

# Eifelian (Middle Devonian) to Lower Frasnian (Upper Devonian) conodont biostratigraphy in the Villech section (Spanish Central Pyrenees)

SOFIE GOUWY, JAU-CHYN LIAO & JOSÉ IGNACIO VALENZUELA-RÍOS



Conodont biostratigraphic research on the Comabella Formation at Villech (Spanish Central Pyrenees), a 54 m thick pinkish-greyish compact hemipelagic limestone section situated in the Compte “subfacies area”, reveals an Eifelian to early Frasnian age for the studied interval. The base of the Formation is of lower Eifelian age (*costatus* Zone), indicated by the lowest local record of *Polygnathus angustipennatus*, associated with *P. partitus*. The *kockelianus* and *eiflius* zones are recognized in the lower half of the section. The uppermost Eifelian and lowermost Givetian (*ensensis* and *hemiansatus* zones, respectively) have not been found so far but might be located in a covered interval. Other biozones recognized in the section are the *timorensis-rhenanus/varcus*, *ansatus*, *semialternans*, *hermanni*, *disparilis* and *norrisi* zones in the Givetian, all indicated by their respective index species and the MN1 Zone (occurrence of *Ad. binodosa* and *Ad. pristina*) in the Frasnian. A black shale and limestone layer in the upper part of the Villech section could represent the local signature of the upper part of the global Taghanic Crisis. • Key words: conodonts, Middle Devonian, biostratigraphy, Spanish Central Pyrenees.

GOUWY, S., LIAO, J.-C. & VALENZUELA-RÍOS, J.I. 2013. Eifelian (Middle Devonian) to Lower Frasnian (Upper Devonian) conodont biostratigraphy in the Villech section (Spanish Central Pyrenees). *Bulletin of Geosciences* 88(2), 315–338 (7 figures, 4 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received February 3, 2012; accepted in revised form June 11, 2012; published online February 4, 2013; issued June 7, 2013.

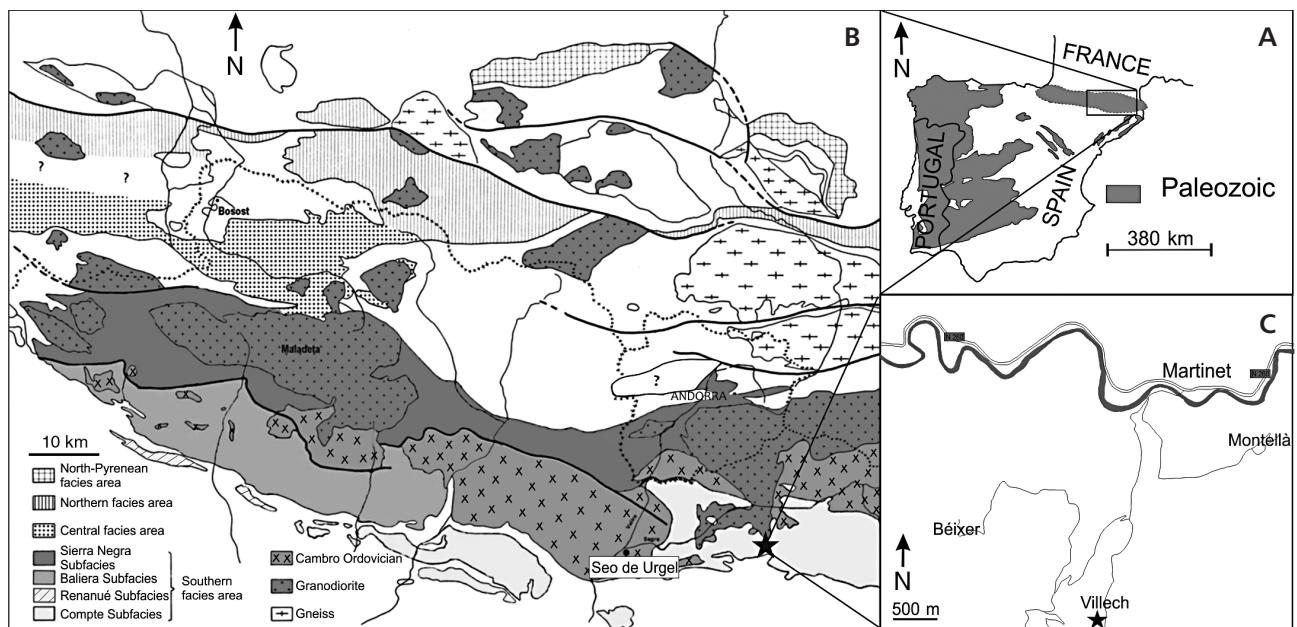
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The Pyrenean Paleozoic rocks are part of the southern flank of the European Variscan Chain where south-verging structures prevail, south of the North Pyrenean Fault Zone. Deformation and magmatism of Paleozoic rocks are mainly Variscan in age while Alpine deformation produced the reactivation of older structures and the structural stacking of Variscan units.

