Conodont ecology in the Early–Middle Frasnian transition on the South Polish carbonate shelf

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Well exposed Early–Middle Frasnian (E–MF, *Palmatolepis transitans* to *Palmatolepis punctata* zonal interval) deposits of the Holy Cross Mountains, in particular the reference Wietrznia section at Kielce, were studied in terms of conodont biofacies dynamics. Frequency of the conodont elements has been controlled mostly by depositional rate in hemipelagic muddy lithofacies and post-mortem gravity sorting during lateral redeposition in storm-generated, talus-like and encrinite layers. The conodont assemblages are dominated by a highly varying proportion of polygnathid, icriodontid, and ancyrodellid fauna. Major biofacies turnovers coincided with the deepening pulses corresponding to Timan, Middlesex, and early Rhinestreet global events. Trends in the conodont dynamics, mortality, and diversity point that the biotic shifts also coincide with the large-scale δ^{13}C excursions as a record of changing trophic conditions during the major biogeochemical perturbation. A gradual decline of the Early Frasnian *Ancyrodella* reef-dwelling community correlates with the minor positive and succeeding larger negative δ^{13}C excursion, and this is paired with a replacement by, mostly sparse, polygnathid and polygnathid-icriodontid biofacies, as well as with a short-term *Belodella* acme in mud-mounds areas. The distinctive habitat deterioration in pelagic and reef ecosystems is broadly correlative with the Domanik Crisis. The progressive biofacies unification is a conodont response to onset of the prolonged (ca. 0.5 Ma) ^{13}C enrichment, probably linked with high-stress life conditions due to eutrophication and partly anoxic regimes. A negative carbon isotope excursion in the late *Pamatolepis punctata* Zone is marked by the second major biofacies turning point during the Rhinestreet transgression, as recorded primarily in a final mesotaxid extinction, and highlighted also by decrease of conodont size and increased mortality of juveniles. After stabilization of δ^{13}C values and a return to the background level across the *Palmatolepis punctata–Palmatolepis hassi* zonal transition, renewed biofacies diversification, in particular re-appearance of reef-related ancyrodellid fauna, took place. In addition, a large-scale migration event among palmatolepids and polygnathids during sea-level rise, mainly from the East European Platform, characterised this Middle Frasnian interval.

Key words: Conodonts, biofacies, palaeoecology, Devonian, Early–Middle Frasnian boundary, Poland.

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Introduction

The Early–Middle Frasnian (E–MF) boundary beds, corresponding to the *Palmatolepis transitans–Palmatolepis punctata* zonal transition (as formally recommended by the IUGS Subcomission on Devonian Stratigraphy; Becker and House 1998; Ziegler and Sandberg 2001), are presented in literature as a time span of distinctive eustatic sea-level fluctuations, with the IIc transgressive-regressive (T-R) cycle of Johnson et al. (1985) starting at the base of the *Pa. punctata* Zone (see e.g., Becker and House 1997, 1998). In North America, the onset of cycle IIc is represented by the Middlesex Shale (Johnson et al. 1985; Over et al. 2003). The sea-level rise and a series of its ecosystem consequences observed globally were named the Middlesex Event (Becker 1993; House 2002). Additionally, recent stable isotope studies have revealed a major carbon cycle perturbation during the same time interval, prolonged to the end of *Pa. punctata* Zone (Racki et al. 2004; Yans et al. in press).

Conodonts were minute, primitive chordates of probable vertebrate affinities (Sweet and Donoghue 2001, but see also Turner et al. 2004) that populated diverse Palaeozoic and Triassic marine habitats, and owing to their sensitivity to physico-chemical parameters are excellent environmental indicators (see Sweet 1988). Well exposed E–MF carbonate rocks of the South Polish-Moravian epicontinental domain (Fig. 1A) were deposited in various, mostly reef-related, environmental settings suitable to a high-resolution conodont biofacies analysis (e.g., Szulczewski 1971; Racki 1993; Racki and Bultynck 1993; Makowska 2001).

Detailed investigation of conodont distribution, undertaken by the present authors in the *Palmatolepis transitans* to *Palmatolepis hassi* zonal interval as a complement to a conodont-based event-stratigraphical study presented in Pisarzowska et al. (2006) and a contribution to an international project "Ecosystem aspects of major carbon isotope anomaly in the Lower–Middle Frasnian transition" (grant 3 P04D 040 22 to G. Racki), supported by the Committee for Scientific Re-

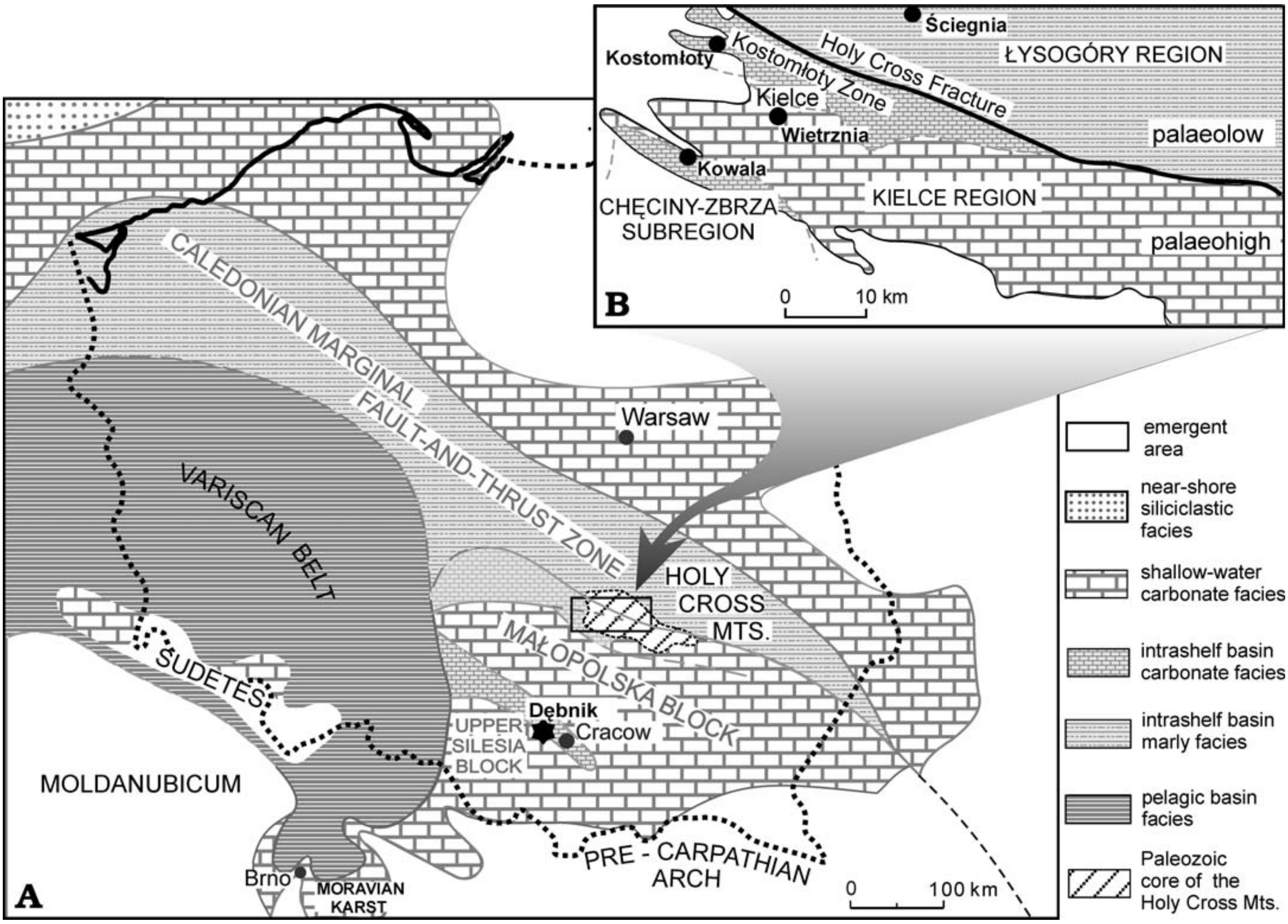

Fig. 1. **A**. Location of Holy Cross Mountains and Dębnik locality within the palaeogeographic and structural framework of the Devonian in Poland (after Racki 1993: fig. 1). **B**. Studied localities against palaeogeographic map of the Givetian to Frasnian of Holy Cross Mountains (based on Racki 1993: fig. 2).

search in Poland, allowed to test the range of environmental perturbation and biotic interactions in the pelagic realm. The main changes in these biotas took place exactly at the *Palmatolepis transitans–Pa. punctata* transition, which allows analysis of the conodont response to sea-level fluctuations and other controlling factors across the eventful E–MF passage in terms of taxonomic composition and relative abundance shifts. The Polish conodont record confirms in detail the general pattern of faunal dynamics and biofacies evolution documented elsewhere (Gouwy and Bultynck 2000; Becker et al. 2001; Zhuravlev et al. 2006), reflecting mostly the complex nature of sea-level changes in late *Pa. transitans* and late *Pa. punctata* zones.

Geological setting

The South Polish-Moravian shelf, up to 600 km in width, formed in the Devonian as a fragment of a pericratonic basin stretching from Western Europe to Ukraine along the periphery of the Laurussian continent. The southern part of this shelf, extending to the Moravian Karst and Sub-Carpathian area (Fig. 1A), is well studied due to numerous outcrops in the Holy Cross Mountains and Silesia-Cracow area, as well as intensive borehole works. Two distinct palaeogeographic-tectonic regions of the Holy Cross area (the Kielce palaeohigh and Łysogóry palaeolow; Fig. 1B) offer an opportunity to compare the event record across the Early–Middle Frasnian boundary in several sedimentary regimes (see Racki 1993; Pisarzowska et al. 2006). The structural framework, obviously related to post-Caledonian erosional relief, induced the central location of the Frasnian Dyminy Reef, surrounded by intrashelf basins: Chęciny-Zbrza to the south and Łysogóry-Kostomłoty to the north (see Szulczewski 1995 for summary). In more general terms, the Dyminy Reef developed over the northern margin zone of the extensive Kielce carbonate platform (Narkiewicz 1988; Racki 1993), that probably extended to the southwestern periphery of the stable Małopolska Block (Sobstel 2003). Late Devonian epicontinental strata indicate continuous but punctuated drowning of the more and more differentiated carbonate platform

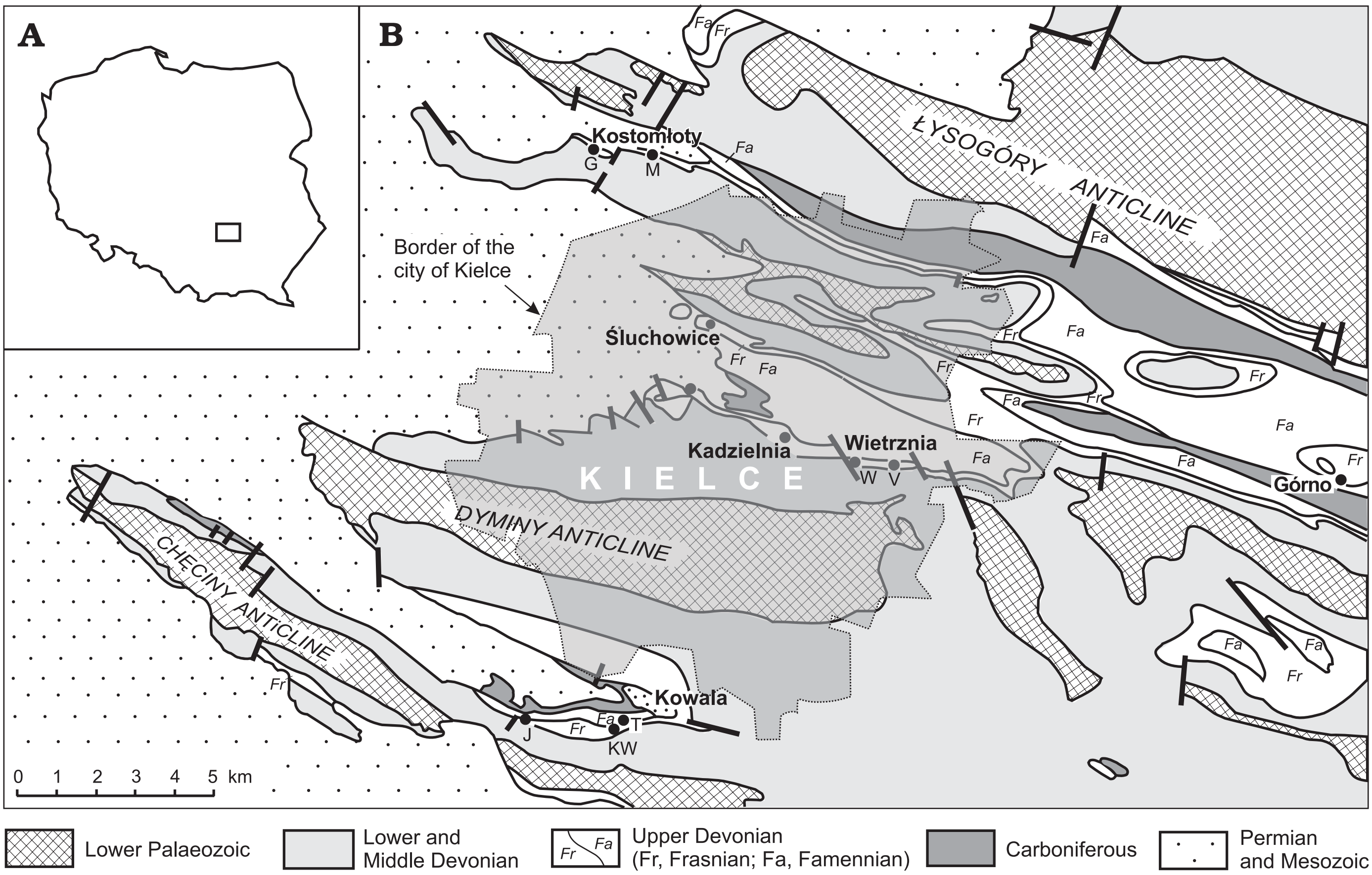

Fig. 2. Location map of studied Early to Middle Frasnian exposures in Poland (**A**) and Holy Cross Mountains (**B**; based on Szulczewski 1971: fig. 1). Abbreviations: KW, Kowala railroad cut; T, Kowala quarry; J, Jaźwica quarry; W, Wietrznia I quarry (see Fig. 6); V, Wietrznia II quarry; G, Kostomłoty-Małe Górki quarry; M, Kostomłoty-Mogiłki quarry.

(e.g., Szulczewski 1971, 1995; Narkiewicz 1988; Racki 1993). The southern closure of the shelf formed the poorly recognised Sub-Carpathian Arch (Narkiewicz 1988, 1996); the Frasnian deposits have been investigated in detail at Dębnik near Cracow (Baliński 1979, 1995; Narkiewicz and Racki 1984).

The E–MF interval has been more or less confidently dated with conodonts in the Holy Cross Mountains, and in other Polish epicontinental successions (e.g., Szulczewski 1971; Narkiewicz and Racki 1984; Racki and Bultynck 1993; Sobstel 2003). The high-resolution study of Pisarzowska et al. (2006) focused on the precise conodont-based recognition of the E–MF boundary against the background of five recognised distinctive ancyrodellid associations and their reliable correlation in bio- and chemo-stratigraphical terms in eight logged sections. Among the accessible outcrops (for details of locations see "Register of localities" in Racki 1993), grouped mostly in the western part of the Holy Cross Mountains (Fig. 2), only the most representative sections are analysed bed-by-bed, and their conodont biofacies are studied, with the corresponding carbon isotopic data taken from Pisarzowska et al. (2006). The continuous sedimentary successions include a record of global and regional geochemical and biotic events in different facies ranging from the intrashelf basin to near-reef (foreslope) setting; the section of Wietrznia was selected for the most comprehensive studies (Figs. 3–7). Significantly, as outlined by Szulczewski (1971: 94–96; see also Narkiewicz 1988 and Racki et al. 1993), the Wietrznia limestones are developed in the transitional facies, comprising both interfingering detrital (i.e., Dyminy Reef-derived) and micritic-marly (intrashelf basin) sediments of the evolving northern flank zone of the Kielce carbonate platform.

Methods

Biofacies analysis of the *Palmatolepis transitans–Pa. hassi* zonal interval was mainly based on conodont faunas from three Wietrznia sections: western (W) and eastern (E) Wietrznia Id, and easternmost Wietrznia Ie (Fig. 3). The samples were taken both from micritic and detrital lithofacies of sets C–D for comparative analysis (see Pisarzowska et al. 2006 for description). Additionally, conodonts extracted from other sections of the Holy Cross area, i.e., Kowala, Śluchowice, Kostomłoty-Mogiłki, and Cracow region, i.e., Dębnik, were used to follow through the equivalence. Weight of samples from all the sections was 0.7–1.5 kg. From a total number of

265 samples from all studied sections 181 were taken for biofacies analysis including 80 of them from Wietrznia section. Some samples, particularly from the E–MF boundary interval, yielded very few conodonts so the determined biofacies are approximate only (and marked with asterisk: see Tables 1–7 in Appendix 1; Figs. 5–11; compare Bultynck et al. 1998).

