Newsletters on Stratigraphy, Vol. 51/3 (2018), 327–342 **Article**

The Frasnian–Famennian boundary in Vietnam and evolutionary meaning of FADs and LADs

Jerzy Dzik[1,2]*, Przemysław Świś[2], and Nguyen Duc Phong[3]

With 10 figures and 1 table

Abstract. The latest Frasnian and earliest Famennian conodont assemblages at the Si Phai section in northernmost Vietnam are similar to those from coeval strata in Europe, but their taxonomic diversity is significantly lower and the order of species appearances is different. Unlike most other localities, where '*Palmatolepis*' *linguiformis* is a very late Frasnian species preceding *Klapperilepis ultima*, it emerges much earlier at Si Phai, already co-occurring with *Ancyrodella lobata*. Its contribution to the assemblage is there many times higher than elsewhere. This allows tentative apparatus reconstruction proving its congenerity with *Manticolepis rhenana*, which at Si Phai occurs only in the lowermost portion of the *M. linguiformis* range. Another peculiar aspect of this Vietnamese section is the abundance of *Avignathus* in its lower part. In a subsequent sudden change of apparently ecological nature, a diverse set of polygnathids *Ctenopolygnathus* and *Polygnathus* species followed by *Klapperilepis ultima* enriched the assemblage. The second dramatic faunal exchange event resulted in the disappearance of all the palmatolepidids except for *K. ultima*. The Si Phai conodont species succession does not differ from those of other regions of the world in that both the first and last occurrences were caused by ecological changes that, apart of this terminal Frasnian event, are not necessarily of global extend. The widely held assumption that most changes in distribution of conodonts were synchronous may not be true. A truly reliable age correlation should not be based on ecologically controlled appearances and disappearances but on well-documented evolutionary transitions. Unfortunately, evolutionary origin of no one of the palmatolepidid species occurring in Si Phai (with possible exception of *Manticolepis winchelli*) has been determined elsewhere. This makes the probably phyletic succession of *Ancyrodella* chronospecies a more reliable tool for age correlation.

Key words. Biostratigraphy, Devonian, Kellwasser Event, evolution, phylogeny, conodonts

1. Introduction

Whatever approach to the biostratigraphic practice is chosen, would it be relying on environmental control of species distribution (e.g., Klapper 2007b), hypothetical phylogeny of guide fossils (e.g., Ziegler and Sandberg 1990) or their phyletic evolution (e.g., Dzik 1995, 2005, 2008, Dzik & Phong 2016), the function of a geological time marker is performed by biological entities: living organisms. Their characteristics include population and ontogenetic variability, the main aspects that change in their phyletic evolution. There are more than enough data showing that so understood evolution is a continuous process (reviewed in e.g.,

Authors' addresses:
[1] Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warszawa, Poland.
[2] Faculty of Biology, University of Warsaw, Aleja Żwirki i Wigury 101, Warszawa 02-096, Poland. dzik@twarda.pan.pl
[3] Vietnamese Institute of Geosciences and Mineral Resources, 67 Chien Thang, Van Quan, Ha Dong, Hanoi, Vietnam. phongcs@yahoo.com
* Corresponding author: dzik@twarda.pan.pl

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Dzik 2005, 2008). If it proceeds in isolated populations, this results in an increase of morphological differences and eventually in genetic isolation, that is in a speciation. To assume that speciation is a punctuational process is intellectually and methodologically counterproductive, as there is no way to distinguish the real beginning of a species from a taphonomic hiatus or migrational event (Dzik 1999). In this paper we will show that such exactly is the nature of first appearances and disappearances of conodont species near the celebrated Frasnian–Famennian boundary (Klapper et al. 1993). We present results of study on a Vietnamese locality, remote in respect to the well-known European, Australian and North American sections of comparable age. The new data show that although evolutionary successions were probably recorded over vast Late Devonian oceanic realms, species successions may differ dramatically in each of them.

2. Geological setting

The Late Devonian carbonate rocks cropping out in the region at the northernmost tip of Vietnam are in continuity with those in the southern Yunnan Province of China (Qiang 1989, fig. 1). This means that in the Late Devonian the region was located near Equator probably not far from Australia (Domeier and Torsvik 2014). The lower part of the Toc Tat Formation exposed at the Si Phai Pass near Dong Van in northernmost Vietnam (105° 22′ 33.05″ 23° 16′ 54.77″) in sedimentological terms represent the Griotte facies (Königshof et al. 2017). They are mainly composed of pelagic limestone (polymict stylobreccia), consisting of tightly packed clasts of pelagic bioclastic wackestone (Königshof et al. 2017). Conodonts from the section were studied by Ta Hoa (2007) who located the Famennian-Frasnian boundary between samples S 12-8 and S 12-9 (Fig. 1) based on occurrence of *Palmatolepis triangularis* (apparently misidentified *Klapperilepis ultima*, as shown on Fig. 8K-S) in bed S 12-9. The thin-bedded part of the section composed of microbial automicrites and brownish shale layers immediately below sample S 12-8 was erroneously proposed to correspond to the Upper Kellwasser Event (Königshof et al. 2017, fig. 6).

Among samples of other sections in the area studied by ourselves only the strongly tectonically deformed Ma Pi Leng Pass (105° 24′ 37.43″ 23° 14′ 26.18″) has yielded conodonts of comparable age. The conodont elements from there are strongly deformed (Fig. 2).

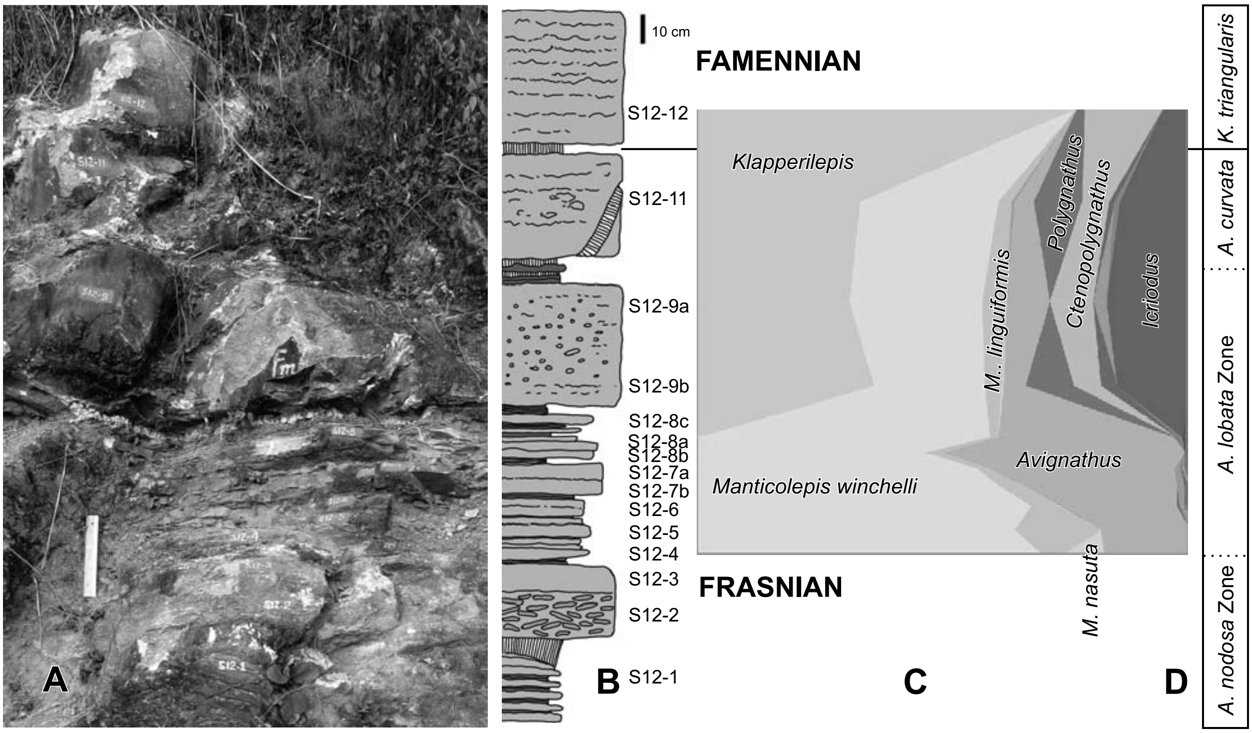

Fig. 1. Si Phai section of the Frasnian–Famennian transition. (A) Exposure with beds' numbers painted by Ta Hoa (2007). (B) Schematic presentation of the rock column with location of samples taken for this study. (C) Log of percent contribution of specimens of conodont species to samples. (D) Proposed *Ancyrodella*-based zonation for the section.

