Famennian (Upper Devonian) conodont zonation: revised global standard

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The revision of the Famennian part of the "Late Devonian Standard Conodont Zonation" is based on the in-equivalence between biozones and time, and the rejection of the presumed single phyletic concept on which the previous zonation was based. It is also intended to simplify the zonation, eliminating the zonal groups named after only one taxon, and biozones that are defined by a Last Appearance Datum (LAD). The proposed revision is largely based on the zonation proposed by Ziegler and Sandberg (1990) and is for the most part correlatable using the same zonal markers. Modifications have only been made when strictly necessary, as the aim of the proposal is to maintain the stability of over 50 years of studies. The 22 zones constituting the revised zonation are defined by the First Appearance Datum (FAD) of species or subspecies that have a well-established stratigraphic range and wide geographic distribution. Each zone is named after the taxon for which the FAD defines the lower boundary. For each zone an association of other species useful for its identification is listed. • Key words: conodonts, Upper Devonian, Famennian, biostratigraphy, biozonation.

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The "Late Devonian Standard Conodont Zonation" of Ziegler & Sandberg (1990), based mainly on the zonation first proposed by Ziegler (1962), utilized a definition of biozones that implies a correspondence with a timespan, against the rules of the International Stratigraphic Guide. This assumes a short time of worldwide diffusion of pelagic species, and the occurrence of species to be near synchronous. It should be clear that a biozone is not a time interval but bodies of strata defined or characterized on the base of their fossil content. A comprehensive discussion on the problem of considering a biozone as equivalent to time is reported in Johnson (1992), for detailed information about terminology see also Owen (1987, 2009).

Ziegler & Sandberg (1990) defined the base of each Upper Devonian conodont zone by "the first occurrence of a diagnostic species that can be or not the zonal name giver", although the base of two zones is defined by the extinction of taxa. The top of each zone was defined by "the first occurrence of another diagnostic species or subspecies which preferably is the phyletically next younger taxon" (Ziegler & Sandberg 1990, p. 12). The correspondence of a biozone with a timespan was "silently" rejected by most conodont workers studying the Upper Devonian, as they continued to use the terms Lower and Upper for the zones, instead of Early and Late as suggested by Ziegler & Sandberg (1990). Apart from this, the "Late Devonian Standard Conodont Zonation" has been widely used since its publication. In the following text, the original zones of Ziegler & Sandberg (1990) will be cited as Lower, Middle, Upper and Uppermost instead of using the original denomination Early, Middle, Late and Latest, as in Fig. 1.

The Frasnian part of the "Standard Zonation" is the result of subsequent revisions of the original zonation of Ziegler (1962, 1971) by Sandberg *et al*. (1988, 1989) and Ziegler & Sandberg (1990). The scheme is still widely used, but it could, and should, be easily substituted by the Frasnian zonation initially proposed by Klapper (1989) for the Montagne Noire and then demonstrated to be valid worldwide by Klapper & Foster (1993), Klapper *et al.* (1996, 2004), and Klapper (2007a). The zonation of Klapper (1989) is based on taxonomic concepts different from those used by Ziegler & Sandberg (1990). For the

identification of species Ziegler and Sandberg, as common practice for Late Devonian faunas, used visual discrimination of P1 (= Pa) elements; Klapper used multielement taxonomy and shape analysis of P1 elements, as well as visual discrimination for zone defining taxa. Zones were delineated by the FAD of species of different genera, several considered by Ziegler & Sandberg (1990) to inhabit more shallow water environments (*e.g. Ancyrodella* and *Ancyrognathus*) than *Palmatolepis* and *Mesotaxis*, which predominate in pelagic environments. Klapper (1989, 1997) demonstrated with graphic correlation that first occurrences of species of *Ancyrodella, Ancyrognathus*, and *Ozarkodina* are as consistent as those of *Palmatolepis* species. The Frasnian zonation (FZ) of Klapper (also known as Montagne Noire Zonation) consists of thirteen zones, the last of which (Frasnian Zone 13) was subdivided into three parts by Girard *et al*. (2005). The FZ is a more detailed subdivision of the Frasnian in respect to the "Standard Zonation", which is composed of nine zones. The graphic correlation scheme for the Frasnian allows an even finer biostratigraphic resolution than 15 zones, but only where faunas are abundant and where sampling is dense. Despite the opinion of some authors (*e.g.* Ziegler & Sandberg 1994) that it is impossible to correlate the two zonal schemes, Klapper & Becker (1999) demonstrated numerous equivalencies and corresponding intervals based on the re-sampling of the Martenberg section – one of the reference sections of Ziegler & Sandberg (1990). The supposed difficulty of applying the taxonomic concept of Klapper is inconsistent as the Frasnian Zonation can be quite easily applied using the "traditional" identification of conodonts through visual discrimination of only the P1 element.

The Famennian part of the "Standard Zonation" of Ziegler & Sandberg (1990) includes subsequent additions and slight modifications of the original zonation of Ziegler (1962) by Ziegler (1969), Sandberg & Ziegler (1973), Sandberg *et al*. (1978, 1989), and Ziegler & Sandberg (1984).

Ziegler & Sandberg (1990) suggested that a zone can be recognized by a distinctive association of conodont elements in the absence of the diagnostic taxon. This suggestion allowed a wide use of the Famennian part of their zonation in the last decades. After the extinction event at the top of the Frasnian, conodonts rapidly recovered and spread worldwide with many representatives of the pelagic genus *Palmatolepis*.

One of the zonal markers of the "Standard Zonation", *Scaphignathus velifer velifer* Helms, already used by Ziegler (1962), was not considered a pelagic species, but an inhabitant of shallow water environments. Ziegler & Sandberg (1984) discussed possible biofacies influences on the formal zonal scheme, but kept *Scaphignathus velifer velifer* as the marker of the Uppermost *marginifera* Zone that replaced the *velifer* Zone of Ziegler (1962). Hartenfels (2011) and Hartenfels & Becker (2016) confirmed that it is a typical dweller of pelagic facies in southern Morocco, reaching frequently the deepest part of the basin.

The lower boundary of two other biozones of Ziegler & Sandberg (1984, 1990) was defined by the LAD of representatives of *Palmatolepis*. The definition of the lower boundary of the Upper *rhomboidea* Zone corresponds to the extinction of *Palmatolepis poolei* Sandberg & Ziegler. The identification of the base of the Upper *rhomboidea* Zone is difficult where *Pa. poolei* – a rare taxon – is not present, as in most sections in the Carnic Alps, Germany, Montagne Noire and Morocco. The definition of the Middle *praesulcata* Zone by the extinction of *Pa. gracilis gonioclymeniae* Müller resulted in a great difficulty for the recognition of this zone (Over 1992, Kürschner *et al.* 1993, Perri & Spalletta 2000, Kaiser 2005), and some authors suggested alternative proposals (Corradini 2008, Kaiser *et al*. 2009, Corradini *et al*. 2016). Ziegler & Sandberg (1994) underlined the phylogenetic character of their zonation, and this was criticised by some authors (*i.e.*, Corradini 2008, Kononova & Weyer 2013) because the lower boundaries of seven biozones of their zonation were defined by the FAD of taxa of five different genera (*Scaphignathu*s, *Pseudopolygnathus*, *Bispathodus*, *Siphonodella*, *Protognathodus*).

The use of *Siphonodella praesulcata* Sandberg as the marker of the uppermost part of the "Standard Zonation" has also been criticized for problems in identification of the species, especially in relation to the discrimination between *Si. praesulcata* and *Si. sulcata* (Huddle) (Kaiser & Corradini 2008, 2011). *Siphonodella praesulcata* was chosen as the marker to connect the last part of the Upper Devonian zonation with the Lower Carboniferous zonation based on representatives of the genus *Siphonodella.* Unequivocal specimens of *Si. praesulcata* are rare, and the taxon should not be used as a marker until the taxonomic problems are resolved.

The rarity of some of the markers used by Ziegler & Sandberg (1990) for the upper part of the "Standard Zonation" drove some authors to propose alternative zonal definitions (Corradini 2008, Kaiser *et al*. 2009, Hartenfels 2011, Corradini *et al*. 2016). The upper part of the zonation here presented corresponds to that proposed by Corradini *et al*. (2016). Some comments can be made on the *costatus–kockeli* Interregnum (CKI) introduced by Kaiser *et al*. (2009) recently used by Kaiser *et al*. (2015) and Becker *et al*. (2016), among others. According to Kaiser *et al*. (2009) the *costatus–kockeli* Interregnum comprises the interval from the base of the Hangenberg Black Shales and their equivalents to the FAD of *Protognathodus kockeli*, and its lower limit corresponds to a sharp and synchronous extinction event. Kaiser *et al*. (2009) defined correctly the *costatus–kockeli* Interregnum as an interval zone, but they also recognized that in sections (Tröpl and Grüne Schneid),

where the carbonatic sedimentation continued, the interval is characterized by an impoverished fauna mainly composed by protognatodids, polygnathids and branmehlids and suggested to name alternatively the interval corresponding to the *costatus–kockeli* Interregnum *meischneri* partial zone. The synchrony of the extinction event and of the beginning of the sedimentation of black shales worldwide has to be proven, even if Becker *et al*. (2016) considered the two events synchronous at geological scale. As with all major global extinction events in the geologic record, the Hangenberg Extinction Event can be easily discriminated globally. Such events have heightened value (specifically as regards correlative value), if they happen to be associated with the first occurrence of a precisely defined morphologic event preferable in a well-characterized lineage and/or with a spectacular 'flood' of a particular species in a biologic lineage immediately after (or even seeming to coincide with) the extinction event. As well as it has been utilized in definition of the base of the biozone following the Frasnian–Famennian (mid-Upper Devonian) and Permian–Triassic global extinctions. Therefore, we use the FAD of *Protognathodus kockeli* to define the base of the biozone following the Hangenberg Extinction Event that falls within the upper part of the *Bispathodus ultimus* Zone.

Ziegler (1962) initially defined zonal groups named after one characteristic species and subdivided a group into "Untere", "Mittlere" and "Obere" zone, when necessary. This concept was maintained in the subsequent modification to the zonation (see Ziegler & Sandberg 1984). Recently this zonal nomenclature gave rise to another problem, as it seems that recent users of the Ziegler & Sandberg biozonation have abandoned subdivisions that have led to inaccuracies in biostratigraphic analyses (*e.g.* referring to the interval from the Lower to the Uppermost *crepida* zones as a "general" *crepida* Zone).

Remarks on the Famennian boundaries

Lower Boundary of the Famennian Stage

The criterion selected for the definition of the Frasnian/Famennian Boundary by the Subcommission on Devonian Stratigraphy (SDS) in 1989 was that the GSSP had to be sought in relation to the base of the Lower *triangularis* conodont Zone. The SDS in 1991 decided to have this coincide precisely with the lower boundary of the Lower *triangularis* Zone. The formal proposal to the International Commission on Stratigraphy (ICS) reported in the SDS Newsletter No. 9 (1993), was: "The recommendation for a GSSP fall at the level though to mark the acme of extinction which is at the base of the Lower *triangularis* Zone". The recommended GSSP was proposed to be drawn at the base of Bed 32a in the Upper Coumiac Quarry in Montagne Noire (southern France). The selected GSSP was ratified by the ICS and the IUGS in 1993. The only criterion used by Ziegler (1962) and Ziegler & Sandberg (1990) for defining the base of the Lower *triangularis* Zone was the FAD of *Palmatolepis triangularis.* Klapper *et al*. (1994) suggested using the flood occurrence of *Palmatolepis triangularis* to "the virtual exclusion of other species of the genus, stratigraphically *above* the fauna dominated by the characteristic upper Frasnian species" so as to exclude "the extremely rare occurrences of *Palmatolepis triangularis* a few centimetres lower, within the uppermost (Frasnian) conodont zone". At the time of the ratification of the GSSP for the lower limit of the Famennian stage there were taxonomic problems regarding *Palmatolepis triangularis*. Ziegler & Sandberg (1996) questioned the presence of *Palmatolepis triangularis* in Bed 31g reported, but not figured, by Klapper *et al*. (1994). Ziegler & Sandberg (1996) not only criticized the taxonomic approach of Klapper, but they also repeated earlier claims (Sandberg *et al.* 1987, unpublished letter to SDS members) that at Coumiac there is a "mineralized (limonitized) contact representing an angular unconformity" at the top of the Frasnian, and therefore in their opinion the basal part of the Famennian is not represented. No detailed sedimentary or lithological data have been presented to support this last assertion; it was only based on the study of conodont biofacies and association (see Ziegler & Sandberg, 1996, pp. 161–163). The angular unconformity claim has been rejected by House *et al.* (2000), based on microfacies studies, which showed several microstromatolithic hardgrounds in the condensed succession that represent minor sedimentary breaks. Klapper (2007b) emphasized that a similar sedimentary break occurs also at Steinbruch Schmidt, the original GSSP contender, and possibly at all marine F/F boundary sections.

Based on the original definition of Klapper *et al*. (1994), the reintroduction of *Pa. ultima* as a discrete species, and the restriction of the concept of *Pa. triangularis* to the original diagnosis of the holotype, entering in this acceptation slightly higher in the Lower *triangularis* Zone, Klapper *et al*. (2004) proposed a redefinition of the Lower *triangularis* Zone as characterized by the flood occurrence of *Palmatolepis ultima* Ziegler immediately above the end Frasnian extinction event. Klapper (2007b) advocated the same definition highlighting the validity of the acme of *Palmatolepis ultima* as supported by graphic correlation. He also wrote (p. 68): "Additionally, the lowest occurrence of *P. subperlobata* Branson & Mehl, 1934 characterizes the lower boundary of the Lower *triangularis* Zone". He did not propose *Palmatolepis subperlobata* Branson & Mehl as a marker because in his opinion the species is too rare to be used as the defining criterion (for the GSSP). Furthermore, he did not want to suggest a possible change of the GSSP criterion. A revised definition of the criterion

used for the formalization of the lower boundary of the Famennian stage (Frasnian/Famnennian Boundary) is highly desirable, following the proposal by Klapper (2007b), and as shown in the revised GSSP section stratigraphic column by Becker *et al.* (2012, fig. 22.8).

The use of fossils as criterion for the definition of GSSPs should require maximum accuracy in avoiding taxonomic problems. Problems arising using biostratigraphy for chronostratigraphic correlations are discussed in Klapper (1991) and Murphy (1994).