The samples were disintegrated by applying a 10% solution of acetic acid to recover the conodonts. The remaining residues were carefully washed in water and separated in lithium metatungstate. The heavy fraction was picked for conodonts. Among them, only the platform elements were included in the biofacies analysis. The biofacies were named after the most common taxa or two dominant genera that constitute 70% or more of the conodont fauna (see methodology in Sandberg et al. 1989 and Ziegler and Sandberg 1990); more diverse (“mixed”) generic composition is often seen as a record of post-mortem transportation and synsedimentary reworking. Ramiform to platform element ratio is considered as a crude proxy of the winnowing by sorting processes (conodont autochthony index; Racki 1993). Moreover, many examples of ecological preferencies at species level for conodonts have been observed (e.g., Racki and Bultynck 1993), and the ecological interpretation was thus strengthened by analysis of distribution of certain species. For example, *Icriodus* is thought to be euphotic, and among its species *Icriodus symmetricus* Branson and Mehl, 1934 lived in a lower portion of water column, frequently together with deep-water *Mesotaxis* (Sandberg and Dreesen 1984). Thus, it is regarded as the most deep-water species among icriodontids.

The Pa elements of *Belodella* were not determined, so the percentage of *Belodella* is reduced to one-fifth to be included in calculations. *Mehlina* does not occur frequently and, as a probable root stock for several narrow-platform species of *Polygnathus* (Sandberg et al. 1992), it was counted together with *Polygnathus* for biofacies assessment.

Biofacies analysis

Wietrznia (Figs. 3–7, Tables 1–3).—The Early Frasnian set C (= middle Wietrznia Beds) exhibits a distinct lateral variation within downslope fore-reef facies from west to east toward more distal variety, traced over distance of ca. 100 m in the studied outcrops (Figs. 3, 4; Pisarzowska et al. 2006). A few centimetres-thick layers of partly knobby and/or wavy-bedded bituminous micrites are intercalated with marly shale partings; autochtonous brachiopod nests are a common character (Racki et al. 1993), and locally rich in styliolinids as well. Thicker, up to 1 m, calcirudites with intra- and bioclast interbeds and erosional bottom surfaces, including flat-pebble conglomerates, are the second dominant lithology. Redepostited corals, stromatoporoids, brachiopods and especially crinoid detritus are abundant in the grained beds. A succession of alternating fossil-impoverished thin-bedded micrites and marly shales form the uppermost part of the set C just below the Early–Middle Frasnian boundary (see Figs. 5–7). The western part of the quarry (Wietrznia Id) was situated most closely to the reef structure so its thick-bedded lithofacies is characterised by the presence of large and unsorted mictitic lithoclasts and broken reef builders forming reef-breccia (Fig. 7). The total thickness of the set amounts to about 8–9.5 m.

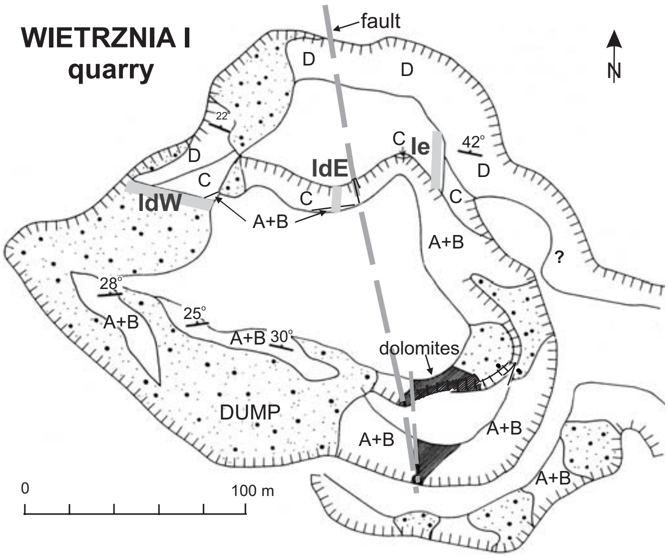

Fig. 3. Location sketch of Wietrznia quarry (sub)sections (Id, IdE, and IdW) at Kielce (see Figs. 2, 5–7; partly after Narkiewicz 1991). Lithologic sets (A–D) after Szulczewski (1971) and Racki and Bultynck (1993).

The Middle Frasnian set D (= upper Wietrznia Beds; Racki 1993) is very well exposed in WId-W and WIe sections. It is distinguished by the appearance of thick-bedded light-coloured calcirudites with redeposited reef-builders, but also with localised renalcid-*Stachyodes* buildups. Alternating thin-bedded poorly fossiliferous micrites and shales occur subordinately at WId-W. The set D splits eastward into D_1 and D_2 subsets at WIe section. The mostly thin-bedded subset D_1 (about 7 m thick) is transitional unit between sets C and D, as defined by Szulczewski (1971), whilst the thick layers of subset D_2 correspond well with set D of the WId-W section.

Micritic layers.—Conodont remains from dominantly micritic layers are of very low abundance, commonly the average number of elements per kilogram of sample is lower than 20. Many of these samples yielded only coniform or ramiform elements so they were not taken into account for biofacies analysis (not included in Tables 1–3). Also, the other phosphatic remains (ichthyoliths, lingulids) are typically scarce (Makowska 2001). However, some micritic samples are especially rich in conodonts, with frequency exceeding 100 elements per kilogram, as exemplified by samples WId-W9, WId-W49/1 and WId-W46.

Micritic lithofacies are characterised by prevalence of deep-water polygnathid-mesotaxid biofacies in the *Palmatolepis transitans* Zone, and by prevalence of polygnathid biofacies (up to 100% of *Polygnathus*) and rarely polygnathid-mesotaxid biofacies within the *Pa. punctata* Zone.

The exception is the thick marly interval of the topmost part of *Palmatolepis transitans* Zone, determined by the very low abundance assemblage of mixed, polygnathid-icriodontid (up to 54% of *Icriodus*) or polygnathid biofacies, paired with an unusually high occurrence of *Belodella* (12% or even 50% of the sample!). *Ancyrodella* usually does not constitute more than a few percent of the elements.

Detrital layers.—Coarse-grained layers of the set C are distinguished by a very high abundance of conodonts in all parts of the Wietrznia successions (up to 400 Pa elements per kilogram), only rarely dropping below 20 elements per sample (Tables 1–3, Figs. 5–7). The abundance and diversity is highest in the lower part of the *Pa. transitans* Zone and it decreases significantly in the uppermost part, just below the *Pa. punctata* Zone boundary. The *Pa. punctata* Zone starts with a relatively diverse and abundant fauna, with diversity slightly decreasing higher up in the succession (set D). Also, the abundance of ichthyoliths is high in older detrital layers, and it gradually decreases in upper parts of the section (Makowska 2001).

The conodont fauna is dominated by *Polygnathus* with the average abundance of about 40% in the *Pa. transitans* and ca. 70% in the *Pa. punctata* zones. The higher contribution of *Ancyrodella* (up to 60% in the middle part of the *Pa. transitans* Zone), as a substitute of the *Mesotaxis–Klapperina* association in comparison to micritic lithofacies, is noticeable in all Wietrznia sections. Thus, polygnathid-ancyrodellid biofacies predominate in the early and middle parts of the *Pa. transitans* Zone. The high icriodontid abundance indicates the polygnathid-icriodontid biofacies in the latest *Pa. transitans* Zone, and the changing contribution of *Ancyrodella*, *Belodella*, and *Mesotaxis* marks the appearance of a mixed biofacies. The conodont fauna from detrital layers of the *Pa. punctata* Zone is very homogenous in terms of biofacies assignment, identified as polygnathid and rarely polygnathid-mesotaxid biofacies. The early *Pa. hassi* Zone conodont biofacies of set D is more diversified, as it evolved from earlier polygnathid to polygnathid-ancyrodellid and palmatolepid-polygnathid assemblages.

Lateral and stratigraphical variation.—The conodont frequency in both micritic and detrital layers of Wietrznia sections in the broad E–MF passage decreases laterally from the western part of the quarry toward the easternmost Wietrznia Ie section (Fig. 3). The average abundance of Pa elements in western Wietrznia Id-W is over 100 per kilogram of sample, while in the eastern, more distal Wietrznia Ie succession it is about 50 Pa elements. However, the overall pattern of frequency and diversity changes throughout the interval under study is the same in all Wietrznia sections. It shows a highly variable diversity in the Early Frasnian, with an abundance peak in the early part, followed by a minimum frequency and diversity interval in the latest *Pa. transitans* Zone. The interval of relative stability is paired with the inception of the Middle Frasnian substage. A slightly decreasing abundance trend starts from late in the *Pa. punctata* Zone and it continues through the early *Pa. hassi* Zone.

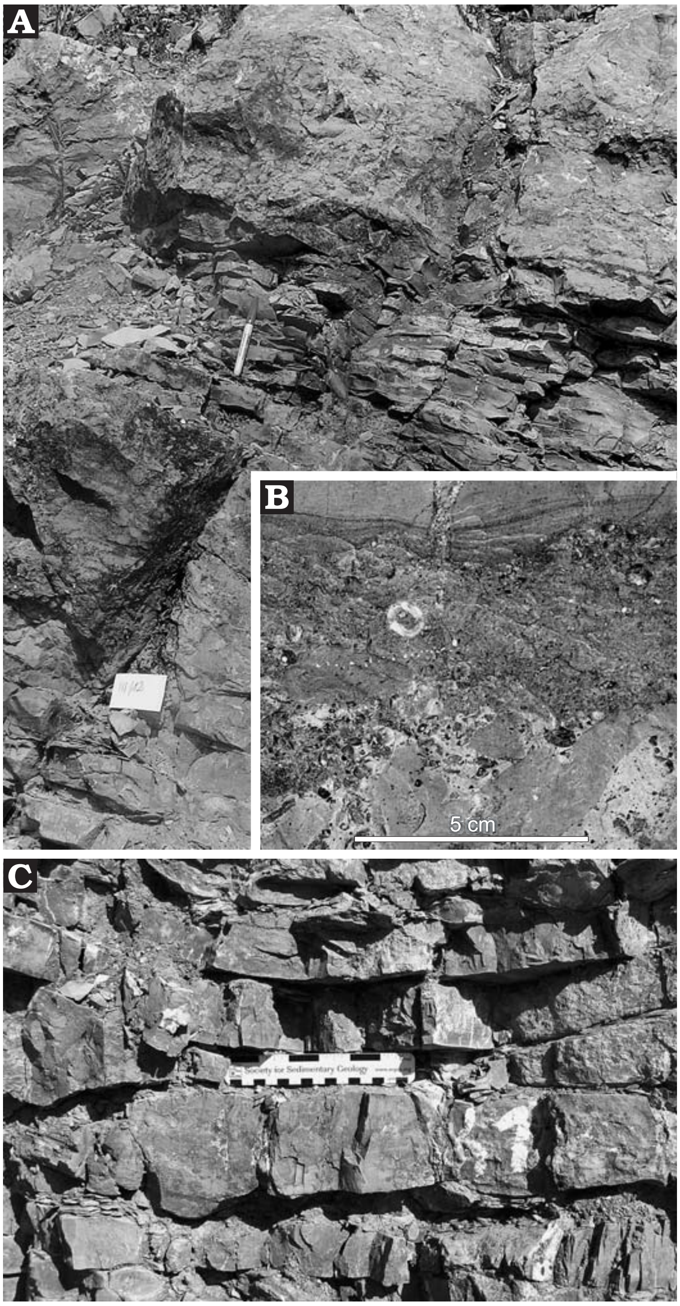

Fig. 4. Field photo of thick detrital layers and thin-bedded micritic lithofacies (**A**) and close-up of graded, partly bioclastic and conglomeratic layer (**B**; bed 70 at Wietrznia Id-E section, Fig. 6) and of micritic-shaly interval (**C**) of set C, middle Wietrznia Beds (Pisarzowska et al. 2006; Vierek in press), in the Wietrznia Id section (see Figs. 3, 6, 7); photos by A. Vierek.

The composition of conodont assemblages in all samples is dominated by *Polygnathus* with a changing a contribution of *Mesotaxis* and *Klapperina*, *Ancyrodella*, and *Icriodus*, so the biofacies are polygnathid and mixed with polygnathids. However, the difference in biofacies for mictitic and detrital layers are clearly expanded vertically in the sections, as well as laterally from the western to eastern part of Wietrznia quarry, but

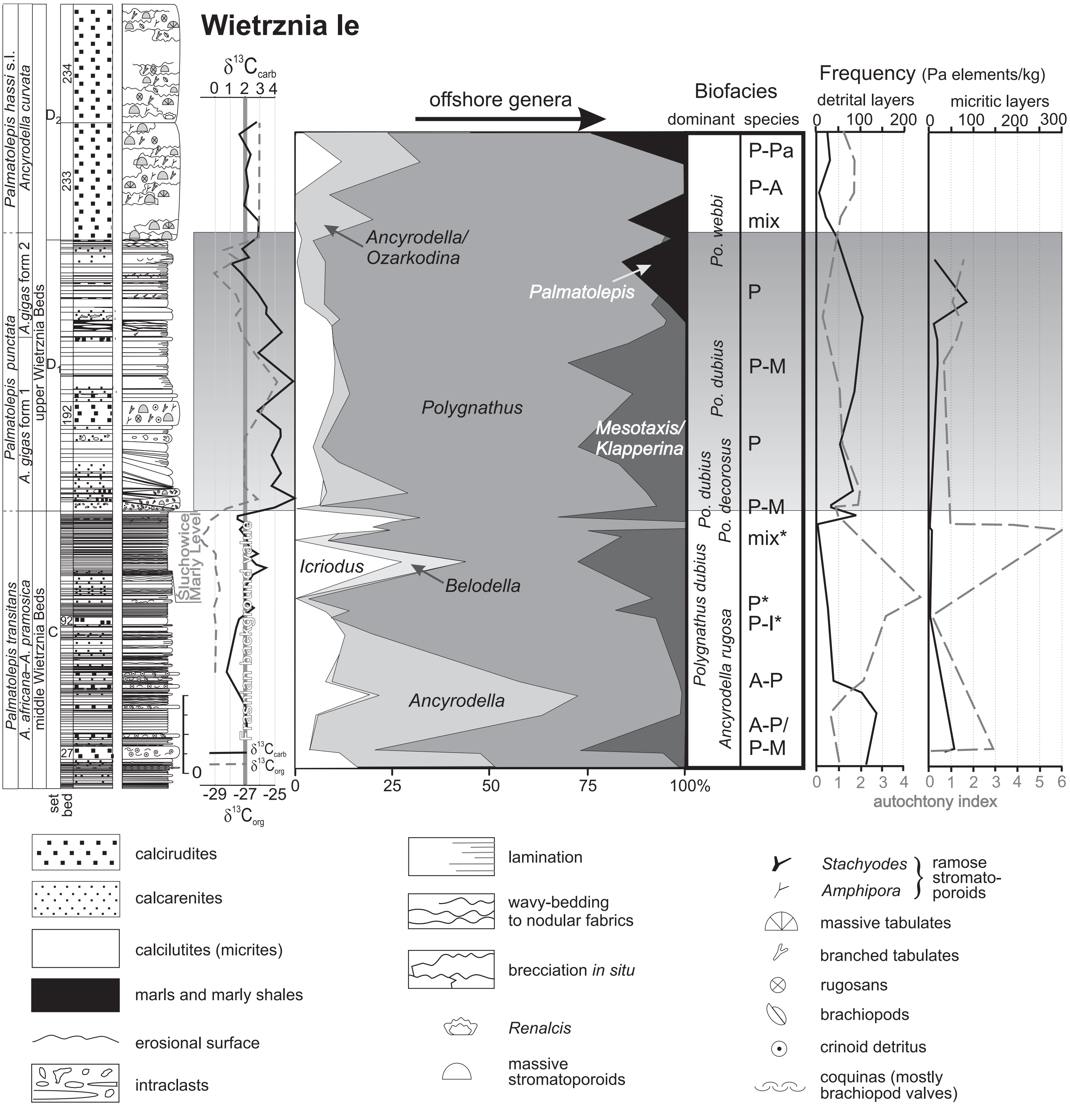

Fig. 5. Conodont biofacies distribution, dominating species, abundance trends and autochtony index (ramiform to platform element ratio; Racki 1993) against carbonate and organic carbon isotopic curves (the results in per mil deviation from the Vienna Peedee Belemnite standard, VPDB; see details in Pisarzowska et al. 2006) for Wietrznia Ie. Note diverse frequency and conodont element ratio within micritic and detrital layers. Biofacies abbreviations: A, ancyrodellid; P, polygnathid; I, icriodontid; M, mesotaxid; Pa, palmatolepid; mix, mixed; *, biofacies determined from low frequency samples (less than 20 Pa elements).

on a generic rather than species level. Micritic lithofacies are paired mostly with polygnathid and polygnathid-mesotaxid biofacies, while detrital deposits are characterised by polygnathid, polygnathid-ancyrodellid and polygnathid-icriodontid biofacies. Mixed biofacies are present in both lithofacies of the late *Palmatolepis transitans* Zone interval.