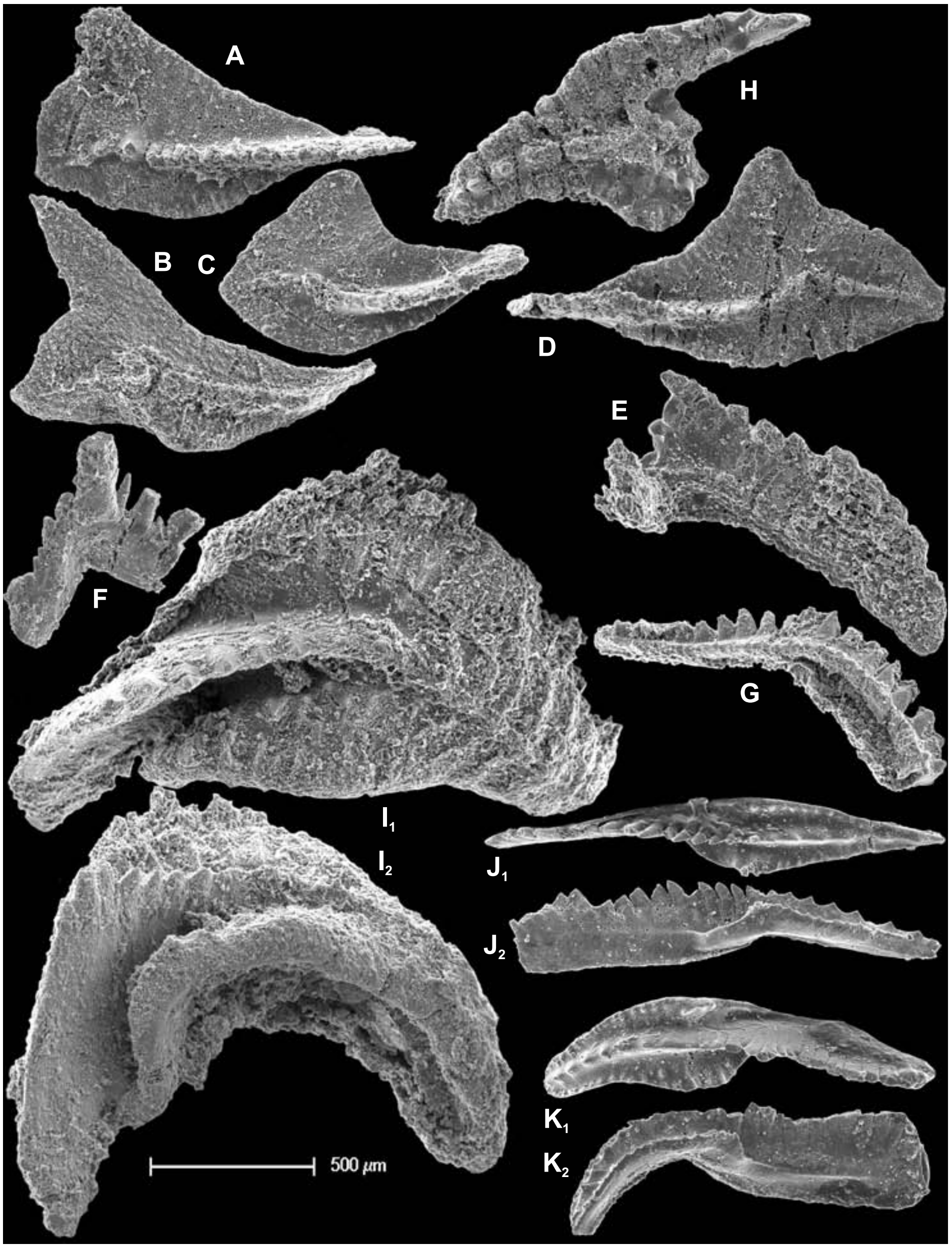

Fig. 2. Tectonically deformed elements from a sample taken from the Ma Pi Leng section. (A–E) *Manticolepis jamieae* (Ziegler and Sandberg, 1990), (A–B) P_1 elements ZPAL 25/102, 103, (C) crushed but only slightly deformed P_1 element ZPAL 25/101, (D) P_2 element ZPAL 25/112, (E) M element ZPAL 25/113. (F–H) *Kielcelepis* cf. *hassi* (Müller and Müller, 1957), (F, G) probably undeformed juvenile and strongly deformed mature P_1 elements ZPAL 25/100 and 122, (H) compressed P_2 element ZPAL 25/111. (I) *Ancyrodella nodosa* Ulrich and Bassler, 1926, P_1 element ZPAL 25/104. (J) *Parapolygnathus brevis* (Miller and Youngquist, 1947), P_1 element ZPAL 25/105. (K, L) *Polygnathus* sp. nov. Dzik, 2002, P_1 elements ZPAL 25/108 and 107.

3. Material and Methods

Sampling for this study followed the beds' numbering (Fig. 1A) of Ta Hoa (2007). Samples of about 2 kg weight were dissolved in 10–15 % formic acid. The residue was enriched for conodonts in the Franz mineralogical electromagnetic separator. Conodont elements were then picked with a wet hair mounted on a preparatory needle handle. Selected specimens were glued to SEM microscope stub with UHU stick glue and coated with carbon and platinum. The elements show color alteration index (CAI) between CAI 4 and

5 (dark brown to black) as already reported by Königshof et al. (2017). Their preservation is generally poor but varies from sample to sample. Generally, thin beds near the base of the section yielded better preserved material than the thick beds above.

Specimens are housed at the Institute of Paleobiology, Polish Academy of Sciences, in Warsaw (abbreviated ZPAL).

4. Identification of conodont apparatus species

Königshof et al. (2017) sampled the whole Si Phai section for conodonts. Our research is concentrated on the Frasnian–Famennian boundary strata. Beds of similar age are widely distributed in the Dong Van Karst Plateau as shown by a sample from Ma Pi Leng Pass (Fig. 2). It has yielded numerous conodont elements but they are strongly tectonically deformed. Resulting bizarre morphologies are difficult to interpret taxonomically. We suggest that most of the new species proposed by Savage (2013) on the basis of a similarly deformed material from near Mae Sariang, Thailand, are preservational artifacts.

It is hard to decide whether relatively high platform lobe proclination angle of a palmatolepidid P_1 element (Fig. 2C) is original or rather a result of deformation. The associated variously deformed P_2 elements with relatively high denticulation and angular bending of the dorsal process may represent the Mid Frasnian *Kielcelepis* (‘*Palmatolepis*’) *hassi* (Müller and Müller, 1957). They match with P_1 elements of generalised morphology and relatively straight carina. If true, S_0 elements with only two processes and M elements with a wide-angle disposition of processes should be expected to co-occur. Instead, the only found incomplete palmatolepidid M element shows a rather low angle between processes. Probably this kind of elements matches with another kind of P_1 elements from the sample showing a relatively large proclination angle of the posterior lobe of the platform and P_2 elements with a wide platform and low denticles, as well as the cusp. Such combination of P_1, P_2 and M elements morphology can be found only in *Lagowilepis*? (‘*Palmatolepis*’) *jamieae* as interpreted by Dzik (2002). It has to be noted that the lobe proclination angle is very variable in the Late Frasnian palmatolepidids (Dzik 2002, fig. 43) and the diagnostic utility of their P_1 elements is probably overvalued.

The only firm basis for the age determination of the Ma Pi Leng sample SS 13-2 is offered by a single P_1 element of *Ancyrodella* (Fig. 2I) that fits in the ontogenetic series of *A. nodosa* (Fig. 3E-J). This species has been already reported from the lower part of the Si Phai section by Ta Hoa (2007). *Parapolygnathus* (‘*Polygnathus*’) *brevis* and a probable member of the *Avignathus* lineage (perhaps at the stage of evolution prior to development of additional lateral processes, thus conspecific with *Polygnathus* sp. nov. Dzik, 2002) support the age determination as *A. nodosa* Zone.

