus* sp., and *Neopolygnathus communis*) occurs in a laminated limestone intercalation about 3 m above the black shale and 2 m below the first occurrence of diagnostic Tournaisian conodonts (Dzik 1997).

The zonal conodont *Dasbergina trigonica* occurs also throughout the sampled section of the Pho Han Formation exposed in the southern part of the Cát Bà Island in the picturesque Ha Long Bay in northern Vietnam (SDTable 1). This means that it represents only a brief episode, in terms of geological time, corresponding to the upper part of the *Wocklumeria* Limestone. Moreover, the sedimentary discontinuity immediately below the Hangenberg black shale (Komatsu et al. 2014) suggests a hiatus



TEXT-FIGURE 2
Rock column of the latest Famennian part of the Kowala section measured in 2017, with location of conodont and cephalopod samples, their correlation with sampling in 2013 and 2016, as well as with that published in Dzik (2006), and the number of cephalopod specimens collected bed-by-bed.



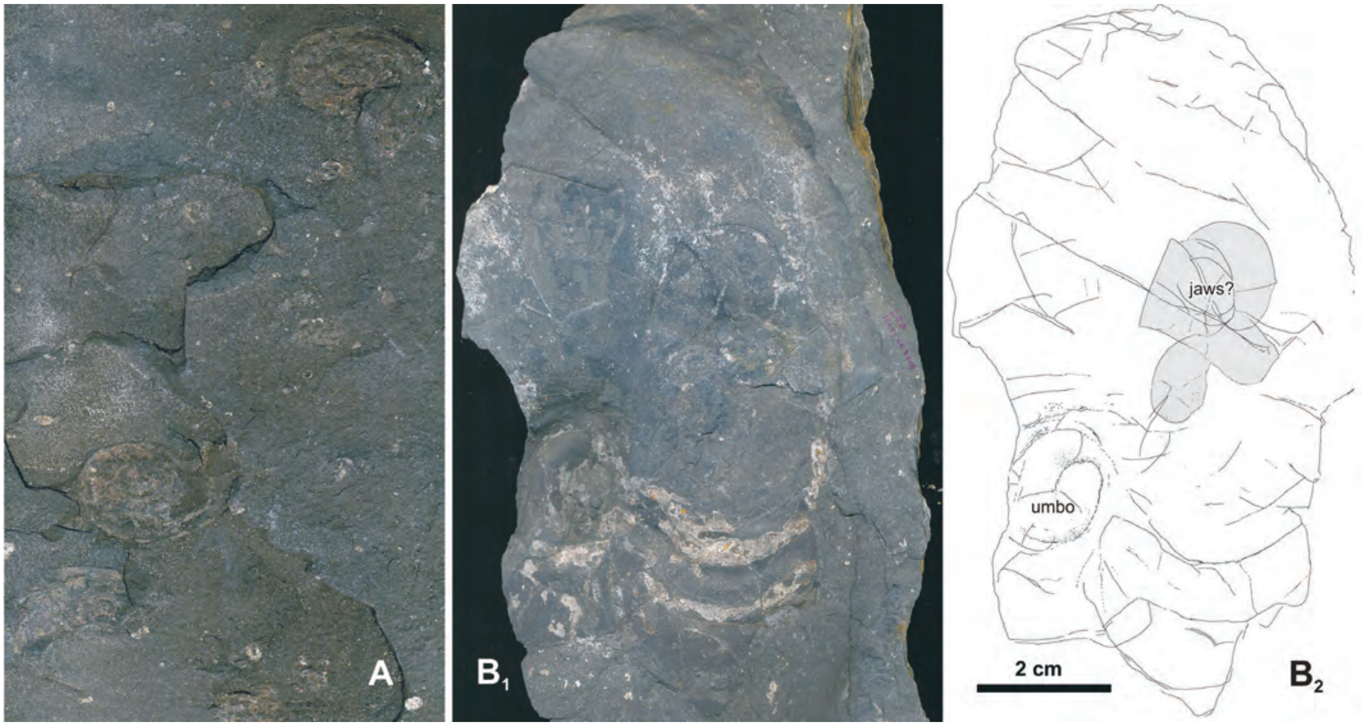
TEXT-FIGURE 3
Discoclymenia (*Alpinites*) sp. aff. *D. zigzag* Becker, 2002, specimen ZPAL AmVII/1895 from a bed between samples Ko-397 and 400.

there. In the Devonian, northernmost Vietnam and the Guizou province of South China were part of the same geotectonic unit and in equivalents of the Hangenberg Black Shale (the Changshun Shale in the Jiarantang section) the clymeniid *Postclymenia* cf. *evoluta* has been identified (Zhang et al. 2019).

MATERIAL

Ammonoids from the Devonian-Carboniferous boundary strata exposed in a trench dug north of the Nowiny II Quarry immediately south of the Kowala Village have been already described by the senior author (Dzik 1997, 2006). Exclusively internal molds of their conchs were found in the trench, as well as in the strata recently exposed in the quarry, although Czarnocki's (1989) material collected before World War II included numerous exquisitely preserved specimens with preserved shells showing growth increments. Only a general attribution to the Famennian 'Stufen' was given in the Czarnocki (1989) monograph and no information regarding exact position of the specimens collected bed-by-bed has survived. Presumably, there was a local lens of limestone with aragonitic shells transformed into calcitic sparite.

Although the Devonian strata exposed in the Kowala Quarry are folded and cut by many faults, sampled conodonts are amber-colored (CAI = 1) without any signs of significant heating. Distribution of elements varies but usually there are enough numerous ramiform specimens to enable apparatus reconstruction (SDTable 2; Dzik 1997, 2006).



TEXT-FIGURE 4
Ammonoids from the Hangenberg shale at Kowala. A. Undetermined clymeniid species, probably *Finiclymenia*. B. Very large specimen of *Cyrtoclymenia* and interpretive drawing showing probable jaws.

The conodont samples from the Cát Bà Island section in northern Vietnam were taken from the same place as those published by Komatsu et al. (2014) and the same numbers are given to them. Conodont elements extracted from the samples are dark brown in coloration (CAI = 3) but well preserved without any signs of tectonic deformation. Proportions between ramiform and platform elements show a relatively low unbalancing as for the Late Devonian (SD Table 1).

The collection is housed at the Institute of Paleobiology of the Polish Academy of Sciences (abbreviated ZPAL) in Warsaw.

METHODS

Conodont sample processing

The conodont samples were dissolved in diluted acetic (pure limestone) or formic (marls, dolomitized limestones) acids. The residue was decanted, dried and enriched in the Franz electromagnetic mineralogical separator. The conodont specimens are kept loose in plastic slides (*Franke Zellen*) to allow their easy separation into classes, overturning and manipulation. SEM photographs of conodonts were taken of specimens mounted on stubs with a sticky tape and coated with carbon or gold.

For measuring conodont elements their whole set was photographed with a digital camera together with a millimeter scale. Particular elements were numbered and contours of elements representing a succession of ontogenetic stages were drawn with Photoshop on the graphic tablet. Specimens that are reasonably complete but with broken tips were then fit into contours of the same size and shape to append the missing part (thirty specimens among 180 in case of *Tripodellus* from a Cát Bà sample). The measurements were done with ImageJ software with 0.01 mm precision.

Biostratigraphic age determination and apparatus reconstructions

We faced difficulty with application of widely used conodont zones, proposed by Ziegler and Sandberg (1984), to the Kowala section, especially with the two topmost ones. Like other Late Devonian zones proposed by these authors, they were established based on evolution within particular lineages. Unfortunately, Ziegler's *Bispathodus costatus* Zone was defined on the appearance of the species of questionable taxonomic identity. *B. costatus* is the type species of its genus. It comes from the Tournaisian Hannibal Shale (Missouri, US) and is presumably conspecific with the co-occurring type species of *Pseudopolygnathus* as its extreme morphotype (Dzik 1997, p. 74; Dzik 2006, p. 152). The valid name for the Late Famennian species traditionally used to define the Zone is *Pseudopolygnathus ziegleri*. Regrettably, the origin of *P. ziegleri* is cryptic and its occurrences are sensitive ecologically, as pointed out by Dzik (1997, 2006), similarly to *P. aculeatus*, believed by Ziegler and Sandberg (1984) to be of biostratigraphic importance. They cannot be direct successors of *Dasbergina stabilis*, mature P_1 elements of which tend to develop a rudimentary platform (Dzik 2006, fig. 116E), not an icrion that is diagnostic for the Devonian species of *Pseudopolygnathus* traditionally classified in *Bispathodus*. Fortunately, the evolutionary origin of another species of the genus, *P. jugosus,* is well documented and deserves to be used as the marker of the basal boundary of its own Zone with the *Neopolygnathus styriacus* Zone (Dzik 2006).

Similar difficulties arise with application of ‘*Palmatolepis expansa*’ and ‘*Siphonodella*’ *praesulcata* as zonal species for the latest Devonian time after the *P. jugosus* Zone. Their evolutionary origin remains to be clarified. The former, its correct apparatus name being *Tripodellus expansus*, does not seem to occur in the Holy Cross Mountains and the Sudetes. Its species-diagnostic aspects develop late in ontogeny and thus a high juvenile mortality may prevent its identification, as shown by the Vietnamese material discussed below. The appearance in Europe of the latter (probably with bizarre apparatus structure and provisionally classified in *Dinodus* as *D*. *praesulcatus*) was ecologically controlled and its ancestry remains unknown (Świś and Dzik 2020). A much better zonal marker in this geological time segment is *Dasbergina trigonica*. Its origin from *Dasbergina marburgensis* was traced in the upper part of the clymeniid limestone at Dzikowiec in the Sudetes (Dzik 2006). At Kowala, *D. trigonica* gradually developes in the middle of the studied nodular limestone succession (sample Ko-104; text-figs 2, 13). At the top of this zone the Hangenberg black shale environmental event took place, which prevents its definition in terms of the conodont zonation. This applies as well to the Devonian-Carboniferous transition strata exposed at Cát Bà Island and makes precise correlation with traditional zones difficult.

Our goal is to separate evolutionary change (in geological time) from results of migrations (in geographic space). Present-day paleontology experiences a fundamental split in methodological approach to the fossil material. Traditionally and declaratively, the main value of fossils is that they document evolution understood as a physical process with a time arrow. Any fossil has its spatial (geographic) and time (geochronological) dimensions that are its unchangeable atributes. The crucial aspect of evolutionary inference is a direct dependance on geological time (stratigraphic succession) as an objective ordering factor. This means that successive states of a morphological transformation recorded in a continuous time succession of fossils within the same locality can be assembled into an anagenetic continuity. If the fossil record is complete enough, biometrics can be applied to produce a stratophenetic presentation of the evolution. Such approach permits reasoning in Popperian terms except that prediction of the subsequent course of evolution is not possible. Instead, retrodiction, that is an inference directed back in time can be used to make the theory about the course of evolution falsifiable. Such a hypothetico-deductive approach is referred to as chronophyletics (Dzik 1995, 2005).

The classic Popperian methodology is used also in conodont apparatus reconstruction (Dzik 1991). A working hypothesis on the apparatus composition is formulated on the basis of morphological similarity of elements within a sample and similarity to elements in other known apparatuses. This may be a completely arbitrary choice. If it is too distant from reality, it would be immediately falsified by analysis of the next studied sample. The testing is based on the assumption that in any sample that contains at least one element included in the hypothetical reconstruction, and large enough to be statistically significant, all other elements should also be represented. Moreover, all the elements should be easily homologized with elements occurring in other members of the same lineage. If they are missing, or unsimilar elements occur, the hypothesis on the apparatus composition is wrong This means that along with the statistical co-occurrence an independent reasoning on evolutionary (chronophyletic) continuity is used to falsify the hypothesis.