Laterally, the contribution of *Mesotaxis* increases toward the eastern part of Wietrznia quarry, while *Ancyrodella* and *Icriodus* are more numerous in western Wietrznia Id-W and middle Wietrznia Id-E sites in the *Pa. transitans* Zone. Distribution of biofacies in the *Pa. punctata* Zone interval is more consistent. Both Id-W and Ie successions are character-

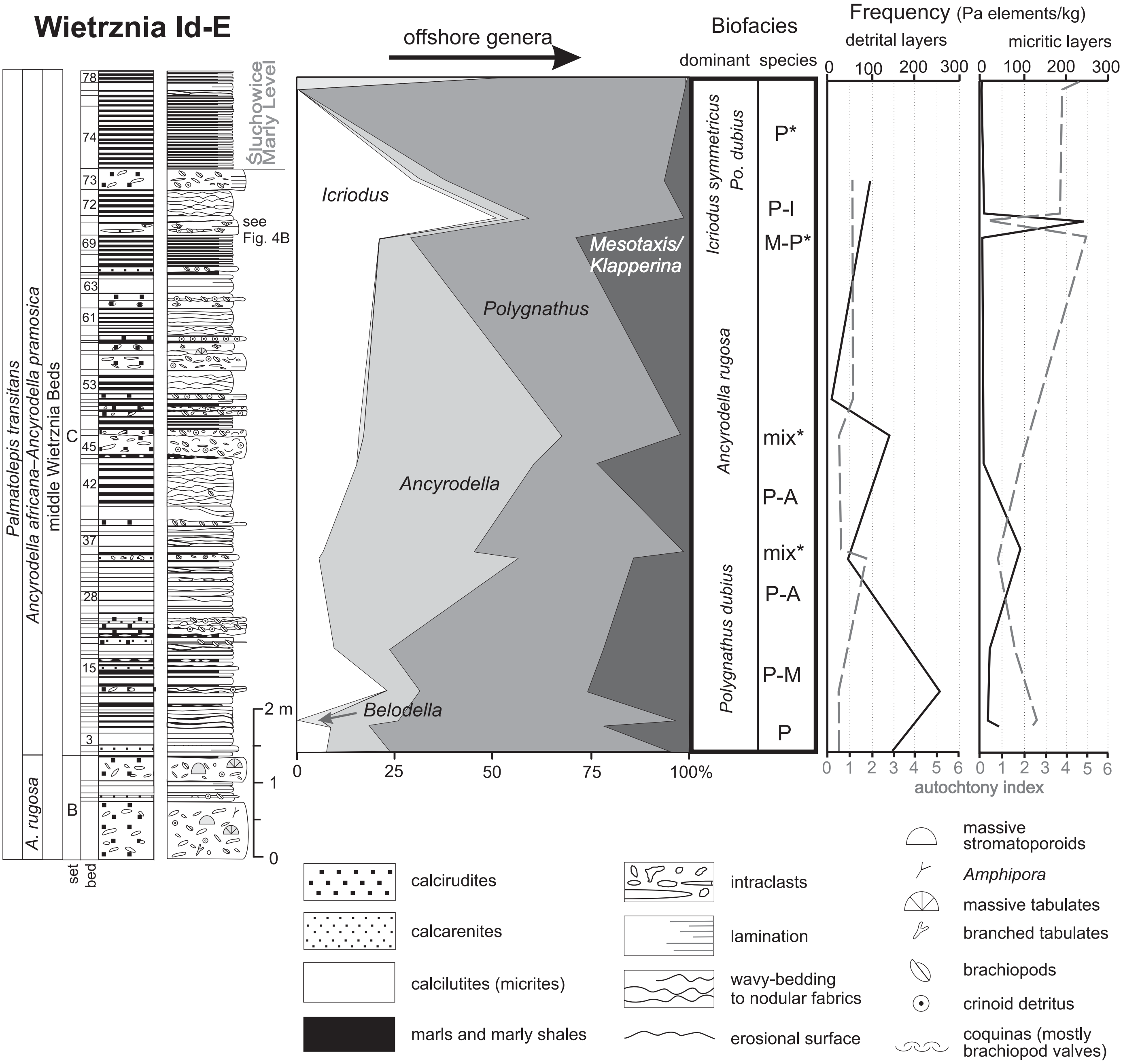

Fig. 6. Conodont biofacies distribution, dominating species, abundance trends and autochtony index for Wietrznia Id-E. Biofacies abbreviations: A, ancyrodellid; P, polygnathid; I, icriodontid; M, mesotaxid; mix, mixed; *, biofacies determined from low frequency samples (less than 20 Pa elements).

ised by polygnathid and rarely by polygnathid-mesotaxid biofacies.

Kowala (Table 4, Fig. 8).—The conodont succession from Kowala roadcut (and active quarry) in the *Palmatolepis punctata* Zone is represented largely by polygnathid biofacies, characterised by very low frequencies despite a variety of lithofacies. Only the lower and uppermost parts are characterised by mixed, polygnathid-icriodontid and palmatolepid-mesotaxid faunas, respectively. *Icriodus* is significantly absent until the late *Pa. punctata* Zone, when it totally replaces an *Ancyrodella* population. The peak of *Icriodus* abundance (25%) falls within the deep-water palmatolepid- polygnathid and mesotaxid-polygnathid biofacies. During the late part of *Pa. punctata* Zone, a shift in polygnathid assemblages took place: *Polygnathus dubius* disappears and *Po. webbi* Stauffer, 1938, *Po. alatus* Huddle, 1934, and *Po. pacificus* Savage and Funai, 1980 start to predominate, comprising the 45% of the population.

Śluchowice (Table 5, Fig. 9).—The Śluchowice section, including diverse lithologies, is exceptionally rich in cono-

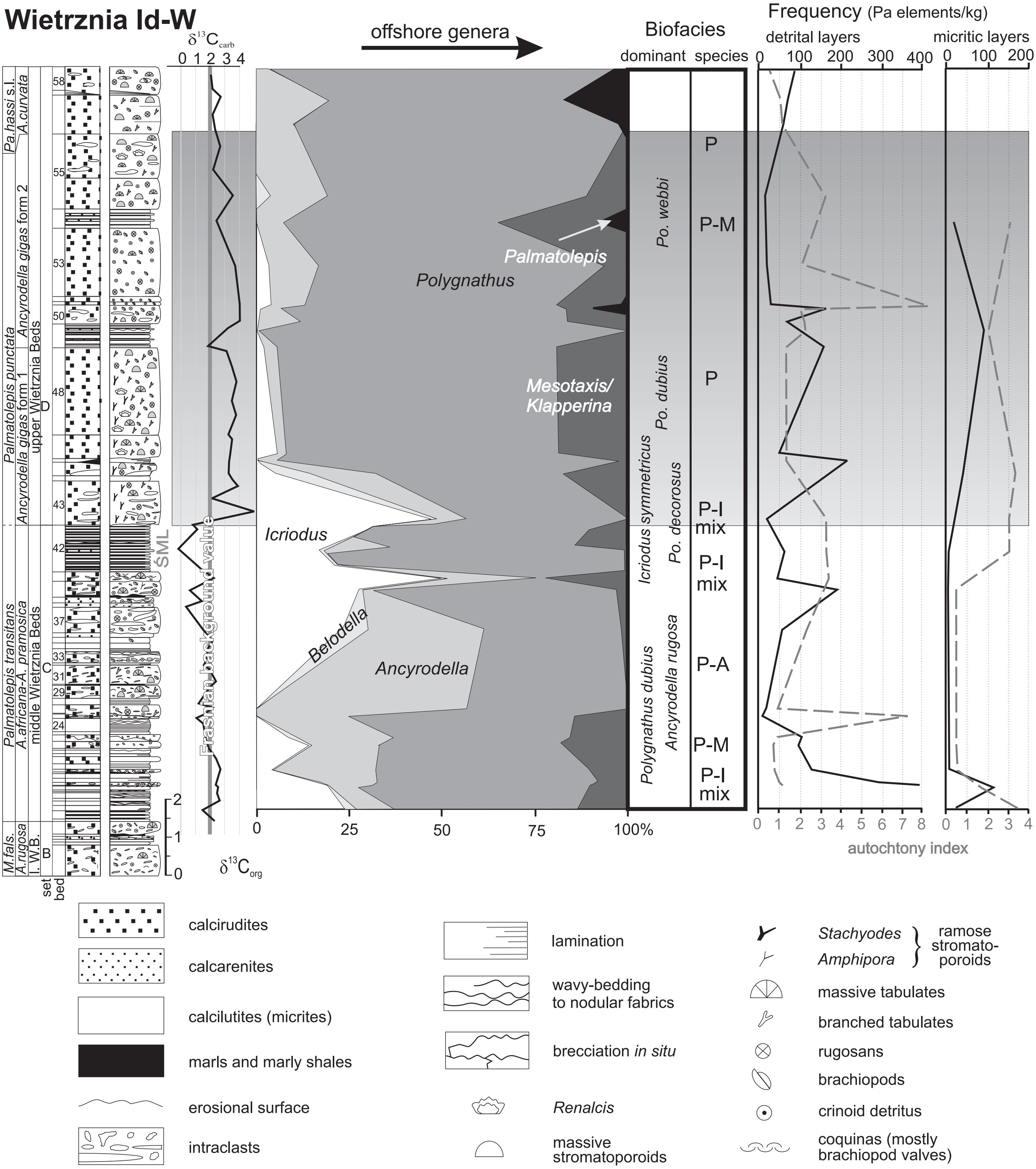

Fig. 7. Conodont biofacies distribution, dominating species, abundance trends and autochtony index against the carbonate isotopic curve for Wietrznia Id-W. Biofacies and other abbreviations: A, ancyrodellid; I, icriodontid; M, mesotaxid; *M. fals.*, *Mesotaxis falsiovalis*; mix, mixed; P, polygnathid; ŚML, Śluchowice Marly Level.

donts (see also Szulczewski 1971; Racki and Bultynck 1993) and all the samples appeared to be productive. Almost the entire conodont succession at Śluchowice is dominated by *Polygnathus.* The second main biofacies component in the E–MF boundary interval is *Icriodus symmetricus*. The peak of its abundance alternates with the distribution of frequent

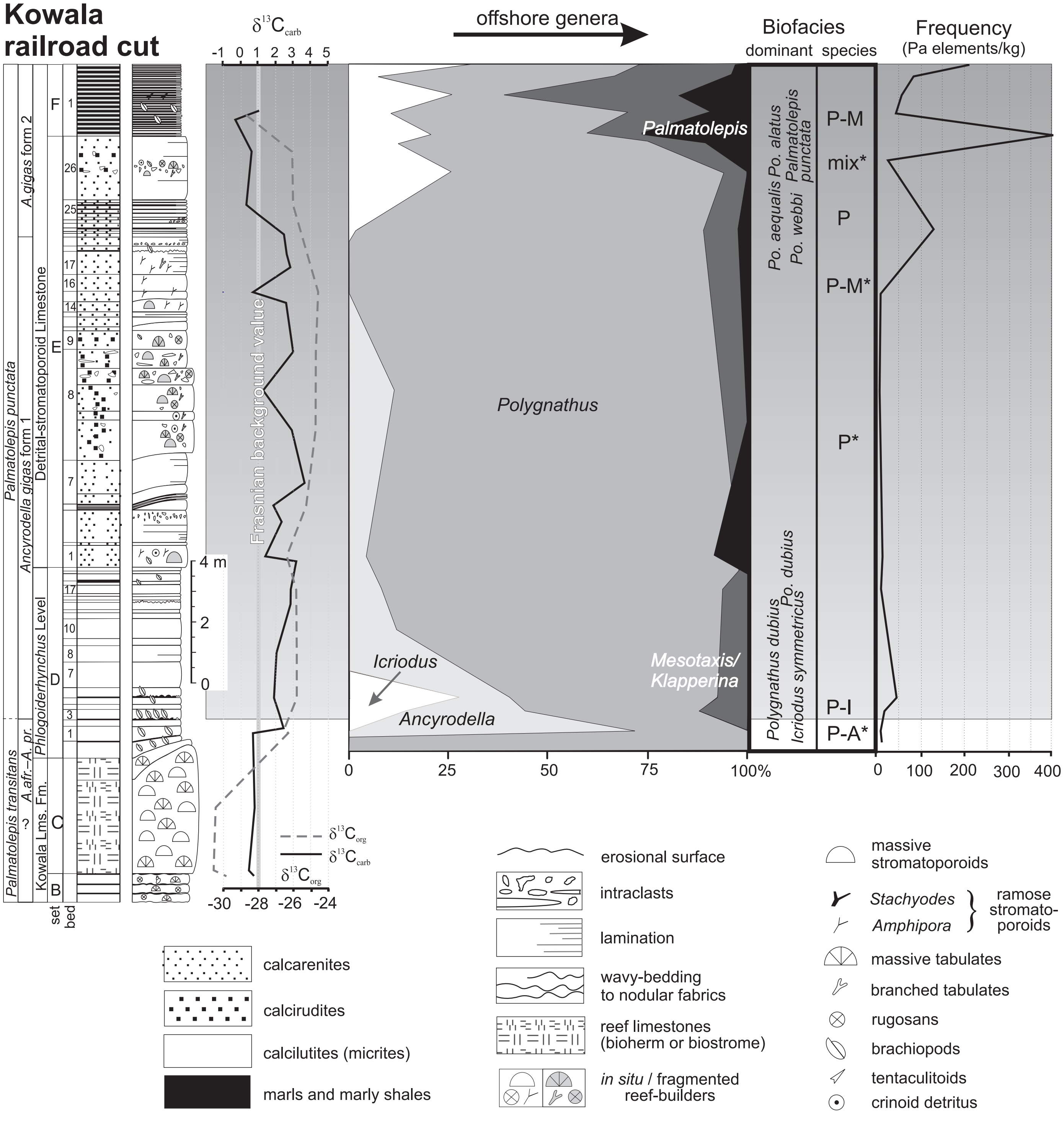

Fig. 8. Conodont biofacies distribution, dominating species and abundance trends against the carbonate and organic carbon isotopic curves for Kowala. Biofacies and other abbreviations: A, ancyrodellid; *A. afr.–A. pr.*, *Ancyrodella africana–A. pramosica*; I, icriodontid; M, mesotaxid; mix, mixed; P, polygnathid; *, biofacies determined from low frequency samples (less than 20 Pa elements); Kowala Lms Fm., Kowala Limestones Formation.

Mesotaxis. *Ancyrodella* is not diversified, reaching its maximum abundance twice: for the first time just above the E–MF boundary with the predomination of *A. pramosica* Perri and Spaletta, 1981, and for the second time within the *Palmatolepis punctata* Zone dominated by *Ancyrodella gigas* Youngquist, 1945. Biofacies change from mixed at the *Pa. transitans–Pa. punctata* boundary toward polygnathid-icriodontid, polygnathid and mesotaxid-polygnathid in the Middle Frasnian strata.

Kostomłoty-Mogiłki (Table 6, Fig. 10).—The youngest, highly diversified fauna of the *Ancyrodella africana–A. pra-*

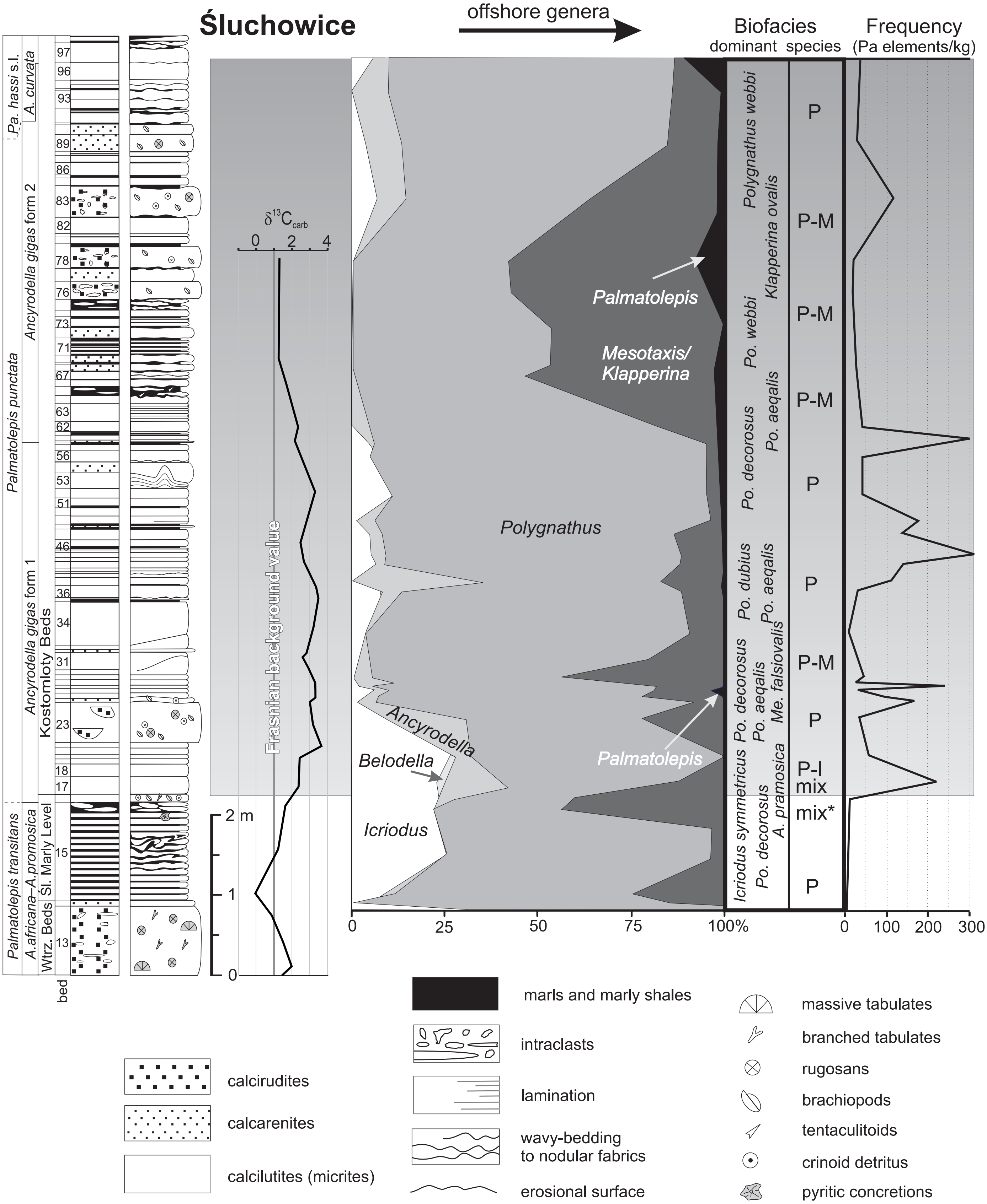

Fig. 9. Conodont biofacies distribution, dominating species and abundance trends against the carbonate carbon isotopic curve for Śluchowice. Biofacies and other abbreviations: A, ancyrodellid; P, polygnathid; I, icriodontid; M, mesotaxid; mix, mixed; *, biofacies determined from low frequency samples (less than 20 Pa elements); *A.*, *Ancyrodella*; *Me.*, *Mesotaxis*; Wtrz., Wietrznia; Śl., Śluchowice.