Upper boundary of the Famennian Stage

The top of the Famennian corresponds to the lower boundary of the Tournaisian Stage, *i.e.*, the Devonian–Carboniferous Boundary (DCB). Problems concerning both the criterion (entry of the conodont *Siphonodella sulcata* Huddle) chosen for the definition of the boundary, and the lithology of the section where the GSSP was established (La Serre trench E', Montagne Noire, France) in 1990 (Paproth *et al*. 1991) have been discussed in several papers (*e.g*. Ziegler & Sandberg 1996; Casier *et al*. 2002; Kaiser 2005, 2009). A redefinition of the boundary was reputed necessary, to which in 2008 the International Commission on Stratigraphy established a working group deputed to propose a new criterion for defining the boundary and identification of a new GSSP. Since then many papers concerning the boundary have appeared (*e.g*. Kaiser *et al*. 2009, 2015; Kaiser & Corradini 2011; Corradini *et al*. 2011, 2013, 2016; Becker *et al*. 2013, 2016; Kumpan *et al*. 2014; Malec 2014; Kalvoda *et al*. 2015; Matyja *et al*. 2015; Mossoni *et al*. 2015). As evidenced in some of the cited papers, siphonodellids with curved shape resembling *Si. sulcata*, are already present in faunas found below the Hangenberg Black Shales or its equivalents, *i.e*., in the higher part of the Devonian. A meticulous taxonomic revision of the early forms of siphonodellids is essential and highly desirable, as curved elements like those cited have variably been identified in different papers as *Siphonodella praseulcata* or *Siphonodella sulcata* on the base of their stratigraphic position and associated fauna. Probably these elements belong to different, not yet named species (see *e.g*. Tragelehn 2010). The zonation presented herein includes the *Protognathodus kockeli* Zone, as proposed by Corradini *et al*. (2016) which comprises the final part of the Famennian and the first part of the Tournaisian according to the current definition of the boundary (see discussion in Becker *et al*. 2016, Corradini *et al*. 2016). This zone corresponds to the *kockeli* and the *sulcata/kuehni* zones of Kaiser *et al*. (2009). Recently, during the International Workshop of the joined Subcommissions on Devonian and Carboniferous Stratigraphy (SDS/SCCS) task group held in Montpellier (France) in September 2016, the "base of *kockeli* Zone, beginning of radiation, top of major regression (top of HSS) and end of mass extinction" was voted as potential boundary horizon and criterion for the redefinition of the base of the Carboniferous. The proposal will be submitted to the ICS for approval.

Zonation

The zonation (Fig. 1) is largely based on the original zonation by Ziegler (1962) and on the "Late Devonian Standard Conodont Zonation" of Ziegler & Sandberg (1990). It partly continues and updates revisions by Kaiser *et al.* (2009) and Hartenfels (2011) respectively for the uppermost and the upper part of the Famennian. A partly coincident new scheme of "standard zones" was introduced without explanations by Becker *et al*. (eds, 2013). Modifications have only been made when strictly necessary. The proposal is intended to simplify the zonation, naming each zone after the taxon for which FAD defines the lower boundary, and to maintain stability of about 50 years of studies. The proposed new zonation is, for the most part, correlatable to the older zonation schemes as most of the same zonal markers are used. The main difference is that each of the 22 zones is defined by the FAD of a species, or subspecies, that have a well-established stratigraphic range, and a wide geographic distribution. For each zone an association of additional species useful for identification is listed. In a few cases the proposed marker of a zone is a relatively uncommon species and/or absent in some geographic areas. For the definition of these zones an alternative marker for local biozonation is indicated.

The stratigraphic distribution of the species cited in the text and of many other Famennian species is reported in Table 1 in Appendix and/or in Figs. 2–9. Not all Famennian species and/or subspecies known from the literature have been included in Table 1. It is noteworthy that some genera (*e.g. Icriodus* and *Polygnathus*) include endemic species and are also characterised by frequent homeomorphy, probably depending on life style and environmental constraints. Since this paper is a proposed standard (global) zonation, we report only taxa that have a documented wide geographical distribution.

Palmatolepis subperlobata Zone

Lower boundary: FAD of *Palmatolepis subperlobata*
Upper boundary: FAD of *Palmatolepis triangularis*

Remarks. – This zone corresponds to the lowest part of the former Lower *triangularis* Zone. The base is defined by the FAD of *Palmatolepis subperlobata* immediately above the highest occurrence of species characteristic of the upper Frasnian (*i.e.*, *Palmatolepis bogartensis*, *Pa. winchelli*,

and last representatives of the genus *Ancyrodella*). The entry of *Palmatolepis subperlobata* corresponds to the acme of *Palmatolepis ultima*, the last representative of *Palmatolepis* that has a FAD within the uppermost part of the Frasnian (Klapper *et al.* 2004, Girard *et al*. 2005, Klapper 2007b). The zone is typically developed in the Famennian GSSP section at Coumiac (Schülke 1995, Klapper 2007b, Becker *et al.* 2012) but it is recognizable worldwide (Klapper 2007a; Huang & Gong 2016; Perri & Spalletta, unpublished data).

The zone is characterized by a low diversity fauna that includes several taxa that survived the upper Frasnian biological crisis, such as *Icriodus alternatus alternatus*, *Ic. alternatus helmsi*, *Ic. iowaensis iowaensis*, *Mehlina gradata*, *Pelekysgnathus planus, Polygnathus angustidiscus,* and *Po. brevilaminus* (Fig. 2).

Conodonts useful for the zonal identification. – *Palmatolepis delicatula delicatula* enters at or immediately above the lower boundary of the zone. *Palmatolepis protorhomboidea* occurs within the zone.

Palmatolepis triangularis Zone

Lower boundary: FAD of *Palmatolepis triangularis*
Upper boundary: FAD of *Palmatolepis delicatula platys*

Remarks. – This zone corresponds to the upper part of the former Lower *triangularis* Zone. The base is defined by the FAD of *Palmatolepis triangularis sensu* Klapper in Klapper *et al*. (2004). The typical locality is the section at the Upper Coumiac Quarry in Montagne Noire (Klapper 2007b).

Conodonts useful for the zonal identification. – The conodont association characteristic of this zone is quite the same of the *Palmatolepis subperlobata* Zone. *Ancyrognathus cryptus* enters within the zone. *Polygnathus tenellus* becomes extinct within the zone (Fig. 2).

Palmatolepis delicatula platys Zone

Lower boundary: FAD of *Palmatolepis delicatula platys*
Upper boundary: FAD of *Palmatolepis minuta minuta*

Remarks. – This zone corresponds exactly to the former Middle *triangularis* Zone of Ziegler & Sandberg (1990). The original Middle *triangularis* Zone of Ziegler (1962) was the interval between the entry of *Palmatolepis marginata clarki* and that of *Pa. tenuipuncata*. For the lower boundary of the zone Ziegler (1962) indicated the entry of both *Palmatolepis marginata clarki* and *Pa. marginata marginata.* Later part of the elements assigned by Ziegler (1962) to *Pa. marginata marginata* were re-assigned to *Pa. delicatula delicatula* and part to *Pa. delicatula platys*

Ziegler (1962,1969)	Ziegler & Sandberg (1990)	NEW GLOBAL ZONATION
S. sulcata - Pr. kockeli	*sulcata*	*Protognathodus kockeli*
Low. *Protogn.* f.	Late *praesulcata*	
Upper *costatus*	Mid. *praesulcata*	*Bispathodus ultimus*
Middle *costatus*	Early *praesulcata*	
	Late *expansa*	
Lower *costatus*	Middle *expansa*	*Bispathodus costatus*
Upper *styriacus*		*Bispathodus ac. aculeatus*
	Early *expansa*	*Palmatolepis gr. expansa*
Middle *styriacus*	Late *postera*	*Palmatolepis gr. manca*
Lower *styriacus*	Early *postera*	*Polygnathus styriacus*
Upper *velifer*	Late *trachytera*	*Pseudopolygnathus granulosus*
Middle *velifer*	Early *trachytera*	*Palmatolepis r. trachytera*
Lower *velifer*	Latest *marginifera*	*Scaphignathus v. velifer*
Upper *quadrantinodosa*	Late *marginifera*	*Palmatolepis marg. utahensis*
Lower *quadrantinodosa*	Early *marginifera*	*Palmatolepis marg. marginifera*
rhomboidea	Late *rhomboidea*	*Palmatolepis gr. gracilis*
	Early *rhomboidea*	*Palmatolepis rhomboidea*
Upper *crepida*	Latest *crepida*	*Palmatolepis gl. pectinata*
	Late *crepida*	*Palmatolepis gl. prima*
Middle *crepida*	Middle *crepida*	*Palmatolepis termini*
Lower *crepida*	Early *crepida*	*Palmatolepis crepida*
Upper *triangularis*	Late *triangularis*	*Palmatolepis min. minuta*
Middle *triangularis*	Middle *triangularis*	*Palmatolepis del. platys*
Lower *triangularis*	Early *triangularis*	*Palmatolepis triangularis*
		Palmatolepis subperlobata

Figure 1. Comparison between the revised global conodont biozonation and the zonation schemes of Ziegler (1962, 1969) and Ziegler & Sandberg (1990). The thickness of zones is calibrated according to their supposed duration, as estimated in the Devonian chapter of *The Geologic Time Scale 2012* (Becker *et al*. 2012).

(Ziegler & Sandberg 1990). The elements assigned by Ziegler (1962) to *Palmatolepis marginata clarki* have been

partly re-assigned to *Pa. clarki* and part to *Pa. protorhomboidea* (see Ziegler & Sandberg 1990 for synonymy list). *Palmatolepis clarki sensu* Ziegler & Sandberg (1990) enters slightly higher than *Pa. delicatula platys*. The only remaining species which has the FAD corresponding with the lower boundary given by Ziegler (1962) for this zone is *Pa. delicatula platys*. According to Schülke (1995) *Pa. delicatula platys* is rare outside the Rhenish Massif whereas *Pa. clarki* is more common and can be used to identify the zone in the absence of the marker.

Conodonts useful for the zonal identification. – *Ancyrognathus sinelaminus* enters at the base of this zone, *Palmatolepis clarki* appears slightly above, *Icriodus cornutus,* and *Ic. iowaensis ancylus* enter within the zone. *Palmatolepis ultima* becomes extinct at the top (Fig. 2).

***Palmatolepis minuta minuta* Zone**

Lower boundary: FAD of *Palmatolepis minuta minuta*
Upper boundary: FAD of *Palmatolepis crepida*

Remarks. – This zone is equivalent to the former Upper *triangularis* Zone of Ziegler & Sandberg (1990). The lower boundary of the original Upper *triangularis* Zone of Ziegler (1962) corresponded to the entry of *Palmatolepis tenuipunctata*. Ziegler & Sandberg (1990) did not explain the change of the taxon defining the lower boundary of the zone. Both *Palmatolepis minuta minuta* and *Pa. tenuipunctata* enter at the base of the zone, therefore the definition given by Ziegler & Sandberg (1990) is maintained. In the Famennian Composite Standard, constructed by graphic correlation, the lowest occurrence of both taxa is in the same sample at the Upper Coumiac Quarry (Klapper, personal communication).

Conodonts useful for the zonal identification. – *Palmatolepis perlobata perlobata*, *Pa. regularis*, *Pa. sandbergi, Pa. tenuipunctata,* and *Pa. werneri* enter at the base of the zone. *Palmatolepis lobicornis*, *Pa. spathula*, *Polygnathus eoglaber,* and *Po. procerus,* in the sense of the holotype by Sannemann 1955, first appear within the zone. *Icriodus deformatus asymmetricus* and *Ic. deformatus deformatus* become extinct (Fig. 2).

***Palmatolepis crepida* Zone**

Lower boundary: FAD of *Palmatolepis crepida*
Upper boundary: FAD of *Palmatolepis termini*

Remarks. – The zone corresponds to the former Lower *crepida* Zone.

Conodonts useful for the zonal identification. – *Palmatolepis minuta loba, Pa. quadrantinodosalobata* M2, and *Pa. wolskajae* have their first appearance at the base of the zone, *Polygnathus communis communis* and *Po. nodocostatus nodocostatus* within the zone. *Palmatolepis clarki, Pa. delicatula platys*, *Pa. sandbergi*, and *Pa. triangularis* become extinct within the zone; *Palmatolepis delicatula delicatula* near the top, and *Pa. spathula* at the top (Fig. 2).

***Palmatolepis termini* Zone**

Lower boundary: FAD of *Palmatolepis termini*
Upper boundary: FAD of *Palmatolepis glabra prima* – M3 of Hartenfels (2011), typical morphotype

Remarks. – This zone is equivalent to the former Middle *crepida* Zone.

Conodonts useful for the zonal identification. – *Ancyrolepis cruciformis* is characteristic of this zone. *Palmatolepis minuta wolskae* enters at the base of the zone; *Mehlina strigosa*, *Pa. circularis*, *Po. lauriformis*, and *Po. semicostatus* within the zone. In the Montagne Noire is registered the lowest occurrence of *Polygnathus glaber glaber*, entering within the biozone (Girard *et al*. 2014). *Polygnathus angustidiscus* becomes extinct within the zone, *Icriodus alternatus helmsi* at the top (Fig. 2).

***Palmatolepis glabra prima* Zone**

Lower boundary: FAD of *Palmatolepis glabra prima* – M3 of Hartenfels (2011), typical morphotype
Upper boundary: FAD of *Palmatolepis glabra pectinata* – M2 of Hartenfels (2011), typical morphotype *sensu* Ziegler & Sandberg (1984)

Remarks. – The zone is equivalent to the former Upper *crepida* Zone.

Conodonts useful for the zonal identification. – *Palmatolepis adamantea* and *Pa. minuta subgracilis* have their first appearance at the base of the zone. *Palmatolepis glabra lepta*, *Pa. klapperi* and *Pa. perlobata schindewolfi* first appear within the zone. *Palmatolepis wolskajae* becomes extinct within the zone, *Pa. circularis*, and *Pa. termini* at the top (Fig. 3).

***Palmatolepis glabra pectinata* Zone**

Lower boundary: FAD of *Palmatolepis glabra pectinata* – M2 of Hartenfels (2011), typical morphotype *sensu* Ziegler & Sandberg (1984)
Upper boundary: FAD of *Palmatolepis rhomboidea*

Remarks. – The zone corresponds to the former Uppermost *crepida* Zone.