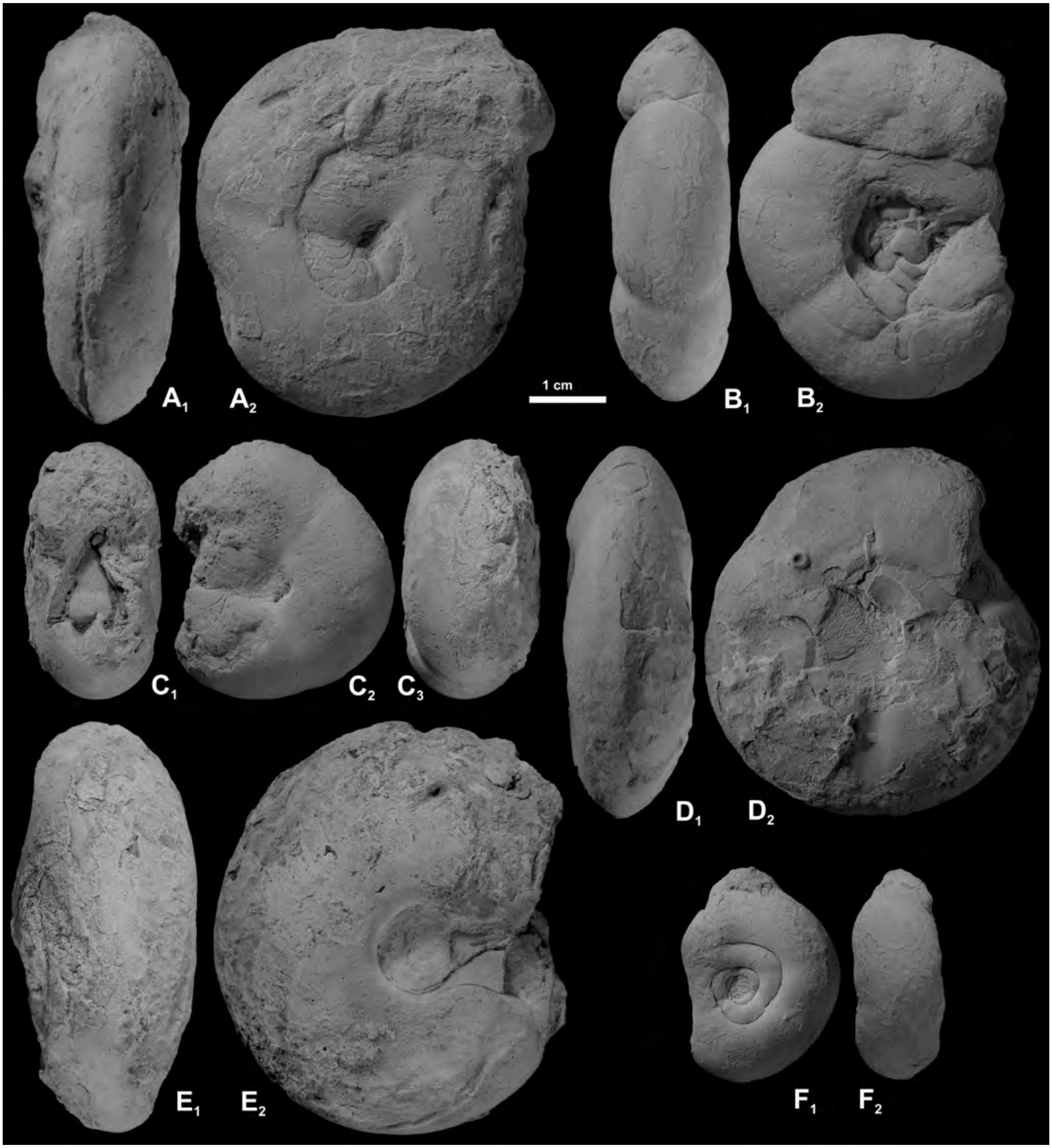
Admittedly, an alternative approach to that presented above is much more commonly chosen by biostratigraphers. It considers taxa understood as hypothetical units that originate suddenly and do not change their morphology until extinction. This implies a vertical, instead of population, concept of chronospecies (reviewed in Dzik 2005 and Klapper 2021).

FAUNAL DYNAMICS OF LATEST FAMENNIAN CEPHALOPODS

Knowledge of growth increments and periodic apertural modifications are necessary to determine most Famennian goniatite and clymeniid species but virtually all specimens from the Kowala section are internal molds lacking shell. This makes bed-by-bed collecting of cephalopod fossils of limited value in tracing stratigraphic distribution of species. Reliable taxonomy is usually possible only to the genus level; sometimes this allows to indicate a group of species, rarely their precise identification. Few samples taken from single beds are numerous enough to provide an estimate of taxonomic diversity. However, taking together all the record (text-fig. 2) one may roughly approximate the population dynamics. Generally, the species diversity seems rather low and only two lineages, *Cymaclymenia* and *Kosmoclymenia*, dominate, being represented in almost all beds yielding ammonoid fossils. Only in the topmost nodular limestone beds the wocklumeriids dominate in number of specimens. Goniatites with a complex suture (*Discoclymenia*, *Posttornoceras*, and *Sporadoceras*) appear only sporadically as single specimens. A surprising aspect of their succession is that the most advanced sharp-edged *Discoclymenia* (*Alpinites*) aff. *zigzag* (text-fig. 3) precedes *Discoclymenia cucullata* with obtuse coils.

The Hangenberg black shale exposed at Kowala is full of ammonoid fossils but they are strongly compressed, which prevents their identification to the species or even genus level (text-fig. 4A). One important addition to knowledge of cephalopods from this stratum (e.g., Korn 1991; Korn and Weyer 2003) is the documentation of a large specimen of *Cyrtoclymenia* (text-fig. 4B, C). Fossils of this genus occur throughout the Famennian of Kowala; the last specimens preserved three-dimensionally was collected from the topmost limestone beds (samples Ko-277 and 342; text-figs 2, 5E, 8E). Apparently, the faunal change at the transition to the Hangenberg black shale was not dramatic and the cause of the decrease in species diversity is mostly taphonomic. A rich ammonoid fossil assemblage similar to those from the latest Famennian emerges with the Tournaisian *Gattendorfia* Limestone. The locality geographically nearest to Kowala with such a record is the classic Dzikowiec (Ebersdorf) locality in the Sudetes (reviewed in Dzik 1997 and Korn et al. 2005). Along with direct successors of the Devonian goniatites having involute adult conchs it has yielded also prolecanitids characterized by a novel evolute conch geometry. Korn et al. (2003) ingeniously explained their origin by progenetic (or even proterogenetic) evolution. Their ancestors had involute mature conchs but evolute juvenile stages that gradually expanded to later stages, *Gattendorfia* representing an intermediate conch geometry. *Eocanites* found in Kowala (Świś and Dzik 2020) represents a late stage of such evolution that remains mostly cryptic and apparently took place in geographically distant regions.

Conchs of many Famennian ammonoids show periodic thickenings of the nacre, which appear as constrictions on internal molds, but they are not expressed on the external surface of the



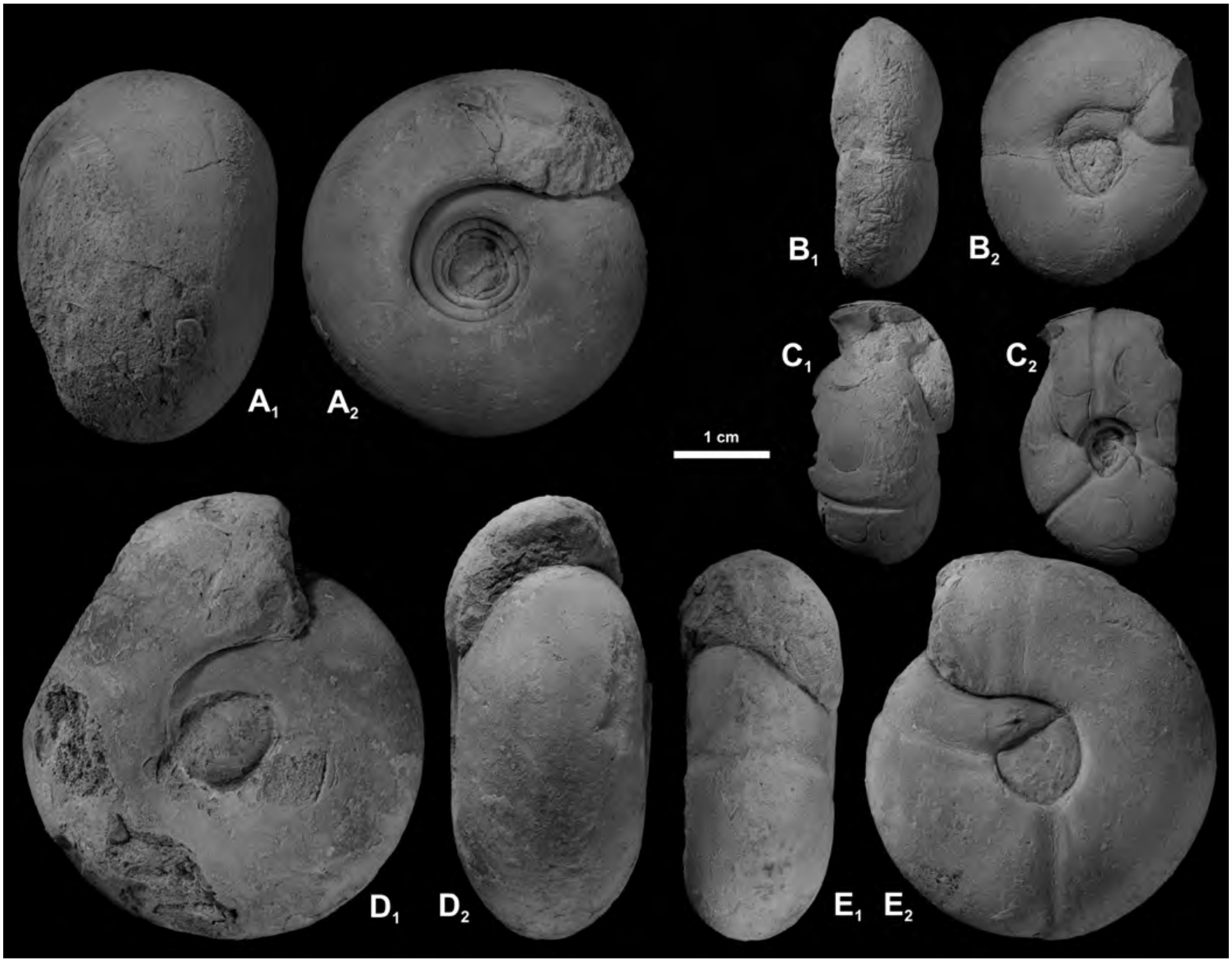
TEXT-FIGURE 5
Late Famennian clymeniids from Kowala in lateral and apertural (or adapertural) views.

A, B, D *Epiwocklumeria bohdanowiczi* (Czarnocki 1989), mature specimens ZPAL AmVII/1871, 1819, and 1868 and from sample Ko-268, undetermined bed of a reddish limestone, Ko-267, and 268, respectively.

C *Epiwocklumeria* sp., juvenile specimen ZPAL AmVII/1892 from sample Ko-282.

E *Cyrtoclymenia* sp. specimen ZPAL AmVII/1891 from sample Ko-277.

F *Parawocklumeria distorta* (Tietze 1870) specimen ZPAL AmVII/1867 from sample Ko-294.



TEXT-FIGURE 6
Latest Famennian clymeniids *Wocklumeria* from Kowala in lateral and apertural (or adapertural) views.

A *Wocklumeria sphaeroides* (Richter, 1848) specimen ZPAL AmVII/1879 from sample Ko-344.