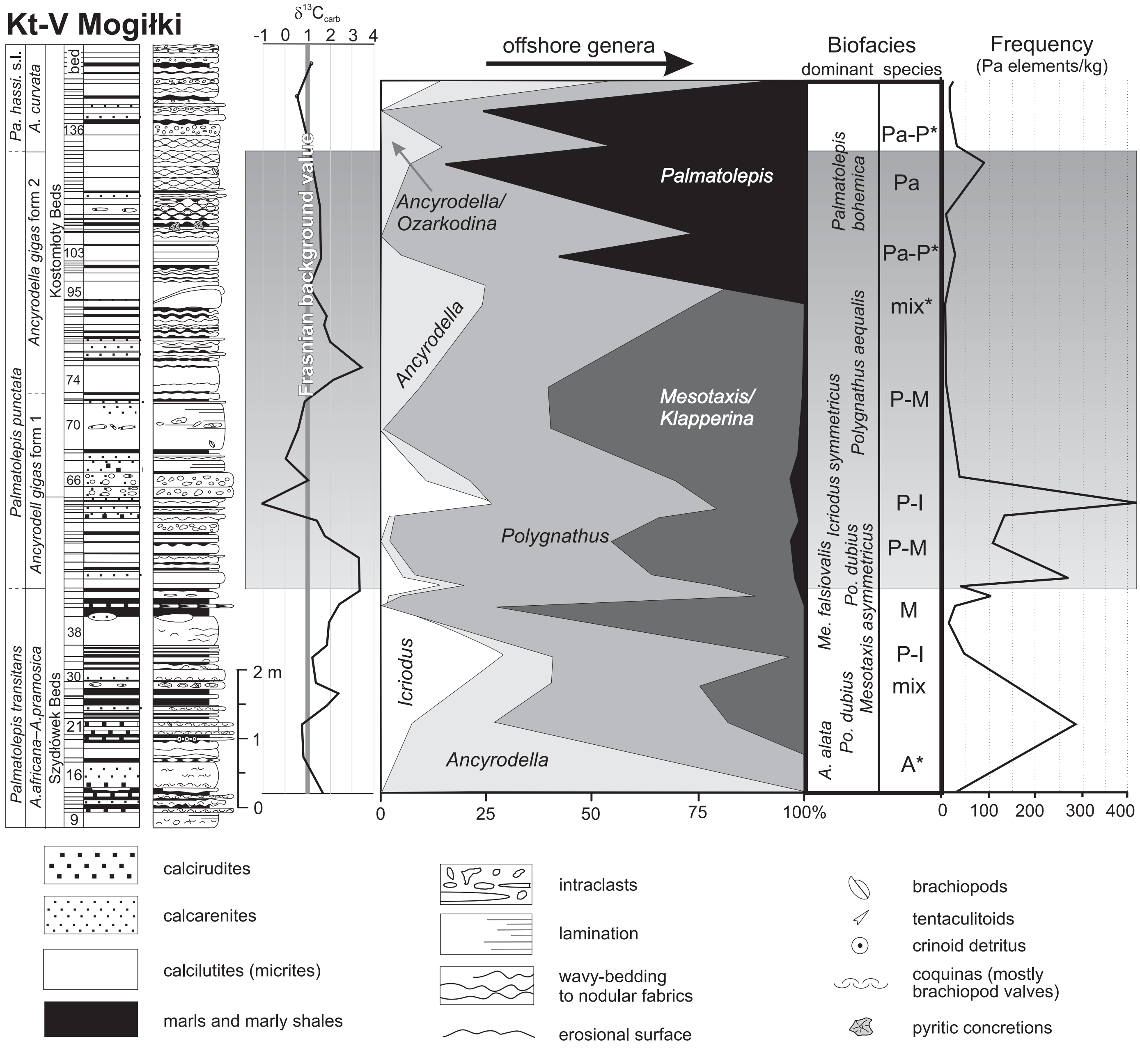

Fig. 10. Conodont biofacies distribution, dominating species and abundance trends against the carbonate carbon isotopic curve for Kostomłoty-Mogiłki. Biofacies: A, ancyrodellid; P, polygnathid; I, icriodontid; M, mesotaxid; Pa, palmatolepid; mix, mixed; *, biofacies determined from low frequency samples (less than 20 Pa elements); *A.*, *Ancyrodella*; *Me.*, *Mesotaxis*.

mosica ancyrodellid level in the late part of the *Palmatolepis transitans* Zone (see Racki and Bultynck 1993; Pisarzowska et al. 2006) reveals the highest percentage of *Ancyrodella*, up to 20%, where *A. alata* Glenister and Klapper, 1966 is the main component as well as *Icriodus* i.e., *I. symmetricus* is up to 35%. A sudden change from polygnathid-icriodontid to mesotaxid-polygnathid biofacies runs within the stylolinid-rich horizon of topmost Szydłówek Beds (see Racki et al. 2004). The following 2 m thick interval of mesotaxid-polygnathid biofacies is exceptionally rich in conodont fauna, as compared to low-abundance late *Pa. punctata* Zone biofacies. The *Mesotaxis*-rich biofacies are interrupted twice, just above the stylolinid horizon and at the base of the Kostomłoty Beds, by an increase in the number of *Icriodus symmetricus* (up to 27% of the conodont fauna). The late *Pa. punctata* Zone biofacies are dominated by *Mesotaxis* and *Palmatolepis* (mesotaxid-polygnathid and palmatolepis-polygnathid biofacies), while *Palmatolepis* prevails in the early *Pa. hassi* Zone (palmatolepid and palmatolepid-polygnathid biofacies).

Dębnik (Table 7, Fig. 11).—The conodont biofacies from Early to Middle Frasnian nodular limestones at Dębnik show gradual evolution (see also Balinski 1995). During the *Pa. transitans* Zone, the biofacies is largely dominated by *Icrio-*

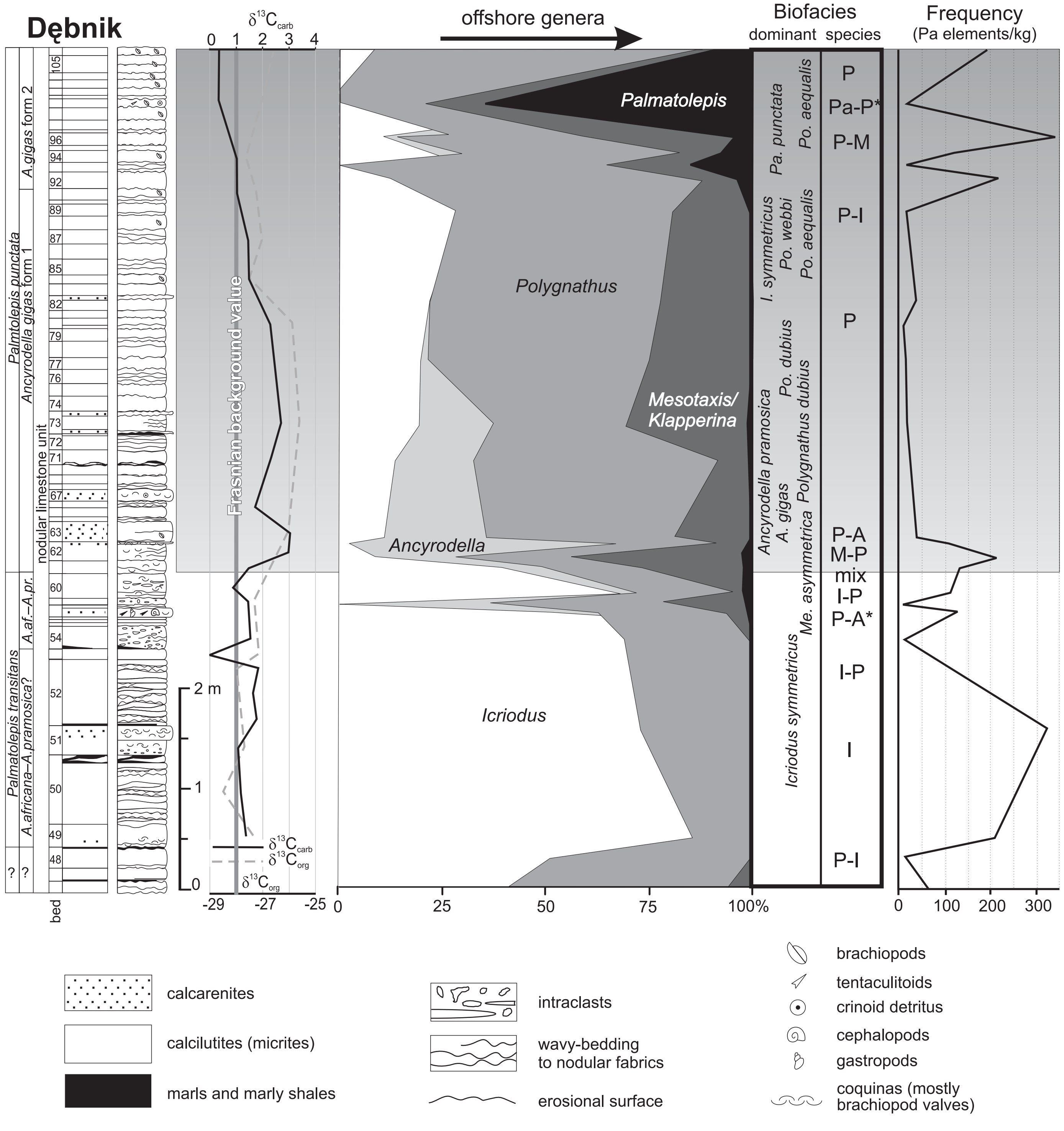

Fig. 11. Conodont biofacies distribution, dominating species and abundance trends against the carbonate and organic carbon isotopic curves for Dębnik. Biofacies and other abbreviations: A, ancyrodellid; P, polygnathid; I, icriodontid; M, mesotaxid; Pa, palmatolepid; mix, mixed; *, biofacies determined from low frequency samples (less than 20 Pa elements); *A. af.–A. pr.*, *Ancyrodella africana–Ancyrodella pramosica* conodont level; *Me.*, *Mesotaxis*; *Pa.*, *Palmatolepis*.

dus, up to 80% of the conodont assemblage constituting polygnathid-icriodontid and icriodontid biofacies. A significant shift to mesotaxid-polygnathid biofacies falls across the E–MF transition. This is preceded by a short-term mixed biofacies and an increase of the conodont relative abundance. The early *Palmatolepis punctata* interval marks an intensified *Ancyrodella* bloom. This genus is almost absent in underlying marly and bioclastic deposits, as well as in wavy-bedded limestone of the late *Pa. punctata* Zone. Significantly, *Ancyrodella* is represented mainly by two species: *A. pramosica* and *A. gigas* (up to 53% of conodont fauna). The middle *Pa. punctata* Zone is characterised by an interval of low abundance and di-

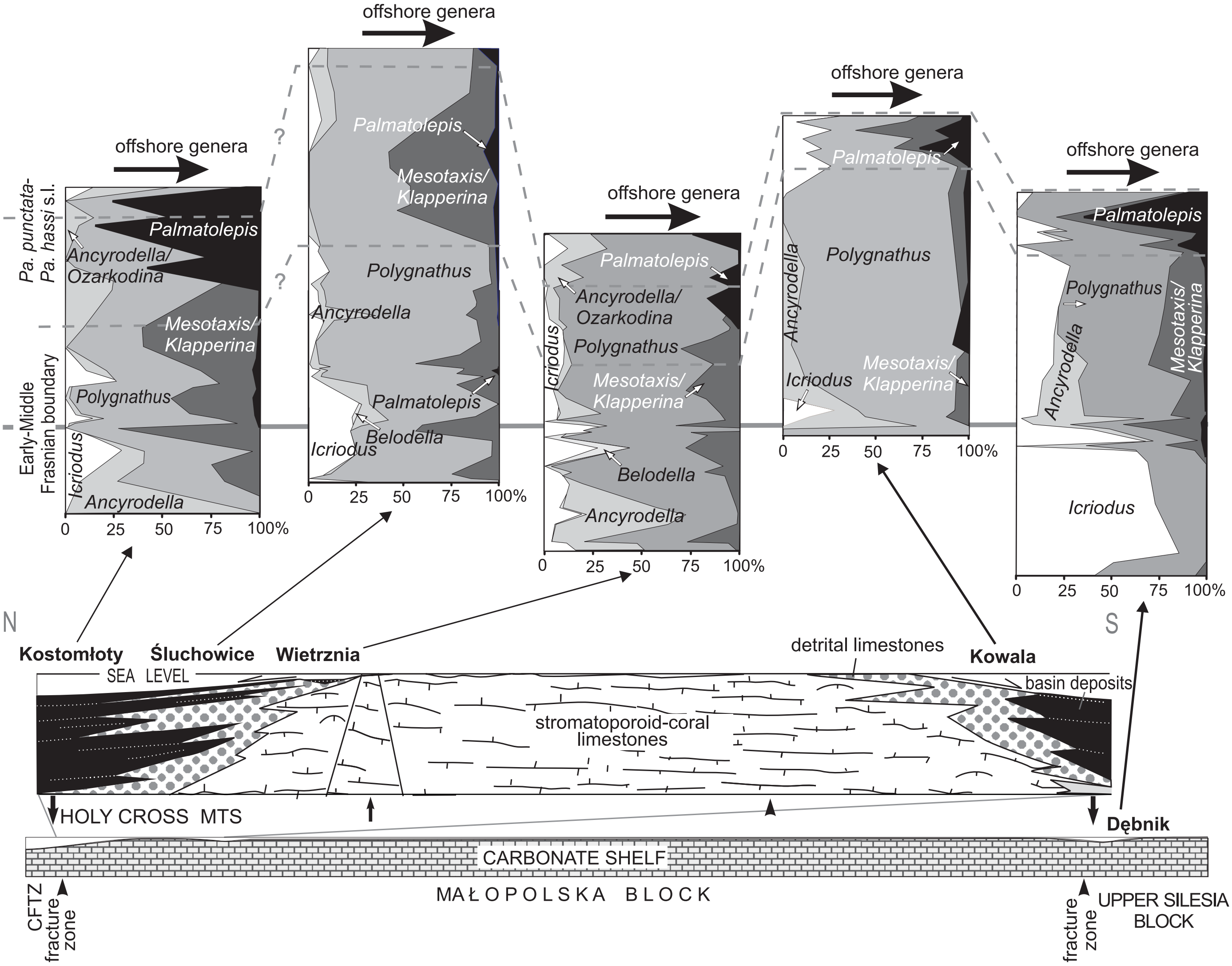

Fig. 12. Generalised biofacies correlation of sections studied against diagrammatic cross-section of the South Polish carbonate shelf to show location of Holy Cross Mountains and Cracow regions (partly after Szulczewski 1971: fig. 11C), as well their geotectonic setting (CFTZ, Caledonian Marginal Fault-and-Thrust Zone; Dadlez et al. 1994).

versity of polygnathid biofacies. The conodont biofacies change from polygnathid to palmatolepid-polygnathid during the late *Palmatolepis punctata* Zone.

Ecological interpretation

Sandberg et al. (1989) recognised five conodont biofacies within the Early Frasnian, which, proceeding shoreward, are: mesotaxid-polygnathid, polygnathid-icriodontid, polygnathid-ancyrodellid, polygnathid, and pandorinellinid. Six biofacies were recognised by Sandberg and Dreesen (1984) and Sandberg et al. (1988) for later Frasnian. In a shoreward direction they are: palmatolepid, palmatolepid-polygnathid, polygnathid-icriodontid, polygnathid, and polygnathid-ancyrodellid biofacies. The latter one occurred mainly around reefs and in mud-mounds settings (Sandberg et al. 1989, 1992).