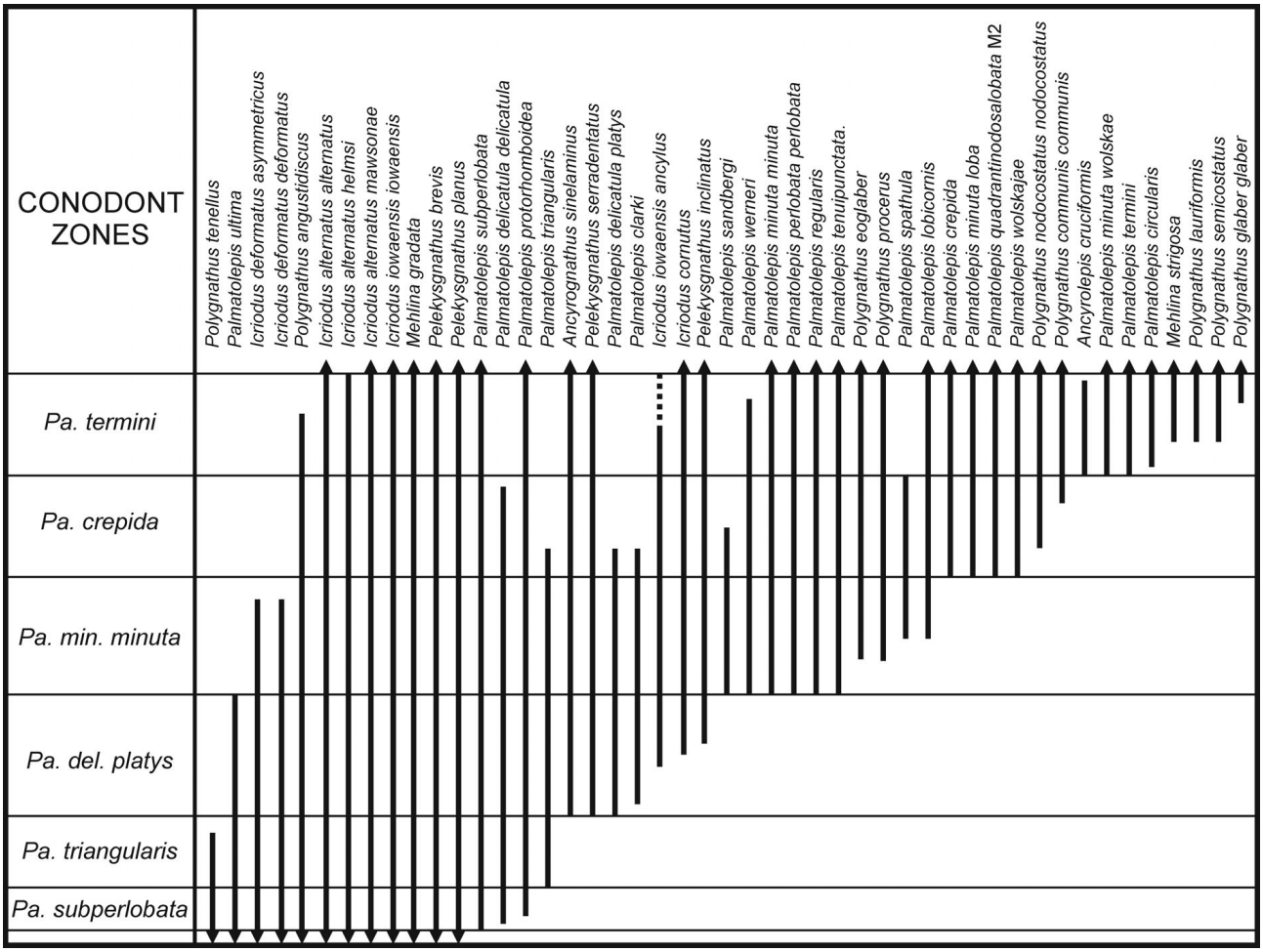

Figure 2. Stratigraphic distribution of the main Famennian conodont species and subspecies from the *Palmatolepis subperlobata* Zone to the *Palmatolepis termini* Zone.

Conodonts useful for the zonal identification. – *Palmatolepis glabra acuta* starts at the lower boundary of the zone. *Icriodus olivierii*, *Polygnathus padovanii*, *Po. rhomboideus* and *Polylophodonta linguiformis* have their first appearance within the zone. *Ancyrognathus cryptus, Anc. sinelaminus*, *Icriodus alternatus alternatus*, *Palmatolepis perlobata perlobata*, *Pa. tenuipunctata*, and *Polygnathus procerus* become extinct within the biozone, *Pa. adamantea* at the top (Fig. 3).

Palmatolepis rhomboidea Zone

Lower boundary: FAD of *Palmatolepis rhomboidea*
Upper boundary: FAD of *Palmatolepis gracilis gracilis*

Remarks. – The zone corresponds to the former Lower *rhomboidea* Zone and the lowermost part of the Upper *rhomboidea* Zone *sensu* Sandberg & Ziegler (1973).

Conodonts useful for the zonal identification. – *Palmatolepis glabra glabra*, *Pa. poolei,* and *Polylophodonta confluens* enter at the base of the zone. The range of *Palmatolepis poolei* is restricted to the zone and it becomes extinct near the top. *Polygnathus diversus* first appears within the zone. *Icriodus chojnicensis,* and *Palmatolepis minuta schleizia* enter near the top of the zone. *Icriodus iowaensis iowaensis*, *Ic. olivierii*, *Palmatolepis lobicornis*, *Pa. minuta wolskae*, *Pa. protorhomboidea*, *Pa. quadrantinodosalobata*, and *Pa. regularis* become extinct within the zone. *Palmatolepis crepida, Pa. minuta loba,* and *Pa. minuta subgracilis* near the top (Fig. 3).

Palmatolepis gracilis gracilis Zone

Lower boundary: FAD of *Palmatolepis gracilis gracilis*
Upper boundary: FAD of *Palmatolepis marginifera marginifera*

Remarks. – This new zone corresponds to most of the former Upper *rhomboidea* Zone. The base is defined by the

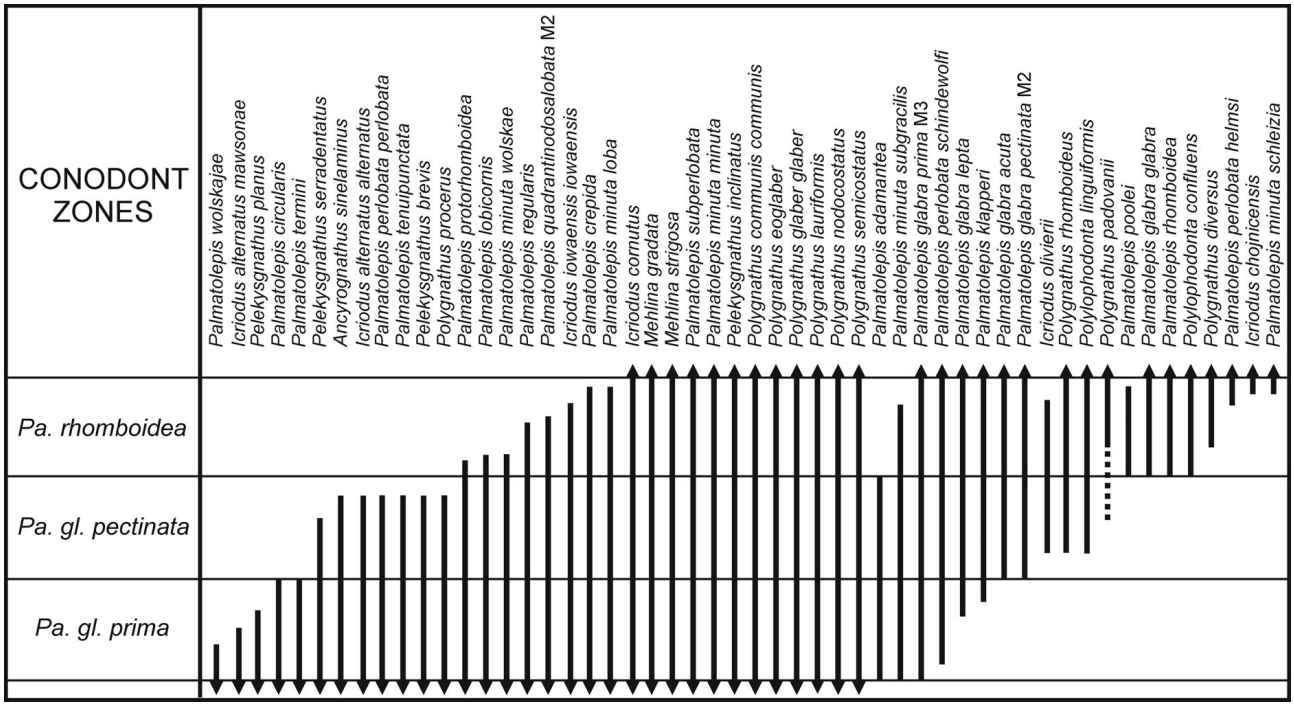

Figure 3. Stratigraphic distribution of the main Famennian conodont species and subspecies from the *Palmatolepis glabra prima* Zone to the *Palmatolepis rhomoboidea* Zone.

FAD of *Palmatolepis gracilis gracilis*, the nominal subspecies, that is easy to recognize and characterized by a worldwide geographic distribution. The FAD of *Palmatolepis gracilis gracilis* is slightly higher than the LAD of *Pa. poolei*, which defined the base of the Upper *rhomboidea* Zone of Sandberg & Ziegler (1973) and Ziegler & Sandberg (1990). The choice of *Palmatolepis gracilis gracilis* as the zonal marker avoids a zonal boundary defined by the LAD of *Pa. poolei*. *Palmatolepis poolei* is rare and it is not present in some geographic areas (*e.g.* Montagne Noire). A possible alternative marker to define a new zone could have been *Palmatolepis minuta schleizia* that according to Ji & Ziegler (1993) enters at the base of the Upper *rhomboidea* Zone of the "Standard Zonation". *Palmatolepis gracilis gracilis* was choosen as it is more common and widespread than *Palmatolepis minuta schleizia*. The best reference section for this zone is the Lali section (China) of Ji & Ziegler (1993).

Conodonts useful for the zonal identification. – *Bispathodus stabilis vulgaris* enters at the base of the zone. *Alternognathus pseudostrigosus, Branmehla disparilis*, and *Palmatolepis quadrantinodosa inflexa* enter slightly above the base of this zone. *Palmatolepis perlobata maxima* enters within the zone. *Polygnathus triphyllatus,* and *Polylophodonta gyratilineata* start in the upper half of the zone. *Palmatolepis stoppeli* first appears near the top. *Polygnathus eoglaber*, and *Po. rhomboideus* disappear within the zone (Fig. 4).

Palmatolepis marginifera marginifera Zone

Lower boundary: FAD of *Palmatolepis marginifera marginifera*
Upper boundary: FAD of *Palmatolepis marginifera utahensis*

Remarks. – The zone is equivalent to the former Lower *marginifera* Zone.

Conodonts useful for the zonal identification. – *Palmatolepis quadrantinodosa quadrantinodosa* is exclusive of this biozone. *Branmehla werneri*, *Palmatolepis glabra distorta*, and *Polygnathus glaber medius* enter at the base of the zone, *Pa. perlobata sigmoidea* slightly above. *Palmatolepis marginifera duplicata, Polygnathus glaber bilobatus,* and *Po. pennatuloideus* enter within the zone. *Polygnathus tryphillatus* becomes extinct within the lower part of the zone, *Palmatolepis klapperi*, *Pa. stoppeli*, *Pa. subperlobata*, and *Polylophodonta gyratilineata* within the zone, *Pa. glabra glabra*, and *Polygnathus brevilaminus* at the top (Fig. 4).

Palmatolepis marginifera utahensis Zone

Lower boundary: FAD of *Palmatolepis marginifera utahensis*
Upper boundary: FAD of *Scaphignathus velifer velifer*

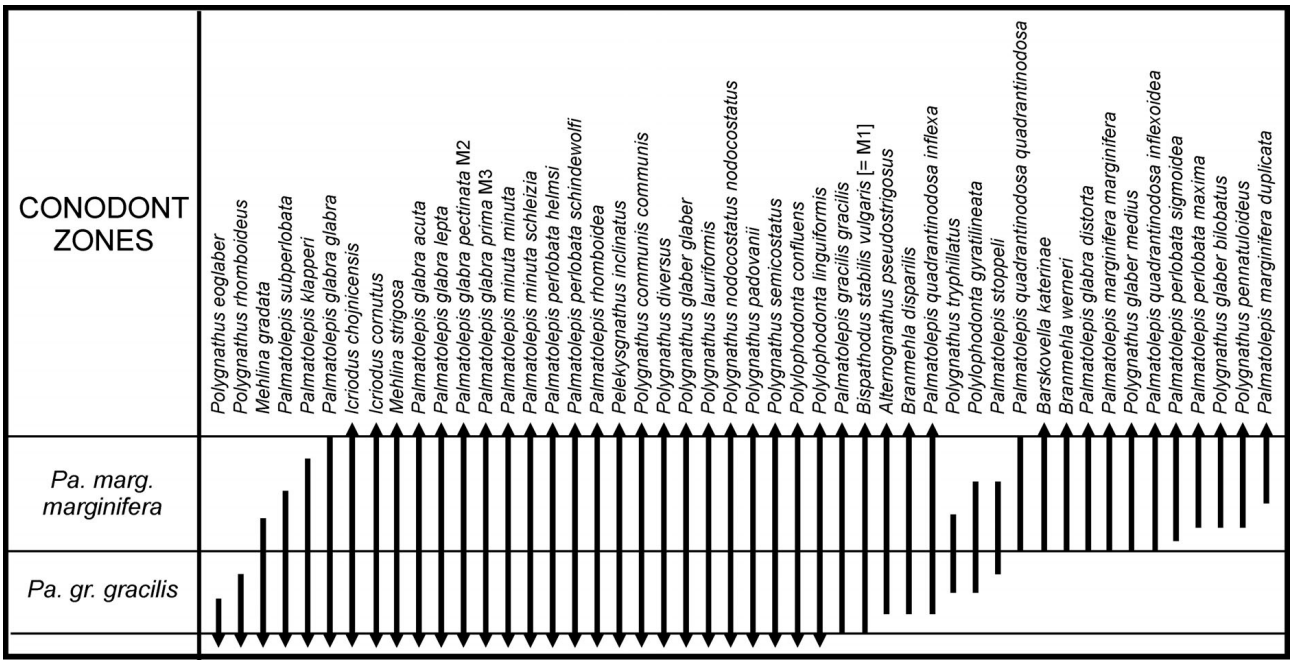

Figure 4. Stratigraphic distribution of the main Famennian conodont species and subspecies from the *Palmatolepis gracilis gracilis* Zone to the *Palmatolepis marginifera marginifera* Zone.

Remarks. – This zone is equivalent to the Upper *marginifera* Zone *sensu* Ziegler & Sandberg (1984) and Ziegler & Sandberg (1990). Sandberg & Ziegler (1973) defined the zone as "characterized by the range of *Palmatolepis marginifera marginifera* between the disappearance of *Pa. quadrantinodosa quadrantinodosa*, *Pa. quadrantinodosa inflexa*, *Pa. quadrantinodosa inflexoidea* and the first appearance of *Scaphignathus velifer*". Ziegler & Sandberg (1984) introduced the new subspecies *Palmatolepis marginifera utahensis* and defined the lower boundary of the present zone by the first appearance of the new taxon.

Conodonts useful for the zonal identification. – *Branmehla inornata* and *Palmatolepis rugosa* cf. *ampla* first appear at the base of the zone. *Polygnathus marginvolutus,* and *Po. perplexus* first appear within the zone. The occurrence of *Branmehla bohlenana bohlenana, Palmatolepis perlobata grossi, Polygnathus granulosus, Po. lagowiensis,* and *Po. nodoundatus* allow the identification of the upper part of the zone. *Palmatolepis glabra acuta, Pa. glabra pectinata, Pa. marginifera duplicata*, *Pa. quadrantinodosa inflexa*, *Pa. quadrantinodosa inflexoidea, Pa. rhomboidea,* and *Polylophodonta linguiformis* go extinct within the zone, *Pa. glabra prima*, and *Polygnathus glaber medius* at the top (Fig. 5).