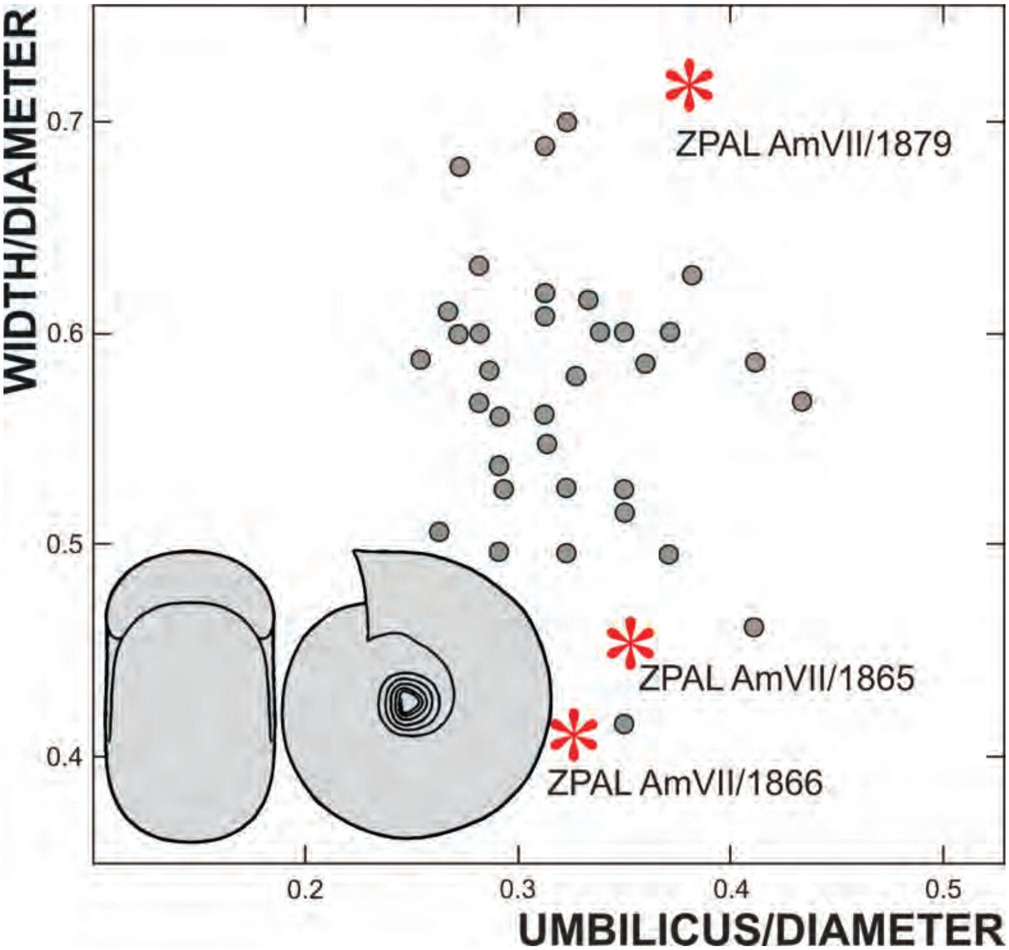
B–E *Wocklumeria plana* Schindewolf 1937 specimens ZPAL AmVII/1889, 1884, 1865, and 1866, respectively, from samples Ko-342 (B, C) and the scree, but of identical lithology (D, E).

shell. The disposition of such thickenings is not parallel to the aperture. The most common example of such constrictions is offered by the cheiloceratids *Prionoceras* and *Sporadoceras*. The conch constriction that characterizes the wocklumeriid clymenias are real and they are parallel to growth increments, being controlled by the mantle margin at the aperture.

The strong conch aperture constrictions in the wocklumeriid ammonoids develop in triplicate (e.g., Ebbinghausen and Korn 2007). This is not an unique phenomenon and many similar cases are known among ammonoids of various geological age, as well as among some extant stenoglossan gastropods. Three episodes of shell thickenings develop by each coil (e.g., in the muricid gastropods) resulting in varices strengthening the conch; the conch growth from one varix to the next one being very rapid (Linsley and Javidpour 1980).

Despite the tremendous increase in knowledge of molecular biology of molluscs (e.g., Aguilera 2017) regulatory mechanism of their shell development remains mostly unknown. One may suppose that regulatory genes control secretion of pigments in the prismatic shell layer (Budd et al. 2014) in a similar way to the secretion of periostracum and the prismatic layer itself. Computer modelling shows that it is enough to differentiate the rate of incremental growth in a region of the mantle margin to produce any of the observed morphologies of the molluscan conch (Okamoto 1988), including changes in evoluteness near termination of its growth. Such was probably also the control of the wocklumeriid conch shape.

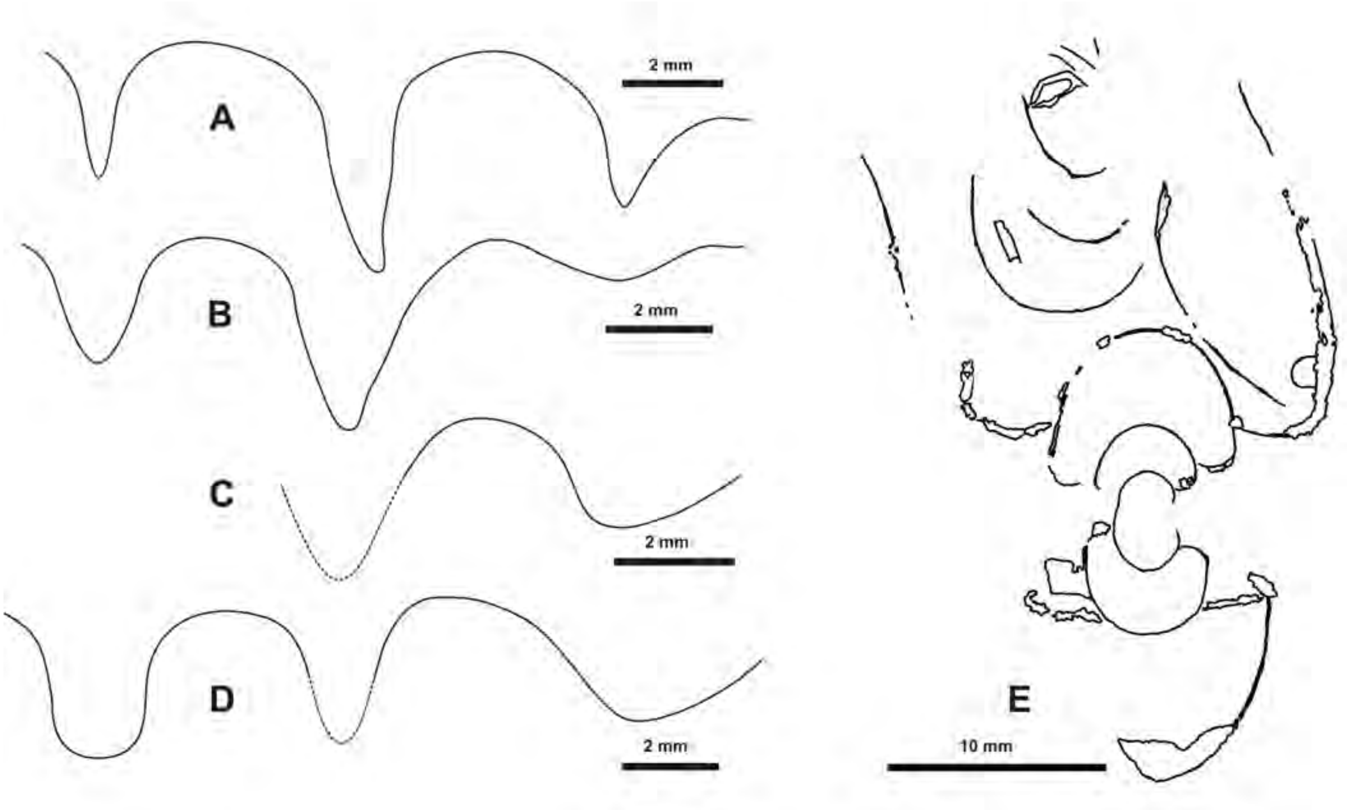
The fossil record of the evolution of the Wocklumeriidae is not complete enough to enable tracing their origin. Probably the oldest member of the family is *Kamptoclymenia* from



TEXT-FIGURE 7
Variability of *Wocklumeria* from Stourscombe Beds of Cornwall (after Selwood 1960) and position of mature specimens of *Wocklumeria* from Kowala (asterisks) on the scattergram.

Hönnental (*K. endogona* co-occurring with *K. trigona*; Becker 2000). It had an evolute conch of minute adult size with a trigonal appearance restricted to early stages. Lateral furrows developed in the mature last whorl near aperture. This suggests that the root of its lineage is close to the *Rhiphaeoclymenia canaliculata* of Bogoslovsky (1981), the predecessor of the Glatziellidae, the sister branch of the wocklumeriids. If *Liroclymenia fundifera* of Czarnocki (1989) is conspecific with *R. canaliculata* (Becker 1997) and truly comes from the red limestone at Kowala (the original specimen being lost; Dzik 2006), this species would be of *P. jugosus* Zone age. Presumably it is older than other glatziellids and the wocklumeriids. Its relatively large adult conch may be a plesiomorphic trait. The oldest unquestionable species of the glatziellid lineage is *Glatziella lethmathensis* from the Rhenish Slate Mountains (Becker 1997). All specimens of *Glatziella* species with relatively evolute conchs were collected at Dzikowiec from the scree but it seems likely that they come from the *P. jugosus* Zone. The finding of the most advanced member of the lineage, *G. glaucopis*, in sample Ko-102 at Kowala in stratum of the earliest *D. trigonica* Zone (Dzik 2006) suggests that the remaining species of the genus occur at Dzikowiec in strata of an older age.

This seems to be contradicted by finding of *Kamptoclymenia trivaricata* Schindewolf, 1937, which represents the first step in the development of trigonal wocklumeriid conch, in a bed 0.1 m below the top of the clymeniid limestone at Dzikowiec (Schindewolf 1937). Also *Parawocklumeria distorta*, with the conch distinctly trigonal at adult stage but with lateral furrows near the terminal aperture comes from the topmost *Wocklumeria* Limestone at Dzikowiec (Schindewolf 1937). Such unexpectedly late geological age would prevent any inference on the evolution of the wocklumeriids based on their stratigraphic succession. Korn (1995, text-fig. 6) considered all the members of the wocklumeriid morphocline coeval, from the evolute *Kamptoclymenia endogona*, through *K. trigona*, *K. trivaricata*, *Parawocklumeria patens*, and *P. distorta* to highly involute *P. paprothae*. If true, such a picture of species distribution would imply that they all originated somewhere other than the central European region of the Rheic Ocean and immigrated there in a quite chaotic order, with no correspondence to their evolutionary advancement. Such puzzling stratigraphical evidence requires confirmation by independent conodont dating. In fact, in parts of the Dzikowiec Quarry where the Famennian section is complete, its top represents the *D. trigonica* Zone, but in other places both the *Gattendorfia* Limestone and the topmost strata of the



TEXT-FIGURE 8
Suture lines of the wocklumeriid ammonoids from the latest Famennian of Kowala.

A *Wocklumeria plana* Schindewolf, 1937 specimen ZPAL AmVII/1884 from sample Ko-342 (see also text-fig. 6C).

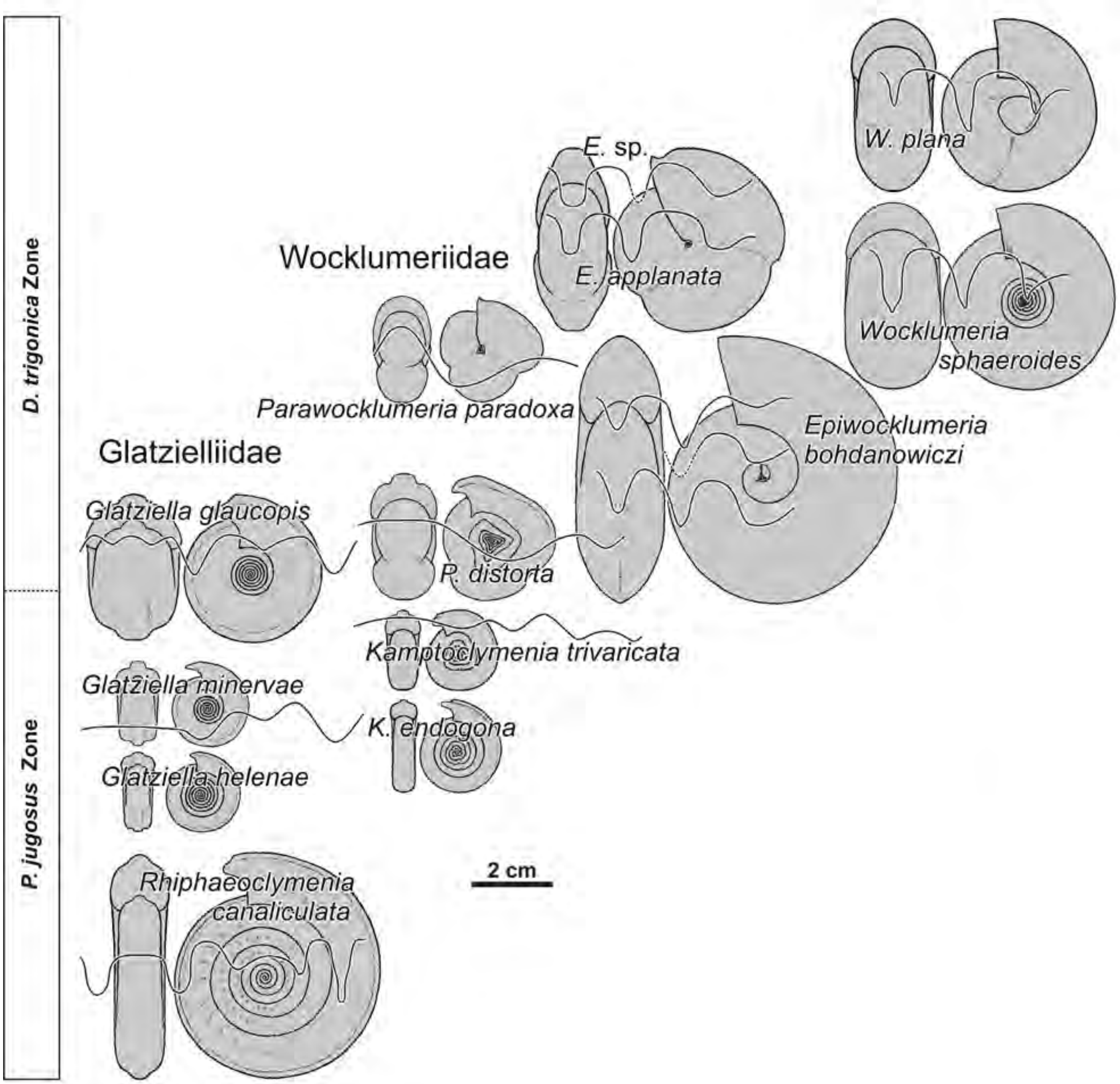
B,C *Epiwocklumeria bohdanowiczi* (Czarnocki, 1989) specimen ZPAL AmVII/1889 from sample Ko-342 (B) and specimen ZPAL AmVII/1877 from the scree of black limestone (C).