The general biofacies temporal trend in the *Palmatolepis transitans* Zone in Wietrznia area as well as and other sites studied points to oscillating bathymetric changes from deep-water mesotaxid-polygnathid through “neritic” polygnathid-ancyrodellid to polygnathid-icriodontid and mixed biofacies. A prominent shift from mixed to homogenous and specialised polygnathid biofacies coincides with the base of the Middle Frasnian. A polygnathid biofacies continues throughout the entire *Pa. punctata* Zone and the very beginning of the early *Pa. hassi* Zone. The early *Pa. hassi* Zone marks the return to more diversified polygnathid-ancyrodellid, palmatolepid-polygnathid, and mixed biofacies (Fig. 12).

However, the E–MF conodont biofacies from the Holy Cross Mountains and Cracow area do not perfectly fit to the biofacies model of Sandberg and Dreesen (1984) and Sandberg et al. (1988), and some modification of biofacies interpretation, especially on species level, has been proposed.

Early Frasnian biofacies diversity.—Thin-layered partly laminated micritic limestones with shaly partings make a sedimentary background for interfingering coarse-grained limestones at Wietrznia. The hemipelagic lithofacies, rich in algal and other reef-derived fine detritus (Skwarek 1990), reflects the environment of distal-tempestite sedimentation specific of deeper slope areas. It is confirmed by the deep-water polygnathid-mesotaxid conodont biofacies. Thus, this "background" polygnathid-mesotaxid biofacies probably represents a largely undisturbed conodont record, as indicated by the abundance of juveniles as well as ramiform elements. The low frequency of conodonts in micrite layers may result mostly from element dilution in hemipelagic ooze blankets. Interestingly, some micritic layers reveal ancyrodellid-polygnathid biofacies characteristic of detrital layers (sample WIe 28), possibly resulting from the presence of small channel lags within the muddy deposits.

Special attention must be paid to interpreting biofacies of fore-reef and marginal-slope sediments represented by detrital lithofacies of the Wietrznia Beds. As evidenced by sedimentological data and microfacies analysis (Szulczewski 1971; Racki and Bultynck 1993; Makowska 2001; Vierek in press), most of detrital deposits in Wietrznia sections display evidence for an allochthonous origin of skeletal grains. The Early and Middle Frasnian downslope sedimentation in Wietrznia area was under the influence of the adjacent Dyminy Reef (Szulczewski 1971; Racki 1993); it was controlled by gravity-flow and turbiditic transport of highly concentrated mud material from reef to slope settings caused by strong current activity or storm events, which interrupted the stability of sediments at the reef slope (Szulczewski 1968, 1971; Vierek in press). As noted, the litho- and bioclastic lithofacies changes gradually to well- and moderately-sorted graded deposits toward the eastern Wietrznia Ie succession, contributing to thin-bedded calcareous crinoid-rich turbiditic intercalations. Reef-derived clasts, mostly crushed and fragmented stromatoporoids and corals, were mixed with deeper-water brachiopods-crinoid detritus and finally deposited in deeper slope areas. The alternating detrital-micritic lithologies of Wietrznia succession (Figs. 4–7), and related rapid changes in conodont biofacies, document an intermittent high energy regime in juxtaposition to the Dyminy Reef.

The detrital ("event") layers contain high concentrations of conodont platform elements derived from different habitats. Such assemblages, characterised by extremely low proportions of ramiform and coniform conodont elements (e.g., samples WIe 28, WIe 48, WId-E 2, WId-E 13; Tables 1–3, Figs. 5–7), can be considered only as mixed-origin conodont death assemblages (see Sandberg et al. 1989, 1992). As stated by Broadhead et al. (1990), the ramiform and coniform elements may be transported up tp 10 times farther in a lateral distance than the platform ones. The conodonts are well or moderately sorted in many samples, which indicates an irregular hydrodynamic sorting of apatite skeletal grains during differential postmortem lateral transport. The most robust platform elements of *Ancyrodella* and *Icriodus* are the ones that remained undamaged during the hydraulic transport (see Weary and Harris, 1994). Most of *Ancyrodella*, especially the Early Frasnian ones, flourished in relatively shallow-water settings, and after death were transported basinward and represent postmortem admixture in deeper water biofacies. The presence of mixed conodont faunas usually represents a high energy regime within storm wave activity or tidal currents range.

The biofacies analysis of detrital Wietrznia limestones shows that this area was in close proximity to reef environments, albeit placed at various distances from its core (Racki and Bultynck 1993). The fore-reef habitats were particularly diversified and peculiar for the conodont biota (see Sandberg et al. 1992). This is reflected in occurrences of taxa typical for reef biotopes, such as *Belodella* and *Ancyrodella*, together with deep-water *Mesotaxis* or *Icriodus symmetricus*, and even *Palmatolepis* (see also Bultynck et al. 1998; Racki and Bultynck 1993). *Ancyrodella* plays a very important role in Wietrznia biofacies, and the shallow and high-energy near-reef settings created an optimum condition for its development. According to Sandberg et al. (1989), *Ancyrodella* usually constitutes 10–30% of the population in the polygnathid and polygnathid-ancyrodellid shallow-water biofacies belts but it is also an important element in pelagic palmatolepid biofacies, especially in the higher Frasnian intervals (Klapper and Lane 1985). In Wietrznia sections, the contribution of *Ancyrodella*, reaching up to 50% in many samples, confirms the role of irregular sorting of conodont elements. *Ancyrodella* is very frequent in the proximal westernmost Wietrznia Id-W section, but, in places, it attained the highest frequency in deeper channels settings in the central and eastern part of the Wietrznia I quarry that are filled with crinoidal bioclastic accumulations (Table 3). When comparing the autochthony index for particular layers, most of them are characterised by very low values, with the most unbalanced ratios established within the early and middle part of the *Palmatolepis transitans* Zone.

The presence of the most offshore biofacies conodonts is indicated by the occurrences of *Mesotaxis*. Mesotaxids lived mainly in pelagic settings, thus characterizing deep-water mesotaxid-polygnathid and polygnathid-icriodontid biofacies (Sandberg et al. 1989). *Mesotaxis* is the most common genus in the micritic lithofacies, even in the shallowest Wietrznia Id-W section, where its presence indicates the temporary reef-slope submergence and establishment of hemipelagic basin regimes (see Pisarzowska et al. 2006). Some *Mesotaxis*-rich assemblages are with abundant post-mortem admixture of *Ancyrodella*, but mostly, the presence of *Ancyrodella* is opposite to the distribution of this deep-shelf dweller. *Ancyrodella* is very frequent in the early and middle part of the *Pa. transitans* Zone at Wietrznia, with the abundance peak in the middle portion. The latter interval is also almost barren of *Mesotaxis*, even in the most off-reef Wietrznia Ie succession. This surely indicates that deposition occurred more shoreward of the ecologic preference of pelagic *Mesotaxis* and suggests a short-term sea withdraw.

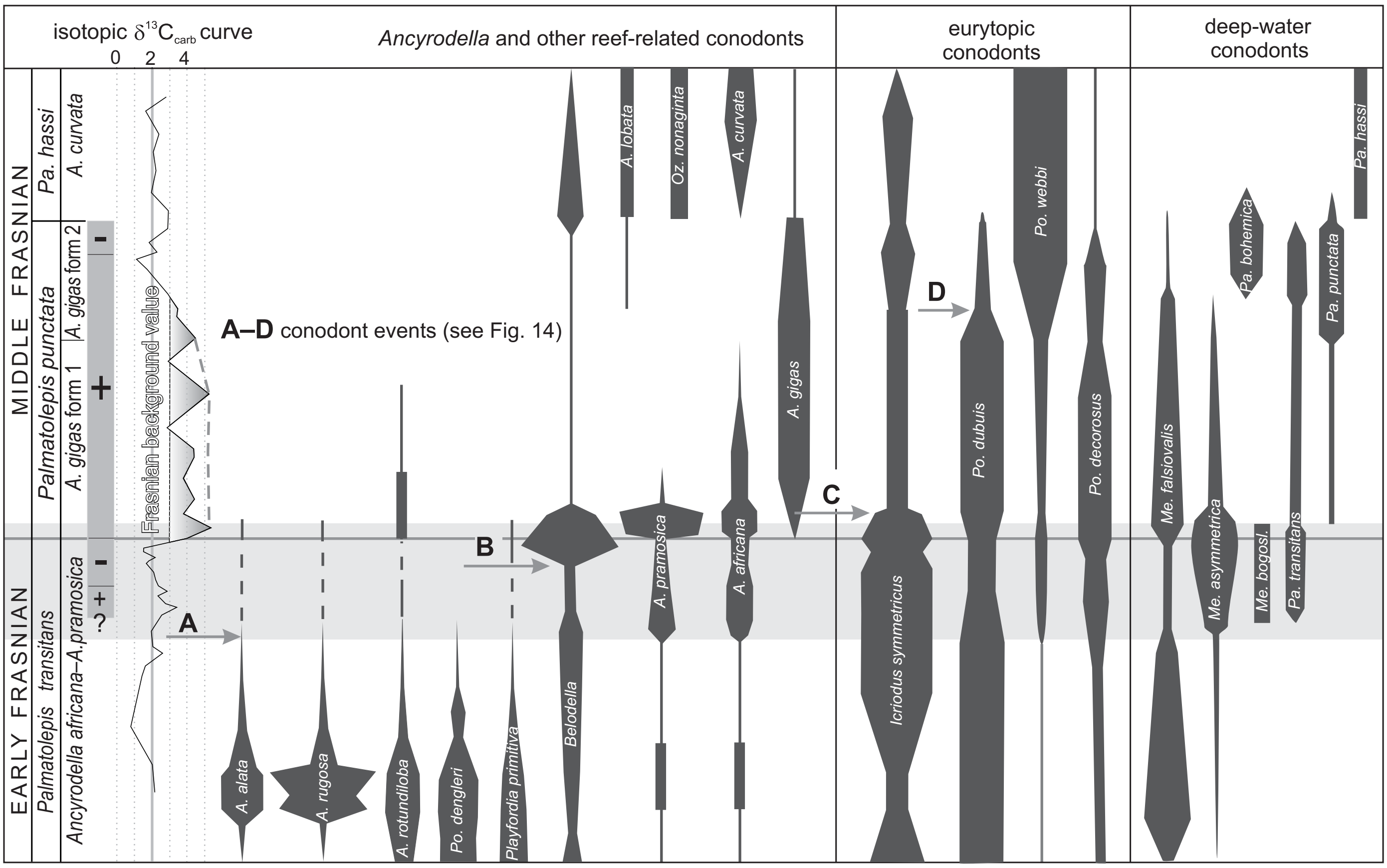

Fig. 13. Diversity development for selected conodont species groups around Early–Middle Frasnian transitional interval. The abundance relationship between reef-related, opportunistic and eurytopic conodont taxa is plotted against $\delta^{13}C$ curve (after Pisarzowska et al. 2006).

Concluding, the Early Frasnian conodont frequency, as a whole, and the contribution of reef-related taxa is significantly lower in the easternmost Wietrznia Ie. The effect of secondary transport of shallow-water taxa to the fore-reef slope is best evidenced in the Wietrznia Id-E section where mixed biofacies predominate through the large part of the Early Frasnian succession.

Early–Middle Frasnian boundary biofacies turnover.—The latest Early Frasnian beds are marked by thicker micritic-marly thin-bedded sets in Wietrznia and Śluchowice localities. This significant level (Śluchowice Marly Level) can be correlated lithostratigraphically on a regional scale (e.g., clayey-nodular set at Jaźwica quarry, Fig. 2; see figs. 23B and 24 in Racki 1993), and to some extent, using conodont biofacies, in all investigated sections. The onset of carbonate-poor deposition characterizes the almost total disappearance of benthos (see Głuchowski 2006; Baliński 2006) and a noticeably impoverished conodont fauna, that indicates significant habitat turnover.

The latest *Palmatolepis transitans* Zone micritic-marly deposits and earliest *Pa. punctata* Zone interval is represented chiefly by sudden biofacies changes, seen mainly in mixed biofacies. This unusual biofacies fluctuation may be a result of fine-grained debris flows and/or muddy turbidites and slumps shed from reef areas to the downslope settings as described for the Wietrznia Beds (Pisarzowska et al. 2006), but on the other hand, the good state of preservation and element ratios point to a mostly autochthonous origin of the assemblage (Figs. 5–7). Sandberg et al. (1988) suggested that mixed biofacies may develop by telescoping of biofacies and projection of shallow-water biofacies directly into deeper water settings as a result of rapid regression. The biofacies dynamic trend shows that the late part of the *Pa. transitans* Zone was indeed a timespan of oscillating sea-level that resulted in the occurrence of mixed biofacies. The general eustatic trend is directed toward deepening followed by shallowing episodes during the E–MF boundary interval.

The late *Pa. transitans* Zone biofacies are characterised by the increased number of *Icriodus* in all the Holy Cross and Dębnik sections (Tables 1–7, Figs. 5–11). *Icriodus* is believed to be a genus that has its optimum habitat in nearshore, relatively high energy and shallow-water settings (e.g. Seddon and Sweet 1971; Sandberg and Dreesen 1984), and its occurrence in pelagic deposits is attributed to nektonic life habit within the upper part of water column (Schülke 2003). However, the late *Pa. transitans* and *Pa. punctata* zones icriodontid faunas in the Holy Cross Mountains are composed almost entirely of *Icriodus symmetricus*, considered as

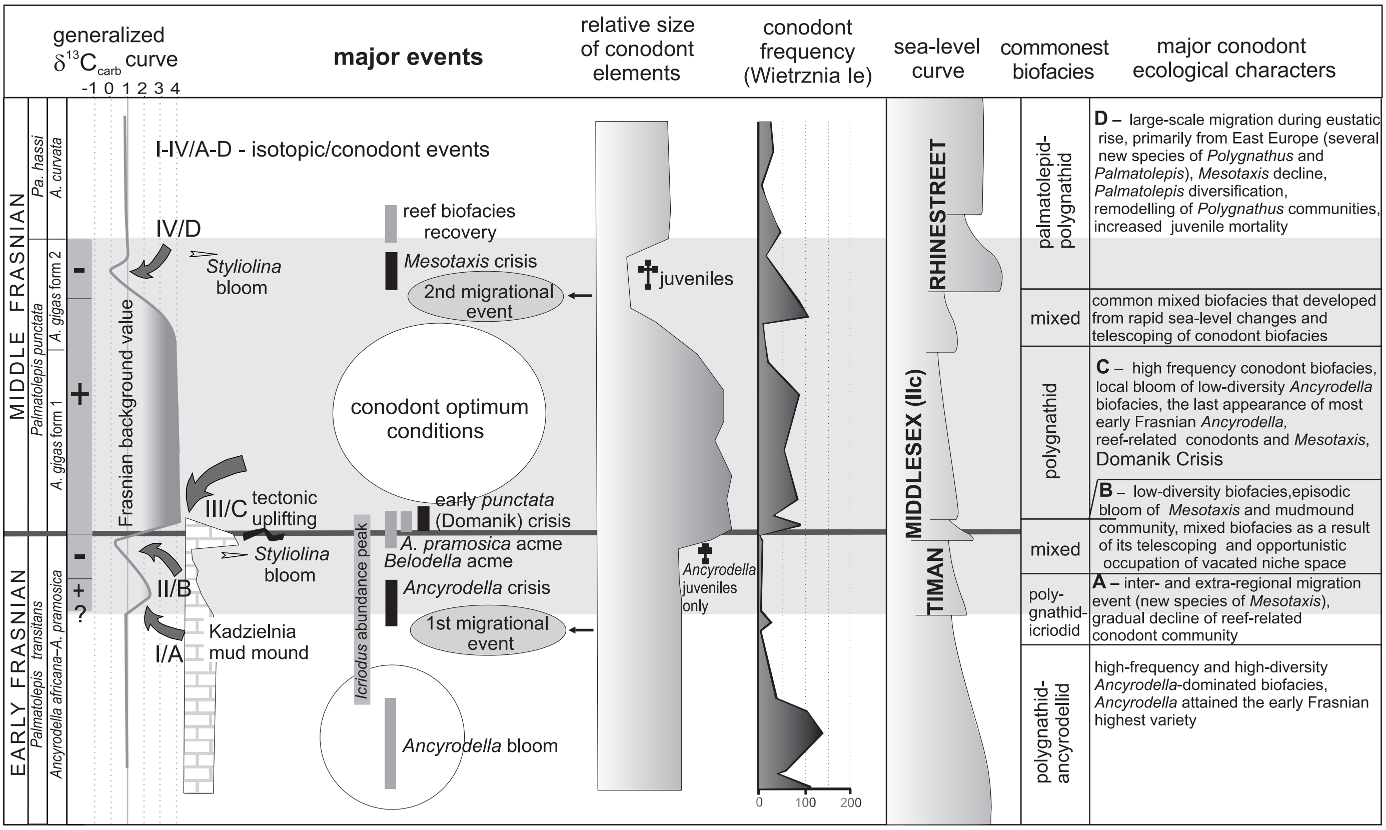

Fig. 14. A synthesis of main conodont events against other biotic and tectonic events, carbon isotopic curve and sea-level changes. Note a response of relative conodonts size to variation in $\delta^{13}C$ curve. The essential biofacies turnovers, a sequence of conodont crisis and recovery episodes correlate positively with sea-level and productivity fluctuation.

the most deep-neritic Frasnian species of *Icriodus* and rarely present in shallow-water settings (Sandberg et al. 1992, 2002; Bultynck 2003). Its relatively high abundance in all the sites studied might thus indicate a deepening episode in the late *Pa. transitans* Zone, the more so because it is accompanied by highly diversified *Mesotaxis* fauna, and first palmatolepids (e.g., delayed *Palmatolepis transitans* Müller, 1956; see Racki and Bultynck 1993). Nevertheless, there is no simple correlation between the co-occurrence of *I. symmetricus* and the other deep-water species of *Mesotaxis* and *Klapperina* to prove conclusively this depth-dependent biofacies change. The percentage of *Icriodus symmetricus* often is opposite of that of *Mesotaxis*. This late Early Frasnian increase in abundance of *Icriodus* in the Holy Cross Mountains coincides markedly with the decline of many species of *Ancyrodella* and carbon isotopic perturbation interval (see summary in Figs. 13, 14).