During the Devonian, a complex sedimentation took place in the Central and Eastern Pyrenees. In this region, important lateral changes in Devonian lithologies prompted Mey (1967) to arrange them into four major facies areas. In this subdivision, the concept of subfacies was introduced in the “Southern facies area” by Mey (1967). He distinguished the Sierra Negra, the Baliera, the Renanué and the Compte “subfacies areas” based on the grouping of similar Devonian sequences (Fig. 1B). Some subsequent authors like Boersma (1973) and Zwart (1979) regrouped the stratigraphic units but in this work the original subdivision of the “Southern facies” into four “subfacies” of Mey (1967) (Fig. 1B) is used.

Middle Devonian rocks are widespread in the Spanish Central Pyrenees but only in the last 40 years, studies on this topic have been intensified (Harteveld 1970, Boersma 1973, Sanz-López 1995, Liao *et al.* 2001, Valenzuela-Ríos & Liao 2006, Liao *et al.* 2008, Liao & Valenzuela-Ríos 2008). One of the most relevant early works for conodont studies was Boersma (1973). He did the initial conodont studies of several important Middle and Upper Devonian sections, among which also the Villech section that is described here in detail. The same section was also sampled by Valenzuela-Ríos in the course of a Geological Survey. He improved the initial dating of Boersma over the entire Villech section (from the Pragian to the Carboniferous) and realized the potential of the section. A significant part of it is studied in this paper.

The Villech section is located in the Compte “subfacies area”, part of the larger “Southern facies area” of Mey (1967) located in the Spanish Central Pyrenees (Figs 1A–C, 2). The upper part of the Emsian, the Middle Devonian and the



**Figure 1.** Devonian Facies areas in the Spanish Central Pyrenees (B – after Zwart 1979) and location of the studied section (B, C). Star indicates the position of the section.

Frasnian of the Compte “subfacies area” are represented by the Villech and Comabella Formations. In most sections, the Villech Formation ends within the *serotinus* Zone (Montesinos & Sanz-López 1999); in the Serra Comabella section, it can reach the lower part of the *patulus* Zone, indicating a possible diachronous top of the Formation. The boundary between the Villech and Comabella formations is situated around the boundary between the upper Emsian *serotinus* and *patulus* zones (Sanz-López 1995, 2002; Valenzuela-Ríos & Sanz-López 2002; Valenzuela-Ríos & Liao 2006).