D *Epiwocklumeria* sp., juvenile specimen ZPAL AmVII1892 from sample Ko-282 (see also text-fig. 5C).

E *Cyrtoclymenia* sp., transverse section of specimen ZPAL AmVII/1998 from sample Ko-342.

Wocklumeria Limestone was eroded (Dzik 1997). The stratigraphic order of occurrences seems to be confirmed by the presence of *P. distorta* in sample Ko-294 of the red limestone of the *P. jugosus* Zone at Kowala (text-figs 2, 5F, 9). This removes partially the alleged lack of consistence between morphology and stratigraphy. There is no doubt that *Parawocklumeria paradoxa* of Wedekind (1918), known from the *D. trigonica* Zone both at Dzikowiec and Kowala, is the youngest species of its lineage. Yet another alternative explanation of the seemingly chaotic stratigraphic distribution of morphologies may be that it is a result of a wide population variability of the wocklumeriids. This calls for its determination by biometrics on large stratigraphically homogenous samples.

The only quantitative estimation of population variability of the wocklumeriids is that of *Wocklumeria sphaeroides* by Selwood (1960, text-fig. 1). It is based on a sample collected from the ‘upper faunal division’ within the Stourscombe Beds exposed in two disused quarries near Stourscombe in Cornwall. According to Selwood (1960, p. 155) *Parawocklumeria* is absent in this ‘division’, being abundant below, where it is represented by *P. paradoxa* (Becker 2000; Ebbinghausen and Korn 2007). This means that the stratum with *Wocklumeria* is truly latest Famennian in age and the fossil assemblage may be homogenous in respect to the rate of evolution of its ammonoids. Ebbinghausen and Korn (2007, text-fig. 9) presented statistics on size frequency distribution of mature conchs of *Wocklumeria* in their thorough study on the conch ontogeny of the wocklumeriids based on bulk samples from particular geographic areas. The enigmatic aspects of the occurrences reported by them is the presence of closely similar species in the same stratigraphic unit (e.g., Korn 1995, text-fig. 6) or even bed (Korn 1992, fig. 3; Becker 2000, fig. 3; Ebbinghausen and Korn 2007, fig. 3). A few specimens of *W. sphaeroides* have been collected bed-by-bed at Kowala (text-figs 2, 6A). They are within the upper part of the *Epiwocklumeria bohdanowiczi* range, except for the topmost bed of the limestone succession. Their conch geometry fits the maximum globosity in the Stourscombe Beds (text-fig. 7). In this respect they strongly differ from the *Wocklumeria* specimens that dominate the sample with the last *E. bohdanowiczi* specimen and are well outside the values on the Selwood’s (1960) scattergram (text fig. 7). Possibly, they are

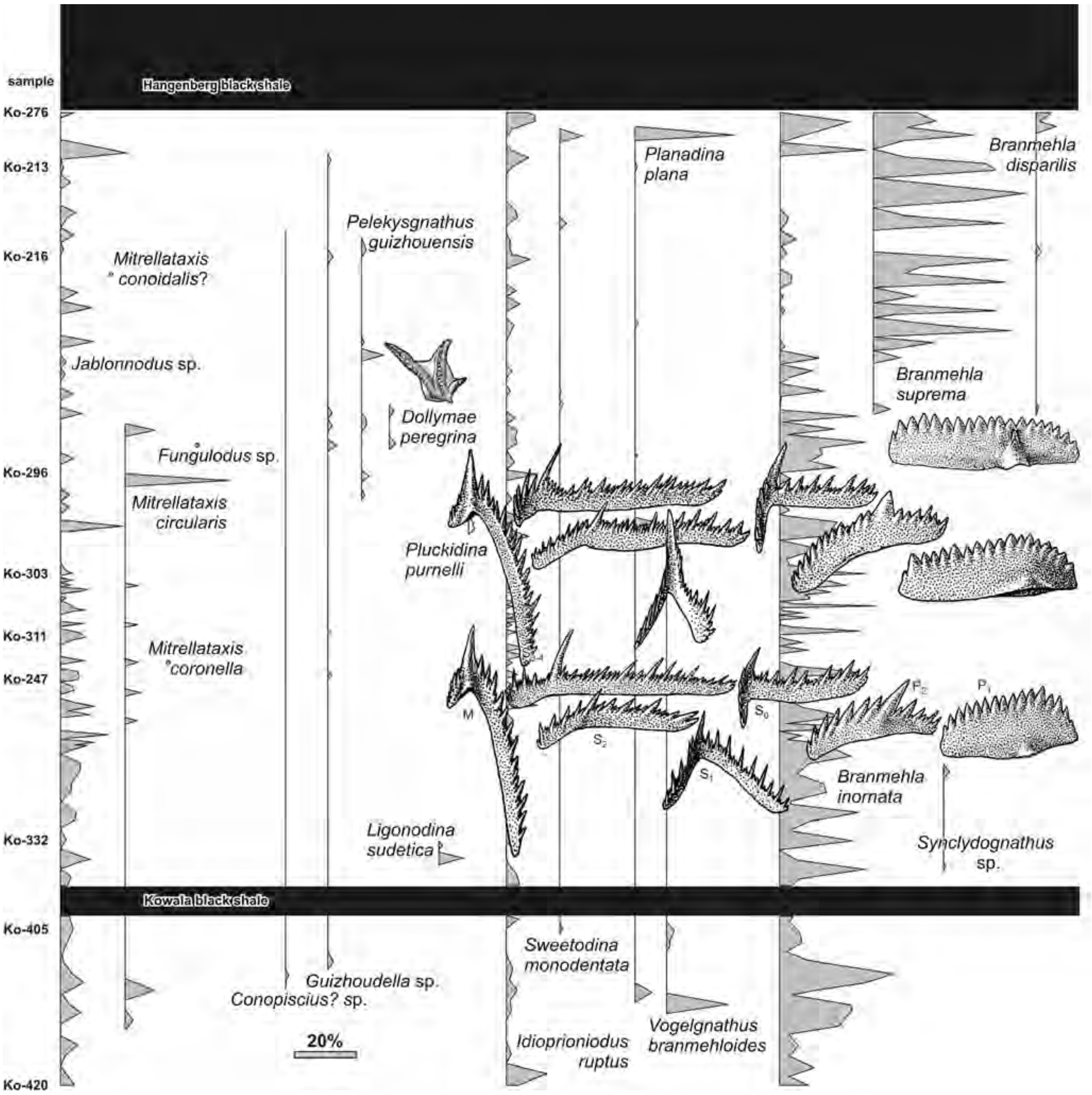


TEXT-FIGURE 9
Proposed hypothetical time distribution of the Glatziellidae and Wocklumeriidae species extrapolated from bed-by-bed collecting in the Kowala section (modified after Dzik 2006).

conspecific with *W. plana* (text fig. 6B-E). Their suture shows a very narrow and acute ventral lobe (text fig. 8A).

Epiwocklumeria bohdanowiczi (Czarnocki, 1989) is a wocklumeriid with the most elaborate modification of the mature body chamber. It lacks constrictions and becomes evolute. In connection with its relatively acute venter, the suture shows a rather narrow ventral lobe as compared with otherwise similar *E. applanata* (text-figs 5A, B, D, 7B, and 8). Czarnocki (1989) introduced genus *Kielcensia* for the species (developed further by Becker 2000) but it seems more likely that this is rather a connecting link between early *Parawocklumeria* and the type species of *Epiwocklumeria*. The oldest mature specimen of *E. bohdanowiczi* (ZPAL CVII/1896 from sample Ko-351) does not differ from those from the youngest specimens of comparable ontogenetic stage. Less clear is the taxonomic status of the two specimens from the black nodular limestone with *Wocklumeria plana* topping the Devonian limestone unit (text-fig. 2; one from the conodont sample Ko-342, the other from the scree). They are openly umbilicate and are similar to specimens of *E. bohdanowiczi* of similar size.

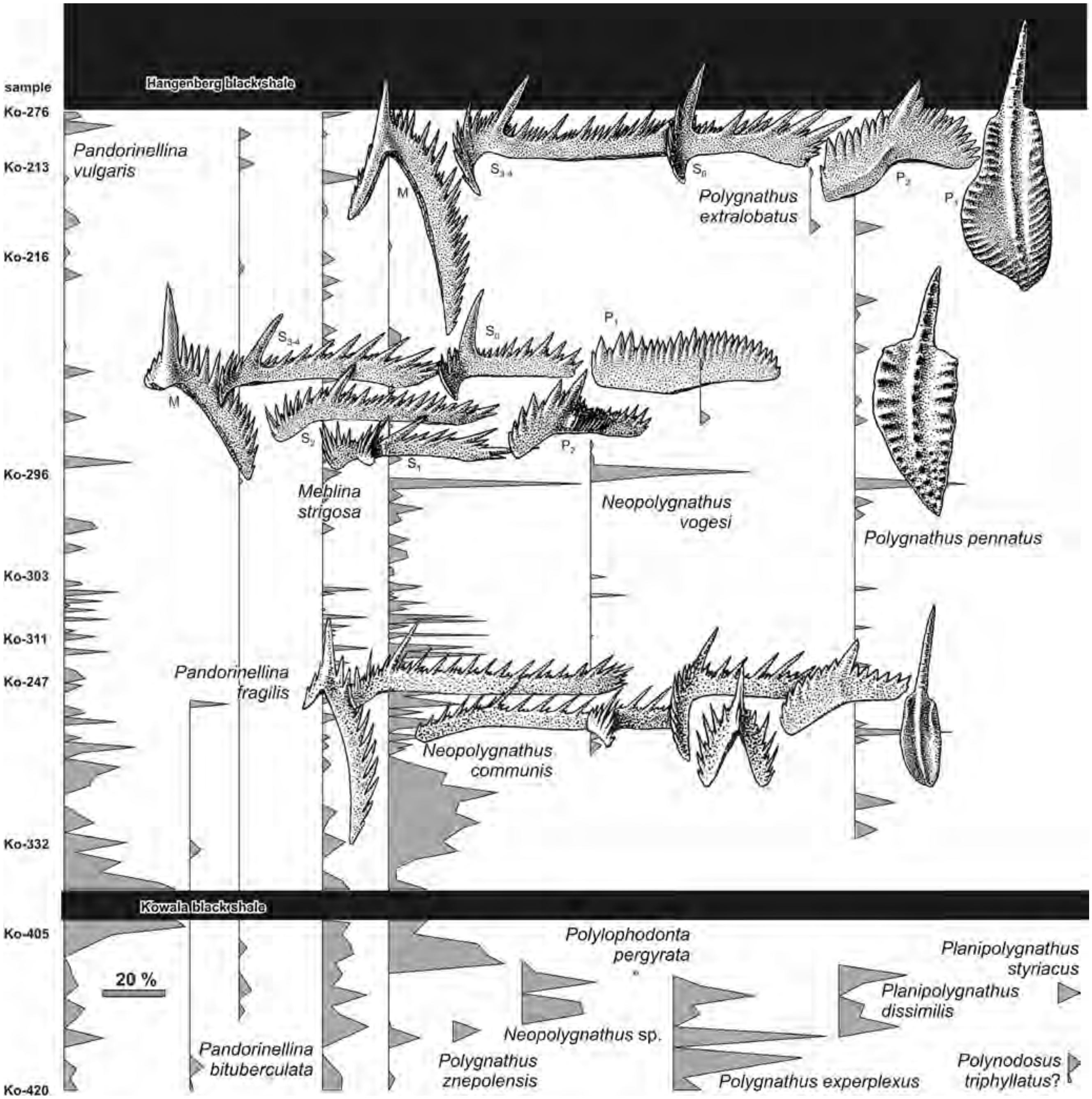
Czarnocki (1989, p. 27) claimed that *E. bohdanowiczi* occurred throughout his 5.54 m thick *Wocklumeria* beds, starting from below the red marly limestone. Our bed-by-bed collecting proves its occurrence in the topmost 3 m of the Famennian limestone (text-fig. 2). Korn (1995) correctly guessed that *Kielcensia* had the same range as *Wocklumeria*, that is the lower two-thirds of the