The samples taken by us from the lowermost part of the Si Phai Pass exposure were barren. Presumably the layers S 12-1 to S 12-3 (the latter bed with flat pebbles) represent too shallow-water environment as for an abundant occurrence of conodonts. The lowermost productive sample is S 12-4. No palmatolepidid S_0 element has been found there and this precludes any reliable species identification of the generalized palmatolepidid, which is represented in the sample by P elements and some S elements tentatively attributed to it. The dominant morphology makes P_1 elements (Fig. 4) more advanced in developing the posterior lobe than *Lagovilepis*? *jamieae* (Ziegler and Sandberg, 1990). This places it at the level of *Manticolepis* (‘*Palmatolepis*’) *gigas* (Miller and Youngquist, 1947) as understood by Dzik (2002). In opinion of Klapper (2007a, p. 531) ‘the holotype of *Palmatolepis gigas* is best considered as just a large specimen of’ *Manticolepis* (‘*Palmatolepis*’) *winchelli*. Ziegler and Sandberg (1990) proposed origin of *M. winchelli* (their *Palmatolepis subrecta*) from *Kielcelepis hassi* (Müller and Müller, 1957) whereas *M. gigas* was proposed by them to be a successor of *L.* ? *jamieae*. These are contradictory interpretations as one is dealing probably with separate lineages strongly differing in morphology of their M elements. In the lineage classified on this basis in *Manticolepis*, the M element processes diverge at a large angle, but in *Lagovilepis* it is of A-profile. Ziegler and Sandberg (1990) gave the stratigraphic range of *P. subrecta* as starting from their Late rhenana Zone, and *P. gigas* as starting from the Early rhenana zone. Until the taxonomic status of these two chronospecies is clarified we propose to use provisionally the name *Manticolepis gigas* for early populations of the *M. winchelli* lineage.

The largest palmatolepidid P_1 element from sample S 12-4 (Fig. 4A) resembles the specimen attributed to *Palmatolepis rhenana nasuta* Müller, 1956 by Ziegler and Sandberg (1990, pl. 12:6). According to these authors (Ziegler and Sandberg 1990, p. 57) this ‘subspecies’ is characterized by terminations of the anterior (physiologically ventral) ends of the platform that

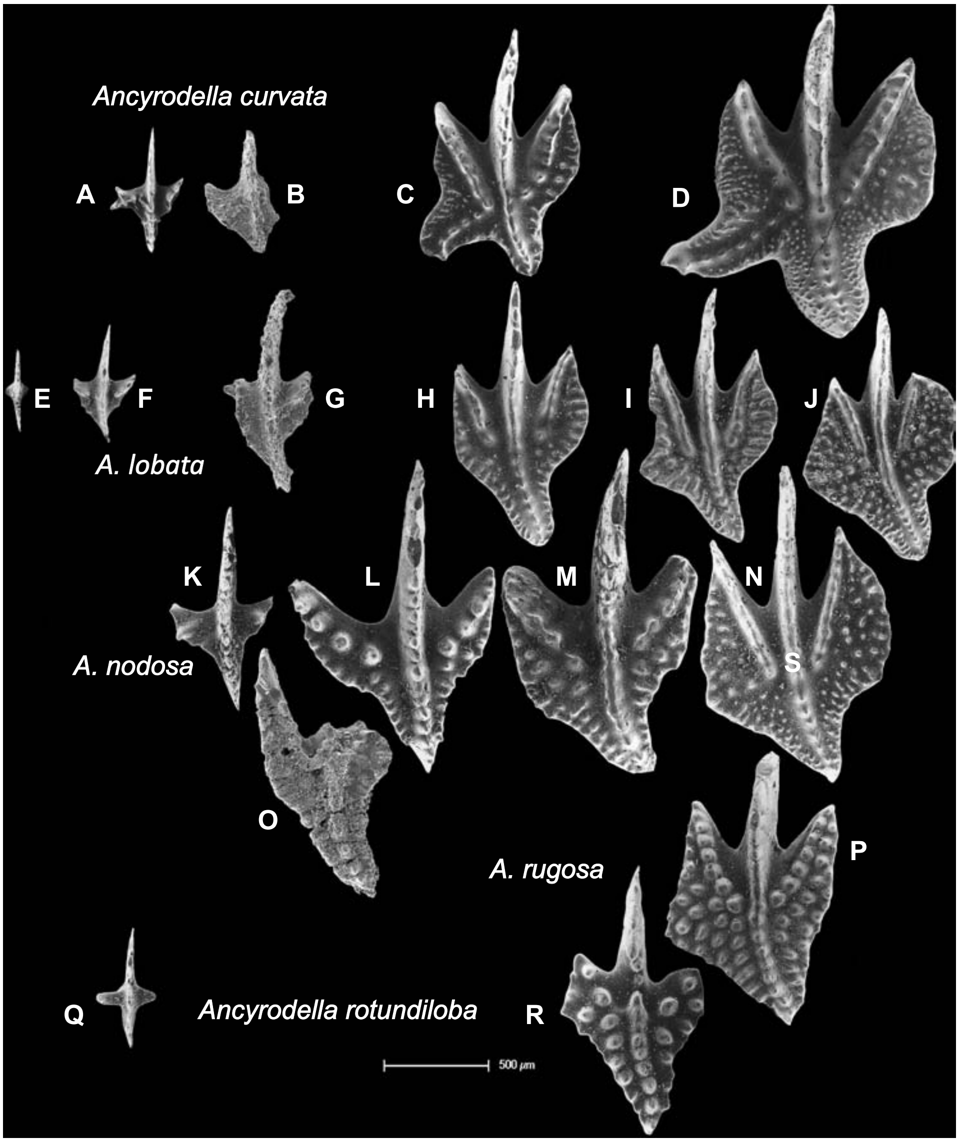

Fig. 3. P_1 elements of *Ancyrodella* from Si Phai and Ma Pi Leng fit into the succession of ontogenetic series of related species from the Holy Cross Mountains, Poland (see also Dzik 2002). (A–D) *Ancyrodella curvata* Branson and Mehl, 1934, (A, C, D) specimens ZPAL CXVI/484, 1184, and 483 from Płucki, sample Pł-391, (B) Specimen ZPAL 25/47 from Si Phai sample S 12-11. (E–J) *Ancyrodella lobata* Branson and Mehl, 1934, (E, F, H, J) specimens ZPAL CXVI/629, 630, 624, 626, 625, and 627 from sample Pł-22, (G) specimen ZPAL 25/04 from Si Phai S 12-6. (K–O) *Ancyrodella nodosa* Ulrich and Bassler, 1926, (K–N) specimens ZPAL CXVI/731, 739, 732, and 788 from Wietrznia, Poland, sample Wtr-5, (O) specimen ZPAL 25/104 from Ma Pi Leng Pass. (P) *Ancyrodella rugosa* Branson and Mehl, 1934, specimen ZPAL CXVI/854 from sample Wtr-13. (Q, R) *Ancyrodella rotundiloba* (Bryant, 1921) specimens ZPAL CXVI/1054 and 1055 from sample Wtr-11.

are not opposed and the outer (anterior) side joins the blade farther anteriorward (ventrally). Such is morphology of the platform in all the palmatolepidid P_1 specimens from sample S 12-4 (Fig. 4A, B) as well as the specimens classified as such by Ziegler and Sandberg (1990), co-occurring with the typical *Manticolepis* (‘*Palmatolepis*’) *rhenana* in the Upper Kellwasserkalk. It is unclear what generic affiliation and taxonomic rank should be given to this taxon. On text-fig. 9 in Ziegler and Sandberg (1990) it is depicted as transitional between *Palmatolepis hassi* and *P. rhenana rhenana* but on the phylogenetic diagram on their text-fig. 2, it co-occurs with the latter after its punctuational speciation near the base of the Late rhenana Zone. The beginning of this zone is defined at this event but its top on the first occurrence of *Palmatolepis lingui-*