Scaphignathus velifer velifer Zone

Lower boundary: FAD of *Scaphignathus velifer velifer*
Upper boundary: FAD of *Palmatolepis rugosa trachytera*

Remarks. – The present zone corresponds to the Uppermost *marginifera* Zone. *Scaphignatus velifer velifer* in some geographic areas is a rare taxon; where absent *Alternognathus beulensis* and/or *Alt. regularis* can be used for the identification of the lower boundary of this zone, as these taxa enter at the same level as *Scaphignatus velifer velifer*. We considered to name the zone after one of the two species of *Alternognathus* but opted for continuity with the original definition. The genus *Alternognathus* was regarded by Ziegler & Sandberg (1984) as characteristic of a more offshore environment, and therefore environmentally less restricted than *Scaphignathus*. The different environment was reputed by the authors as sufficient reason to define a new genus, but in fact elements attributed by Ziegler & Sandberg (1984) to their new genus were previously considered as representatives of *Scaphignathus.* The use of *Scaphignathus velifer velifer* as nominal marker of the same biozone was already suggested at local or supraregional level by Corradini (2008) and Hartenfels (2011).

Conodonts useful for the zonal identification. – *Alternognathus beulensis* and *Alt. regularis* have their FAD at the lower boundary of the zone. *Icriodus costatus*, and *Ic. raymondi* start near the lower boundary of the zone, and *Scaphignathus velifer leptus* slightly above. *Palmatolepis marginifera utahensis*, *Polygnathus lauriformis*, and *Po. lagowiensis* become extinct within the biozone, *Icriodus chojnicensis*, and *Polylophodonta confluens* at the top (Fig. 5).

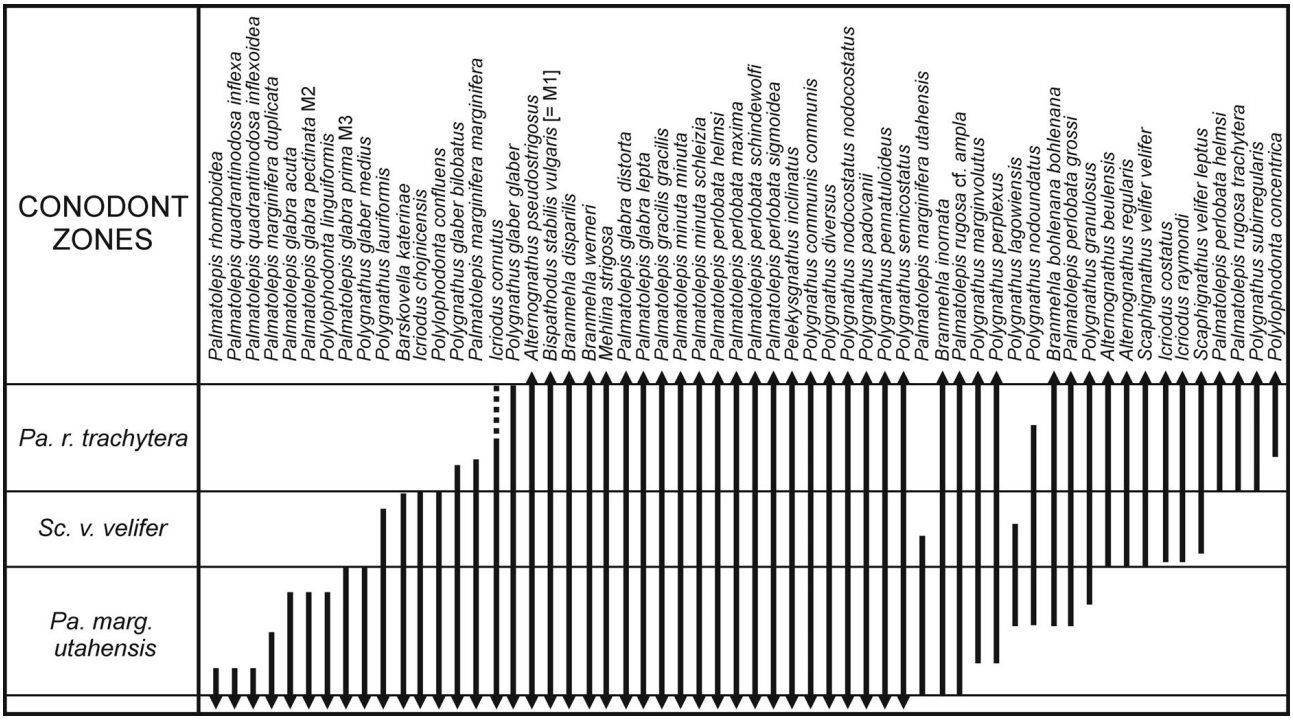

Figure 5. Stratigraphic distribution of the main Famennian conodont species and subspecies from the *Palmatolepis marginifera uthaensis* Zone to the *Scaphignathus velifer velifer* Zone.

Palmatolepis rugosa trachytera Zone

Lower boundary: FAD of *Palmatolepis rugosa trachytera*
Upper boundary: FAD of *Pseudopolygnathus granulosus*

Remarks. – The zone is equivalent to the former Lower *trachytera* Zone.

Conodonts useful for the zonal identification. – *Palmatolepis perlobata helmsi* and *Polygnathus subirregularis* enter at the lower boundary of the zone. *Palmatolepis marginifera marginifera*, and *Polygnathus glaber bilobatus* become extinct in the lower part of the biozone, *Po. nodoundatus* within it, and *Po. glaber glaber* at the top (Fig. 5).

Pseudopolygnathus granulosus Zone

Lower boundary: FAD of *Pseudopolygnathus granulosus*
Upper boundary: FAD of *Polygnathus styriacus*

Remarks. – The zone is equivalent to the former Upper *trachytera* Zone. The zone was subdivided by Hartenfels (2011) into three regional subzones recognized also in other geographic areas (Hartenfels & Becker 2016). The *Palmatolepis gracilis sigmoidalis* subzone of Hartenfels (2011) can be useful for the recognition of the middle part of the zone. The *trachytera–styriacus* Interregnum of Hartenfels (2011) is the interval zone between the disappearance of *Palmatolepis rugosa trachytera* and the appearance of *Polygnathus styriacus*, which corresponds to the interval comprising the lower and upper *Annulata* extinction events in the uppermost part of the Zone.

Conodonts useful for the zonal identification. – *Palmatolepis gracilis sigmoidalis*, *Polygnathus homoirregularis*, *Po. protostyriacus*, and *Pseudopolygnathus micropunctatus* first appear within the central part of the zone. *Pseudopolygnathus granulosus* and *Ps. micropunctatus* are the first representatives of the genus. *Palmatolepis gracilis sigmoidalis* enters in the middle part of the zone. *Bispathodus stabilis stabilis* (Girard *et al*. 2017; Perri & Spalletta, unpublished data), *Polygnathus margaritatus* and *Po. obliquicostatus* enter in the upper part. *Palmatolepis glabra distorta* and *Pa. glabra lepta*, the last representatives of the species, became extinct within the zone, as well as *Pa. minuta minuta* and *Polygnathus padovanii*. *Palmatolepis perlobata grossi, Pa. rugosa trachytera*, and *Scaphignathus velifer velifer* become extinct at different levels near the top of the zone during the lower and upper *Annulata* extinction events. *Icriodus cornutus* become extinct at the top (Fig. 6).

Polygnathus styriacus Zone

Lower boundary: FAD of *Polygnathus styriacus*
Upper boundary: FAD of *Palmatolepis gracilis manca*

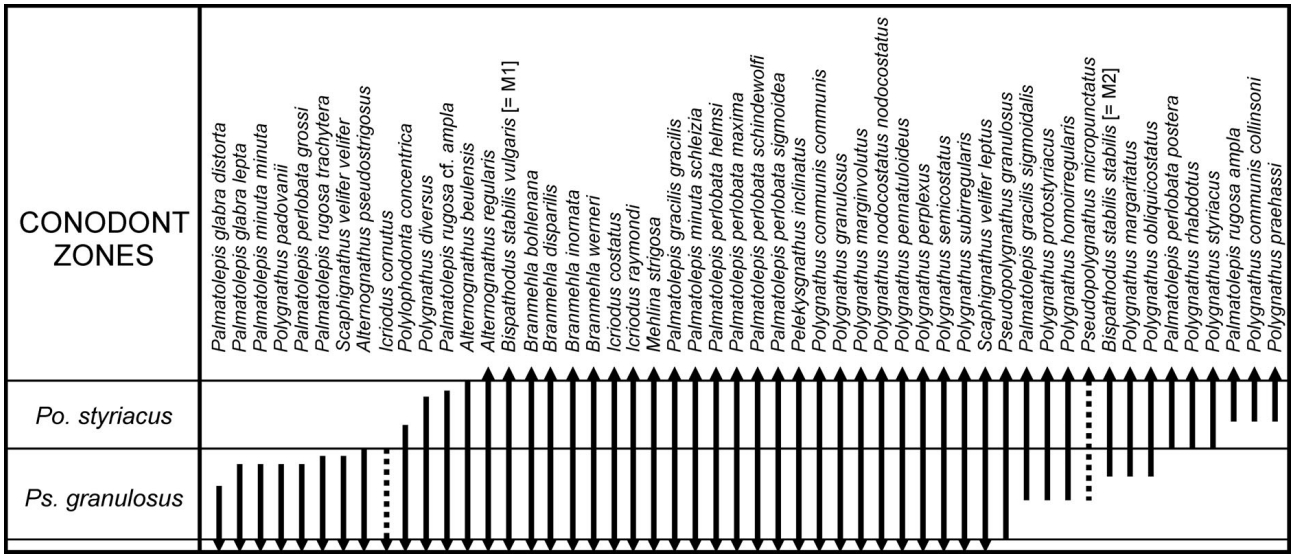

Figure 6. Stratigraphic distribution of the main Famennian conodont species and subspecies from the *Pseudopolygnahtus granulosus* Zone to the *Polygnathus styriacus* Zone.

Remarks. – This zone corresponds to the former Lower *postera* Zone. *Palmatolepis perlobata postera* is a rare species, and in some localities (*i.e.*, the Carnic Alps) the species enters in higher levels. *Polygnathus styriacus* is preferred as a zonal marker due to a wider geographic distribution in respect to *Palmatolepis perlobata postera*, and for historical reasons, as it was chosen as the zonal marker by Ziegler (1962). Ziegler and Sandberg (1984) substituted the Lower *styriacus* Zone of Ziegler (1962) with the Lower *postera* Zone in order to name all the zonal groups after species of *Palmatolepis*. Recently some authors (Corradini 2008, Hartenfels 2011) re-introduced a local or supraregional *styriacus* Zone for European and North Africa regions, where *Palmatolepis perlobata postera* is very rare or absent.

Polygnathus styriacus is widely distributed, common in Europe, although rare in the western United States (Sandberg 1979). Where *Polygnathus styriacus* is rare, the base of the zone can be identified by the entry of *Palmatolepis perlobata postera*. Typically where *Polygnathus styriacus* is common *Palmatolepis perlobata postera* is very rare or absent, and vice versa.

Conodonts useful for the zonal identification. – *Palmatolepis perlobata postera* and typical *Polygnathus rhabdotus* enter at the lower boundary of the zone. *Palmatolepis rugosa ampla*, *Polygnathus praehassi,* and *Polygnathus communis collinsoni* enter within the zone. The presence of *Polygnathus praehassi* can be used to recognize the upper part of the zone. *Palmatolepis rugosa* cf. *ampla*, and *Polygnathus diversus* become extinct near the top of the biozone, *Alternognathus beulensis* at the top (Fig. 6).

Palmatolepis gracilis manca Zone

Lower boundary: FAD of *Palmatolepis gracilis manca*
Upper boundary: FAD of *Palmatolepis gracilis expansa*

Remarks. – This zone corresponds to the former Upper *postera* Zone. In Sardinia the zonal marker is not present, for this reasons a local, not subdivided, *styriacus* Zone has been used by Corradini (2008). The zonal index species is extremely rare or absent in North Africa (Hartenfels 2011).

Conodonts useful for the zonal identification. – *Bispathodus stabilis bituberculatus* (*Bi. stabilis* M3) and *Clydagnathus ormistoni* enter at the base of the zone. *Bispathodus bispathodus*, *Pseudopolygnathus controversus*, *Ps. inordinatus*, and *Scaphignathus peterseni* appear within the zone, *Palmatolepis rugosa rugosa* and *Polygnathus experplexus* in the uppermost part. *Palmatolepis perlobata sigmoidea*, and *Pseudopolygnathus granulosus* become extinct within the zone, *Alternognathus regularis*, *Palmatolepis minuta schleizia*, and *Scaphignathus velifer leptus* at the top (Fig. 7).

Palmatolepis gracilis expansa Zone

Lower boundary: FAD of *Palmatolepis gracilis expansa*
Upper boundary: FAD of *Bispathdus aculeatus aculeatus*

Remarks. – The zone is equivalent to the former Lower *expansa* Zone. The entry of *Bispathodus stabilis stabilis* (*Bi. stabilis* M2) was used by Hartenfels (2011) as the index taxon of a zone considered equivalent to the Lower *expansa* Zone. The *Bispathodus stabilis stabilis* Zone of

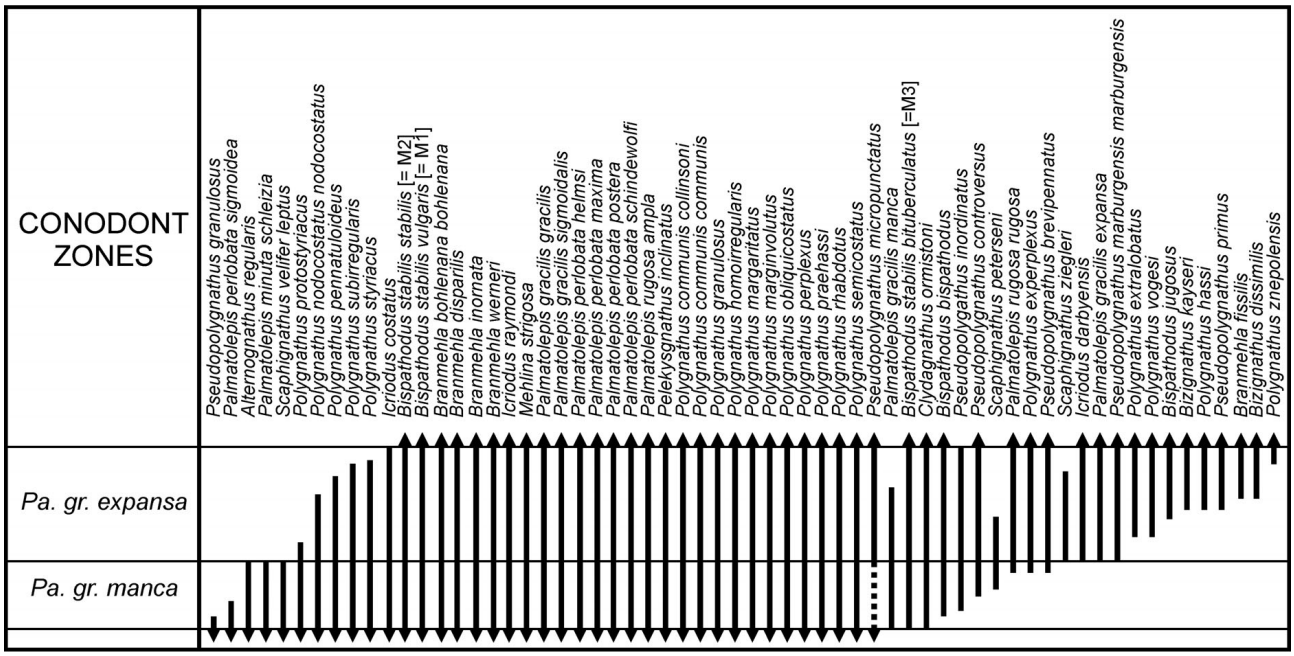

Figure 7. Stratigraphic distribution of the main Famennian conodont species and subspecies from the *Palmatolepis gracilis manca* Zone to the *Palmatolepis gracilis expansa* Zone.