TEXT-FIGURE 10
Frequency contribution to samples of icriodontid, prioniodinid and ozarkodinid conodonts elements in the topmost Famennian of the Kowala Nowiny II Quarry in the Holy Cross Mountains, Poland.

upper *paradoxa* Zone. Becker and Mapes (2010) interpreted the bed of the Woodford Shale at the Ryan Quarry in the Arbuckle Mountains, Oklahoma, from which probably comes their *Kielcensia vagabunda* and the conodont sample R19 taken by Over (1992), as being older than *Wocklumeria*. Over's (1992, SD Table 6) conodont sample was barren and samples from the section did not yield conodont species that could be used for precise biostratigraphic dating. The relatively high contribution from *Branmehla inornata* to the assemblage dominated with *Dasbergina stabilis* suggests a rather cold-water environment, as a *Branmehla* species apparently dominated the Famennian high latitude assemblage of Amazonia (probably misidentified as a Frasnian species by Cardoso et al. 2015, specimens illustrated on their fig. 3 N, T, U seem to represent P_1, S_1, and M elements of *Branmehla suprema*).

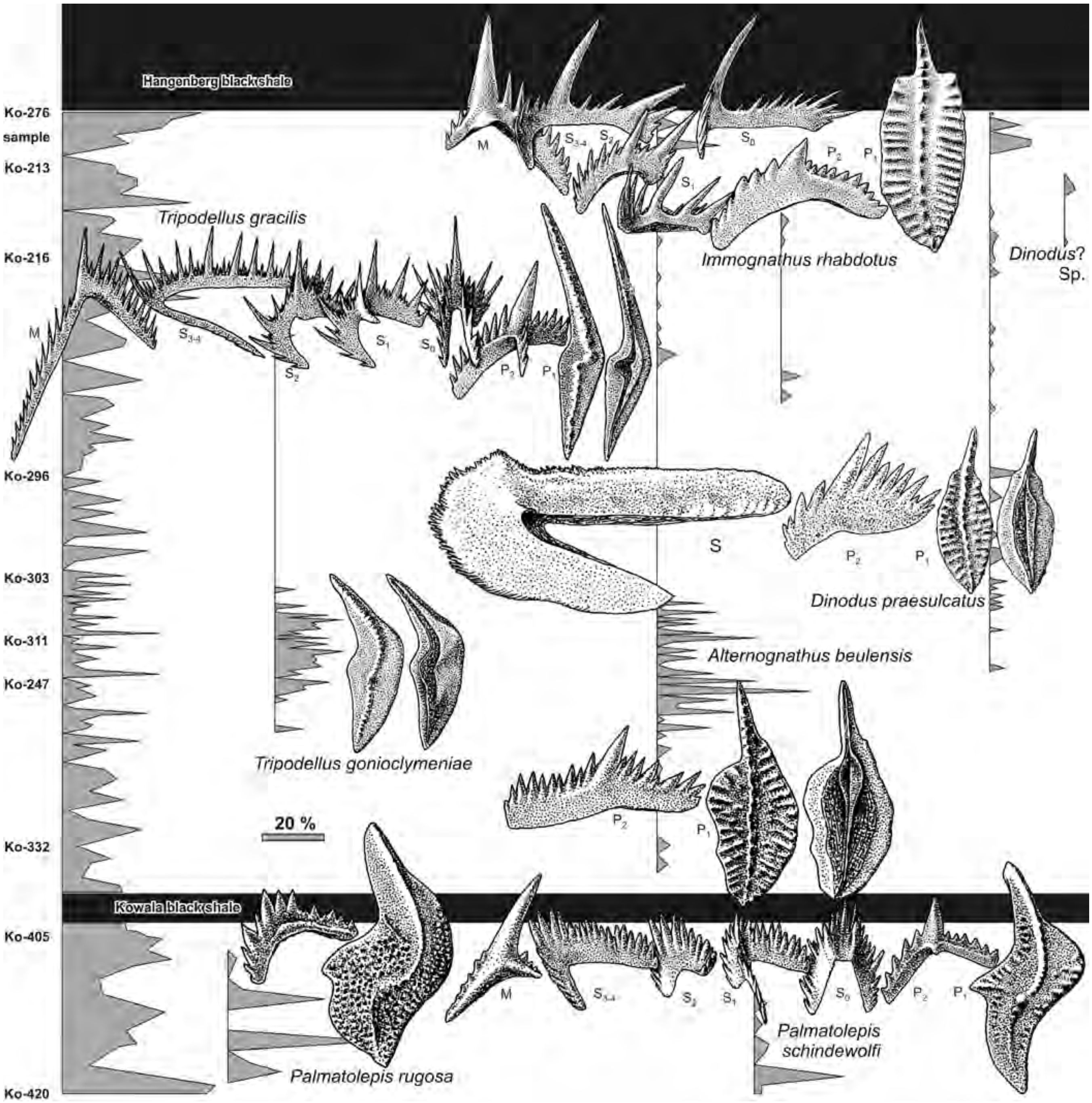
Czarnocki (1989, p. 30) reported a mass occurrence (34 specimens) of *Epiwocklumeria applanata* in the grey nodular limestone unit at the Kowala section. The exact position of this layer (as well as the source layer of specimens illustrated by



TEXT-FIGURE 11
Frequency contribution to samples of polygnathid conodonts elements in the topmost Famennian of the Kowala Nowiny II Quarry in the Holy Cross Mountains, Poland.

Halamski 2003) cannot be determined on the basis of simplified presentation of the trench section published in his monograph (Czarnocki 1989, fig. 21). No apertural modifications have been reported so it remains unknown if these are adults with constrictions developing until their maturity. The species differs from *E. bohdanowiczi* in ventrolateral furrows on its flat discoidal conch (text fig. 9). One enigmatic specimen, ZPAL AmVII/1892, from sample Ko-282, that is within stratigraphic range of *E. bohdanowiczi* (text fig. 5C), differs from its juveniles (and *Epiwocklumeria applanata*) in a more globose appearance and may represent a new species of the genus. Its suture (text fig. 8D) shows a rounded ventral sinus, which corresponds to the conch globosity.

The general picture of species succession in the Kowala section (text-figs 2 and 9) is far from being conclusive in respect to the basic question: how much evolution and what contribution from migrations? In fact, no one ammonoid lineage represented there has its fossil record complete enough to show evolution at place.This does not necessarily mean that only shifts in geo-

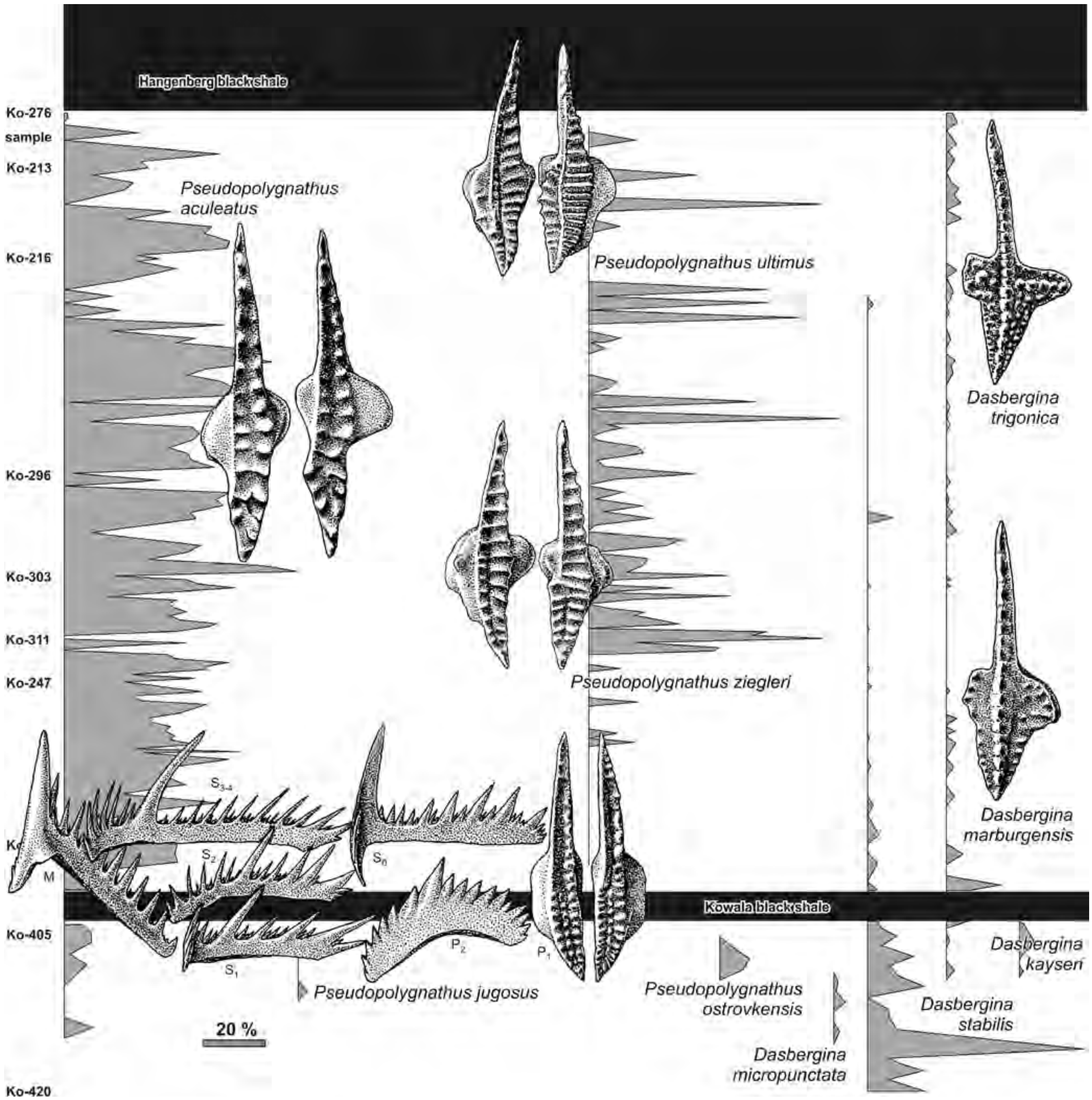


TEXT-FIGURE 12
Frequency contribution to samples of palmatolepidid and elictognathid conodonts elements in the topmost Famennian of the Kowala Nowiny II Quarry in the Holy Cross Mountains, Poland.

graphic distribution of population controlled its vertical range in the section. Admittedly, much more work with bed-by-bed collecting is necessary to achieve a reliable picture of the latest Devonian ammonoid faunal dynamics. At the moment, we are closer to this target with data on microfossils, that is on conodonts.

FAUNAL DYNAMICS OF CONODONTS

The quantitative apparatus approach to conodonts reveals aspects of faunal dynamics near the end of Devonian not accessible in other ways. De Vleeschouwer et al. (2013) estimated time of deposition of the part of the Kowala section sampled by us on the basis of inferred climatic cyclicity at 1.2 million years, somewhat less than the 2 milion year estimate of Kaufmann



TEXT-FIGURE 13
Frequency contribution to samples of idiognathodontid conodonts elements in the topmost Famennian of the Kowala Nowiny II Quarry in the Holy Cross Mountains, Poland.