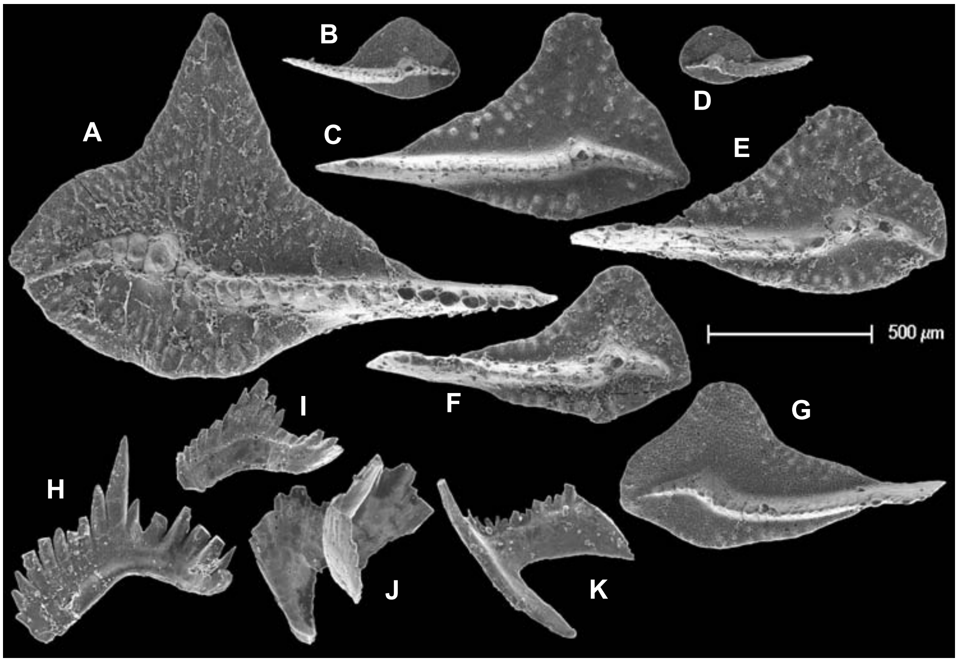

Fig. 4. *Manticolepis gigas* (Miller and Youngquist, 1947) from sample Si Phai S 12-4. (A–G) P_1 elements ZPAL 25/72, 76, 71, 77, 74, 75, and 70. (H–I) P_2 elements ZPAL 25/80 and 82. (J) S_1 element ZPAL 25/83. (K, L) S_{3-4} elements ZPAL 25/92 and 91.

formis. If taken literally, sample S 12-4 would be within the linguiformis Zone. However, specimens of unquestionable species affiliation to *M. rhenana* from the Upper Kellwasserkalk in Poland differ from these apparently much earlier forms found in Vietnam not only in the morphology of P_1 elements, which show the characteristic convexity of the platform but also in P_2 and other elements of the apparatus, characterized by a more uniform denticulation (Dzik 2002). Because of these differences and co-occurrence it does not seem likely that *M. nasuta* and *M. rhenana* represent successive chronospecies within a single lineage.

We interpret the *Manticolepis* ('*Palmatolepis*') *nasuta*-like large specimen from sample S 12-4 as an end-member of the ontogenetic series represented by smaller specimens with a shallower incision at the dorsal part of posterior lobe from the same sample (Fig. 4E).

It seems that the palmatolepidid P_1 elements with a narrow platform and acute posterior lobes occurring in the same sample (Fig. 5A, B) represent an early member of the proper *Manticolepis rhenana* (Ziegler, 1958) lineage. They do not show any convexity so typical for the population of the species from the Upper Kellwasserkalk. Associated are robust ramiform elements of the apparatus (Fig. 5), which differ from homologous elements of typical *M. rhenana* in a less regular denticulation. They may be conspecific with associated M elements of *Manticolepis* morphology but it is not possible to decide whether they belong to this species or rather to '*Palmatolepis*' *linguiformis* Müller, 1956, or perhaps even to *M. gigas*, the probable member of the *Manticolepis winchelli* lineage, both represented in the sample.

Specimens of '*P.*' *linguiformis* found in sample S 12-4 apparently represent one of the earliest records of the species (Fig. 5). They are closely similar to the holotype of *Palmatolepis linguiformis* from the lower, nodular layer of the Upper Kellwasserkalk at Schmidt quarry near Bad Wildungen, Germany (Ziegler 1973, p. 283). Despite a rather unsimilar P_1 elements outline, Ziegler and Sandberg (1990) proposed origin of '*P.*' *linguiformis* from '*P.*' *hassi*. This makes *M. rhenana* a 'sister' species of '*P.*' *linguiformis* and implies similarity in their apparatuses composition. In Europe, '*P.*' *linguiformis* is a rare species which prevents collecting enough ramiform elements to restore its apparatus. Dzik (2002, fig. 35) suggested that some ramiform elements associated with P_1 elements of the species in the Olentangy Shale at the Lazarus Camp, Ohio, belong to '*P.*' *linguiformis*. No such elements occur in Si Phai section, despite unusual richness of P_1 elements of *P. linguiformis*, which falsifies this hypothesis. Instead, the *M. rhenana*-like ramiform elements in sample S 12-4 may be associated with *P. linguiformis*, which corroborates both identification of P_2 element by Dzik (2002, fig. 35D) and the phylogenetic hypothesis of Ziegler and Sandberg (1990). Thus, *P. linguiformis* appears to be a species of *Manticolepis*.

The juvenile *Ancyrodella* P_1 element from Si Phai sample S 12-6 fits specimens of comparable size of *A. lobata* Branson and Mehl, 1934. A ramosity of lateral processes in S_0 element of the associated palmatolepidid (Fig. 6M) identifies it as the early *Manticolepis winchelli* (Stauffer, 1938). Strata of comparable age in the Holy Cross Mountains, Poland contain specimens of early *Manticolepis linguiformis* (Müller, 1956) populations as well.

In sample S 12-8b two different morphotypes of the palmatolepidid M elements occur (Fig. 6F, G, Q, R). One of them shows processes diverging at an angle of about 110° and seems to be a part of the *M. winchelli* apparatus. The other, with unusually wide disposition of processes, at angle of about 130°, must represent another species. Most likely it is *Manticolepis linguiformis* (Müller, 1956), which is the only palmatolepidid represented by P_1 elements numerous enough to make similarly high frequency of M elements likely. Also the P_2 elements with a rather uniform size of denticles may belong to this species. They are similar to homologous elements of *M. rhenana* but no its P_1 element is present in the sample.

A rather unexpected similarity of the Vietnamese conodont succession to that in Poland is expressed by the abundance of *Avignathus* ('*Polygnathus*') *decorosus* (Stauffer, 1938) in the part of the section where *An-*

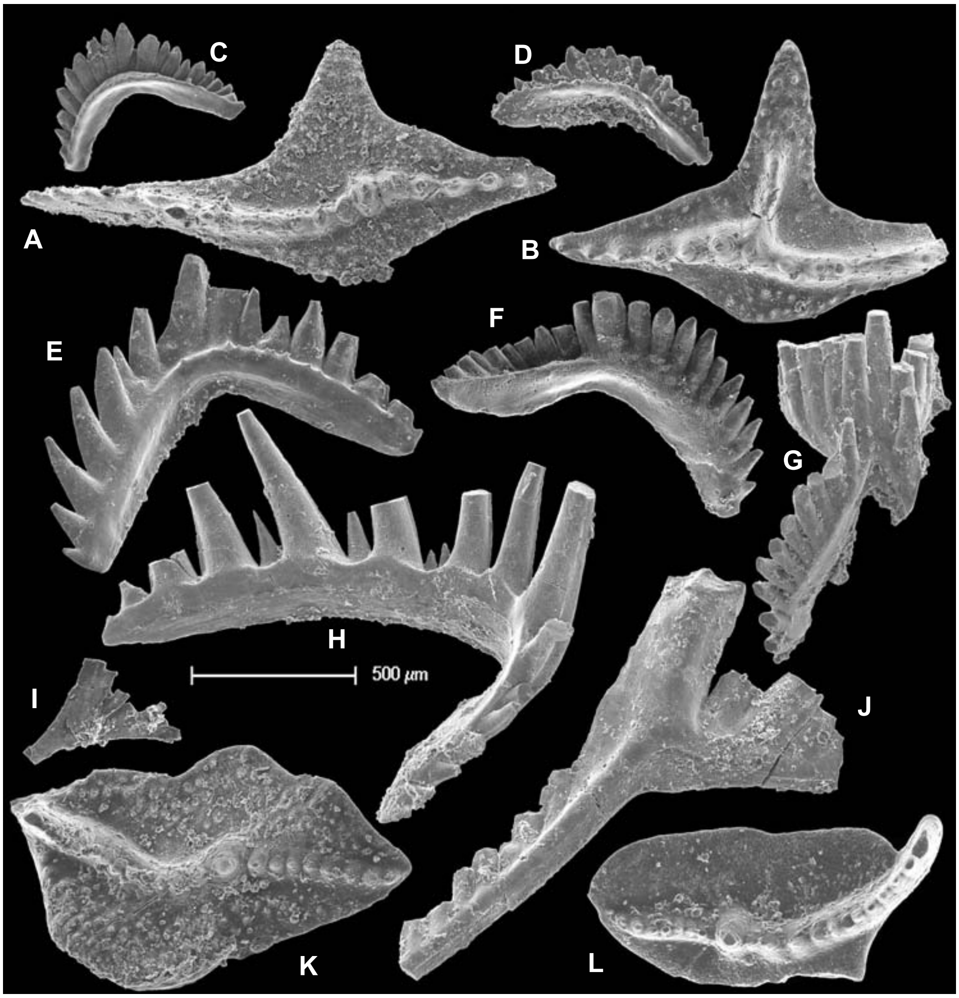

Fig. 5. Advanced palmatolepidids from sample Si Phai S 12-4. (A–J) *Manticolepis rhenana* (Ziegler, 1958), (A, B) P_1 elements ZPAL 25/86 and 88, (C–F) P_2 elements ZPAL 25/90, 89, 93, and 79, (G) S_1 element ZPAL 25/94, (H) S_{3-4} element ZPAL 25/97, (I, J) M elements ZPAL 25/85 and 98. (K, L) *Manticolepis linguiformis* (Müller, 1956), P_1 elements ZPAL 25/92 and 91.