According to some authors (e.g., Belka and Wendt 1992; Wang and Ziegler 2002; Schülke 2003), there is no clear causal connection between sea-level changes and *Icriodus* distribution, indeed its blooming is attributed to other ecological factors, such as temperature, salinity, food supply, oxygenation, energy level, and clastic influx (e.g., Nicoll 1984; Klapper and Barrick 1978; Pohler and Barnes 1990; Belka and Wendt 1992).

Belka and Wendt (1992) indicated that the Late Frasnian icriodontids are more frequent in shallow-water carbonate deposits with a high clastic influx. Among the areas of the present study, *Icriodus* is most common in the nearshore Dębnik area where a clayey admixture is noticeable and other "neritic" conodonts like *Ancyrodella* are absent. A short-term bloom of *Ancyrodella* at the beginning of the *Pa. punctata* Zone leads to transient impoverishment of icriodontids (Fig. 11). The faunal replacement within *Icriodus* and *Ancyrodella* populations is clearly visible in the late *Pa. transitans* Zone sections of the Holy Cross Mountains, and it coincides with a regularity of fine detrital quartz and paramagnetic mineral particles input (Grażyna Bzowska and Jerzy Nawrocki, personal communications 2006). Although a significant cooling episode is not attributed to the E–MF transition, oxygen isotopes indicate a gradual temperature decrease of global oceans initiated at E–MF boundary (Agnieszka Pisarzowska, personal communication 2006; but see also Joachimski et al. 2004). Probably these and other environmental disturbances (see below) stressed the Early Frasnian reef biota and many of the reef-related conodonts. The most sensitive are species of *Ancyrodella*, i.e., *A. rugosa* and *A. alata*, but the whole diverse group of early Frasnian ancyrodellids are eliminated. Such species as the broad-platform *Polygnathus dengleri* (Bischoff and Ziegler, 1957), *Po. pennatus* Hinde, 1879, and *Playfordia primitiva*

(Bischoff and Ziegler, 1957), mostly associated with *Ancyrodella*-dominated biofacies, disappear at the E–MF boundary or in the earliest *Pa. punctata* Zone beds (see also Becker at al. 2001). Only isolated specimens of Early Frasnian conodont species appear as relics in the Early Middle Frasnian (e.g., Wietrznia Id-W 46, Pisarzowska et al. 2006: tables 1–7). Surprisingly, these species of *Ancyrodella* selected by environmental stress found quite favorable living conditions in moderately-deep Śluchowice and nearshore Dębnik basins around the E–MF boundary. The *Ancyrodella* bloom is significantly dominated by *A. pramosica* populations, again contributing to development of mixed biofacies, but this time as a result of rapid occupation of abandoned niches after the ecological crisis (see Morrow 2000). This acme ended just after the *Mesotaxis* decline and simultaneously with the next transgressive episode.

Consequently, *Icriodus symmetricus* is seen as a eurytopic species, which replaced *Ancyrodella*-dominated biota during the reef ecosystem instability in the latest *Palmatolepis transitans* Zone by expanding into the vacated ancyrodellid niche. Similarly, icriodontids went unaffected by the Frasnian–Famennian (F–F) extinction event, and the Early Fammenian icriodontid spike, recognised even in relatively deep basins, may not be explained as a response to shallowing, but as an occupation of the abandoned ecological niches during the end-Frasnian *Palmatolepis* collapse (e.g., Sandberg at al. 1988, 2002; Belka and Wendt 1992; Morrow 2000; Yiang and Ziegler 2002). The increased percentage of *Icriodus* coincides similarly with transient carbonate production crisis and the *Ancyrodella* demise (see summary in Pisarzowska et al. 2006). The changes in conodont biofacies toward icriodontid-dominated occurred synchronously both in shallow peri-reefal settings and deep-water off-reef areas.

The latest *Palmatolepis transitans* Zone succession is unique, marked in the diversity of *Mesotaxis* faunas similar to those occurring in the age-equivalent strata from South Timan (Becker et al. 2001). By analogy, many of these species did not successfully pass through the E–MF crisis (see Kuzmin et al. 1997). Significantly, they become extinct with the final decline of most species of the early Frasnian *Ancyrodella* and just after the first appearance of *A. gigas* (Pisarzowska et al. 2006). As it is shown by biofacies analysis, the faunal change may be explained by the rapid shallowing, probably of eustatic nature (see e.g., Walliser 1998). Kuzmin et al. (1997) point to changes in water circulation and spreading of sea bottom anoxia developed by deepening. In this case, the extinction should have quite selective character, because at the same time diversification of *Palmatolepis*, another deep-water conodont, occurred.

Surprisingly, many micritic samples from the latest *Pa. transitans* Zone marly interval of Wietrznia yield an increased number of *Belodella*. This genus is usually thought to live mainly in Devonian stromatoporoid-coral reefs, associated with polygnathids and rarely ancyrodellids, the main mud-mound biofacies components (Sandberg et al. 1992). *Belodella* is more frequent within the Early Frasnian strata of Wietrznia, but it only constitutes about 1 percent of the conodont fauna. The late *Pa. transitans* Zone and E–MF boundary interval yield 9, 12, and about 50% of *Belodella* of the whole, however, together with considerably low-frequency assemblages. The bloom of this genus within the E–MF transitional facies is surprising in light of the high environmental sensitivity of *Belodella* (Dzik 2002). Most probably it is a reflection of intense growth of low-energy Kadzielnia-type mud-mounds (e.g., Racki 1993), supposed to be the optimum habitat for *Belodella*. Furthermore, the percentage of *Belodella* derived from mud-mound lithofacies in the southernmost part of Małopolska Block (Fig. 1A) is also very high, reaching 30–40% of the low-diversity and impoverished conodont populations (Sobstel 2003). The local high contributions would be an effect of increased transport from the adjacent midslope mud-mounds (see Pisarzowska et al. 2006).

The equivalents of the buildup biofacies in the Holy Cross Mountains are polygnathid-icriodontid biofacies that are widespread within the transitional E–MF sequences (Fig. 15). The comparable relationships of litho- and biofacies are observed in the mud-mound of the Ardenne Arche Mbr and its lateral equivalent marly Chalon Mbr (Vandelaer et al. 1989), as well as in younger middle Frasnian Lion Mudmound (Sandberg et al. 1992).

Middle Frasnian stabilization phase.—The most distinct changes of conodont biofacies are the ones from Dębnik, probably because the area was not affected by synsedimentary tectonic activity at that time (see summary in Pisarzowska et al. 2006). The same trends in the Holy Cross Mountains are not always clear or do not change significantly at the E–MF boundary, as the biofacies pattern may be blurred by intraformational erosion and/or synsedimentary mixing (Kostomłoty, Wietrznia), and condensation (Śluchowice, Kowala), paired with generally very low frequencies of conodonts in all the sections. At Wietrznia Ie, biofacies did not change to deeper ones, contrary to other successions. The contribution of deep-water *Mesotaxis* remains at the same level. The changes concern mostly the degree of conodont diversification. The *Pa. punctata* Zone biofacies are more uniform, represented entirely by polygnathid biofacies. Such a biofacies development in Wietrznia slope habitats seems to be partly a result of block uplifts counterbalancing the deepening pulse observed clearly in other sections across the E–MF transition (Pisarzowska et al. 2006).

The base of the *Pa. punctata* Zone is characterised by a fluctuation in biofacies record, with the domination of mixed and polygnathid-icriodontid biofacies initiated at the end of the *Pa. transitans* Zone. In the most complete record at Dębnik, after a sharp deepening pulse just below the base of the zone, expressed by an entry of open-marine mesotaxids, there is an increase in the number of *Polygnathus decorosus* or *Po. timanicus* Ovnatanova, 1969 regarded as deeper water species and domination of *Icriodus symmetricus* among icriodontidis. A shallowing episode starts later in the Middle

Frasnian, and it is demonstrated by a bloom of *Ancyrodella pramosica* supplemented by *A. gigas*, paired with simultaneous reduction of mesotaxids to just a few percent. A similar pattern is more or less recognizable in all the sections. Also, a prominent depositional event took place just after the deepening episode at the beginning of the *Palmatolepis punctata* Zone, probably bound to the synsedimentary tectonic pulse. The biofacies re-arrangement, clearly manifested as a shift to monotonous polygnathid-dominated assemblages, is paired with the final demise of peri-reefal conodonts, some mesotaxids, and the end of the shallowing episode. Almost the entire *Pa. punctata* Zone interval lies within polygnathid biofacies, only occasionally punctuated by deeper polygnathid-mesotaxid biofacies. The latter are mostly associated with distinct micritic-marly intercalations of Wietrznia Id-W section (set D) and stylolinid-rich horizons at Wietrznia Ie (set D_1). The contribution of mesotaxids in the Kostomłoty and Dębnik areas is significantly higher. It points to a deeper bathymetric position of these two sections. The evidently deep-water biofacies are not seen till the late *Palmatolepis punctata* Zone.

The earliest Middle Frasnian is overall significantly impoverished in *Ancyrodella*. Probably only the deeper water *Ancyrodella pramosica* and *A. africana* survived the stressful environmental processes and gave rise to *A. gigas* near the start of the *Pa. punctata* Zone. In comparison, the Early Frasnian polygnathid populations persisted almost unaffected. The most frequent taxa in the early *Pa. punctata* Zone biofacies are *Polygnathus dubius*, *Po. aeqalis*, and *Po. decorosus*. These polygnathids are some of the commonest eurytopic Frasnian species (Ziegler et al. 2000), and *Po. decorosus* is also widely represented in deep-water palmatolepid biofacies (Klapper and Lane 1985). The increased abundance of *Po. decorosus*, often opposite to *Po. dubius*, may be connected with subordinate deepening episodes (samples Deb 60, WIe 164, WId-W 40). At Dębnik, for example, it appears more abundantly together with deep-water *Po. timanicus* and *Mesotaxis*, as well as in the reef-distant Śluchowice area.

After the *Icriodus* profusion episode during the late part of the *Pa. transitans* Zone, its abundance rapidly drops to a few percent. In the Kowala section *Icriodus* is absent completely until the late part of the *Pa. punctata* Zone. Although *Icriodus* was unaffected by level-bottom anoxia during the Late Frasnian anoxic Kellwaser Event (Belka and Wendt 1992; Schülke 1998), the sudden loss of *I. symmetricus*, even in shallow-water neritic biofacies, often is connected with dysaerobic conditions (Sandberg et al. 1989, 1994). Its synchronous disappearance in both deep-water and shallow-water settings may reflect changes not so much in basin depth but as a result of a stratified water column producing anoxic layers within the lower part of water column. The presence of dysoxic and anoxic conditions, even in the photic zone, has been confirmed by geochemical data for the Middle Frasnian set D at Kowala (Leszek Marynowski, personal communication 2006), and indirectly by the total lack of benthos. *I. symmetricus* disappears together with the advent of anoxia in the water column, suggesting that oxygen-deficient water was probably an important controlling distribution factor, moreover, it suggests its nekto-benthic mode of life as postulated by some conodont workers for various taxa (Sweet 1988). The early *Pa. punctata* Zone conodont fauna from Kowala is also extremely sparse (Table 4; Fig. 8). This impoverished succession, probably due to sluggish circulation within the partly(?) isolated Chęciny-Zbrza intrashelf basin, is sharply interrupted by the event-related intercalation correlated with pronounced eustatic rise late in the *Pa. punctata* Zone.

The distinctive feature of the early *Pa. punctata* Zone conodont fauna is a noticeable increase in conodont abundance (Fig. 14). Zhuravlev (2001) and Zhuravlev et al. (2006) point to a significant increase in average cell imprint size during the *Pa. punctata* Zone timespan, probably an indicator of optimal environment condition for conodonts. Our data evidently show the general increase in size of conodont elements of early to middle *Pa. punctata* Zone faunas, when compared with stratigraphically older individuals. The latter are especially characterised by the relatively small size and increased number of juvenile elements per sample, but these observations must be regarded as preliminary and need verification by further biometric analysis (see example in Renaud and Girard 1999).

Late *Palmatolepis punctata* Zone biofacies turnover.—The late *Pa. punctata* Zone coincides with the onset of more open-sea biofacies in all the areas studied (Figs. 12–14). A shift from polygnathid to palmatolepid-polygnathid biofacies falls within the fine-grained, laminated, locally stylolinid-rich marly deposits that record a deepening episode (Pisarzowska et al. 2006). The polygnathid biofacies is still present in the late *Pa. punctata* Zone in the upper Wietrznia beds, but the new habitats are marked there by invasion of new deep-water polygnathid species, as seen in the other sections as well. Many species of *Polygnathus* immigrated from the East European shelf, where they are known to occur beginning from the earliest *Pa. punctata* Zone. These are mostly *Po. uchtensis* Ovnatanova and Kuzmin, 1991 and *Po. lodinensis* Pölsler, 1969, the highest abundance of which is more frequent in relatively deep and lower energy environmental regimes (Ziegler et al. 2000). Some species, like *Po. timanicus*, are already present from the commencement of the *Pa. punctata* Zone at Dębnik, spread over the whole Holy Cross area at that time. *Po. dubius*, so common in the Early Frasnian, is replaced by fauna predominated by *Po. webbi* Stauffer, 1938. Three polygnathid species, *Po. webbi*, *Po. aequalis* Klapper and Lane, 1985, and *Po. alatus*, are the most frequent species of the newly established fauna, all of them are eurytopic generalist species (Fig. 13; Pisarzowska et al. 2006: tables 1–7); the long-ranged marker species of the *Po. dubius* and *Po. webbi* groups indicate wide geographic and ecological distribution, having their local abundance peaks in different sites through the entire Frasnian (Ziegler et al. 2000). The temporal ranges of these species are not bound with any extinction or even environmental turnover, but probably resulted from the appearance of new competitor taxa, i.e., a wave of immigrants from the East European epeiric seas into the South Polish outer shelf.

This deepening was marked by a gradual but significant decline in *Mesotaxis* (Fig. 14). The decline of mesotaxids was concurrent with diversification and increased abundance of the genus *Palmatolepis*, due to expansion of *Palmatolepis* into habitats formerly occupied by its ancestor, *Mesotaxis* (Sandberg et al. 1994). This shift within the pelagic deep-water communities took place worldwide in the late *Pa. punctata* Zone (Ziegler and Sandberg 2001).

Generally open-sea palmatolepids flourish even in quite shallow-water peri-reefal habitats recorded in Wietrznia Id section, but they are represented mainly by delayed *Pa. transitans*, appearing together with rare *Ancyrognathus ancyrognathoideus* (Ziegler, 1958) that preferentially occurr in neritic, quiet-water habitats (Sandberg et al. 1992). Palmatolepids from the *Pa. punctata* Hinde, 1879 group (Klapper and Foster 1993), in turn, are almost absent in moderately shallow regimes. *Pa. punctata* is more frequent in open-shelf facies of Kostomłoty, Kowala, and Dębnik, and *Pa. bohemica* Klapper and Foster, 1993 occurs only in deep-water Kostomłoty and in Dębnik. At Kostomłoty, huge populations of *Pa. bohemica* dominate the latest *Pa. punctata* assemblages (Pisarzowska et al. 2006: table 6), constituting 50% of the fauna.

The environmental changes during the late *Pa. punctata* Zone interval triggered a distinct decrease in size of conodonts and a higher juvenile mortality. It probably coincides with a differentiation in shape of palmatolepid P1 elements, being a morphological response to the altered habitats (see Renaud and Girard 1999). A true palmatolepid radiation is also bound with this time interval, as new *Palmatolepis* species, like *Pa. bohemica* and possibly new *Pa.* sp. A (Pisarzowska et al. 2006), appear for the first time. Some of them, for example *Pa. triquetra* Kuzmin, 1998 immigrated from deep shelf domains of the East European Platform, where they originated earlier in the *Pa. punctata* Zone (Kuzmin 1998).

Early *Palmatolepis hassi* Zone recovery.—The start of the *Pa. hassi* Zone is placed within a regressive episode of a large-scale deepening phase initated in the latest *Pa. punctata* Zone. The entry of *Pa. hassi* s.l. Müller and Müller, 1957 is coupled with this short-term shallowing. The species probably preferred relatively shallow-water environments, as proved by its more frequent occurence in peri-reefal Wietrznia areas, where microbial buildups were developed. Dzik (2002) suggests that *Pa. hassi* occurs abundantly in near-reef (“inshore”) settings (Wietrznia Ie, Kowala). Palmatolepids, regarded as the pelagic conodont proxy, had a wide ecological tolerance, however, as examplified by “neritic” *Pa. semichatovae* Ovnatanova, 1976; the biofacies with a considerable contribution of this genus occupied a relatively wide spectrum of environments from the deep-basin to the inner shelf (Belka and Wendt 1992). In studied areas, polygnathid and palmatolepid fauna dominates both in deep-water settings (Kostomłoty) and in peri-reefal biotopes (Wietrznia).