(2006) and much less than 3.9 million years in Gradstein et al. (2020, p. 750). This time segment is bracketed by radical changes in the environment of sedimentation that apparently influenced the conodont faunal dynamics. The first event is recorded by the Kowala black shale (Marynowski and Filipiak 2007).

Rather unexpectedly, the Kowala black shale sedimentation event near the base of the studied section did not influence succession of conodont communities. The probable icriodontid *Jablonnodus*, the prioniodinid *Idioprioniodus*, the gondolellid *Branmehla* (text-fig. 10), the polygnathids *Pandorinellina*, *Mehlina*, and *Neopolygnathus* (text-fig. 11), the palmatolepidid *Tripodellus*, as well as the idiognathodontids *Pseudopolygnathus* and *Dasbergina* (text-fig. 12), all continue to occur above the black shale bed. Their contribution to conodont assemblages immediately below and above the bed is more or less the same.

This does not mean that changes in environmental conditions of the late Famennian are not reflected by the conodont faunal dynamics. The change is evident about one meter below the black shale, expressed by a gradual reduction of diversity of the platform-bearing polygnathids, including *Polygnathus experplexus,* virtually homeomorphic with advanced Tournaisian *Dinodus* species like *D. cooperi* (text fig. 11), palmatolepidids with ornate platform (text fig. 12), but also in idiognathodontids with an extremely robust icrion (*Pseudopolygnathus ostrovkensis*; text fig. 13). The immediate result is a significant reduction in species diversity. It took some time, corresponding to about two meters of the section above the Kowala black shale, to restore most of the lost diversity. Conodonts with robust platform of P_1 elements are subordinate, represented by elictognathids (text fig. 12) or idiognathodontids (*Dasbergina*; text fig. 13) but contributions to the fossil assemblage (that is biological productivity) of those with a deep basal cavity and icrion increased (admittedly, with some taphonomic bias).

Species of *Pseudopolygnathus*, *Tripodellus* or *Branmehla* dominate in almost every sample within the main part of the studied section, representing the latest *P. jugosus* and *D. trigonica* Zones. The boundary between occurrences of *Dasbergina marburgensis* and its successor *D. trigonica* extends for a significant time span, being of phyletic, not ecological nature (text-fig. 13). Species of *Pseudopolygnathus* were more ecologically sensitive than those of *Dasbergina*, co-occuring or replacing one another in the succession. The most stable is the occurrence of *Tripodellus gracilis*, although in the middle of its occurrence its contribution to particular samples may differ dramatically. This was coeval with the *Alternognathus beulensis* acme (text-fig. 12). Such lack of stability in biological productivity is the general aspect of the conodont faunal dynamics in the late Famennian at Kowala.

Included with the palmatolepidid *Tripodellus gracilis,* the early gondolellid *Branmehla inornata* and the idiognathodontid *Pseudopolygnathus aculeatus* are species that dominate throughout almost the whole section, although they disappear many times from the record for a while (text-figs 10, 12, and 13). Such sporadic appearances and disappearances mark the distribution of species with a low contribution to the biological

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TEXT-FIGURE 14

Latest Famennian conodonts from the Cát Bà Island locality in northern Vietnam.

A, B *Mitrellataxis coronella* Chauff and Price 1980, specimens ZPAL C25/125 and 126 from sample CB 115a.

C P_1 element of *Pelekysgnathus planus* Sanneman 1955, specimen ZPAL C25/127, same sample.

D–F *Mitrellataxis asymmetrica* Dzik 2006, specimens ZPAL C25/122–124, same sample.

G–J *Apatognathus varians* Branson and Mehl 1934, specimens ZPAL C25/146–147, elements P from samples SB 110, S from sample 115a, and two M from sample CB 110, respectively.

K–O *Idioprioniodus ruptus* Dzik 2006, specimens ZPAL C25/128–132, elements P_2 and S_0, from sample CB 115/2, S_2 from sample CB 110, $S_{3\text{-}4}$ and M from sample CB 115/2, respectively.

P–U *Lagovidina*? sp., specimens ZPAL C25/133–138, elements P_1, P_2, and S_0 from sample CB 115/2, S_1 from sample CB 115a, S_2, $S_{3\text{-}4}$, and M from sample CB 115/2, respectively.

V–AB *Branmehla inornata* (Branson and Mehl 1934), specimens ZPAL C25/139–145, elements P_1 from sample CB 115a, P_2 from sample CB 115/2, S_0, S_1, S_2, $S_{3\text{-}4}$ from sample CB 110, and M from sample CB 115/2, respectively.

AC–AJ *Dasbergina stabilis* (Branson and Mehl 1934), specimens ZPAL C25/172, 150–156, two elements P_1 and one P_2 from sample CB 115/2, S_0 from sample CB 115a, S_1 from sample CB 110, S_2 from sample CB 115/2, and $S_{3\text{-}4}$ and M from sample CB 110, respectively.

AK–AR *Mehlina strigosa* (Branson and Mehl 1934), specimens ZPAL C25/157–164, elements P_1 from sample CB 110, P_2 and S_0 from sample CB 115a, S_1 and S_2 from sample CB 115/2, and $S_{3\text{-}4}$ and M from sample CB 115a, respectively.

AS–AT *Neopolygnathus communis* (Branson and Mehl 1934), specimens ZPAL C25/177–178, elements P_1 from sample CB 115a.

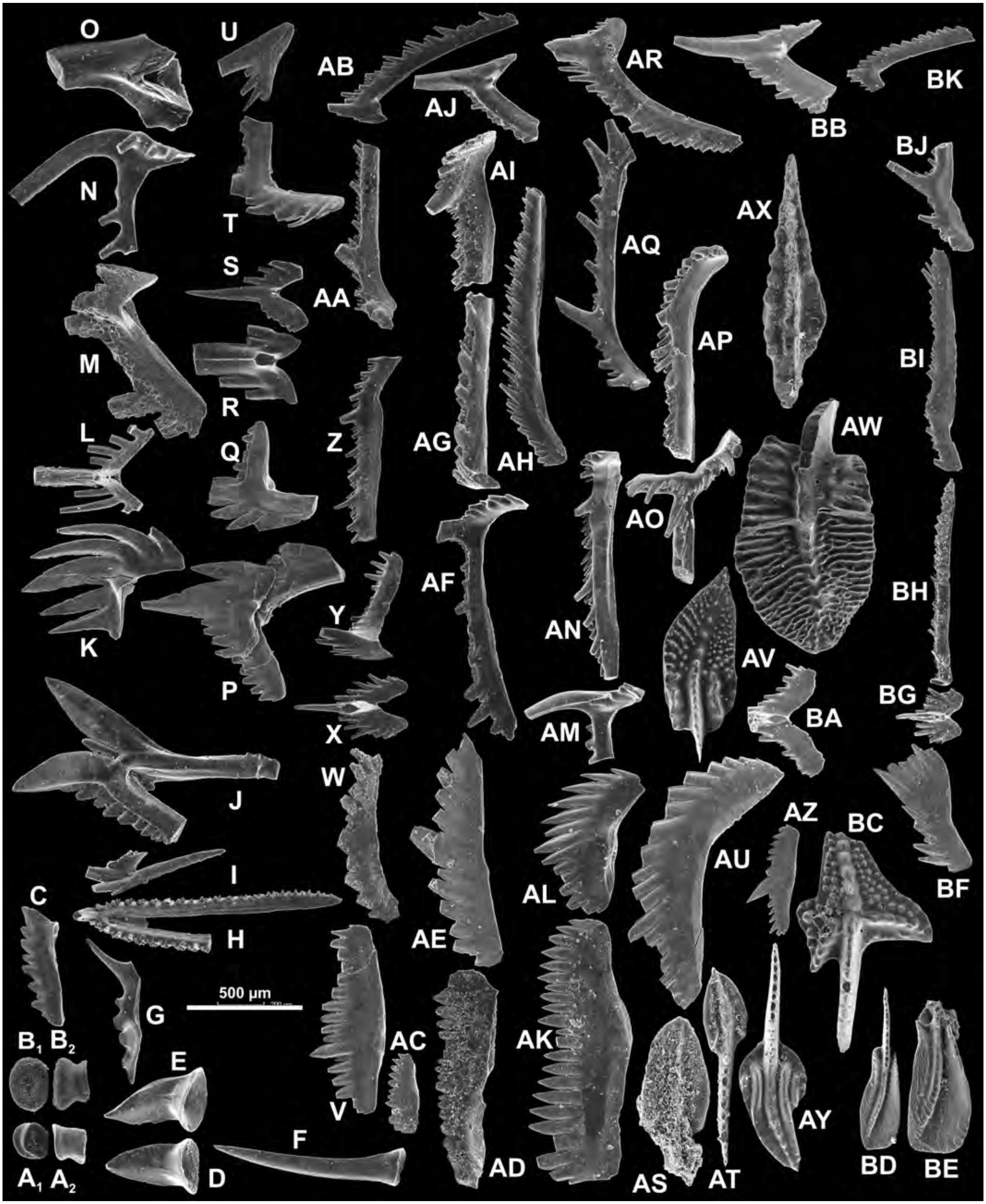
AU–AW *Planipolygnathus*? *bicristatus* (Mossoni et al. 2015)., specimens ZPAL C25/171, 170, and 169, element P_2 and two P_1 from sample CB 115/2, respectively.

AX *Pseudopolygnathus* sp., element P_1 from sample CB 115/2.

AY–BB *Polynodosus diversus* (Helms 1959, specimens ZPAL C25/173, 174, 176, and 175, elements P_1, P_2, S_0, and M from sample CB 115/2, respectively.

BC *Dasbergina trigonica* (Ziegler 1962), specimen ZPAL C25/166 from sample CB 115/2.

BD–BK *Polygnathus znepolensis* Spassov, 1965, specimens ZPAL C25/179–186, element P_1 from sample CB 115a, and elements P_1, P_2, S_0, S_1, S_2, $S_{3\text{-}4}$, and M from sample CB 115/2, respectively.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productivity of the conodont community; for example *Pandorinellina vulgaris*, *Neopolygnathus communis* and *Polygnathus pennatus* (text-figs 10 and 11). None of these species show any evolutionary change in the studied late Famennian strata. Apparently, this interval was not long enough to document evolution of slowly evolving lineages. This is exemplified by the evolution of the *Tripodellus* lineage throughout the whole Famennian of the Kowala and other sections in the Holy Cross Mountains (Dzik 2008). There are some tachytelic lineages in the late Famennian that show anagenetic evolutionary change probably within a few hundred thousand years. The most impressive is the lineage *Dasbergina marburgensis* → *D. trigonica*, in which the platform of P_1 elements changed from robust tuberculation to developing incipient processes, the posterior one (in anatomical terms) being bifurcated. This gradual change can be traced in the middle of the studied section between samples Ko-338 and Ko-333 (text-figs 2 and 13).

Another such evolutionary change is within the lineage *Pseudopolygnathus ziegleri* → *P. ultimus*, in which tranverse ridges of the icrion became more and more densely distributed. The change is recorded in the uppermost part of the section (text-fig. 13). This was already used for biostratigraphic age correlation (e.g., Spaletta et al. 2011; Corradini et al. 2017).

More problematic is the evolutionary transition between *Branmehla inornata* and *B. disparilis* (text-fig. 10). Processes in the P_1 elements, characteristic for the latter species, develop late in ontogeny and its identification depends on population dynamics; that is samples with mature specimens preserved.

The faunal transformations associated with sedimentation of the Hangenberg black shale resemble the conodont faunal succession at the Kowala black shale. Polygnathids and probable elictognathids with robust apperance of P_1 elements (text-figs 10 and 12) and species of *Pseudopolygnathus* (text-fig. 13) gradually disappear well below the black shale. Instead, *Tripodellus gracilis* increases in abundance (text-fig. 13). Species of *Branmehla* (text-fig. 10), *Dinodus praesulcatus*, and *Dasbergina trigonica* apparently continue to occur near the black shale without any change, although in low abundances (text-figs 11, 13).