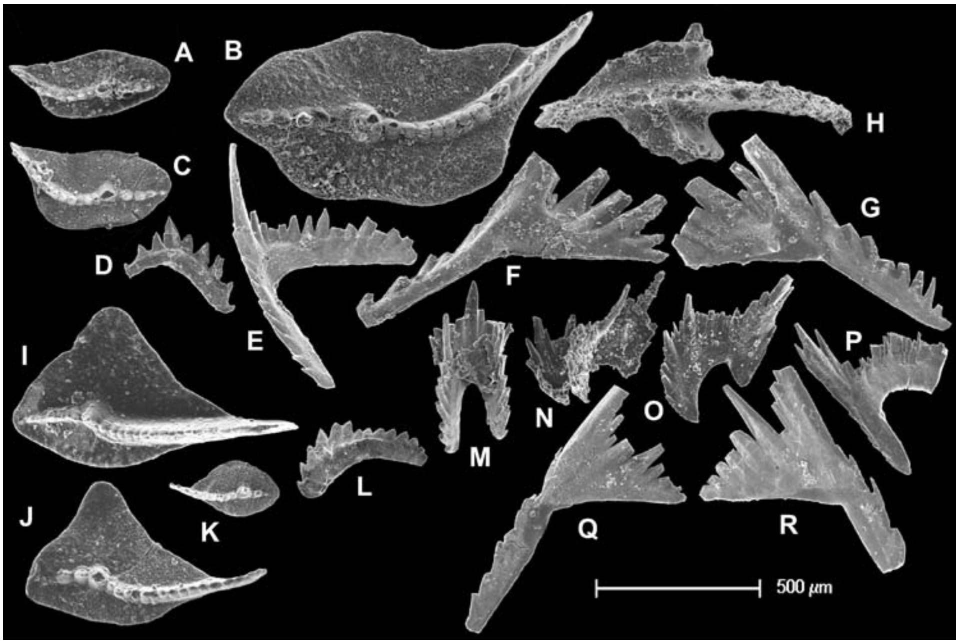

Fig. 6. (A–G) *Manticolepis linguiformis* (Müller, 1956) from samples Si Phai S 12-6 (A, B) and Si Phai S 12-8b (C–G), (A–C) P_1 elements ZPAL 25/02, 03, and 34, (D) P_2 element ZPAL 25/35, (E) $S_{3–4}$ element ZPAL 25/38, (F, G) M elements ZPAL 25/36 and 37. (H) *Ancyrodella lobata* Branson and Mehl, 1934; juvenile P_1 element from sample Si Phai S 12-6, ZPAL 25/04. (I–R) *Manticolepis winchelli* (Stauffer, 1938) from sample Si Phai S 12-8b, (I, K) P_1 elements ZPAL 25/26, 24 and 25 (L) P_2 element ZPAL 25/28, (M) S_0 element ZPAL 25/27, (N) S_1 element ZPAL 25/29, (O) S_2 element ZPAL 25/30, (P) aberrant $S_{3–4}$ element ZPAL 25/31, (Q, R) M elements ZPAL 25/33 and 32.

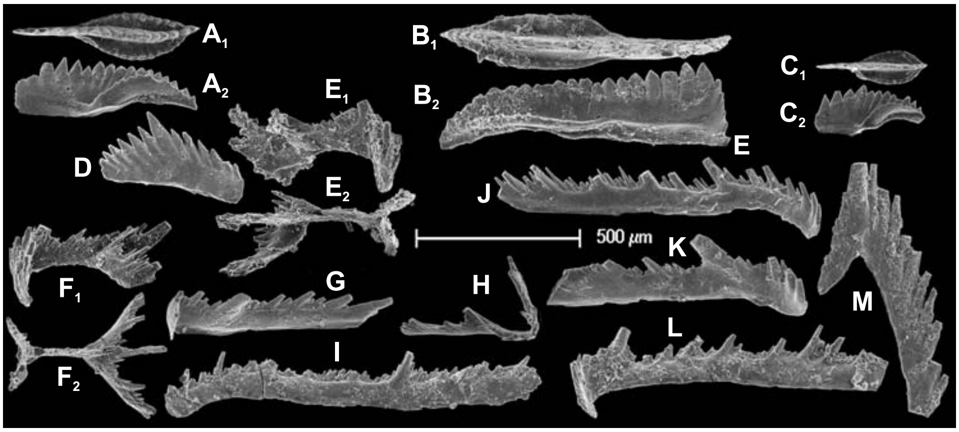

Fig. 7. *Avignathus decorosus* (Stauffer, 1938) from samples Si Phai S 12-8a (A–C) and Si Phai S 12-8b (D–M). (A–C) P_1 elements ZPAL 25/20, 18 and 21. (D) P_2 element ZPAL 25/17. (E, F) S_0 elements ZPAL 25/15 and 13. (G, H) S_1 elements ZPAL 25/11 and 12. (I, J) S_2 elements ZPAL 25/06 and 07. (K, L) $S_{3–4}$ elements ZPAL 25/08 and 09. (M) M element ZPAL 25/10.

cyrodella lobata occurs. This is a bizarre species characterized by additional lateral processes in S_0 elements (Fig. 7). The remaining part of the apparatus is as in a generalized polygnathid (van dem Boogaard 1983). Elements are gracile in form. In the Holy Cross Mountains this species seems to be replaced, probably phyletically, by *Avignathus bifurcatus* Dzik, 2002, distinct in having the medial process of S_0 element reduced immediately in front of the bifurcation. Unfortunately, only one fragmentary S_0 element lacking the diagnostic process has been found in the bed with *Ancyrodella curvata* at Si Phai (sample S 12-11).

There is a dramatic change in conodont species composition between samples S 12-8a and S 12-9b, which probably misled Ta Hoa (2007) who placed there the Frasnian–Famennian boundary. A set of generally shallow-water species of *Icriodus*, *Ctenopolygnathus*, and *Polygnathus webbi* Stauffer, 1938 entered the environment that time together with abundant *Klapperilepis ultima* (Ziegler, 1958). Other palmatolepidids remained at the place and the whole assemblage achieved status similar to that of the European Upper Kellwasser Event assemblage. Most of the *K. ultima* P1 elements are juveniles with a relatively narrow platform as for the species. Savage (2013) identified "*Palmatolepis ultima*" in his sample 11B from the geographically closest locality near Mae Sariang, Thailand, where it co-occurs with "*Palmatolepis triangularis*" and eight other palmatolepidid species. Such assemblage composition is typical for the late triangularis Zone (Ziegler and Sandberg 1990; Klapper 2007b). Apparently, these taxa have been understood by Savage (2013) as morphotypes within the population variability of biological species.