## The Villech section

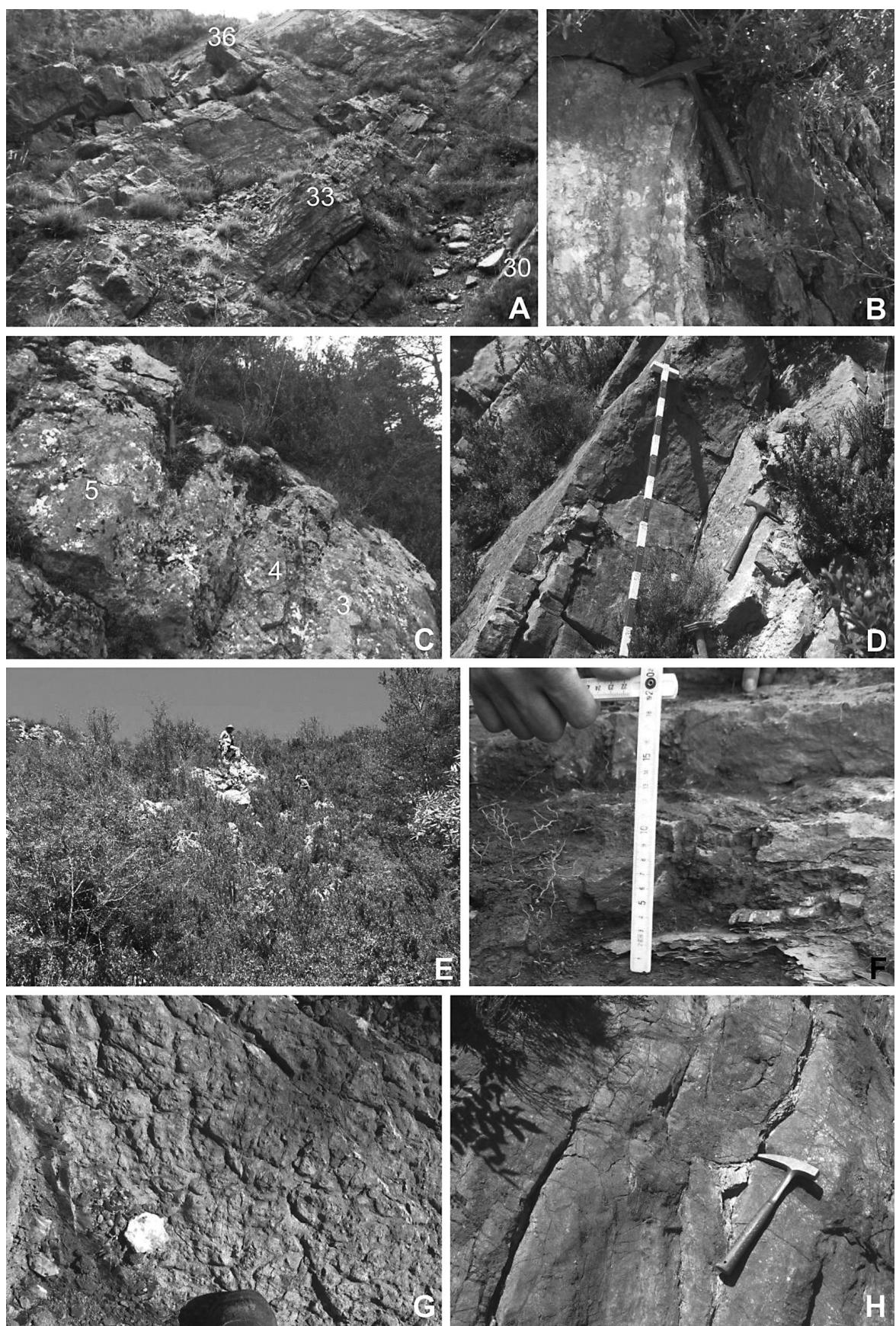
The section is partly exposed near the road on the eastern slope of a hill and partly in an abandoned quarry along the road close to the small village of Villech (Fig. 1C). The 54 m long section is easily accessible with a bit of climbing.

Two lithological formations are exposed in a series of almost continuous outcrops of which only two are studied here (Fig. 2A–H). The Villech Formation is composed of nodular and argillaceous limestones with different amounts of red and green shales. The overlain Comabella

Formation consists of nodular reddish limestones and condensed red beds in the lowermost part of the formation (Fig. 2B, C, E) followed by condensed pinkish-greyish limestones (Fig. 2A, D, H) with hard-ground development (Fig. 2G) and synsedimentary tectonics (Fig. 2H) especially in the uppermost part of the section. The limestone beds are rather poor in number of conodont specimens, although they have a high diversity of conodont taxa.