Hartenfels (2011) may have local value but it cannot be used in a standard zonation, as in other localities it has a lower entry, *e.g.* in the Carnic Alps *Bispathodus stabilis stabilis* has been found in samples attributed to the *Pseudopolygnathus granulosus* Zone (Perri and Spalletta, unpublished data).

Conodonts useful for the zonal identification. – *Icriodus darbyensis, Pseudopolygnathus brevipennatus*, and *Ps. marburgensis marburgensis* have their first appearance at the base of the zone. *Scaphignathus ziegleri* is limited to this zone. *Bispathodus jugosus*, *Bizignathus dissimilis*, *Biz. kaiseri*, *Branmehla fissilis*, *Polygnathus extralobatus, Po. hassi*, *Po. vogesi*, and *Ps. primus* enter within the zone, and *Po. znepolensis* in the uppermost part. The upper part of the zone can be identified by the presence of *Branmehla fissilis*, *Polygnathus hassi* and *Pseudopolygnathus primus. Polygnathus nodocostatus nodocostatus* and *Scaphignathus peterseni* become extinct within the zone; *Icriodus costatus*, *Polygnathus styriacus*, *Po. subirregularis*, and *Pseudopolygnathus inordinatus* near or at the top (Fig. 7).

***Bispathodus aculeatus aculeatus* Zone**

Lower boundary: FAD of *Bispathodus aculeatus aculeatus*
Upper boundary: FAD of *Bispathodus costatus*

Remarks. – The zone corresponds to the lower part of the Middle *expansa* Zone. It was proposed by Corradini *et al*. (2016). It is equivalent to the lower subzone of the *Bispathodus aculeatus aculeatus* Zone of Hartenfels (2011).

Conodonts useful for the zonal identification. – *Bispathodus aculeatus anteposicornis*, *Bi. spinulicostatus*, and *Clydagnathus plumulus* first appear at or near the base of the zone. *Palmatolepis perlobata helmsi* and *Palmatolepis gracilis manca* become extinct above the base of the zone, *Bispathodus stabilis bituberculatu*s (= *Bi. stabilis* M3), *Bizignathus dissimilis*, *Branmehla werneri*, *Clydagnathus ormistoni* and *Palmatolepis perlobata maxima* within the zone (Fig. 8).

***Bispathodus costatus* Zone**

Lower boundary: FAD of *Bispathodus costatus*
Upper boundary: FAD of *Bispathodus ultimus*

Remarks. – The zone is equivalent to the upper part of the Middle *expansa* Zone, and to the Lower *costatus* Zone of Ziegler (1962). It is the same as proposed by Corradini *et al*. (2016). It also corresponds to the *Bispathodus costatus* Subzone of Hartenfels (2011) raised to zonal rank by Corradini *et al*. (2016).

Conodonts useful for the zonal identification. – *Polygnathus spicatus* enters within the zone. *Polygnathus hassi*, *Po. rhabdotus*, and *Pseudopolygnathus controversus* become extinct within the zone, *Icriodus raymondi, Polygnathus experplexus, Po. homoirregularis,* and *Po. margaritatus* at the top (Fig. 8).

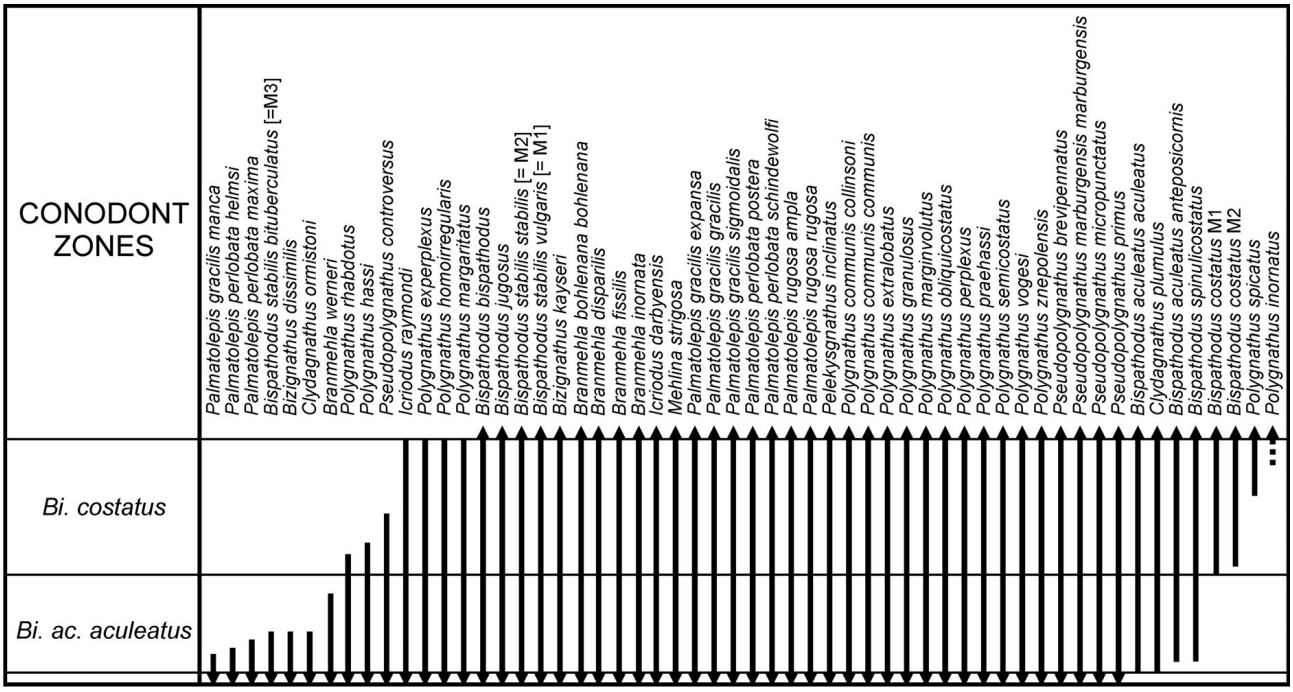

Figure 8. Stratigraphic distribution of the main Famennian conodont species and subspecies from the *Bispathodus aculeatus aculeatus* Zone to the *Bispathodus costatus* Zone.

Bispathodus ultimus Zone

Lower boundary: FAD of *Bispathodus ultimus*
Upper boundary: FAD of *Protognathodus kockeli*

Remarks. – The re-defined zone is equivalent to the Upper *expansa*, Lower and Middle *praesulcata* zones of Ziegler & Sandberg (1984), as well as to the Upper *expansa* and *praesulcata* zones and the *costatus–kockeli* Interregnum of Kaiser *et al.* (2009). It corresponds also to the *ultimus ultimus* and *praesulcata* zones and *costatus–kockeli* Interregnum of Becker *et al.* (2016). The name *ultimus* Zone was first used regionally in the Pyrenees (Perret 1988), and then adopted internationally in the sense of the Upper *expansa* Zone by Hartenfels & Becker (2012). The zone was then re-defined and enlarged by Corradini *et al*. (2016). It extends for an interval quite long when compared to the other Famennian zones. Here it is not subdivided, as *Siphonodella praesulcata,* which entry was used by Ziegler & Sandberg (1984, 1990) to define the Lower *praesulcata* Zone, is a taxon rare and difficult to identify (Kaiser & Corradini 2011). The occurrence of *Si. praesulcata* could be useful as an indication of the middle part of the zone, which can be identified by the entry of *Protognathodus meischneri* and *Pr. collinsoni.* The lower and middle parts of the zone are characterized by a fauna with high diversity. The upper part, corresponding to the "*costatus–kockeli* Interregnum" of Kaiser *et al*. (2009), is characterized by an impoverished fauna following the extinction associated with the Hangenberg Event. Kononova & Weyer (2013) named a new subspecies of *Bi. ultimus* - *Bi. ultimus bartzschi* but here this subspecies is not considered valid.

Conodonts useful for the zonal identification. – *Branmehla suprema, Palmatolepis gracilis gonioclymeniae*, and *Pseudopolygnathus marburgensis trigonicus* enter near the base of the zone; *Polygnathus purus purus*, and *Po. symmetricus* enter in the lower part. The first occurrences of the two last species are probably not synchronous worldwide as delayed occurrences are common in the basal Tournaisian. *Protognathodus collinsoni*, *Pr. meischneri*, and *Siphonodella praesulcata* and other early *Siphonodella* species enter in the middle part of the zone. *Polygnathus marginvolutus*, *Po. perplexus*, *Po. praehassi*, and *Peudopolygnathus brevipennatus* become extinct in the basal part of the zone. In the middle part of the zone *Bizignathus kaiseri*, *Branmehla bohlenana bohlenana*, *Br. fissilis*, *Icriodus darbyensis*, *Ps. marburgensis marburgensis*, and several polygnathids became extinct (see Fig. 9). *Bispathodus bispathodus*, *Bi. costatus*, *Bispathodus jugosus*, *Bi. ultimus*, *Branmehla disparilis*, *Palmatolepis gracilis expansa, Pa. gracilis gonioclymeniae*, and *Pseudopolygnathus marburgensis trigonicus* disappear in the upper part (Fig. 9). *Palmatolepis perlobata postera*, *Pa. perlobata schindewolfi*, *Pa. rugosa ampla*, *Pa. rugosa rugosa* were reported by Ji & Ziegler (1993) to range to the top of the Upper *expansa* Zone, but according to Becker *et al.* (2015) these taxa come only from mixed fauna and the late findings are due to reworking.

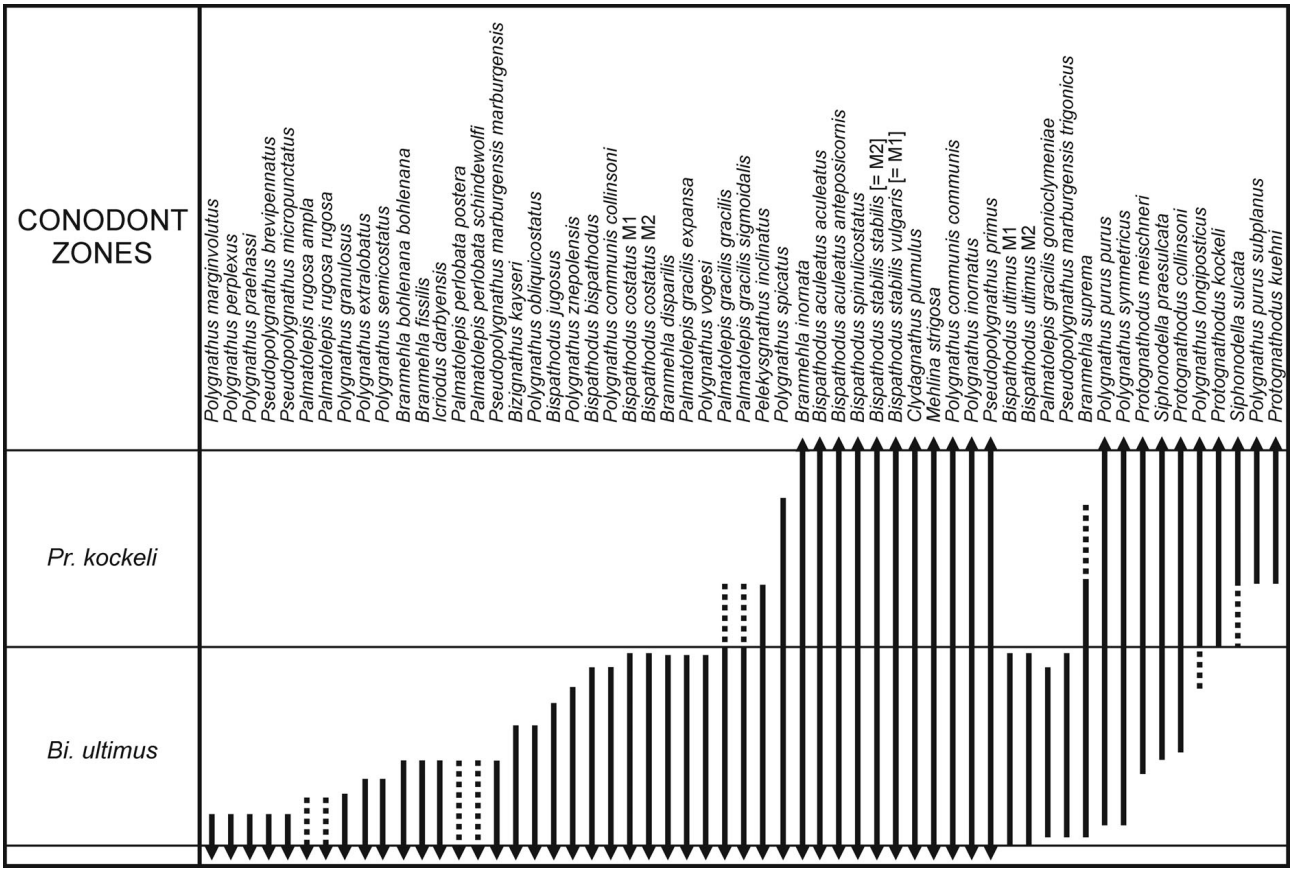

Figure 9. Stratigraphic distribution of the main Famennian conodont species and subspecies from the *Bispathodus ultimus* Zone to the *Protognathodus kockeli* Zone.

***Protognathodus kockeli* Zone**

Lower boundary: FAD of *Protognathodus kockeli*
Upper boundary: FAD of *Siphonodella bransoni*

Remarks. – The revised zone is equivalent to the Upper *praesulcata* and *sulcata* zones of Ziegler & Sandberg (1984), and to the *kockeli* and *sulcata/kuehni* zones of Kaiser *et al*. (2009). The zone in its present form was proposed by Corradini *et al*. (2016), which spans from the uppermost part of the Famennian to the lowest part of the Tournaisian, including the present position of the Devonian/Carboniferous Boundary.