Sample Si Phai S 12-11 yielded a juvenile specimen of *Ancyrodella* (Fig. 3B; 8F), with incipient bifurcation of the anterior lobe, a characteristic aspect of *A. curvata* Branson and Mehl, 1934. As expected, it is associated with *M. linguiformis* but contrary to the generally held opinion (e.g., Klapper 2007b) *M. linguiformis* is hardly diagnostic for the latest Frasnian age as it occurs throughout the whole Si Phai section. Its contribution to samples is many times higher than in corresponding strata in Europe. As commented above, P_1 elements of *M. linguiformis* co-occur in sample S 12-4 with specimens probably representing an

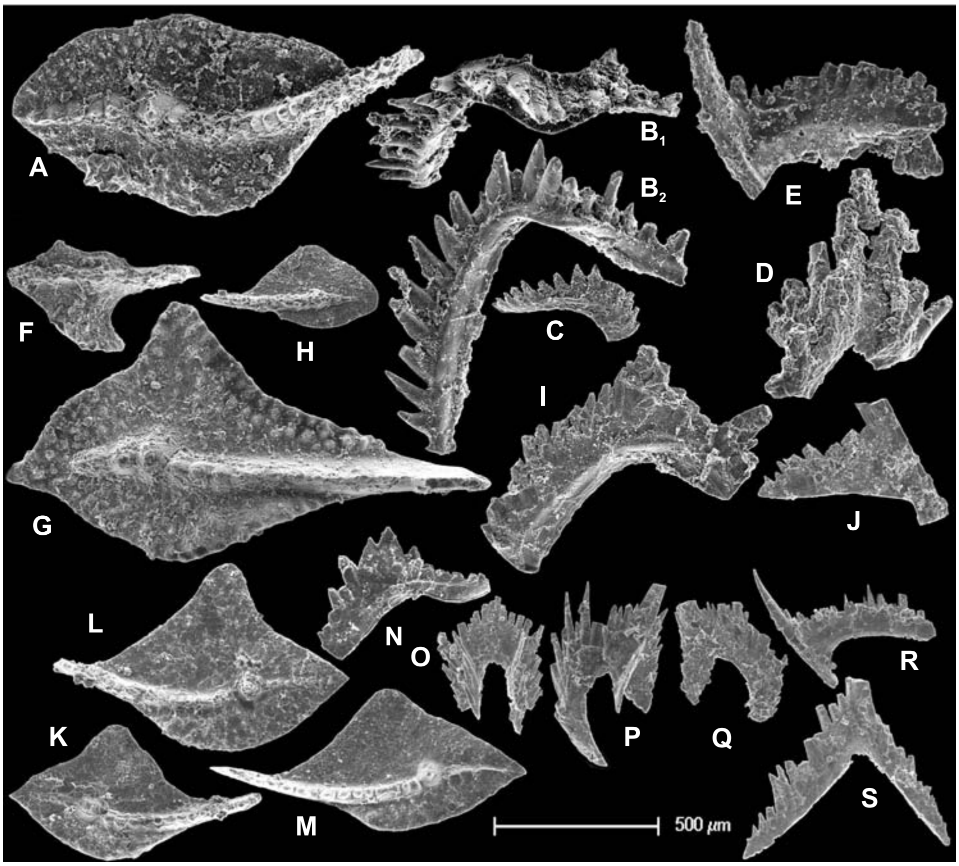

Fig. 8. (A–E) *Manticolepis linguiformis* (Müller, 1956) from sample Si Phai S 12-9b, (A) P_1 element ZPAL 25/39, (B) P_2 element ZPAL 25/40, (C) juvenile P2 sample S 12-9a ZPAL 25/114, (D) S_0 element ZPAL 25/42, (E) S_{3-4} element ZPAL 25/44. (F) *Ancyrodella curvata* Branson and Mehl, 1934 from sample Si Phai S 12-11, P_1 element ZPAL 25/47. (G–J) *Manticolepis winchelli* (Stauffer, 1938) from sample Si Phai S 12-11, (G–H) P_1 elements ZPAL 25/45 and 50, (I) P_2 element ZPAL 25/51, (J) M element ZPAL 25/52. (K–S) *Klapperilepis ultima* (Ziegler, 1958), sample S 12-9b (K–R) and 9a (S), (K–M) P_1 elements ZPAL 25/115, (N) P_2 element ZPAL 25/116, (O) S_0 element ZPAL 25/117, (P) S_1 element ZPAL 25/118, (Q) S_2 element ZPAL 25/121, (R) S_{3-4} element ZPAL 25/119, (S) M element ZPAL 25/120.

early population of its probably sister species *M. rhenana*, which prevents separation of their apparatuses elements. Single elements P_1 of morphology typical for the late *M. rhenana* has been encountered in samples S 9-6 and S 12-9b but elements P_2 from these and neighbouring samples differ from those associated with *M. rhenana* in the Polish Upper Kelwasserkalk. Their processes are elongated and high-arched, also the outline of the platform in occlusal view is sinuous (Fig. 8). Altogether ninety P_1 specimens of *M. linguiformis* have been collected at Si Phai and only five of the *M. rhenana* group. This makes likely that associated other apparatus elements belong rather to the former species than to the latter. Possibly, there is an evolutionary change in morphology of P_2 elements from sample S 12-6 to S 12-9b but the material is too small to prove this suspicion. Although an almost complete set of elements possibly representing the *Manticolepis linguiformis* apparatus has been assembled, the number and preservation of ramiform elements are not sufficient to enable anything more than just its tentative reconstruction. We present it here to stimulate its falsification or corroboration.

The topmost bed of the Si Phai succession (sample S 12-12) contains *Klapperilepis* as the only palmatolepidid (Fig. 9). There is a continuity in its population variability in this Famennian sample, thus it seems that only one species is represented. The modal length to width ratio is apparently higher than in the Frasnian *K. ultima* from underlying samples 9b, 9a and 11 although population variability is invariably large. This makes sample S 12-12 similar not to that immediately above the Frasnian–Famennian boundary at Płucki in the Holy Cross Mountais, Poland (Dzik 2002, fig. 47, sample Pł-20) but to that from the bed above, prior to the immigration of other Famennian species of *Klapperilepis* (sample Pł-16). This may substantiate attribution of specimens from sample S 12-12 to the *K. triangularis* chronospecies. Even if the calcite vein below the bed 12 corresponds to a tectonic gap, its extend was probably insignificant as long as the Si Phai succession remains comparable to that observed in the Płucki section in the Holy Cross Mountains (Dzik 2002, 2006).

5. Ecological succession

The conodont assemblages from the basal part of the Si Phai section differ from those of comparable age in central Europe in their low taxonomic diversity. This refers mostly to the virtual lack of the icriodontids, and the *Polygnathus webbi* group (Fig. 10), diverse at this time in Europe. In Vietnam, *Avignathus* and *Manticolepis* dominated. Both lineages had apparently roots in strata preceding those exposed at the Si Phai pass, as shown by composition of the Ma Pi Leng pass sample. Probably local bathymetric and climatic factors supplemented the global ones there. The presence of *Belodella* suggests that this was a sea shallowing (Sob-

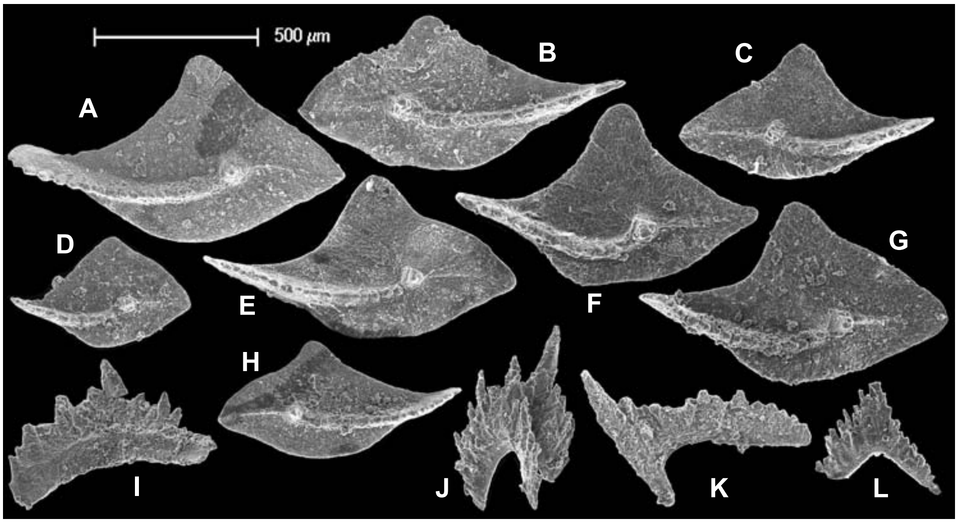

Fig. 9. *Klapperilepis triangularis* (Sannemann, 1955) from sample Si Phai S 12-12. (A) P_1 element ZPAL 25/54, 55, 60, 61, 56, 58, 59, and 57. (I) P_2 element ZPAL 25/62. (J) S_1 element ZPAL 25/63. (K) S_{3-4} element ZPAL 25/64. (L) M element ZPAL 25/64.