In this road-cut section, Boersma (1973) recognized the uppermost part of the Basibé Formation, the Villech Formation and what he called the Compte (A–C) Formation; his Compte A Fm approximately corresponds to the current Comabella Formation. The studied part of the Villech section represents the uppermost Villech Formation and most of the Compte A Member of Boersma (1973). He placed the base of his A Member of the Compte Formation at the base of some thick-bedded grey limestones; about 11 m above the top of the Villech Formation as conceived in the present study (see Fig. 3). Boersma (1973) situated this level in the *kockelianus* Zone (1973), corresponding to the present *australis-ensensis* zones (upper Eifelian) based on the first occurrence of *Spathognathodus intermedius*. From his uppermost sample of the Compte A Member (sample 435), he mentioned a list of species from which

**Figure 2.** Images of the Villech section. • A – upper part of the Villech section in the quarry (samples 30–36) scale: the two thick limestone beds in the middle of the picture measure together 3.6 m. • B – contact between the Villech Formation (right) and Comabella Formation (left). • C – reddish nodular limestones in the lowermost part of the section (samples 2–5). • D – bedded massive grey limestone in the upper part of the section (here samples 25–26). • E – fieldwork conditions in the lower part of the section (around sample 23). • F – thin layer of black shales and limestone (sample 29). • G – hardground with limonite (sample Q-1/1). • H – synsedimentary tectonics (slumping) around sample 34.



many, according to present conodont biostratigraphy, cannot occur together. The sample either contained pieces from different beds or his identifications are, at least, not all correct. In any case these data should no longer be considered.

Sanz-López (2002) places the nodular lower part of the Comabella Fm. in the *costatus* Zone; the more condensed red beds are located in the *kockelianus* Zone and the condensed hemipelagic limestones with hardgrounds in the upper Givetian.

The Villech section (Fig. 3) was sampled during two field campaigns in the summers of 2007 and 2008. During the first field campaign the section was measured in detail and 31 samples were taken for conodont research, during the second campaign 20 extra samples were taken for the refining of the conodont biostratigraphy, based on the preliminary results of the first sampling. Samples from V500 = Vi-I/1 to V620, V1/2, Q-1/1 and Q-1/2 are from the earlier geological survey campaign by Valenzuela-Ríos.

## Results

The conodont elements retrieved from the studied part of the Villech section are moderately preserved (no deformed conodonts, but a lot of broken specimens) and have a colour alteration index of 4–4.5 (dark brown). The diversity of the species in the samples increases with younger age of the samples. The abundance of the conodonts fluctuates though the section although the richest samples are found in the upper part of the section.

Our conodont biostratigraphic study reveals an Eifelian to early Frasnian age for the sampled interval in the Comabella Fm. (Fig. 3, Tables 1–3).

The base of the Comabella Fm. is placed in the lower part of the Eifelian, indicated by the lowest local record of *Polygnathus angustipennatus* found right above the contact with the underlying Villech Formation (sample Vi-I/1). According to Belka *et al.* (1997) this species appears in the lowermost part of the *costatus* Zone.

In sample Vi-I/2, a higher diversity of taxa is found: *P. partitus*, *P. bulytnicki*, *P. robusticostatus* and *P. angustipennatus*, an assemblage that places the sample in the lower part of the *costatus* Zone (Belka *et al.* 1997, Gouwy & Bultynck 2002).

The index species of that zone, *P. costatus* first appears in sample Vi-I/3, together with *I. cf. regularicrescens*; *Polygnathus angusticostatus* and *P. linguiformis linguiformis* make their entry in sample Vi-I/5. These are two species that normally appear within the *costatus* Zone and both range up into the Givetian.

*Tortodus kockelianus australis*, the index species for the *australis* Zone, was not found, so the presence of this

zone cannot be stated. *T. kockelianus kockelianus* appears in sample Vi-I/15, defining the base of the *kockelianus* Zone and coinciding with the first occurrence of *P. pseudofoliatus* morphotype β. *Polygnathus eiflius* in sample Vi-I/17 marks the base of the *eiflius* Zone. The finding of *P. trigonicus* in sample Vi-I/17t in combination with *P. eiflius* limits this sample to the *eiflius* Zone (Belka *et al.* 1997).

A typical Givetian fauna appears first in sample Vi-I/18A following a covered interval in the section: *P. ensensis*, *P. hemiansatus* and *P. xylus*, a combination that does not occur below the base of the Lower *varcus* Zone. The covered interval in the section does not allow sampling between Vi-I/17t and 18A, impeding the recovery of data that might indicating the presence of the *ensensis* and *hemiansatus* zones.