Conodonts useful for the zonal identification. – *Polygnathus purus subplanus*, and *Protognathodus kuehni* enter in the middle part of the zone. Curved elements identified as representatives of *Siphonodella sulcata* enter within the zone, most likely in the basal part. The stratigraphic position of the entry of typical *Siphonodella sulcata* is still uncertain. *Palmatolepis gracilis gracilis*, *Pa. gracilis sigmoidalis*, the last representatives of the Upper Devonian genus *Palmatolepis, Branmehla suprema*, and *Pelekysgnathus inclinatus* become extinct. Kaiser *et al*. (2009) suggested that all the occurrences of palmatolepids after the Hangenberg extinction Event are due to reworking, as they have never been found above the level of the extinction in undisturbed sequences. *Polygnathus spicatus* becomes extinct within the zone. *Branmehla inornata* becomes extinct within the zone, or possibly it goes higher (Fig. 9).

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Appendix

Table 1. Stratigraphic distribution of common and widespread Famennian conodont species and subspecies. Biostratigraphic range is based on the lowest- and highest occurrence that has been reported for the taxon with the relevant citation. Notes: 1 – The reported range corresponds to that of typical *Pa. glabra pectinata*, M2 according to Hartenfels (2011); 2 – The reported range corresponds to that of typical *Pa. glabra prima*, M3 according to Hartenfels (2011); 3 , 4 – The question mark for the upper range indicates that occurrences of the species after the Hangenberg extinction event may be due to reworking; 5, 12, 16 – According to Hartenfels (2011) the species does not reach the top of the *Ps. granulosus* Zone; 6 – Metzger (1994) lowered the range of *Pa. p. maxima* to a "generic" *rhomboidea* Zone but in his sections it occurs above the disappearance of *Pa. poolei*, therefore we suppose its entry is within the Upper *rhomboidea* Zone; 7, 8, 10, 11 – The upper range of the species reported by Ji & Ziegler (1993) is not supported by undoubted evidences (see text for comment); 9 – Here with *Pa. quadrantinodosalobata* M2 we refer to the typical forms; 13 – According to Hartenfels (2011) the upper range may extend to the Middle *expansa* Zone; 14 – The given range refers to typical forms of *Po. procerus* according to the holotype; 15 – This species was defined by Ziegler (1962b, pre-print 1960) as *Polylophodonta*? *triphyllata* but before the paper was published Helms (1961) transferred it to the Genus *Polygnathus*; 17 – Typical forms of *Si. sulcata* occur in the *sulcata* Zone of Sandberg *et al*. (1978) and therefore within the *Pr. kockeli* Zone.

Taxon	Biostratigraphic range from literature	Biostratigraphic range according to the new global zonation	Notes
Alternognathus beulensis Ziegler & Sandberg, 1984	Uppermost *marginifera* – Lower *postera* (Ziegler & Sandberg 1984)	*Sc. vel. velifer – Po. styriacus*	
Alternognathus pseudostrigosus (Dreesen & Dusar, 1974)	Upper *rhomboidea* (Ziegler & Sandberg 1984) – Upper *trachytera* (Perri & Spalletta 1998a)	*Pa. gr. gracilis – Ps. granulosus*	
Alternognathus regularis continuus Hartenfels, 2011	Lower *trachytera* – Lower *postera* (Hartenfels 2011)	*Pa. r. trachytera – Po. styriacus*	
Alternognathus regularis regularis Ziegler & Sandberg, 1984	Uppermost *marginifera* (Ziegler & Sandberg 1984) – Upper *postera* (Perri & Spalletta 1998a)	*Sc. vel. velifer – Pa. gr. manca*	
Ancyrognathus bifurcatus (Ulrich & Bassler, 1926)	Upper *crepida* (Over 2007) – Lower *marginifera* (Wang *et al*. 2016)	*Pa. glabra prima – Pa. marg. uthaensis*	
Ancyrognathus cryptus Ziegler, 1962a	Lower *triangularis* – Uppermost *crepida* (Schülke 1996)	*Pa. triangularis – Pa. gl. pectinata*	
Ancyrognathus sinelaminus (Branson & Mehl, 1934a)	Middle *triangularis* – Uppermost *crepida* (Ziegler & Sandberg 1990)	*Pa. del. platys – Pa. gl. pectinata*	
Ancyrolepis cruciformis Ziegler, 1959	Middle *crepida* (Schülke 1996)	*Pa. termini*	
Antognathus mowitzaensis (Sandberg & Ziegler, 1979)	?Upper *trachytera* (Bultynck 2003) – Lower *expansa* (Gatovsky 2008)	*?Ps. granulosus – Pa. gr. expansa*	
Antognathus volnovachensis Lipnjagov (*in* Kozitskaya *et al*.), 1978	Lower *expansa* – Middle *expansa* (Gatovsky 2008)	*Pa. gr. expansa – Bi. costatus*	
Antognathus vjatsheslavi Gatovsky, 2008	Lower *rhomboidea* – Upper *rhomboidea* (Gatovsky 2008)	*Pa. rhomboidea – Pa. gr. gracilis*	
Barskovella katerinae Gatovsky, 2009	Lower *marginifera* – Uppermost *marginifera* (Gatovsky 2009)	*Pa. marg. marginifera – Sc. vel. velifer*	
Bispathodus aculeatus aculeatus (Branson & Mehl, 1934a)	Middle *expansa* (Ziegler & Sandberg 1984) – *texanus* (Lane *et al.* 1980)	*Bi. ac. aculeatus* – Visean	
Bispathodus aculeatus anteposicornis (Scott, 1961)	Middle *expansa – sandbergi* (Ziegler *et al*. 1974)	*Bi. ac. aculeatus* – Tournaisian	
Bispathodus bispathodus Ziegler *et al*., 1974	Upper *postera* – Middle *praesulcata* (Kaiser *et al*. 2009)	*Pa. gr. manca – Bi. ultimus*	

Table 1 – continued

Taxon	Biostratigraphic range from literature	Biostratigraphic range according to the new global zonation	Notes
Bispathodus costatus (Branson, 1934) M1	Middle *expansa* – Middle *praesulcata* (Ziegler & Sandberg 1984)	*Bi. costatus – Bi. ultimus*	
Bispathodus costatus (Branson, 1934) M2	Middle *expansa* – Middle *praesulcata* (Ziegler & Sandberg 1984)	*Bi. costatus – Bi. ultimus*	
Bispathodus jugosus (Branson & Mehl, 1934a)	Lower *expansa* (Ziegler & Sandberg 1984) – Lower *praesulcata* (Corradini 2003)	*Pa. gr. expansa – Bi. ultimus*	
Bispathodus spinulicostatus (Branson, 1934)	Middle *expansa* (Ziegler *et al*. 1974) – Lower *crenulata* (Sandberg *et al*. 1978)	*Bi. ac. aculeatus* – Tournaisian	
Bispathodus stabilis bituberculatus (Dzik, 2006) [M3]	Upper *postera* (Ziegler & Sandberg 1990) – Middle *expansa* (Hartenfels 2011)	*Pa. gr. manca – Bi. ac. aculeatus*	
Bispathodus stabilis stabilis (Branson & Mehl, 1934a) [M2]	Upper *trachytera* (Girard *et al*. 2017) – Lower *crenulata* (Sandberg *et al*. 1978)	*Ps. granulosus* – Tournaisian	
Bispathodus stabilis vulgaris (Dzik, 2006) [M1]	Upper *rhomboidea* (Girard *et al*. 2014) – Lower *crenulata* (Sandberg *et al*. 1978)	*Pa. gr. gracilis* – Tournaisian	
Bispathodus stabilis zizensis Hartenfels, 2011	Upper *trachytera* – Lower *expansa* (Hartenfels 2011)	*Ps. granulosus – Pa. gr. expansa*	
Bispathodus ultimus (Bischoff, 1957) M1 and M2	Upper *expansa* – Middle *praesulcata* (Ziegler & Sandberg 1984)	*Bi. ultimus*	
Bizignathus dissimilis (Helms & Wolska, 1967)	Lower *expansa* – Middle *expansa* (Corradini 1998)	*Pa. gr. expansa – Bi. ac. aculeatus*	
Bizignathus kayseri (Bischoff & Ziegler, 1956)	Lower *expansa* – Lower *praesulcata* (2009)	*Pa. gr. expansa – Bi. ultimus*	
Branmehla ampla (Branson & Mehl, 1934a)	?Upper *rhomboidea* (Dreesen & Dusar 1974) – Middle *expansa* (Hartenfels 2011)	*?Pa. gr. gracilis – Bi. ac. aculeatus*	
Branmehla bohlenana bohlenana (Helms, 1959)	Upper *marginifera* (Spalletta & Perri 1994) – Upper *expansa* (Corradini 2003)	*Pa. marg. utahensis – Bi. ultimus*	
Branmehla bohlenana gediki (Capkinoglu, 2000)	Lower *marginifera* – Middle *expansa* (Capkinoglu 2000)	*Pa. marg. marginifera – Bi. ac. aculeatus*	
Branmehla disparilis (Branson & Mehl, 1934a)	Upper *rhomboidea* (Perri & Spalletta unpubl.) – Middle *praesulcata* (Spalletta *et al.* 1998)	*Pa. gr. gracilis – Bi. ultimus*	
Branmehla fissilis (Branson & Mehl, 1934a)	Lower *expansa* – Upper *expansa* (Ziegler & Sandberg 1984)	*Pa. gr. expansa – Bi. ultimus*	
Branmehla inornata (Branson & Mehl, 1934a)	Upper *marginifera* (Ziegler & Sandberg 1984) – ?*hassi* (Kaiser *et al.* 2009)	*Pa. marg. uthaensis* – Tournaisian	
Branmehla suprema (Ziegler, 1962a)	Upper *expansa* (Ziegler & Sandberg 1984) – Upper *praesulcata* (Kaiser *et al.* 2009)	*Bi. ultimus – Pr. kockeli*	
Branmehla werneri (Ziegler, 1962a)	Lower *marginifera* (Ziegler & Sandberg 1984) – Middle *expansa* (Hartenfels 2011)	*Pa. marg. marginifera – Bi. ac. aculeatus*	
Clydagnathus ormistoni Beinert *et al*., 1971	Upper *postera* (Ziegler & Sandberg 1984) – Middle *expansa* (Hartenfels 2011)	*Pa. gr. manca – Bi. ac. aculeatus*	
Clydagnathus plumulus (Rhodes *et al.*, 1969)	Middle *expansa* (Hartenfels 2011) – Lower *duplicata* (Kaiser 2005)	*Bi. ac. aculeatus* – Tournaisian	
Dasbergina schaeferi Luppold (*in* Korn & Luppold), 1987	?Lower *postera* (Korn & Luppold 1987) – Upper *expansa* (Savage 2013)	*?Po. styriacus – Bi. ultimus*	
Dasbergina ziegleri Schäfer, 1976	Lower *expansa* – Middle *expansa* (Hartenfels 2011)	*Pa. gr. expansa – Bi. ac . aculeatus*	
Icriodus alternatus alternatus Branson & Mehl, 1934a	Upper *rhenana* – Uppermost *crepida* (Bultynck 2003)	Frasnian – *Pa. gl. pectinata*	
Icriodus alternatus helmsi Sandberg & Dreesen, 1984	Upper *rhenana* – Middle *crepida* (Ji & Ziegler 1993)	Frasnian – *Pa. termini*	
Icriodus alternatus mawsonae Yazdi, 1999	FZ 13c – Upper *crepida* (Perri & Spalletta unpubl.)	Frasnian – *Pa. gl. prima*	
Icriodus cornutus Sannemann, 1955b	Middle *triangularis* (Sandberg & Dreesen 1984) – ?Upper *trachytera* (Bultynck 2003)	*Pa. del. platys – Ps. granulosus*	

Table 1 – continued

Taxon	Biostratigraphic range from literature	Biostratigraphic range according to the new global zonation	Notes
Icriodus costatus (Thomas, 1949)	Uppermost *marginifera* – Lower *expansa* (Bultynck 2003)	*Sc. vel. velifer – Pa. gr. expansa*	
Icriodus chojnicensis Matyja, 1972	Upper *rhomboidea* – Uppermost *marginifera* (Bultynck 2003)	*Pa. rhomboidea – Sc. vel. velifer*	
Icriodus darbyensis Klapper, 1958	Lower *expansa* – Upper *expansa* (Bultynck 2003)	*Pa. gr. expansa – Bi. ultimus*	
Icriodus deformatus asymmetricus Ji & Ziegler, 1993	FZ 13c (Perri & Spalletta unpubl.) – Upper *triangularis* (Ji & Ziegler 1993)	Frasnian – *Pa. min. minuta*	
Icriodus deformatus deformatus Han, 1987	FZ 13b (Perri & Spalletta unpubl.) – Upper *triangularis* (Ji & Ziegler 1993)	Frasnian – *Pa. min. minuta*	
Icriodus iowaensis ancylus Sandberg & Dreesen, 1984	Middle *triangularis* – Middle *crepida* (Bultynck 2003)	*Pa. del. platys – Pa. termini*	
Icriodus iowaensis iowaensis Youngquist & Peterson, 1947	Lower *rhenana* (Bahrami *et al*. 2013) – Lower *rhomboidea* (Bultynck 2003)	Frasnian – *Pa. rhomboidea*	
Icriodus olivierii Corradini, 1998	Uppermost *crepida* – Lower *rhomboidea* (Corradini 2003)	*Pa. gl. pectinata – Pa. rhomboidea*	
Icriodus raymondi Sandberg & Ziegler, 1979	Uppermost *marginifera* – Middle *expansa* (Bultynck, 2003)	*Sc. vel. velifer – Bi. costatus*	
Mehlina gradata (Branson & Mehl, 1934a)	Late *falsiovalis* (Ziegler & Sandberg 1990) – Lower *marginifera* (Klapper & Ziegler 1979)	Frasnian – *Pa. marg. marginifera*	
Mehlina strigosa (Branson & Mehl, 1934a)	Middle *crepida* (Perri & Spalletta unpubl.) – *bransoni* (Kaiser *et al*. 2009)	*Pa. termini* – Tournaisian	
Palmatolepis adamantea Metzger, 1994	Upper *crepida* – Uppermost *crepida* (Metzger 1994)	*Pa. gl. prima – Pa. gl. pectinata*	
Palmatolepis arta Klapper *et al*., 2004	Upper *crepida* (Klapper *et al*. 2004) – Uppermost *crepida* (Over 2007)	*Pa. gl. pectinata*	
Palmatolepis circularis Szulczewski, 1971	Middle *crepida* – Upper *crepida* (Ji & Ziegler 1993)	*Pa. termini – Pa. gl. prima*	
Palmatolepis clarki Ziegler, 1962a	Middle *triangularis* (Ziegler & Sandberg 1990) – Lower *crepida* (Perri & Spalletta unpubl.)	*Pa. del. platys – Pa. crepida*	
Palmatolepis crepida Sannemann, 1955b	Lower *crepida* – Lower *rhomboidea* (Ji & Ziegler, 1993)	*Pa. crepida – Pa. rhomboidea*	
Palmatolepis delicatula delicatula Branson & Mehl, 1934	Lower *triangularis* (Ziegler & Sandberg 1990) – Lower *crepida* (Perri & Spalletta unbubl.)	*Pa. subperlobata – Pa. crepida*	
Palmatolepis delicatula platys Ziegler & Sandberg, 1990	Middle *triangularis* (Ziegler & Sandberg 1990) – Lower *crepida* (Perri & Spalletta unpubl.)	*Pa. del. platys – Pa. crepida*	
Palmatolepis glabra acuta Helms, 1963	Uppermost *crepida* – Upper *marginifera* (Ji & Ziegler 1993)	*Pa. gl. pectinata – Pa. marg. utahensis*	
Palmatolepis glabra distorta Branson & Mehl, 1934a	Lower *marginifera* (Ji & Ziegler 1993) – Upper *trachytera* (Over *et al*. 2009)	*Pa. marg. marginifera – Ps. granulosus*	
Palmatolepis glabra glabra Ulrich & Bassler, 1926	Lower *rhomboidea* – Lower *marginifera* (Ji & Ziegler 1993)	*Pa. rhomboidea – Pa. marg. marginifera*	
Palmatolepis glabra lepta Ziegler & Huddle, 1969	Upper *crepida* – Upper *trachytera* (Ji & Ziegler 1993)	*Pa. gl. prima – Ps. granulosus*	
Palmatolepis glabra pectinata Ziegler, 1962b M1 Sandberg & Ziegler, 1973	Uppermost *crepida* – Upper *rhomboidea* (Ji & Ziegler 1993)	*Pa. gl. pectinata – Pa. gr. gracilis*	
Palmatolepis glabra pectinata Ziegler, 1962b	Uppermost *crepida* – Upper *marginifera* (Ji & Ziegler 1993)	*Pa. gl. pectinata – Pa. marg. utahensis*	1
Palmatolepis glabra prima Ziegler & Huddle, 1969	Upper *crepida* – Upper *marginifera* (Ji & Ziegler 1993)	*Pa. gl. prima – Pa. marg. utahensis*	2
Palmatolepis gracilis expansa Sandberg & Ziegler, 1979	Lower *expansa* – Middle *praesulcata* (Ji & Ziegler 1993)	*Pa. gr. expansa – Bi. ultimus*	
Palmatolepis gracilis gonioclymeniae Müller, 1956	Upper *expansa* – Lower *praesulcata* (Ziegler & Sandberg 1984)	*Bi. ultimus*	
Palmatolepis gracilis gracilis Branson & Mehl, 1934a	Upper *rhomboidea* (Klapper & Ziegler 1979) – ?Upper *praesulcata* (Ji & Ziegler, 1993)	*Pa. gr. gracilis – ?Pr. kockeli*	3