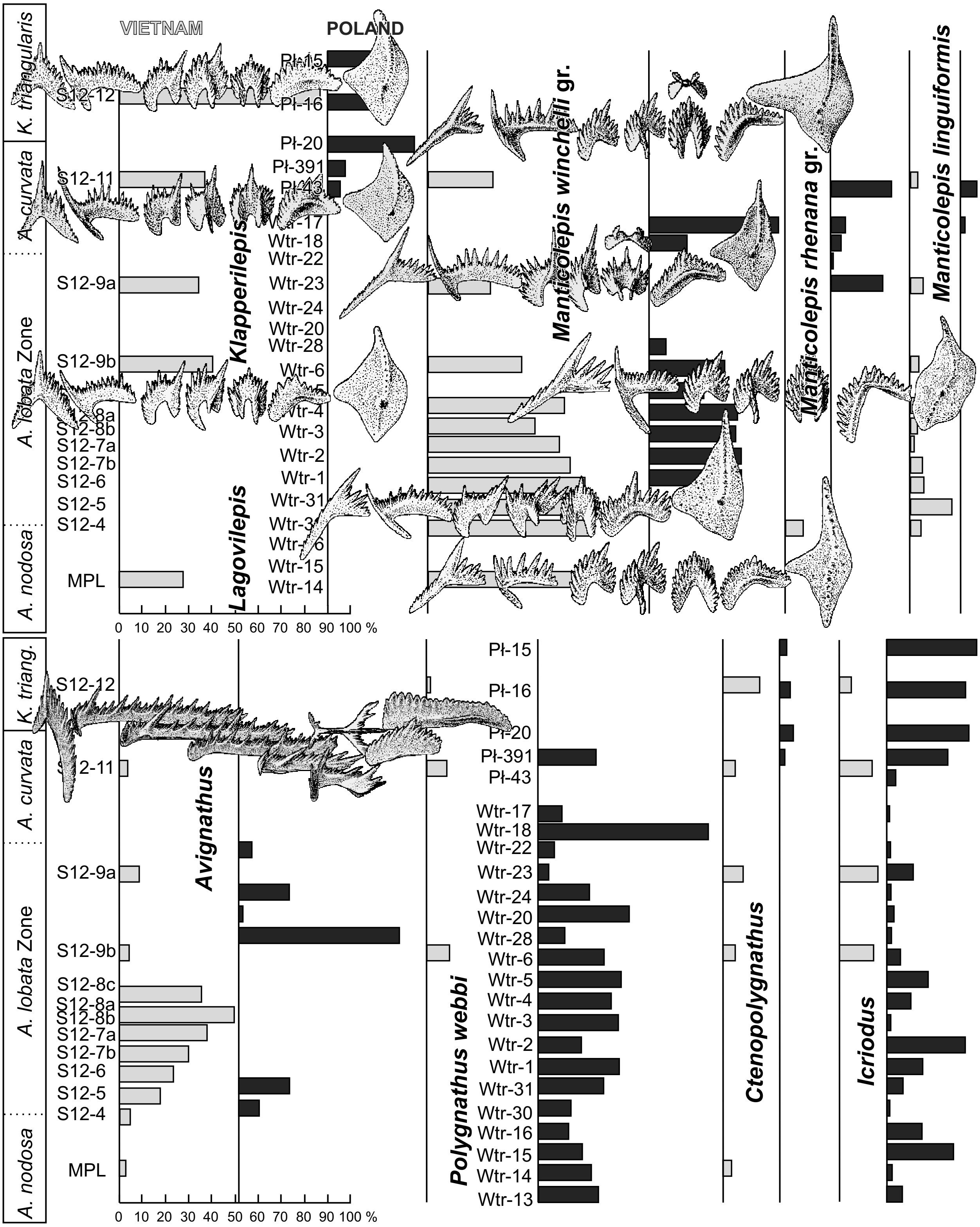

Fig. 10. Pairwise comparison of percent contribution of conodont elements representing biostratigraphically the most important lineages between the Si Phai and Ma Pi Leng (MPL) sections in Vietnam and the corresponding part of Wietrznia and Płucki sections in the Holy Cross Mountains, Poland. Diagrammatic representation of the palmatolepidids apparatuses are shown in the upper part of the figure, *Avignathus* below.

stel et al. 2006). Most importantly, *Manticolepis linguiformis* occurs continuously and in relatively high numbers throughout the *Ancyrodella lobata* and *A. curvata* ranges. This probably refers also to *M. rhenana* represented by few specimens in the succession.

Another transformation of the environment and conodont communities resulted in a dramatic increase of species diversity. *Icriodus* and *Ctenopolygnathus* increased their contribution to the assemblage. The *Klapperilepis* lineage entered the Vietnamese sea. Possibly this corresponds with its emergence in the Lower Kellwasserkalk of the Płucki section in the Holy Cross Mountains (Rakociński et al. 2016, fig. 3T mislabeled as *Polygnathus webbi*). The apparent increase of contribution of *Avignathus* to the Holy Cross Mountains assemblages in the upper part of *Ancyrodella lobata* range correspond to an environmental change of unknown nature. The Kellwasser Event in Vietnam is unlike that in Europe in showing high contribution from *Klapperilepis ultima* and *Manticolepis linguiformis*, together dominating over *Manticolepis winchelli*. *M. linguiformis* is a relatively common species, in respect to associated palmatolepidids, also in Thailand (Savage 2013, Mae Sariang sample 18A) as a member of an assemblage dominated with *Avignathus* and *Ancyrodella*.

The Frasnian–Famennian boundary has the same nature in Europe and Vietnam. In both regions all but *Klapperilepis* palmatolepidids disappeared.

6. Discussion

Klapper (2007b), in his seminal review of difficulties with defining the Frasnian–Famennian boundary, explicitly presented the methodological aspect of the biostratigraphic inference he uses. His discussion refers to two sets of palmatolepidid species. One pair is ‘*Palmatolepis*’ *ultima* and ‘*P.*’ *triangularis*, the other is ‘*P.*’ *winchelli* and ‘*P.*’ *bogartensis*. According to him, ‘*Palmatolepis ultima* appeared abruptly in the higher part of Frasnian Zone 13c as a result of punctuated evolution. This follows from the observation that there does not seem to be an obvious ancestral species in Frasnian Zone 13’ (Klapper 2007b, p. 69). On his text-fig. 1, ‘*P.*’ *ultima* originated after extinction of ‘*P.*’ *linguiformis*. Evidently such is the actual succession of species in sections studied by him but in Polish sections the ranges of these two species strongly overlap; in fact they appear together in the Lower Kellwasserkalk, although admittedly their contribution to the fossil assemblage is very low (Dzik 2002). In Vietnam, the range of ‘*P.*’ *linguiformis* extends even deeper in time. It begins with the conodont fossil record in the exposure. One may guess that its origin from the ancestral member of the *Manticolepis rhenana* lineage took place much earlier. This is evidenced by co-occurrence of already developed *M. linguiformis* with its sister lineage without interbreeding, as evidenced by the lack of transitional morphologies. There was enough time to develop a genetic barrier between them. Actually, the ingression of ‘*P.*’ *ultima* in Vietnam coincides with a significant environmental change expressed in composition of the whole conodont community. It was an immigration, not ‘punctuated evolution’.

Both in Poland and Vietnam the ‘*P.*’ *ultima* lineage crosses the Frasnian/Famennian boundary without any recognizable modification of its morphology or apparatus structure (Dzik 2002, 2006) despite environmental factors (e.g., Joachimski et al. 2001) that caused elimination of other palmatolepidid lineages probably worldwide. Its ‘flood abundance’ (e.g., Klapper 2007b) is an artifact of disappearance of other palmatolepidid species, not a real increase in productivity. In fact, the ecospace left after disappearance of other palmatolepidids and *Polygnathus webbi* was filled by prioniodinids, platformless polygnathids and icriodontids (Dzik 2002, fig. 48). There was no real acme. The post-Frasnian history of the lineage was biometrically documented by Dzik (2002, fig. 47). Initially, the probable release of competition pressure from other palmatolepidids resulted in an increased population variability. Then the immigration of already genetically isolated populations rooted in *Klapperilepis ultima* resulted in a character displacement. In effect, a narrower platform morph started to dominate in the main lineage, referred to as *K. triangularis*. But this means that both *K. ultima* and *K. triangularis* are chronospecies, that is arbitrarily demarcated segments of a continuous lineage.