The early *Pa. hassi* Zone was also a time of recovery of *Ancyrodella* and its diversification after a long-term impoverishment. This changeover was simultaneous with resurgence of reef habitats. On the other hand, the commonest *Ancyrodella* species in the early *Pa. hassi* Zone is *A. curvata* (Branson and Mehl, 1934), quite widespread in moderate water depth but also found in deeper settings of the Kostomłoty Beds.

The polygnathid fauna did not change considerably since the late *Pa. punctata* Zone. Only *Polygnathus zinaidae* Kononova, Alekseev, Barskov, and Reimers, 1996, a species widely represented on the East European Platform, becomes widespread in shallow-water Wietrznia faunas.

Conodont biofacies evolution *versus* eustasy

Conodont fauna successions from the different sites of the Holy Cross Mountains and Cracow area show a broadly similar replacement pattern (Figs. 12, 13) which is biased, mostly by depositional changes promoted by regional tectonic movements in the Holy Cross Mountains basin. This dynamic analysis allows construction of a sea-level curve by the E–MF transition timespan for the Polish part of the Laurussian carbonate shelf (Fig. 14). After an Early Frasnian deepening pulse (II b/c subcycle of Racki 1993; see discussion in Pisarzowska et al. 2006) and the onset of combined detrital and hemipelagic deposition (e.g., set C in Wietrznia succession), many deep-water pelagic conodonts appear and co-exist with reef dwellers (Racki and Bultynck 1993). A strongly fluctuating biofacies development during the *Pa. transitans* Zone remains a clear reflection of rhythmic deposition and lateral transport influence. A noticeable regressive trend in the Holy Cross area is observable in the middle part of the *Pa. transitans* Zone, as indicated by a shift to highly diversified *Ancyrodella*-dominated biofacies. The following change toward polygnathid-icriodontid biofacies marks the late part of the *Pa. transitans* Zone both in the Holy Cross Mountains and Cracow region. That important biofacies replacement was initiated by basin deepening, recorded as a uniquely goniatitid-rich pyritic horizon in Kostomłoty basin (Racki et al. 2004). Although the bathymetric changes are not unambiguously noticeable in all sections or evidenced as only a slightly higher contribution of deeper water conodont taxa, the biofacies shift is synchronously observed both in lithofacies diversity and conodont faunas enriched by biogeographically new conodont species. This gradually accelerated transgressive tendency may be reflected by an increase of the number of deep-water *Icriodus symmetricus*, *Mesotaxis*, and a reduction of the abundance of *Ancyrodella.* Probably the conodont community remodeling was additionally provoked by other physico-chemical perturbations of the marine environment (see discussion in Racki et al 2004; Pisarzowska et al. 2006). According to the conodont and goniatitid dating, this transgression is a regional

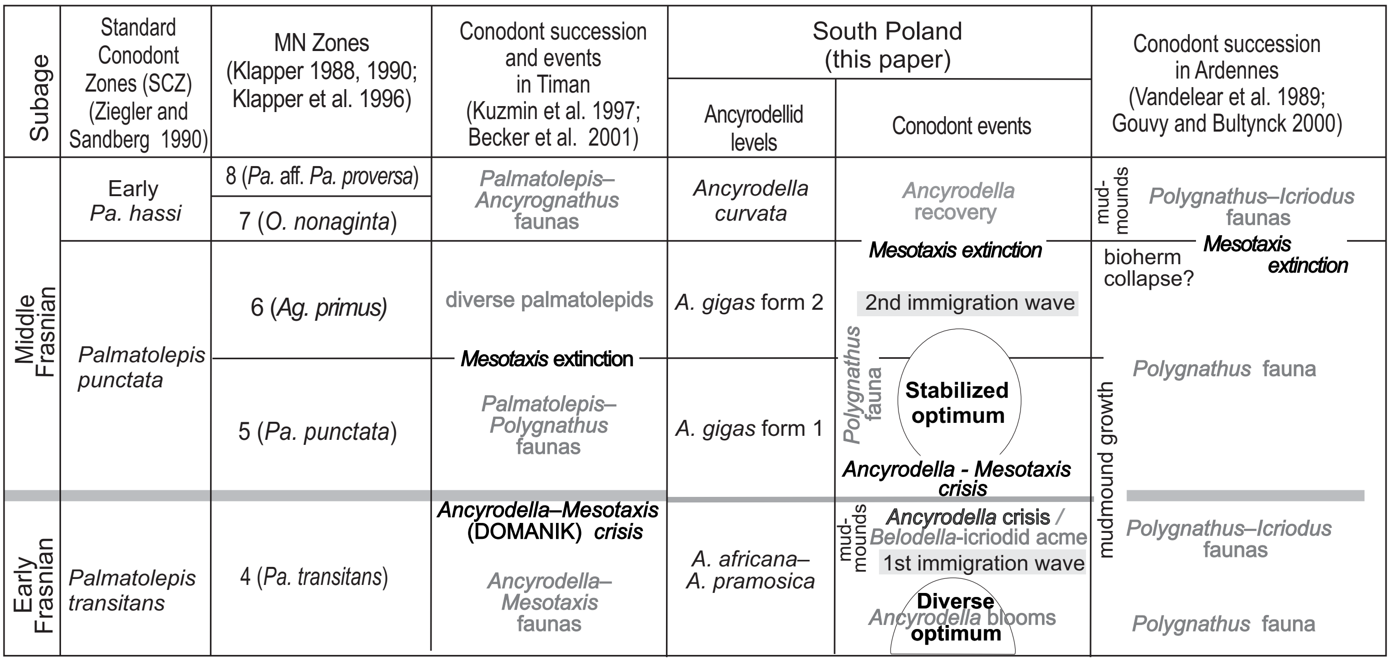

Fig. 15. Comparison of conodont successions and events in South Poland, Timan, and Ardennes against alternative conodont zonation across the Early–Middle Frasnian transition.

record of the Timan Event (Becker and House 1997; see Racki et al. 2004).

The transgressive pulse was followed by considerable shallowing, markedly recorded as a biotic-impoverished marly interval in the Wietrznia downslope succession. During the latest *Palmatolepis transitans* Zone regressive episode, short and rapid relative sea-level fluctuations (due to local tectonics?) are possible, expressed by common mixed biofacies, and locally by invasion of deep-water taxa (*Mesotaxis*, *Palmatolepis*). The pulsatory drowning of the carbonate platform stimulated the intensive development of the Kadzielnia mud-mound, as it is shown by a biofacies composition dominated by *Belodella* in the Wietrznia sections.

A sharp and extensive eustatic deepening occurs just before the E–MF boundary, as indicated by strictly deep-water mesotaxid-polygnathid biofacies and the dark, micriticmarly styliolinid-rich deposits, formed in hypoxic settings, at least in the Holy Cross Mountains (see also Racki et al. 2004). The widespread deepening pulse corresponds to the time of Middlesex Shale deposition in New York State (Over et al. 2003) that marks the base of the IIc cycle of Johnson et al. (1985). In the intrashelf basins of the East European Platform, the initiation of transgression at the same time led to accumulation of the bituminous-cherty Domanik Formation (Kuzmin and Yatskov 1997), where the similar pattern of biofacies changes around the E–MF boundary can be observed (see summary Becker et al. 2001; Fig. 15).

The conodont data from the earliest *Pa. punctata* Zone after the entry of *Ancyrodella gigas*, especially significant reduction of *Mesotaxis* percentage, imply a shallowing episode and the last, although impoverished, bloom of the surviving Early Frasnian conodonts and other biota (Pisarzowska et al. 2006). The involvement of tectonic activity in the biofacies change may be considered, since the sedimentological and carbon isotopic data point to substantial erosional phenomena and/or sedimentary starvation at this time. On the other hand, the Dębnik area, marked by tectonic quiescence, shows a similar biofacies development as in the Holy Cross Mountains, which proves the predominantly eustatic nature of this shallowing episode in the early Middle Frasnian interval.

Compared to the other regional T-R charts from the E–MF boundary interval, a highly complex and fluctuating passage from IIb toward IIc cycle is indicated (see summary in Pisarzowska et al. 2006). For example, according to Gouwy and Bultynck (2000), the E–MF boundary interval in the Ardennes falls within the small regression episode separating the two cycles (see also Walliser 1998). Similarly, in central Alberta, Canada, a sea-level drop was initated at the end of Early Frasnian time (Uyeno and Wendte 2005). The top of the Early Frasnian shallow-water Sargaevo deposits in the East European Platform is marked as well by a short-term break in sedimentation and hiatus (Ovnatanova and Kononova 2001; Zhuravlev et al. 2006), while the next transgressive episode took place in the *Pa. punctata* Zone, when the zonal marker appears for the first time. In the studied Polish sections, *Pa. punctata* enters quite late in the *Pa. punctata* Zone with a return to off-shore conditions (Pisarzowska et al. 2006).

Almost the entire *Pa. punctata* Zone, both in the Holy Cross Mountains and Cracow region, remains uniform in terms of conodont biofacies, that indicates the relative stability of sea level. The new vast transgression starts in the late part of the *Pa. punctata* Zone, preceded by a slight regressive tendency; these sea-level fluctuation are recorded as common mixed biofacies (Fig. 14). The eustatic rise was emphasised by the second immigration wave of various new conodont species and spread of the mostly deep-water Frasnian genera (*Palmatolepis*). The first pulse resulted in rebuilding of polygnathid assemblages and the second one, resulted in replacements within the deep-water *Mesotaxis–Palmatolepis* community. It is recorded by stylolinid-rich horizons deposited in temporary oxygen-depleted conditions, and strictly correlates with the first step of the Rhinestreet Event (House and Kirchgasser 1993; House 2002). This latest *Palmatolepis punctata* Zone deepening pulse is distinctly stronger when compared to the early *Pa. punctata* sea level change (see also Becker and House 1997; Walliser 1998). In fact, record of the Middlesex Event in the Australian Canning Basin and South China reefal succession is not clearly defined (Becker and House 1997; Tsien and Fong 1997), and a series of weak transgressive-regressive pulses is suggested for this time interval in the distant domains. The base of the early *Pa. hassi* Zone coincides with a small-scale regressive tendency over the South Polish carbonate shelf.

The conodont response to environmental perturbation

The late *Palmatolepis transitans*–early *Pa. punctata* time interval is not regarded as time of significant biotic remodeling (see summary in Yans et al. in press; Pisarzowska et al. 2006). Moreover, the *Pa. punctata* Zone is even thought as representing most favorable environmental conditions for conodonts (Zhuravlev 2001; Zhuravlev et al. 2006). On the other hand, only the stress-resistant conodonts, that went through the E–MF boundary perturbation episode, thrived during the long-term stabilization phase in the early Middle Frasnian. The E–MF conodont diversity loss has definitely a stepwise nature and four main biotic events can be distinguished during this crucial timespan, alongside cyclic biogeochemical changes (Figs. 13, 14):

In the late part of *Pa. transitans* time, a gradual decline of many species of Early Frasnian reef-related conodonts occured. *Ancyrodella* suffered major diversity and abundance reductions. There is a correlative rise in abundance of *Icriodus* from a few percent to as much as 80%. This faunal change is seen as an opportunistic capture of the abandoned niche in the course of intermittent deepening, partial reef collapse, and thus restriction of *Ancyrodella* habitat. The onset of this ecological remodeling corresponds to the short-term positive carbon isotope excursion (inception event I of Pisarzowska et al. 2006). The later part of this interval is paired with sudden appearance of *Belodella*-rich biofacies being a probable record of renewed mud-mound accretion in nearby areas.

Subsequent rapid shallowing resulted in a decrease of conodont abundance, reaching a minimum just below the E–MF boundary level. The absence or rarity of conodonts corresponds to a negative δ^{13}C spike (event II). After the spreading of new low-abundance and low-diversity conodont populations, the short-term bloom of highly diversified *Mesotaxis* is significant. The local increase of frequency of some species is associated with the major positive δ^{13}C incursion (event III; "*punctata* event" of Yans et al. in press; = *Pa. punctata* Event) and a sudden, but short-term, transgressive episode.

The start of the *Pa. punctata* Zone is distinctly marked by the loss in *Mesotaxis* species diversity and a fall of *Icriodus* abundance to the background level. After small-scale eustatic fluctuations, the biofacies becomes uniformly represented by polygnathid and polygnathid-mesotaxid assemblages. The conodont abundance is relatively high reaching the pre-crisis values, however reduced sharply in the oxygen-depleted Kowala basin and possibly also in the Kostomłoty area. The faunas of all sections exhibit a similar level of species diversity paired with a positive carbon-isotopic "plateau".

After the late *Pa. punctata* transgressive episode, shifts in conodont assemblages are observed and their taxonomic diversity rises rapidly; they are caused by recovering pelagic habitats and by effects of migrations. On the other hand, the reduction of conodont element size and increased juvenile mortality are bound to synchronous ^{12}C enrichment (event IV), ending the prolonged anomalous carbon cycling.

The causes of the late *Pa. transitans* environmental perturbations are undoubtedly complex and mostly conjectural, even if controlled mainly by the sea-level fluctuations (Sandberg et al. 1992). In fact, the Late Devonian mass extinctions at the Frasnian–Fammenian or Devonian–Carboniferous boundaries occurred during severe sea-level falls, immediately following major eustatic rises (Sandberg et al. 2002). The present data show that the significant shifts in conodont communities are also strictly bound to short-term and rapid eustatic sea-level fluctuations across the E–MF transition. During a deepening phase of the T-R couplets the conodont frequencies rise, while their reduction is noticeable during regressions (see also Zhuravlev et al. 2006). Intermittent short-term eustatic changes led to temporary rise of oceanic oxygen-depleted bottom waters, as recorded even in the photic zone of neritic domains (according to biomarker signature; Leszek Marynowski, personal communication 2006). The local disappearance of *Icriodus symmetricus* in anoxia-affected habitats suggests that only this species was influenced by the changes in oxygenation within the lower portion of the water column, forcing the population to migrate.

Compared to *Ancyrodella* and some specialised conodonts associated with reef habitats, polygnathids and icriodontids were unaffected through the E–MF transition. Many polygnathids and icriodontids were probably ecologic generalist able to adopt to environmental extremes during such a large-scale crisis as exemplified by the Kellwasser events (Wang and Ziegler 2002). Most polygnathids were probably uppermost photic-zone dwellers (Schülke 2003), so the changes in oxygenation did not affect their natural habitat. Moreover, the long-term positive C-isotopic anomaly, possibly indicating an increased nutrient influx and phytoplankton productivity (e.g., Racki et al. 2004; Pisarzowska et al. 2006), resulted in an increase in size of polygnathids and other conodonts; in contrast, size reductions coincide with negative isotopic signal, when near-surface productivity was probably generally lowered and/or at least destabilised. On the other hand, the start of a carbon isotopic perturbance is synchronous with the *Ancyrodella* decline, but most probably, the changes in productivity itself did not result directly in extermination of *Ancyrodella* populations. The series of events such as sea-level fluctuation, eutrophication pulses and promoted hypoxia, increased detrital input, and seismic activity led to destabilization of reef ecosystem, devastation of the *Ancyrodella* niche and stepwise collapse of trophic structure. One may speculate that *Ancyrodella* preferably inhabited nurtient-poor settings, but its population bloomed in off-reef areas of increased primary production (e.g., Dębnik, Śluchowice). Icriodontids, in turn, are commonly present in the nearshore settings, which should be easily affected by rapid environmental changes, but *Icriodus* probably had a wide depth range (Schülke 2003), which enabled it to adapt quickly to altered conditions. The correlation with secular $\delta^{13}C$ trends shows that icriodontids are the most abundant in nutrient-deficient or nutrient-extreme sites that gives the genus eurytopic status and explains its abundance spikes throughout the stressful E–MF interval. The significant replacements within the polygnathid communities in the *Pa. punctata* Zone provide additional evidence of the positive relationship between species competition and shifts in food availibility.

Concluding, we can emphasize that nutrient level fluctuation leading to changes in trophic structure and therefore food supply, coupled with such factors as sea level changes and oxygen deficiency, influenced Early–Middle Frasnian conodont fauna distribution to the largest extent. This causal connection was already strongly suggested by Belka and Wendt (1992). The conodont abundance trends around the E–MF boundary follow a similar pattern to those already documented by Kuzmin et al. (1997). The biodiversity decline and the gradual disappearance of some conodont taxa, summarised as a small-scale conodont extinction, was termed the "Domanik Crisis". Its synchronicity in both areas indicates its supraregional nature (Figs. 14, 15).

Conclusions

Early–Middle Frasnian conodont faunas of the Holy Cross Mountains and Cracow region tend to be dominated by *Polygnathus*, with some bloom occurrences of neritic *Ancyrodella* or *Icriodus* in the *Palmatolepis transitans* Zone and pelagic *Mesotaxis* or *Palmatolepis* in the *Pa. punctata* and early *Pa. hassi* zones, respectively. Prominent biofacies shifts and conodont fauna replacement coincided with the eustatic deepening correlated with Timan, Middlesex, and early Rhinestreet global events, respectively. The E–MF transitional interval is distinguished by a change from relatively diversified biofacies to more homogenous, mostly polygnathid biofacies.