Table 1 – continued

Taxon	Biostratigraphic range from literature	Biostratigraphic range according to the new global zonation	Notes
Palmatolepis gracilis manca Helms, 1963	Upper *postera* (Ziegler & Sandberg 1984) – Middle *expansa* (Hartenfels 2011)	*Pa. gr. manca – Bi. ac. aculeatus*	
Palmatolepis gracilis sigmoidalis Ziegler, 1962a	Upper *trachytera* – ?Upper *praesulcata* (Ji & Ziegler, 1993).	*Ps. granulosus – ?Pr. kockeli*	4
Palmatolepis klapperi Sandberg & Ziegler, 1973	Upper *crepida* (Metzger 1994) – Lower *marginifera* (Ji & Ziegler 1993)	*Pa. gl. prima – Pa. marg. marginifera*	
Palmatolepis lobicornis Schülke, 1995	Upper *triangularis* (Schülke 1999) – Lower *rhomboidea* (Perri & Spalletta unpubl.)	*Pa. min. minuta – Pa. rhomboidea*	
Palmatolepis marginifera marginifera Helms, 1959	Lower *marginifera* – Lower *trachytera* (Ziegler & Sandberg 1984).	*Pa. marg. marginifera – Pa. rug. trachytera*	
Palmatolepis marginifera duplicata Sandberg & Ziegler, 1973	Lower *marginifera* – Upper *marginifera* (Ji & Ziegler 1993)	*Pa. marg. marginifera – Pa. marg. utahensis*	
Palmatolepis marginifera utahensis Ziegler & Sandberg, 1984	Upper *marginifera* (Ji & Ziegler 1993) – Uppermost *marginifera* (Perri & Spalletta 1990)	*Pa. marg. utahensis – Sc. vel. velifer*	
Palmatolepis minuta loba Helms, 1963	Lower *crepida* – Lower *rhomboidea* (Ji & Ziegler 1993)	*Pa. crepida – Pa. rhomboidea*	
Palmatolepis minuta minuta Branson & Mehl, 1934a	Upper *triangularis* – Upper *trachytera* (Ji & Ziegler 1993)	*Pa. min. minuta – Ps. granulosus*	
Palmatolepis minuta schleizia Helms, 1963	Upper *rhomboidea* – Upper *postera* (Ji & Ziegler 1993)	*Pa. rhomboidea – Pa. gr. manca*	
Palmatolepis minuta subgracilis Bischoff, 1956	Upper *crepida* – Lower *rhomboidea* (Klapper & Ziegler 1979)	*Pa. gl. prima – Pa. rhomboidea*	
Palmatolepis minuta wolskae Szulczewski, 1971	Middle *crepida* Zone – Lower *rhomboidea* (Corradini 2003)	*Pa. termini – Pa. rhomboidea*	
Palmatolepis perlobata grossi Ziegler (in Kronberg *et al*.) 1960	Upper *marginifera* Zone – Upper *trachytera* (Ziegler & Sandberg 1984)	*Pa. m. utahensis – Ps. granulosus*	5
Palmatolepis perlobata helmsi Ziegler, 1962a	Lower *rhomboidea* (Hartenfels 2011) – Middle *expansa* (Ziegler & Sandberg 1984)	*Pa. rhomboidea – Bi. ac. aculea*tus	
Palmatolepis perlobata maxima Müller, 1956	?Upper *rhomboidea* (Metzger 1994) – Middle *expansa* (Hartenfels 2011)	*?Pa. gr– gracilis – Bi. ac. acu*leatus	6
Palmatolepis perlobata perlobata Ulrich & Bassler, 1926	Upper *triangularis* – Uppermost *crepida* (Ziegler & Sandberg 1984)	*Pa. min. minuta – Pa. gl. pectinata*	
Palmatolepis perlobata postera Ziegler (in Kronberg *et al*.) 1960	Lower *postera* – Upper *expansa* (Ji & Ziegler 1993)	*Po. styriacus – ?Bi. ultimus*	7
Palmatolepis perlobata schindewolfi Müller, 1956	Upper *crepida* – Upper *expansa* (Ji & Ziegler 1993)	*Pa. gl. prima – ?Bi. ultimus*	8
Palmatolepis perlobata sigmoidea Ziegler, 1962a	Lower *marginifera* – Upper *postera* (Ji & Ziegler 1993)	*Pa. marg. marginifera – Pa. gr. manca*	
Palmatolepis poolei Sandberg & Ziegler, 1973	Lower *rhomboidea* (Ji & Ziegler 1993)	*Pa. rhomboidea*	
Palmatolepis protorhomboidea Sandberg & Ziegler, 1973	Lower *triangularis* – Lower *rhomboidea* (Ji & Ziegler 1993)	*Pa. subperlobata – Pa. rhomboidea*	
Palmatolepis quadrantinodosa inflexa Müller, 1956	Upper *rhomboidea* (Ji & Ziegler 1993) – Upper *marginifera* (Perri & Spalletta 1998c)	*Pa. gr. gracilis – Pa. marg. utahensis*	
Palmatolepis quadrantinodosa inflexoidea Ziegler, 1962a	Lower *marginifera* (Ji & Ziegler 1993) – Upper *marginifera* (Savage 2013)	*Pa. marg. marginifera – Pa. marg. utahensis*	
Palmatolepis quadrantinodosa quadrantinodosa Branson & Mehl, 1934a	Lower *marginifera* (Ji & Ziegler 1993)	*Pa. marg. marginifera*	
Palmatolepis quadrantinodosalobata Sannemann, 1955a M1 Sandberg & Ziegler, 1973	Uppermost *crepida* – Lower *rhomboidea* (Sandberg & Ziegler 1973)	*Pa. gl. pectinata – Pa. rhomboidea*	
Palmatolepis quadrantinodosalobata Sannemann, 1955a M2 Ji & Ziegler, 1993	Lower *crepida* – Lower *rhomboidea* (Ji & Ziegler 1993)	*Pa. crepida – Pa. rhomboidea*	9

Table 1 – continued

Taxon	Biostratigraphic range from literature	Biostratigraphic range according to the new global zonation	Notes
Palmatolepis regularis Cooper, 1931	Upper *triangularis* – Lower *rhomboidea* (Ji & Ziegler 1993)	*Pa. min. minuta – Pa. rhomboidea*	
Palmatolepis rhomboidea Sannemann, 1955a	Lower *rhomboidea* (Klapper & Ziegler 1979) – Upper *marginifera* (Corradini 2003)	*Pa. rhomboidea – Pa. marg. utahensis*	
Palmatolepis robusta Schülke, 1995	Upper *triangularis* – Lower *crepida* (Schülke 1999)	*Pa. min. minuta – Pa. crepida*	
Palmatolepis rugosa ampla Müller, 1956	Lower *postera* (Perri & Spalletta 1991) – Upper *expansa* (Ji & Ziegler 1993)	*Po. styriacus – ?Bi. ultimus*	10
Palmatolepis rugosa cf. *ampla* Müller, 1956, *sensu* Ziegler (in Kronberg *et al*.) 1960	Upper *marginifera* (Ji & Ziegler 1993) – Lower *postera* (Mossoni 2014)	*Pa. marg. utahensis – Po. styriacus*	
Palmatolepis rugosa rugosa Branson & Mehl, 1934	Upper *postera* (Hartenfels 2011) – Upper *expansa* (Ji & Ziegler 1993)	*Pa. gr. manca – ?Bi. ultimus*	11
Palmatolepis rugosa trachytera Ziegler (in Kronberg *et al*.) 1960	Lower *trachytera* – Upper *trachytera* (Ji & Ziegler 1993)	*Pa. rug. trachytera – Ps. granulosus*	12
Palmatolepis sandbergi Ji & Ziegler, 1993	Upper *triangularis* – Lower *crepida* (Ji & Ziegler 1993)	*Pa. min. minuta – Pa. crepida*	
Palmatolepis spathula Schülke, 1995	Upper *triangularis* – Lower *crepida* (Schülke 1995)	*Pa. min. minuta – Pa. crepida*	
Palmatolepis stoppeli Sandberg & Ziegler, 1973	Upper *rhomboidea* – Lower *marginifera* (Ji & Ziegler 1993)	*Pa. gr. gracilis – Pa. marg. marginifera*	
Palmatolepis subperlobata Branson & Mehl, 1934	Lower *triangularis* (Klapper 2007b) – Lower *marginifera* (Ji & Ziegler 1993)	*Pa. subperlobata – Pa. marg. marginifera*	
Palmatolepis tenuipunctata Sannemann, 1955b	Upper *triangularis* – Uppermost *crepida* (Ji & Ziegler 1993)	*Pa. min. minuta – Pa. gl. pectinata*	
Palmatolepis termini Sannemann, 1955b	Middle *crepida* – Upper *crepida* (Ji & Ziegler 1993)	*Pa. termini – Pa. gl. prima*	
Palmatolepis triangularis Sannemann, 1955a	Lower *triangularis* – Lower *crepida* (Ziegler & Sandberg 1990)	*Pa. triangularis – Pa. crepida*	
Palmatolepis ultima Ziegler, 1958	FZ 13c – Middle *triangularis* (Klapper 2007b)	Frasnian – *Pa. del. platys*	
Palmatolepis weddigei Ji & Ziegler, 1993	Upper *triangularis* – Middle *crepida* (Ji & Ziegler 1993)	*Pa. min. minuta – Pa. termini*	
Palmatolepis werneri Ji & Ziegler, 1993	Upper *triangularis* – Middle *crepida* (Ji & Ziegler 1993)	*Pa. min. minuta – Pa. termini*	
Palmatolepis wolskajae Ovnatanova, 1969	Lower *crepida* – Upper *crepida* (Schülke 1999)	*Pa. crepida – Pa. gl. prima*	
Pelekysgnathus brevis Sandberg & Dreesen, 1984	*kockelianus* – Uppermost *crepida* (Bultynck 2003)	Eifelian – *Pa. gl. pectinata*	
Pelekysgnathus inclinatus Thomas, 1949	Middle *triangularis* (Huang & Gong 2016) – Upper *praesulcata* (Sandberg & Dreesen 1984)	*Pa. del. platys – Pr. kockeli*	
Pelekysgnathus planus Sannemann, 1955b	Lower *rhenana* – Upper *crepida* (Corradini 2003)	Frasnian – *Pa. gl. prima*	
Pelekysgnathus serradentatus Capkinoglu, 1991	Middle *triangularis* (Capkinoglu & Gedik 2000) – Uppermost *crepida* (Bahrami *et al*. 2013)	*Pa. del. platys – Pa. gl. pectinata*	
Polygnathus angustidiscus Branson & Mehl, 1934a	Upper *subterminus* Fauna (Witzke *et al.* 1989) – Middle *crepida* (Perri & Spalletta unpubl.)	*Givetian – Pa. termini*	
Polygnathus brevilaminus Branson & Mehl, 1934a	*linguiformis* (Schülke 1995) – Upper *trachytera* (Hartenfels 2011)	Frasnian – *Ps. granulosus*	13
Polygnathus buzmakovi Kuz'min, 1990	Upper *triangularis* (Perri & Spalletta unpubl.) – Lower *marginifera* (Molloy *et al.* 1997)	*Pa. min. minuta – Pa. marg. marginifera*	
Polygnathus communis collinsoni Druce, 1969	Lower *postera* (Druce 1976) – Middle *praesulcata* (Ji & Ziegler 1993)	*Po. styriacus – Bi. ultimus*	
Polygnathus communis communis Branson & Mehl, 1934b	Lower *crepida* (Schülke 1998) – *texanus* (Lane *et al*. 1980)	*Pa. crepida* – Visean	
Polygnathus communis dentatus Druce, 1969	Uppermost *marginifera* – Lower *crenulata* (Ji & Ziegler 1993)	*Sc. v. velifer* – Tournaisian	