The relationship between ‘*P.*’ *winchelli* and ‘*P.*’ *bogartensis* is of fundamentally different nature. These are co-occurring, genetically isolated true biological species. They differ not so much in the morphology of their P_1 elements as in the M and especially S_0 ones. As shown by biometrics of a very large sample from the Upper Kellwasserkalk at Płucki in the Holy Cross Mountains, Poland (Dzik 2002, fig. 43) there is a complete gradation between morphologies arbitrarily chosen as typical for each of these species. The sample is overdominated with ‘*P.*’ *bogartensis*: 232 of the most characteristic M elements of this species have been found and only 2 such elements of ‘*P.*’ *winchelli* (Dzik

2002, table 5). The ancestry of '*P.*' *winchelli* seems rather obvious. It is rooted in populations with closely similar M elements morphology but with a weak bifurcation of lateral processes in S_0 elements, referred to as *Manticolepis gigas* in Dzik (2002). In Vietnam the lineage continues throughout the Si Phai Frasnian portion of the exposure.

Lagovilepis ('*Palmatolepis*') *bogartensis* is characterized by a rather primitive appearance of M elements and the S_0 elements lacking any bifurcation. This difference in the apparatus structure is so deep that using taxonomic criteria applied to apparatus conodont taxa in other geological periods its separation to another genus is hard to avoid (unless the Devonian conodont taxonomy is based on different principles that that of other periods). The ancestry of *L. bogartensis* is not as apparent as that of *M. winchelli*. *Lagovilepis jamieae* as understood by Dzik (2002) is its predecessor and possible ancestor. There is only a small time gap in their ranges in the Holy Cross Mountains but they occur in different environments (Dzik 2002, fig. 49). This lineage seems to be missing in Vietnam.

The available data on the distribution of palmatolepidid species in the Si Phai section provide evidence for only one stratigraphic datum that can be safely determined. This refers to the disappearance of *Manticolepis* species between samples S 12-11 and S 12-12. The application of other markers proposed by Ziegler and Sandberg (1990) to be the basis of their Late Devonian Standard Zonation fails because the appearances and disappearances of conodont species in Si Phai (and most other sections of the world; Dzik 1995) reflect immigration rather than evolutionary events. This is most striking in the cases of *Klapperilepis ultima* and *M. linguiformis*. Both appear in Si Phai well before the Upper Kellwasser Event, the latter being present almost throughout the section in relatively high numbers. To date the actual succession of events more precisely one needs an independent source of evidence.

It appears that as usual, local appearances of all these lineages both in Poland and Vietnam are controlled by environmental changes and are useless for global rank correlative purposes. The only alternative to the palmatolepidid appearances in the Si Phai section are rarely occurring *Ancyrodella* species. They are represented only by juvenile P_1 specimens (Table 1) but owing to the standard succession in the Holy Cross Mountains it seems possible to use them for the age correlation based on the evolutionary succession (Fig. 3), which is less precise than correlation based on environmental signals but more reliable.

7. Conclusions

Two aspects of the Si Phai section conodonts make them of interest. The first one is that the relatively, as for the Late Devonian, balanced samples enable at least tentative restoration of the apparatus composition. No doubt that other than P_1 elements of the apparatus provide information of high taxonomic value, in many cases enabling identification of species otherwise undeterminable (e. g., Lange 1968; van dem Boogaard 1983; Metzger 1994; Schülke 1995, 1999; Dzik 2002, 2006). There is no excuse for ignoring such evidence.

The second issue that has to be highlighted in connection with the Vietnamese conodont succession is that ranges of particular species are clearly diachroneous in respect to the record in other localities, considered to represent reference standard for the Late Devonian biostratigraphy. This should not be a surprise. It is rather obvious that distribution of fossils in sedimentary strata is controlled mainly by environmental conditions, not necessarily strictly expressing differences in time. This means that influence of both these factors making fossils useful in determining the geological age of strata has to be considered.

Even a very fast and subtle change of the environment may find expression in distribution of fossil species. They did not differ in this respect from extant ones. Horizontal shifts of habitats are the main cause of organisms' migrations. Increase or lowering of biological productivity of particular species in the community may change proportions of skeletons supplied by them to the sediment. This line of reasoning offers opportunity to obtain a very fine temporal subdivision of the fossil record. The only problem is that such changes are reversible and not specific. The same pattern may be endlessly repeated with, say, rhythmic changes of the environment. The problem then emerges, which of the acmes in one rock section corresponds to that in another section? Magnetostratigraphy and geochemistry suffers from the same pitfall of being based on events that are not unique.

A different limitation is imposed on species successions caused not directly by the environment but connected solely with the passing geological time. These are mostly evolutionary transitions. Because phyletic evolution is very slow ('Haldane Paradox' of Levinton 2001) inference based on such data does not allow resolution comparable to that offered by environmentally controlled succession. But evolutionary changes are unrepeatable and unique. This is a directional

Table 1 Distribution of conodont elements in samples from the Si Phai section.

Sample		**4**	**5**	**6**	**7b**	**7a**	**8b**	**8a**	**9b**	**9a**	**11**	**12**	**Sum**
Belodella robusta	P, S						2	1					3
Belodella devonicans	P, S			3	3	9	5	5					26
	M			1									
Belodella minutidentata					1	1		1					3
Guizhoudella	S_0										1		1
Icriodus sp.	P_1								33	19	72	3	181
	P_2, M				1	1	1		20	6	22	3	
Ligonodina sp.	P_1												15
	P_2					1					1		
	S_0					2		2					
	S_1					1					4		
	S_2					1							
	S_{3-4}							2			1		
	M												
Pluckidina sp.	P_1												26
	P_2					1							
	S_0			1	1	2		1		2			
	S_1					1				1			
	S_2				4	1							
	S_{3-4}	1			4	1				1			
	M			1	1	2							
Dyminodina sp.	P_1								1				20
	P_2								2				
	S_0			1	1								
	S_1			1							2		
	S_2								4				
	S_{3-4}								3				
	M								1		4		
Ctenopolygnathus sp.	P_1								8	2	20	9	86
	P_2								2	1	5	3	
	S_0								1	3	1	2	
	S_1								1	2	3		
	S_2								1	1	1		
	S_{3-4}								4	1	4	3	
	M								2	3	2	1	
Polygnathus webbi	P_1							1	4		29	2	106
	P_2								1		8		
	S_0								3		3		
	S_1								4		9		
	S_2								6		4		
	S_{3-4}								12		5		
	M								6		9		

Table 1 Continued.

Sample		**4**	**5**	**6**	**7b**	**7a**	**8b**	**8a**	**9b**	**9a**	**11**	**12**	**Sum**
Avignathus spp.	P_1	30	5	50	84	98	108	68	11	5	16		1125
	P_2	2		2	8	22	13	11			4		
	S_0			2	3	19	33	9			1		
	S_1			3	12	15	30	7					
	S_2			3	11	36	53	13	1	3			
	S_{3-4}	2	2	7	26	46	98	27	1	4	1		
	M			4	20	31	40	18	3	1	3		
Ancyrodella spp.	P_1			1							1		2
	P_2												
	S_0												
	S_1												
	S_2												
	S_{3-4}												
	M												
Parapolygnathus brevis	P_1												0
	P_2												
	S_0												
	S_1												
	S_2												
	S_{3-4}												
	M												
Manticolepis rhenana group	P_1	3		1					1				18
	P_2	4											
	S_0	1											
	S_1	1											
	S_2												
	S_{3-4}	3											
	M	4											
Manticolepis linguiformis	P_1	5	1	10	19	8	16	5	4	6	16		148
	P_2	2	1	1			1		1	1	1		
	S_0												
	S_1		1	1	1			3	4				
	S_2	1	1	1									
	S_{3-4}		2	2	4	1	5		4		4		
	M	2	2	3	3	4				1			
Manticolepis winchelli group	P_1	105	19	171	222	250	218	190	64	33	139		2000
	P_2	21	1	5	10	11	5	7	8	6	9		
	S_0		1	2	15	11	10	3			3		
	S_1			4	17	19	23	5			7		
	S_2	3		2	20	22	11	4			6		
	S_{3-4}	6	2	8	28	41	44	16			8		
	M	4	2	12	19	43	39	27	7	1	11		
Klapperilepis spp.	P_1								105	31	164	68	470
	P_2								9	6	33	7	
	S_0												
	S_1								1	2	2	2	
	S_2								2	2	3	2	
	S_{3-4}								6	2	5	2	
	M								3	2	6	5	
Sum		**199**	**39**	**302**	**539**	**701**	**756**	**427**	**354**	**148**	**653**	**112**	

process, that could be to some degree compared with radioactive decay. This gives evolutionary inference a high degree of confidence and makes first (FADs) and last (LADs) occurrences in the rock sections not reliable.

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