Conodonts are rare in strata immediately above the Hangenberg black shale (samples Ko-71–73 in Dzik 1997, table 3) but the composition of their assemblage does not seem to be different from that below the black shale. The mass occurrence of *Acutimitoceras* in the tuffite (Dzik 2006) shows that a tremendous reduction in diversity of ammonoids took place during sedimentation of the Hangenberg Sandstone. The conodont-yielding horizon next in succesion is the laminated marly limestone (probable equivalent of the Stockum Limestone). The fossil assemblage (sample Ko-51) is impoverished and dominated by *Protognathodus* with thin-walled basal cavity of P_1 elements, but juveniles of *Tripodellus* and *Branmehla* continue to occur. Immediately above (sample Ko-24), these two typically Famennian species are replaced with *Pseudopolygnathus* and supplemented with *Dinodus* (‘*Siphonodella’*) above (Dzik 1997, table 3). *Protognathodus* re-appears about 19 m above the Hangenberg black shale (sample Ko-31; Dzik 1997, table 3).

Quantitative data (Kaiser 2007; also Kaiser et al. 2016) on frequencies of conodonts across the Famennian-Tournaisian boundary in the continuous (but highly condensed and not necessarily complete) limestone succesion at Grüne Schneid in the Carnic Alps shows gradual replacement of faunas. This seems consistent with observations at Kowala.

FAMENNIAN ROOTS OF CARBONIFEROUS CONODONTS

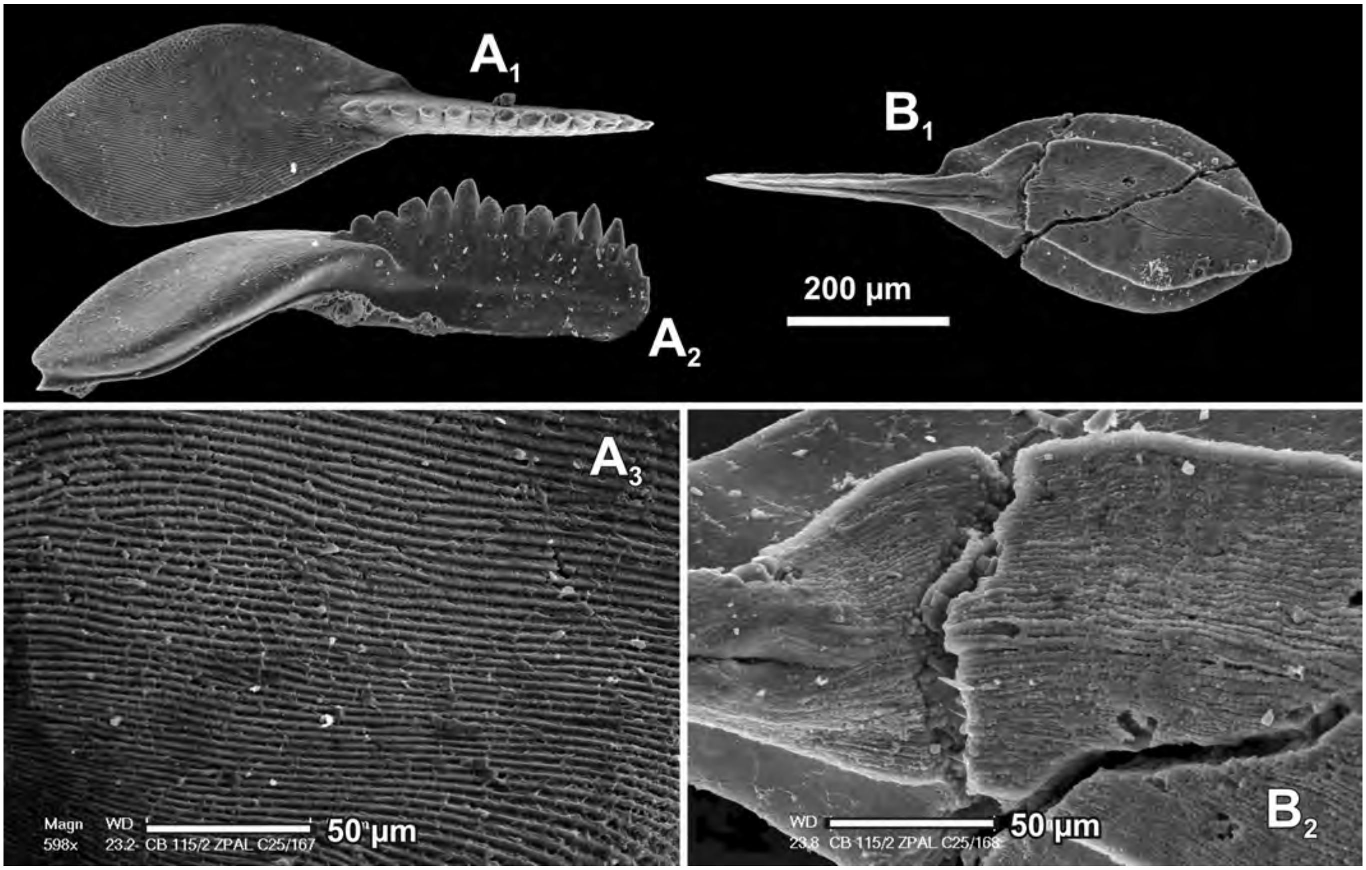
The newly obtained material from the topmost Famennian provide some evidence on the long term evolution of conodonts from the Devonian to Carboniferous. The most important seems to be identification of Devonian ancestors (or at least their close relatives) of typically Carboniferous lineages. They can be found among almost every family rank group, ranging from icriodontids to elictognathids.

The icriodontids were ecologically very sensitive shallow-water conodonts and already relic in the Famennian. Two icriodontid lineages crossed the Devonian-Carboniferous boundary: *Mitrellataxis* (e.g., Baranov et al. 2018) and *Dollymae* (e.g., Hass 1959; Groessens 1971; Tian and Coen 2005). Their occurrences in the Famennian were stratigraphically and geographically isolated. They mostly contributed to assemblages of conodonts with simple-cone units, representing denticles from non-mineralized processes of ramiform S elements of their apparatuses (Dzik 1991, p. 292). In some species P elements were probably lost, whereas simple-cone units were enlarged, as exemplified by *Jablonnodus* and *Mitrellataxis* (Dzik 2006; Zhuravlev and Garasimova 2017; Zhuravlev and Sokiran 2020). The Famennian *Mitrellataxis*, with its bizarre morphology is very similar to its Carboniferous successor (Chauff and Price 1980; Dzik 2006). A more elaborate morphology of P_1 elements in the apparatus characterizes the Tournaisian *Dollymae*, which probably developed in the Famennian, with *D. peregrina* from sample Ko-229 being its ancestor (text-fig. 10; Świś 2021).

The blade-like P_1 elements of *Branmehla* are dominant components in the Kowala conodont fossil assemblages. Its apparatus structure, with characteristic ‘enantiognathid’ S_1 element and a tendency to reduce the (anatomically) dorsal process in P_1 elements, indicates its transitional phylogenetic position between prioniodinids (like *Pluckidina*) and the late Carboniferous gondolellids (Dzik 2006). Occurring throughout the section is *B. inornata*, which originated probably from the mid-Famennian *B. bohlenana*, although the exact transition has not been traced and these lineages are allopatric for most of their ranges (Dzik 2006). In fact, all species of *Branmehla* appeared in Europe by immigration from unknown sources and they gradually disappeared before the *Gattendorfia* Limestone sedimentation (Dzik 1997). High contributions of *Branmehla* to samples also characterize the Woodford Shale of Oklahoma (Over 1992) and probably Amazonia (Cardoso et al. 2015).

Several species of *Neopolygnathus* and *Pseudopolygnathus* crossed the Devonian-Carboniferous boundary connecting the *Wocklumeria* Limestone with *Gattendorfia* Limestone without significant transformations of their morphology.

The biostratigraphically most important Tournaisian conodont lineage with Famennian roots is probably *Dinodus* (‘*Siphonodella’*). The oldest member of this lineage is *D. praesulcatus* (Paproth and Streel 1984; Paproth et al. 1991; Ziegler and Sandberg 1990) that in the Kowala section appears in sample Ko-116 (of Dzik 2006, see text-fig. 2), being very rare throughout the studied section. Its ancestry remains unknown and is complicated by the lack in the Devonian fossil record of any ap-



TEXT-FIGURE 15
Morphology of element P_1 of *Rhodalepis inornata* Druce 1969, specimens ZPAL C25/167 and 168 from sample CB 115/2, the Cát Bà Island locality in northern Vietnam.

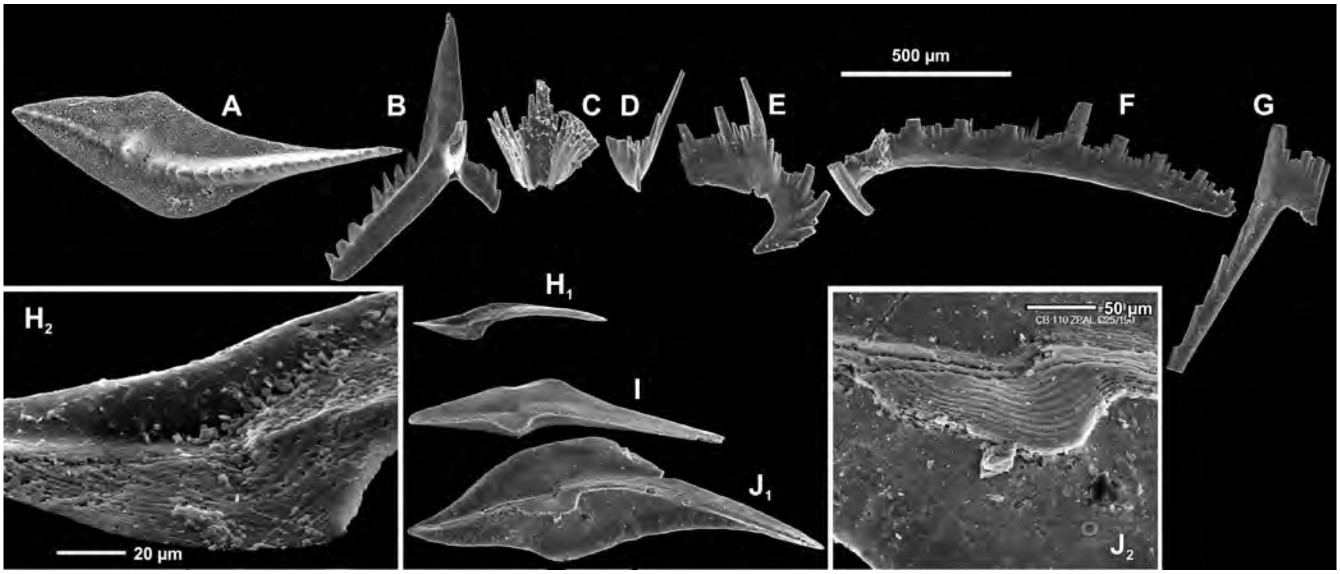
paratus elements that could be homologized with those of its probable Tournaisian relatives. The rather unusual platform-bearing 'elictognathid' P_2 element and bizarre S series and M elements make members of this lineage completely isolated from coeval conodonts. The documentation of similar S or M elements associated with P_1 elements of *D. praesulcatus* in the topmost limestone sample Ko-276 at Kowala (Swis and Dzik 2020) seems to root the apparatus structure in the Devonian, but too few specimens are available to be sure of such an interpretation. The origin of *D. praesulcatus* remains a mystery. Species of *Alternognathus* were proposed as probable closest relatives and ancestors based on similar P_1 elements (Ziegler and Sandberg 1984; Pazukhin 2008) but their apparatuses are completely different (Swis 2019). Another possible relative is *Immognathus rhabdotus* of probably *Ctenopolygnathus* affinity (Dzik 2006; Swis et al. 2020).

The review presented above shows that the latest Famennian conodont succession at Kowala was mostly controlled by immigration and disappearance of conodont lineages. Only a few of them lasted for long enough time and changed their morphology fast enough to record their evolution. These were *Pseudopolygnathus ziegleri* → *P. ultimus*, *Dasbergina marburgensis* → *D. trigonica* and, less likely, *Branmehla inornata* → *B. disparilis*. Evolutionary roots of other species occurring in Kowala, excluding those continuously recorded in older strata at the site, have to be looked for elsewhere in the world. This requires apparatus study. We attempted to do this with the Vietnamese material from the Cát Bà Island locality.

CÁT BÀ CONODONTS

The species composition of the Cát Bà Island conodont asemblage is identical with that from the Kowala with the exception of just two species, *Tripodellus expansus* and *Rhodalepis inornata*, but this makes a major difference. The first species dominates the assemblage, with almost half of all elements belonging to it. The second in number is *Mehlina strigosa*, with less than 10% ten percent contribution. In these aspects the Vietnamese fossil assemblage is unlike those from Poland.