Table 1 – continued

Taxon	Biostratigraphic range from literature	Biostratigraphic range according to the new global zonation	Notes
Polygnathus communis renatae Corradini & Spalletta (*in* Corradini *et al*.), 2003	Lower *praesulcata* – Lower *duplicata* (Mossoni *et al*. 2015)	*Bi. ultimus* – Tournaisian	
Polygnathus delicatulus Ulrich & Bassler, 1926	Upper *styriacus* – Lower *costatus* (Klapper *in* Ziegler 1975)	*Pa. gr. manca – Bi. costatus*	
Polygathus diversus Helms, 1959	Lower *rhomboidea* (Corradini 2003) – *styriacus* (Glenister & Klapper 1966)	*Pa. rhomboidea – Po. styriacus*	
Polygnathus doulingshanensis Ji & Ziegler, 1993	Uppermost *marginifera* – Upper *trachytera* (Ji & Ziegler 1993)	*Sc. vel. velifer – Ps. granulosus*	
Polygnathus eoglaber Ji & Ziegler, 1993	Upper *triangularis* – Upper *rhomboidea* (Ji & Ziegler 1993)	*Pa. min. minuta – Pa. gr. gracilis*	
Polygnathus experplexus Sandberg & Ziegler, 1979	Upper *postera* (Hartenfels 2011) – Middle *expa*nsa (Ji & Ziegler 1993)	*Pa. gr. manca – Bi. costatus*	
Polygnathus extralobatus Schäfer, 1976	Lower *expansa* – Upper *expansa* (Ji & Ziegler 1993)	*Pa. gr. expansa – Bi. ultimus*	
Polygnathus glaber bilobatus Ziegler, 1962a	Lower *marginifera* – Lower *trachytera* (Ji & Ziegler 1993)	*Pa. marg. marginifera – Pa. rug. trachytera*	
Polygnathus glaber glaber Ulrich & Bassler, 1926	Middle *crepida* (Girard *et al*. 2014) – Lower *trachytera* (Ji & Ziegler 1993)	*Pa. termini – Pa. rug. trachytera*	
Polygnathus glaber medius Helms & Wolska, 1967	Lower *marginifera* – Upper *marginifera* (Ji & Ziegler 1993)	*Pa. marg. marginifera – Pa. marg. utahensis*	
Polygnathus granulosus Branson & Mehl, 1934a	Upper *marginifera* (Corradini 2003) – Upper *expansa* (Ji & Ziegler 1993)	*Pa. marg. utahensis – Bi. ultimus*	
Polygnathus guttiformis Khalymbadzha *et al*., 1992	Middle *triangularis* – Lower? *marginifera* (Schülke 1995)	*Pa. delicatula platys* – ?*Pa. marg. marginifera*	
Polygnathus hassi Helms, 1961	Lower *expansa* – Middle *expansa* (Ziegler & Sandberg 1984)	*Pa. gr. expansa – Bi. costatus*	
Polygnathus homoirregularis Helms, 1961	Upper *trachytera* – Middle *expansa* (Ji & Ziegler 1993)	*Ps. granulosus – Bi. costatus*	
Polygnathus inornatus Branson & Mehl, 1934b	Middle?*expansa – anchoralis* (Bahrami *et al.* 2011)	?*Bi. costatus* – Tournaisian	
Polygnathus lagowiensis Helms & Wolska, 1967	Upper *marginifera* – Uppermost *marginifera* (Klapper *in* Ziegler 1975)	*Pa. marg. utahensis – Sc. vel. velifer*	
Polygnathus lauriformis Dreesen & Dusar, 1974	Middle *crepida* (Dreesen & Dusar 1974) – Uppermost *marginifera* (Perri & Spalletta 1990)	*Pa. termini – Sc. vel. velifer*	
Polygnathus longiposticus Branson & Mehl, 1934b	?Lower *praesulcata* (Wang & Yin 1988) – *isosticha*–Upper *crenulata* (Sandberg *et al.* 1978)	*?Bi. ultimus* – Tournaisian	
Polygnathus margaretae Kononova & Weyer, 2013	Lower *praesulcata* (Kononova & Weyer 2013)	*Bi. ultimus*	
Polygnathus margaritatus Schäfer, 1976	Upper *trachytera* – Middle *expansa* (Hartenfels 2011)	*Ps. granulosus – Bi. costatus*	
Polygnathus marginvolutus Gedik, 1969	Upper *marginifera* (Perri & Spalletta 1998b) – Upper *expansa* (Ziegler & Sandberg 1984)	*Pa. marg. utahensis – Bi. ultimus*	
Polygnathus nodocostatus nodocostus Branson & Mehl, 1934a	Lower *crepida* – Lower *expansa* (Ji & Ziegler 1993)	*Pa. crepida – Pa. gr. expansa*	
Polygnathus nodocostatus ovatus, Helms, 1961	Upper *crepida* – Lower *postera* (Hartenfels 2011)	*Pa. glabra prima – Po. styriacus*	
Polygnathus nodoundatus Helms, 1961	Upper *marginifera* – Lower *trachytera* (Perri & Spalletta 1990)	*Pa. marg. utahensis – Pa. rug. trachytera*	
Polygnathus obliquicostatus Ziegler, 1962a	Upper *trachytera* (Hartenfels 2011) – Lower *praesulcata* (Corradini *et al*. 2003)	*Ps. granulosus – Bi. ultimus*	
Polygnathus padovanii Perri & Spalletta, 1990	Uppermost?*crepida* – Upper *trachytera* (Hartenfels 2011)	*?Pa. gl. pectinata – Ps. granulosus*	
Polygnathus pennatuloideus Holmes, 1928	Lower *marginifera* (Perri & Spalletta unpubl.) – Lower *expansa* (Ji & Ziegler 1993)	*Pa. marg. marginifera – Pa. gr. expansa*	

Table 1 – continued

Taxon	Biostratigraphic range from literature	Biostratigraphic range according to the new global zonation	Notes
Polygnathus perplexus Thomas, 1949	Upper *marginifera* (Dreesen & Dusar 1974) – Upper *expansa* (Ziegler & Sandberg 1984)	*Pa. marg. utahensis – Bi. ultimus*	
Polygnathus planirostratus Dreesen & Dusar, 1974	Lower *rhomboidea* – Lower *trachytera* (Dreesen & Dusar 1974)	*Pa. rhomboidea – Pa. rug. trachytera*	
Polygnathus pomeranicus Matyja, 1993	Upper/Uppermost *crepida* (Wang *et al*. 2016) – Uppermost *marginifera* (Matyja 1993)	*Pa. gl. prima/Pa. gl. pectinata – Sc. vel. velifer*	
Polygnathus praecursor Mattyja, 1993	Beginning of Famennian – Lower *crepida* (Dzik 2006)	*Pa. subperlobata – Pa. crepida*	
Polygnathus praehassi Schäfer, 1976	Lower *postera* (Mossoni 2014) – Upper *expansa* (Ziegler & Sandberg 1984)	*Po. styriacus – Bi. ultimus*	
Polygnathus procerus Sannemann, 1955b	Upper *triangularis* (Perri & Spalletta unpubl.) – Uppermost *crepida* (Corradini 2003)	*Pa. min. minuta – Pa. gl. pectinata*	14
Polygnathus protostyriacus Tragelehn & Hartenfels, 2011	Upper *trachytera* – Lower *expansa* (Hartenfels 2011)	*Ps. granulosus – Pa. gr. expansa*	
Polygnathus purus purus Voges, 1959	Upper *expansa* – Lower *crenulata* (Corradini *et al*. 2003)	*Bi. ultimus* – Tournaisian	
Polygnathus purus subplanus Voges, 1959	*sulcata* – Upper *duplicata* (Sandberg *et al*. 1978)	*Pr. kockeli* – Tournaisian	
Polygnathus ratebi Yazdi, 1999	Upper *triangularis* – Uppermost *crepida* (Bahrami *et al*. 2013)	*Pa. min. minuta – Pa. gl. pectinata*	
Polygnathus restrictus Vorontsova, 1993	Lower *styriacus* – Middle *praesulcata* (Vorontsova 1993)	*Po. styriacus – Bi. ultimus*	
Polygnathus rhabdotus Schäfer, 1976	Lower *postera* (Schäfer 1976) – Middle *expansa* (Hartenfels 2011)	*Po. styriacus – Bi. costatus*	
Polygnathus rhomboideus Helms, 1961	Uppermost *crepida* – Upper *rhomboidea* (Perri & Spalletta unpubl.)	*Pa. gl. pectinata – Pa. gr. gracilis*	
Polygnathus semicostatus Branson & Mehl, 1934a	Middle *crepida* – Upper *expansa* (Ji & Ziegler 1993)	*Pa. termini – Bi. ultimus*	
Polygnathus spicatus Branson, 1934	*Middle expansa* (Kalvoda & Kukal 1987) – *sulcata* (Sandberg *et al.* 1974)	*Bi. costatus – Pr. kockeli*	
Polygnathus spiculiferus Hartenfels, 2011	Lower *expansa* (Hartenfels 2011)	*Pa. gr. expansa*	
Polygnathus styriacus Ziegler (*in* Flügel & Ziegler), 1957	Lower *postera* – Lower *expansa* (Ji & Ziegler 1993)	*Po. styriacus – Pa. gr. expansa*	
Polygnathus subirregularis Ziegler & Sandberg, 1979	Lower *trachytera* – Lower *expansa* (Ziegler & Sandberg 1984)	*Pa. rug. trachytera – Pa. gr. expansa*	
Polygnathus subnormalis Vorontsova & Kuz'min, 1984	Lower *rhomboidea* – Upper *trachytera* (Kuz'min 1990)	*Pa. rhomboidea – Ps. granulosus*	
Polygnathus symmetricus Branson, 1934	Upper *expansa* – Upper *sandbergi* (Perri & Spalletta 2001)	*Bi. ultimus* – Tournaisian	
Polygnathus tenellus Ji & Ziegler, 1993	Lower *rhenana* – Lower *triangularis* (Ji & Ziegler 1993)	Frasnian – *Pa. triangularis*	
Polygnathus triphyllatus Helms, 1961	Upper *rhomboidea* – Lower *marginifera* (Klapper & Ziegler 1979)	*Pa. gr. gracilis – Pa. marg. marginifera*	15
Polygnathus vogesi Ziegler, 1962a	Lower *expansa* (Ji & Ziegler 1993) – Upper *duplicata* (Bardasheva *et al*. 2004)	*Pa. gr. expansa* – Tournaisian	
Polygnathus zikmundovae Zhuralev, 1991	Upper *praesulcata* – *sulcata* (Vorontsova 1993)	*Bi. ultimus – Pr. kockeli*	
Polygnathus znepolensis Spassov, 1965	Lower *expansa* (Hartenfels 2011) – Lower *praesulcata* (Ziegler & Sandberg 1984)	*Pa. gr. expansa – Bi. ultimus*	
Polylophodonta concentrica (Ulrich & Bassler, 1926)	Lower *trachytera* – Lower *postera* (Hartenfels 2011)	*Pa. rug. trachytera – Po. styriacus*	
Polylophodonta confluens (Ulrich & Bassler, 1926)	Lower *rhomboidea* – Uppermost *marginifera* (Over *et al.* 2009)	*Pa. rhomboidea – Sc. vel. velifer*	

Table 1 – continued

Taxon	Biostratigraphic range from literature	Biostratigraphic range according to the new global zonation	Notes
Polylophodonta gyratilineata Holmes, 1928	Upper *rhomboidea* – Lower *marginifera* (Klapper & Ziegler 1979)	*Pa. gr. gracilis – Pa. marg. marginifera*	
Polylophodonta linguiformis Branson & Mehl, 1934	Uppermost *crepida* (Ziegler & Sandberg 1973) – Upper *marginifera* (Perri & Spalletta 1990)	*Pa. gl. pectinata – Pa. marg. utahensis*	
Protognathodus collinsoni Ziegler, 1969	Lower *praesulcata* – Upper *duplicata* (Corradini *et al*. 2011)	*Bi. ultimus* – Tournaisian	
Protognathodus meischneri Ziegler, 1969	Upper *expansa* – Upper *duplicata* (Corradini *et al*. 2011)	*Bi. ultimus* – Tournaisian	
Protognathodus kockeli (Bischoff, 1957)	Upper *praesulcata* – Lower *crenulata* (Corradini *et al*. 2011)	*Pr. kockeli* – Tournaisian	
Protognathodus kuehni Ziegler & Leuteritz (*in* Koch *et al*.), 1970	*sulcata – sandbergi* (Corradini *et al*. 2011)	*Pr. kockeli* – Tournaisian	
Pseudopolygnathus brevipennatus Ziegler, 1962a	Upper *postera* (Hartenfels 2011) – Upper *expansa* (Ziegler & Sandberg 1984)	*Pa. gr. manca – Bi. ultimus*	
Pseudopolygnathus controversus Sandberg & Ziegler, 1979	Upper *postera* – Middle *expansa* (Ziegler & Sandberg 1984)	*Pa. gr. manca – Bi. costatus*	
Pseudopolygnathus granulosus Ziegler, 1962a	Upper *trachytera* – Upper *postera* (Hartenfels 2011)	*Ps. granulosus – Pa. gr. manca*	
Pseudopolygnathus inordinatus Tragelehn & Hartenfels, 2011	Upper *postera* – Lower *expansa* (Hartenfels 2011)	*Pa. gr. manca – Pa. gr. expansa*	
Pseudopolygnathus marburgensis marburgensis Bischoff & Ziegler, 1956	Lower *expansa* – Upper *expansa* (Ziegler & Sandberg 1984)	*Pa. gr. expansa – Bi. ultimus*	
Pseudopolygnathus marburgensis trigonicus Ziegler, 1962a	Upper *expansa* – Middle *praesulcata* (Ziegler & Sandberg 1984)	*Bi. ultimus*	
Pseudopolygnathus micropunctatus Bischoff & Ziegler, 1956	Upper *trachytera* (Perri & Spalletta 1991) – Upper *expansa* (Corradini 2003)	*Ps. granulosus – Bi. ultimus*	
Pseudopolygnathus primus Branson & Mehl, 1934	Lower *expansa* (Klapper *in* Ziegler 1981) – Lower *crenulata* (Sandberg *et al.* 1974)	*Pa. gr. expansa* – Tournaisian	
Scaphignathus peterseni Sandberg & Ziegler, 1979	Upper *postera* – Lower *expansa* (Ziegler & Sandberg 1984)	*Pa. gr. manca – Pa. gr. expansa*	
Scaphignathus velifer leptus Ziegler & Sandberg, 1984	Uppermost *marginifera* – Upper *postera* (Ziegler & Sandberg 1984)	*Sc. vel. velifer – Pa. gr. manca*	
Scaphignathus velifer velifer Helms, 1959	Uppermost *marginifera* – Upper *trachytera* (Ziegler & Sandberg 1984)	*Sc. vel. velifer – Ps. granulosus*	16
Scaphignathus ziegleri Druce, 1969	Lower *expansa* (Ziegler & Sandberg 1984)	*Pa. gr. expansa*	
Siphonodella praesulcata Sandberg (*in* Sandberg *et al*.), 1972	Lower *praesulcata* – Lower *duplicata* (Sandberg *et al.* 1978)	*Bi. ultimus* – Tournaisian	
Siphonodella sulcata (Huddle, 1934)	?Upper *praesulcata* (Kaiser & Corradini 2011) – Lower *crenulat*a (Sandberg *et al*. 1978)	*Pr. kockeli* – Tournaisian	17