The conodont biofacies indicate that late *Pa. transitans* and late *Pa. punctata* zones were in fact marked by significant bathymetry fluctuations during initiation of the IIc or Middlesex sea-level rise. The late *Pa. transitans* Zone biofacies provides evidence for two rapid and short sea-level rises followed by a noticeable eustatic drop. Similarly, late *Pa. punctata* Zone is marked by a large-scale T-R cycle. Change in the global sea level, as indicated by change in conodont dynamic trends, should constitute an additional and valuable tool for a high-resolution stratigraphic correlation for this time interval.

The biofacies interpretation imply a wide extent of lateral redeposition and post-mortem sorting in the downslope fore-reef habitats. The conodont assemblages of the Wietrznia area are dominated by highly varying proportions within the overall sedimentologically mixed biofacies, containing polygnathid, icriodontid, and ancyrodellid fauna.

The temporal trends in the conodont dynamics, mortality, and diversity clearly indicate that the major faunal changes correlate meaningfully with the main $\delta^{13}C$ excursions and probably evolving trophic conditions during this large-scale biogeochemical perturbation. The first conodont diversity loss is simultaneous with a transient reef ecosystem collapse and carbonate production crisis, broadly correlative with the Domanik Crisis of Kuzmin et al. (1997). A gradual decline of the Early Frasnian *Ancyrodella* community correlates with the minor positive and succeeding larger negative $\delta^{13}C$ excursion. The biofacies unification is a conodont response to the beginning of the prolonged (ca. 0.5 Ma) positive $\delta^{13}C$ anomaly, probably paired with eutrophication and partly anoxic regimes, but, on the other hand, it is marked by an increase in size of conodont elements. The late *Pa. punctata* negative carbon isotope excursion is linked with the second major biofacies turning point in the Rhinestreet transgression, recorded primarily in mesotaxid extinction, and highlighted also by decrease of conodont size and increased juvenile mortality. After stabilization of $\delta^{13}C$ values and the return to their background level across the *Pa. punctata*–*Pa. hassi* zonal transition, renewed biofacies diversification, in particular re-appearance of reef-related ancyrodellid fauna took place. In addition, a large-scale migration event among palmatolepids and polygnathids during sea-level rise, mainly from East European Platform, characterised this Middle Frasnian interval.

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Appendix 1

Table 1. Conodont biofacies for Wietrznia Ie derived from the percentages of specific conodont genera. Biofacies and other abbreviations: A, ancyrodellid; Po, polygnathid; M, mesotaxid; Pa, palmatolepid; I, icriodontid; mix, mixed; *, biofacies approximated from low frequency faunas (less than 20 Pa elements).

conodont zones		*Palmatolepis transitans*														*Pa. punctata*													*Pa. hassi* s.l.					
ancyrodellid level		*Ancyrodella africana–A. pramosica*														*A. gigas* form 1							*A. gigas* form 2					*A. curvata*			*A. gigas* f. 3		
sample number / taxa		27	28	31	48	60	66	99	105	111	135	157	160	165	168	169	171	172	179	189	195	201	206	208	209	213	225	233/1	233/2	233/3	233/4	233/5	235
Ancyrodella	%	40	36	13	58	48	45	0	8	100	0	12	0	0	0	8	17	0	16	2	6	5	0	0	4	5	7	3	9	10	15	9	9
Polygnathus		42	48	56	35	30	40	82	65	0	29	63	50	80	75	41	67	80	62	70	71	50	77	71	80	77	80	89	66	90	63	50	69
Palmatolepis		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	0	0	0	0	1	8	13	3	12	0	0	24	7
Mesotaxis/Klapperina		4	6	29	4	0	3	9	19	0	29	12	25	0	0	29	17	10	15	22	11	30	11	7	9	8	0	2	0	0	0	0	0
Icriodus		11	9	0	5	19	8	9	8	0	29	0	25	20	25	22	0	7	5	4	11	10	11	7	6	1	0	2	0	0	12	3	6
Ozarkodina		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	12	0	10	12	0
Belodella		0	0	>1	>1	2	3	0	>1	0	14	12	0	0	>1	0	0	0	1	0	0	0	0	0	0	0	0	0	>1	0	>1	0	>1
number of Pa elements/kg		117	33	62	192	99	37	2	26	1	6	8	4	5	8	85	30	30	74	52	87	20	18	14	107	84	15	47	23	7	31	24	35
Pb, M and S elements		118	1	171	131	158	80	0	81	5	42	48	19	12	23	87	26	47	141	56	98	8	23	18	17	75	23	56	36	11	49	30	15
biofacies		Po-A	Po-A	Po-Me	A-Po	A-Po	A-Po	Po*	Po-Me	A*	mix*	mix*	mix*	Po-I*	Po-I*	Po-Me	mix	Po	mix	Po	Po	Po-Me	Po*	Po*	Po	Po	Po*	Po	mix	Po*	Po-A	Po-Pa	Po-A

Table 2. Conodont biofacies for Wietrznia Id-E counted as the contribution of particular conodont genera. Biofacies and other abbreviations: A, ancyrodellid; Po, polygnathid; M, mesotaxid; Pa, palmatolepid; I, icriodontid; mix, mixed; *, biofacies approximated from low frequency faunas (less than 20 Pa elements).

conodont zones		*Palmatolepis transitans*														
ancyrodellid level		*Ancyrodella africana–A. pramosica*														
sample number / taxa		2	5	6	13	18	35	36	43	46	52	70	71	73	77	78
Ancyrodella	%	16	8	19	9	15	60	38	41	46	60	0	6	4	0	0
Polygnathus		73	60	73	41	37	25	52	16	30	20	33	36	57	100	50
Mesotaxis/Klapperina		4	23	4	26	41	10	2	25	5	20	67	2	8	0	0
Icriodus		7	6	0	22	7	7	8	16	18	0	0	54	29	0	0
Ozarkodina		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Belodella		0	>1	4	>1	0	0	0	>1	1	0	>1	>1	1	0	50
number of Pa elements/kg		146	47	24	264	23	44	88	9	135	5	3	226	94	3	2
Pb, M and S elements		93	111	61	172	41	78	65	17	81	6	21	71	121	11	37
biofacies		Po	Po-Me	Po	Po-Me	Me-Po	A-Po	Po-A	mix*	A-Po	mix*	Me-Po*	I-Po	Po-I	Po*	Po-Be*

Table 3. Conodont biofacies for Wietrznia Id-W counted as the contribution of particular conodont genera. Biofacies and other abbreviations: A, ancyrodellid; Po, polygnathid; M, mesotaxid; Pa, palmatolepid; I, icriodontid; mix, mixed; *, biofacies approximated from low frequency faunas (less than 20 Pa elements).

conodont zones		*Palmatolepis transitans*																*Pa. punctata*												*Pa. hassi* s.l.				
ancyrodellid level		*Ancyrodella africana–A. pramosica*																*A.gigas* form1				*A. gigas* form 2								*A. curvata*		*A. gigas* f.3		
sample number taxa		3	9	10	11	15	21	22	25	27	35	37	40	41	42/1	42/2	42/3	43	45	46	47	49/1	49/2	50/1	50/2	51	53	54	55	56/1	56/2	58	60	62
Ancyrodella	%	6	8	7	17	26	14	26	15	55	75	23	3	29	0	14	0	7	10	1	1	1	0	6	5	3	11	6	7	9	14	4	2	3
Polygnathus		44	64	65	60	55	68	49	60	45	25	38	64	2	72	50	55	51	37	97	70	77	100	76	79	73	79	59	67	89	52	89	89	79
Palmatolepis		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	9	9	3	0	6	0	2	17	2	1	3
Mesotaxis/Klapperina		12	10	8	7	11	20	16	15	0	0	2	3	21	0	16	22	0	17	2	18	17	0	4	5	13	7	29	11	0	8	0	0	6
Icriodus		19	8	17	16	4	14	7	0	0	0	19	28	46	14	16	22	39	3	0	3	2	0	2	1	3	4	0	0	0	2	4	4	0
Ancyrognathus		0	0	0	0	0	0	0	0	0	0	0	>1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	4	>1	0
Ozarkodina		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	3	9
Belodella		19	0	5	2	0	2	2	10	0	0	17	1	2	14	3	>1	2	32	0	7	0	0	0	0	5	0	0	15	0	0	0	0	0
number of Pa elements/kg		32	102	396	284	123	97	104	15	19	2	59	186	41	5	56	9	30	62	212	50	158	92	33	116	25	20	11	18	53	64	81	219	34
Pb, M and S elements		93	183	390	231	92	61	92	110	17	13	123	105	178	23	172	24	89	142	278	66	191	186	64	205	198	36	34	42	39	62	55	92	36
biofacies		mix	mix	Po-I	Po-A	Po-A	Po-Me	Po-A	mix*	A-Po*	A*	mix	Po-I	I-A	Po*	mix	mix*	Po-I	Po-Be	Po	Po	Po	Po	Po	Po	Po	Po	Po-Me*	Po*	Po	Po-Pa	Po	Po	Po

Table 4. Conodont biofacies for Kowala counted as the contribution of particular conodont genera. Biofacies and other abbreviations: A, ancyrodellid; Po, polygnathid; M, mesotaxid; Pa, palmatolepid; I, icriodontid; mix, mixed; *, biofacies approximated from low frequency faunas (less than 20 Pa elements).

conodont zone		*Pa. tran.*		*Palmatolepis punctata*														
ancyrodellid level		*A.af–A.pr*		*A.gigas* form 1						*Ancyrodella gigas* form 2								
sample number taxa		C3	D1	D3	D5	D16	E1	E8c	E16	E24	E26	E29	F1	F2	F5	F7	F9	F10
Ancyrodella	%	0	67	24	11	10	8	100	0	0	0	0	1	0	0	1	1	0
Polygnathus		100	33	46	49	80	77	0	40	87	70	42	40	62	27	60	34	82
Palmatolepis		0	0	0	0	0	15	0	20	3	0	16	30	4	17	4	3	6
Mesotaxis		0	0	15	11	10	0	0	40	7	5	8	8	24	47	26	25	11
Icriodus		0	0	15	27	0	0	0	0	3	25	16	20	9	25	7	33	1
Ozarkodina		0	0	0	2	0	0	0	0	0	0	16	0	0	0	2	3	0
number ofl Pa elements/kg		5	3	13	45	10	13	2	5	129	20	12	401	40	68	85	169	89
Pb, M, and S elements		11	3	10	39	10	8	0	3	89	6	7	112	27	41	49	97	107
biofacies		Po*	A-Po*	Po-A*	Po-I	Po*	Po*	A*	Po-Me*	Po	Po	mix*	Po-Pa	Po-Me	Me-Po	Po-Me	mix	Po

Table 5. Conodont biofacies for Śluchowice counted as the contribution of particular conodont genera. Biofacies and other abbreviations: A, ancyrodellid; Po, polygnathid; M, mesotaxid; Pa, palmatolepid; I, icriodontid; mix, mixed; *, biofacies approximated from low frequency faunas (less than 20 Pa elements).

conodont zones		*Pa.transitans*					*Pa. punctata*																												*Pa. hassi* s.l.
ancyrodellid level		*A.africana-A.pramosica*					*A. gigas* form 1																			*A. gigas* form 2									*A. curvata*
sample number / taxa		13	14	15A	15B	15C	16	17	19	23	24	25	26	27	28	29	34	36	37	41	43	47	49	52	56	59	62	67	68	76	78	83	89	94	97
Ancyrodella	%	0	0	6	0	0	27	17	2	21	5	5	5	3	5	6	0	4	30	1	3	3	3	0	0	1	4	0	0	5	0	6	8	10	4
Polygnathus		66	89	47	74	33	22	45	69	50	85	69	67	78	79	50	82	78	52	82	82	80	93	80	87	88	71	39	53	38	41	53	71	76	79
Palmatolepis		0	0	6	0	0	>1	0	0	0	0	1	5	2	0	0	0	0	1	0	1	1	0	0	0	0	0	2	0	0	8	2	2	0	12
Mesotaxis /Klapperina		0	11	23	5	44	36	12	0	21	9	21	14	16	10	44	9	11	17	10	9	11	4	4	6	6	20	55	47	57	52	34	14	14	2
Icriodus		33	0	18	0	22	0	23	27	9	1	3	9	1	5	0	9	7	0	6	4	4	1	16	6	5	4	0	0	0	0	4	4	0	4
Ancyrognathus		0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Ozarkodina		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Belodella		0	>1	0	>1	0	>1	>1	>1	0	0	0	0	0	0	0	0	0	0	>1	0	>1	0	0	0	0	0	0	0	0	0	0	0	0	0
number of Pa elements/kg		5	9	17	23	12	421	218	55	34	163	93	30	244	27	45	15	38	118	140	314	141	162	45	45	300	45	31	36	21	17	120	49	50	56
Pb, S and M elements		12	28	26	57	35	266	161	36	31	76	76	45	104	18	13	16	48	44	192	161	93	97	48	15	109	34	48	28	36	9	63	40	74	69
biofacies		Po-I*	Po*	mix*	Po	mix*	mix	mix	Po-I	Po-I	Po	Po-M	Po-M	Po	Po	Po	Po*	Po	Po-A	Po	Po	Po	Po	Po	Po	Po	Po	Po-M	Po-M	Po-M	Po-M*	Po-M	Po	Po	Po

Table 6. Conodont biofacies for Kostomłoty counted as the contribution of particular conodont genera. Biofacies and other abbreviations: A, ancyrodellid; Po, polygnathid; M, mesotaxid; Pa, palmatolepid; I, icriodontid; mix, mixed; *, biofacies approximated from low frequency faunas (less than 20 Pa elements).

conodont zones		*Pa. transitans*						*Palmatolepis punctata*																*Pa. hassi* s.l.		
ancyrodellid level		*A. afr.–A. pr.*						*Ancyrodella gigas* form 1								*A. gigas* form 2								*A. curvata*		
sample number / taxa		21	29	33	38	40	42	44	45	48	52	57	61	66	70	74	93	95	103	104	117	119	128	133	139	147
Ancyrodella	%	16	19	7	20	0	4	4	4	5	3	2	>1	9	0	11	25	0	0	0	0	0	0	13	0	15
Polygnathus		56	28	56	60	30	82	57	49	64	54	59	50	38	40	22	50	80	24	73	80	64	12	47	25	42
Palmatolepis		0	0	0	0	0	2	2	4	11	6	1	2	5	0	11	25	20	67	27	20	18	80	40	65	5
Mesotaxis/Klapperina		17	31	2	0	70	10	20	32	19	41	34	20	38	59	61	0	0	0	0	0	0	0	0	0	0
Ancyrognathus		0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	5	0	0	0	0	0	0	0
Icriodus		11	22	35	20	0	2	16	11	2	0	3	27	9	0	0	0	0	0	0	0	0	3	0	0	16
Ozarkodina		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	18	5	0	0	21
number of Pa elements/kg		282	132	45	5	22	100	45	271	64	103	138	414	21	29	18	4	5	21	15	2	11	80	16	11	19
Pb, M and S elements		91	74	50	8	38	148	72	354	110	132	295	269	33	46	37	8	10	26	37	5	14	64	6	14	22
biofacies		Po-Me	mix	Po-I	Po-I*	Me	Po	Po-Me	Po-Me	Po-Me	Po-Me	Po-Me	Po-I	Po-Me	Po-Me	Po-Me*	mix*	Po*	Po-Pa	Po*	Po-Pa*	mix*	Pa	Po-Pa*	Pa-Po*	mix*

Table 7. Conodont biofacies for Dębnik counted as the contribution of particular conodont genera. Biofacies and other abbreviations: A, ancyrodellid; Po, polygnathid; M, mesotaxid; Pa, palmatolepid; I, icriodontid; mix, mixed; *, biofacies approximated from low frequency faunas (less than 20 Pa elements).

conodont zones		?		*Pa.transitans*						*Palmatolepis punctata*																
ancyrodellid level		?		*A. af.–A. pr.*						*Ancyrodella gigas* form 1										*A. gigas* form 2						
sample number / taxa		46	48	49	51A	54	58	59	60	61	62A	62B	63	71	73	77	80	82	86	89	92	93	94	96	100	106
Ancyrodella		2	0	0	0	0	6	40	2	11	15	67	23	14	12	3	0	0	0	0	0	0	2	1	0	0
Polygnathus		62	50	17	27	29	22	40	19	28	30	24	51	64	25	29	12	58	52	55	80	44	39	72	23	85
Palmatolepis		0	0	0	0	0	0	0	4	2	1	0	0	0	6	0	0	0	0	0	7	56	14	6	54	4
Mesotaxis/Klapperina	%	5	0	1	>1	0	7	20	4	23	44	7	17	9	38	23	44	22	23	16	3	0	17	5	23	9
Icriodus		32	50	81	73	71	64	0	68	34	9	2	9	14	18	35	44	20	25	22	9	0	28	16	0	1
Belodella		0	>1	1	0	0	0	0	>1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ozardkodina		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5	0	0	0	0	0	1
number of Pa elements/kg		63	16	150	322	14	138	5	123	172	203	106	25	22	16	17	9	41	48	18	155	18	111	247	18	185
Pb, M and S elements		108	13	76	94	9	46	14	49	201	132	132	25	16	17	5	6	16	25	16	2	8	98	178	8	74
biofacies		Po-I	Po-I*	I	I	I-Po*	I-Po	A-Po*	I-Po	mix	M-Po	A-Po	Po-A	mix	M-Po*	mix*	M-I*	Po-I	mix	Po-I*	Po	Pa-Po*	Po-M	Po	mix*	Po