As expected, the Cát Bà conodont community was very similar to open-sea communities from other parts of the world and identification of most species was rather easy. Difficulties, if met, were of a standard kind for conodont apparatuses research. Thus, attribution of extremely simplified icriodontid non-P_1 elements was a difficult task. We provisionally classify elements too large to fit associated P_1 elements of *Pelekysgnathus planus* as representing *Mitrellataxis asymmetrica* (text-fig. 14A–F) although the sample size is too small to delimit particular species. *Apatognathus varians* shows a characteristic enlarged denticle in the M element (text-fig. 14J). Less certain is taxonomic determination of the prioniodinids. The relatively underived elements may represent a late population of *Idioprioniodus ruptus* (text-fig. 14K–O).



TEXT-FIGURE 16
Ontogeny of the conodont *Tripodellus expansus* (Sandberg and Ziegler, 1979) from the Cát Bà Island locality in northern Vietnam, specimens ZPAL C25/187–190 and 192–190, elements P_1 from sample CB 115a (A) and CB 110 (H–J); P_2, S_0, S_1, S_2, $S_{3\text{-}4}$, and M from sample CB 115/2, respectively.

Rather surprising is the presence of M elements (text-fig. 14U) of the morphology typical for *Lagovidina* species, elsewhere known only from the early Famennian (Dzik 2006). It cannot be excluded that some of the non-M elements represent actually a species of *Sweetodina*.

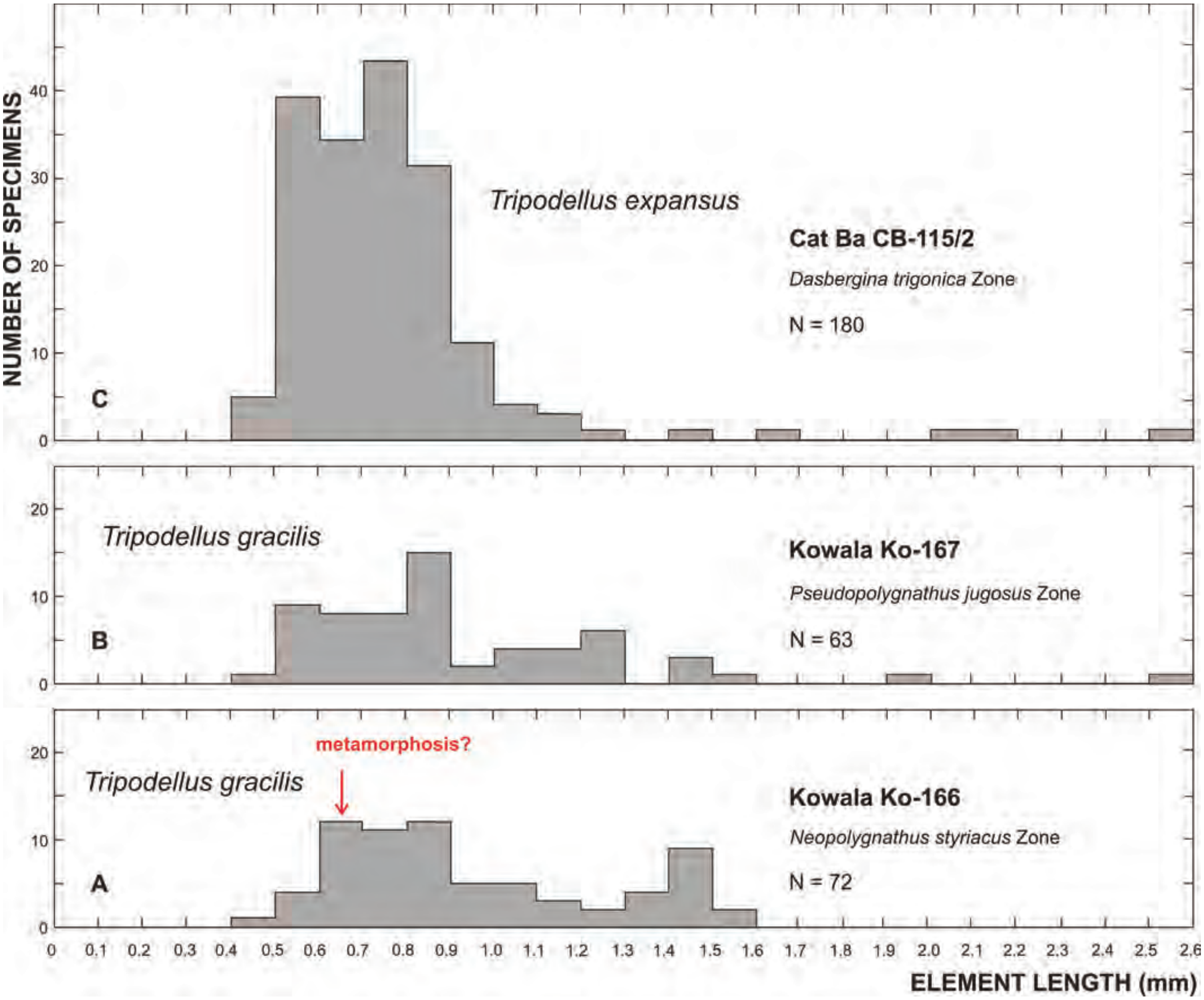
Despite its low contribution to samples, a complete set of element types of *Branmehla inornata* has been identified in the Cát Bà assemblage (text-fig. 14V–AB). The generalized appearance of S and M elements of *Dasbergina stabilis* makes their attribution to the species uncertain and arbitrary (text-fig. 14AC–AJ). Actually, this refers to most Famennian polygnathid and cavusgnathid species. Elements P_2 of *Mehlina strigosa* differ from those of other polygnathids in more or less developed undulation of dorsal (in anatomical terms) process and its S_1 elements are triramous (text-fig. 14AO). Other elements are not especially characteristic and their identification is rather subjective, based on similarity to specimens from more prolific samples from elsewhere. Specimens tentatively determined as *Planipolygnathus*? *bicristatus* (text-fig. 14AU–AW) may actually represent a species of *Polygnathus* but the sample size is too small to provide information on the ontogeny and range of variability. The most complete of a few P_1 elements of *Pseudopolygnathus* sp. (text-fig. 14AX) resembles more the Tournaisian *P. primus* than its Famennian congeners but the limited material does not enable species identification.

Dasbergina trigonica is the biostratigraphically most important conodont species in the assemblage, with well documented gradual origin from the preceding *D. marburgensis* (Dzik 2006). Its occurrence throughout the whole Devonian Cát Bà section (text-fig. 14BC; Komatsu 2014) shows that only a brief episode of the latest Famennian is there represented.

Most of the conodont species recovered from the Cát Bà samples are either cosmopolitan or undeterminable because of inadequate number of specimens preventing apparatus reconstruction and estimation of their population variability. Among those unknown from most of the world except for Australia, China, and Vietnam, with peculiar morphology of P_1 elements and still awaiting apparatus reconstruction, is *Rhodalepis inornata* (text-fig. 15). The fine fingerprint-like ornamentation of the platform of its P_1 elements does not have any analogue among other conodonts. According to R.S. Nicoll (in Jones 2004) the type specimens of *Rhodalepis inornata* bear the same delicate subconcentric ribbing on the platform as *R. polylophodontiformis* from the Rongxian Formation, Guangxi, of early to mid-*praesulcata* Zone age, although the ribbing is not visible in Druce (1969, pl. 38, figs 1b, 2b) photographs because of thick cover of ammonium chloride. This makes also *Polylophodonta* sp. A of Druce (1969) conspecific (Jones 2004) and means that the very fine riblets of juvenile specimens changed in ontogeny to mimic the platform of the early Famennian *Polylophodonta* that originated in evolution and developed in ontogeny in a quite different way.

THE *TRIPODELLUS EXPANSUS* PROBLEM

Among numerous conodont lineages represented in the Famennian of the Holy Cross Mountains, the one leading to *Tripodellus gracilis* shows the most complete fossil record. It exposes a monotonous evolution of all the elements of the apparatus (Dzik 2006) but the platform P_1 elements are the most useful for quantitative studies, being most robust and thus least effected by destructive taphonomy. As in many polygnathids, these elements had a conical basal cavity at the beginning of their ontogeny and then suddenly changed their geometry to inverted basal cavity and developed massive thickening (platform) on both sides of the element blade (carina). It was suggested by Dzik (2008) that the change corresponds to metamorphosis from the ‘sinuosa larva’ to juveniles. Regularly rhythmic, possibly daily growth increments visible within the basal cavity enabled calibration of the ontogeny and its evolutionary change presumably in days. In the latest Famennian *N. styriacus, P. jugosus*, and probably also *D. trigonica* zones in Poland, the stage in evolution of *Tripodellus* is characterized by



TEXT-FIGURE 17
Changes in population dynamics in the Late Famennian segment of the *Tripodellus* lineage; note probable timing of metamorphosis from the '*sinuosa* larva' demarcated by increase in mortality and its decrease in later ontogenetic stages (also in geological time). A. *T. gracilis* sample Ko-166 from the *Neopolygnathus styriacus* Zone at Kowala in the Holy Cross Mts, Poland. B. *T. gracilis* sample Ko-167 from the *Pseudopolygnathus jugosus* Zone. C. *T. expansa* sample CB 115/2 from the *Dasbergina trigonica* Zone in Cát Bà Island, Vietnam.

the mature P_1 elements with narrow platform and relatively large basal cavity of the '*sinuosa* larva'.

Much value was given to coeval lineage of *Tripodellus, T. expansus*, with the holotype from the Sappington Member of the Three Forks Formation of Montana, Late *styriacus* Zone (Sandberg and Ziegler 1979). Large, mature P_1 elements of *Tripodellus* from the Cát Bà locality fit the diagnostic aspects of this taxon (text-fig. 16A, J; Komatsu et al. 2014). This means that the lineage continued its occurrence almost to the end of the Famennian, which makes its use in biostratigraphy of limited value. Remarkably, the Vietnamese samples are dominated by juveniles representing the '*sinuosa* larva' and stages immediately following it (text-figs 16H, I and 17C). They are indistinguishable at this stage of ontogeny from corresponding stages in *T. gracilis*. Such a tremendous increase in mortality was apparently connected with a peak in life risk in the development, possibly the metamorphosis. Adult specimens are rare also in latest Famennian of Poland, which might be used to explain the lack of determinable *T. expansus* there. This is not likely, however, because adult specimens are well represented in strata coeval with the type population of the species, as well as in those significantly younger. Moreover, adults are there relatively more common in respect to the '*sinuosa* larvae' than in the latest Famennian Cát Bà samples (text-fig. 17A, B). This may mean that the latest Famennian environment was more oppressive to larvae. The question of evolutionary roots of *T. expansus* remains to be settled before its occurrence is used to define a biostratigraphic zone. Apparently it is missing in many regions and appears in others at different times (Hartenfels and Becker 2009).

The general trend in replacing conodont species with robust, platform-bearing P_1 elements (some polygnathids and palmatolepidids) by those with deep, conical basal cavity and thin basal cone wall can be used in support of limited availability of calcium in the environment. These aspects of the conodonts morphology were clearly connected with climate in the Ordovician; the Early Carboniferous expansion of idiognathodontids may have been controlled by climate cooling (Dzik 1997) in a similar way as with invertebrate calcareous shells (Watson et al. 2012).

CONCLUSIONS

The Kowala section probably offers the most complete record of faunal changes in the latest Famennian among those sampled bed-by-bed for ammonoids and conodont apparatuses. It appears that the faunal dynamics of both cephalopods and conodonts was controlled by environmental changes that resulted in immigration and disappearance of particular lineages. Only a few lineages persisted for long enough time and transformed their morphology fast enough to leave a record of their evolution in the studied sections. Most of the evolution apparently took place elsewhere. During deposition of the Kowala and Hangenberg black shale events these were remote refugia. Their locations remain to be identified. The predominance of long range migrations resulted in a false view of homogeneity of the Late Devonian faunas over the world. The Vietnamese locality Cát Bà shows for the southern margin of the South China Plate dramatically different conodont species contribution and presence of lineages unknown from Poland for a brief time of the *Dasbergina trigonica* Zone of the latest Famennian.

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DATA AVAILABILITY

Supplementary data including specimen counts at both localities can be found at:
https://www.micropress.org/microaccess/stratigraphy/issue-378/article-2270, an open-source online repository hosted by Micropaleontology Press.

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