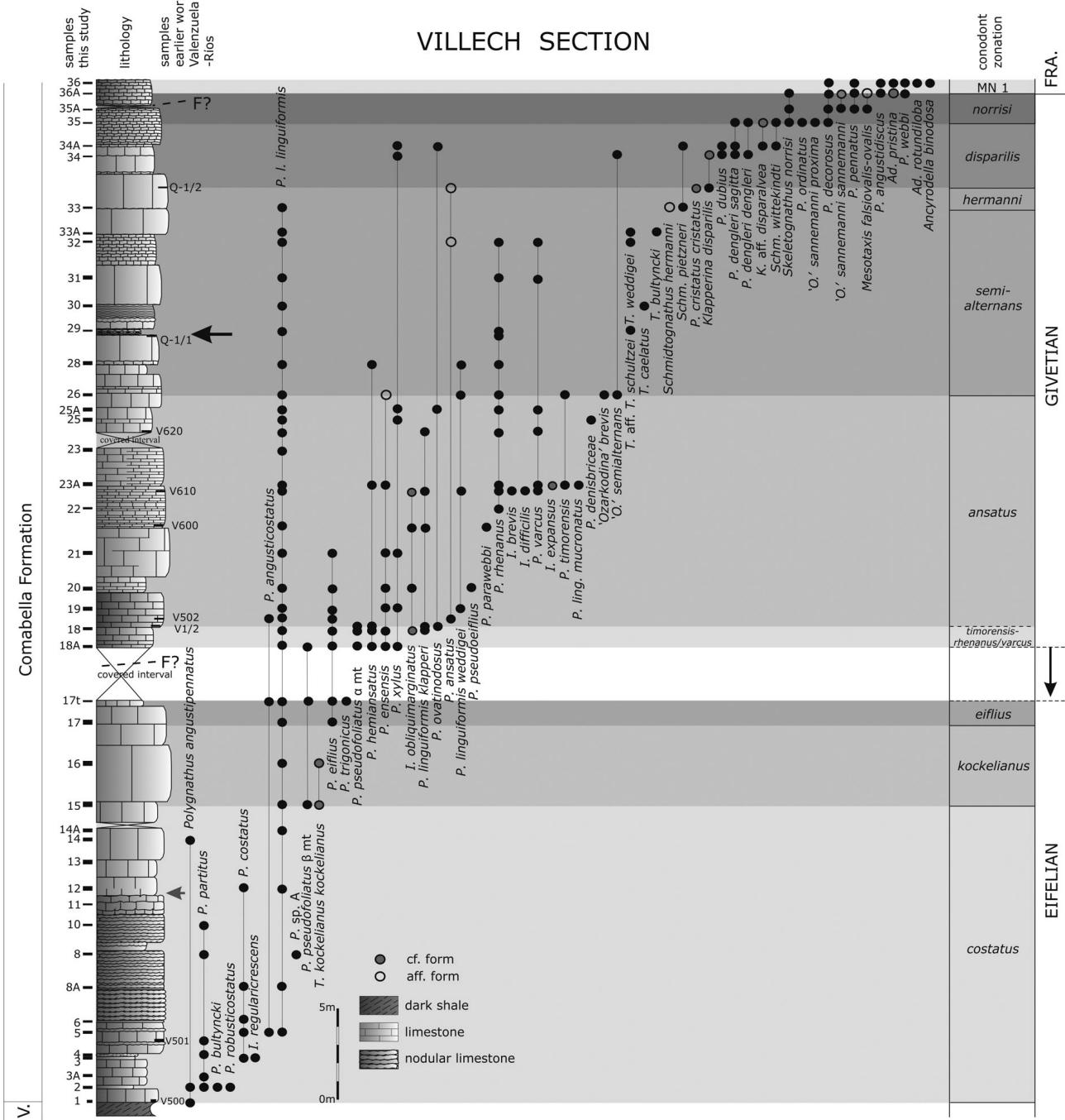
The *ansatus* Zone starts almost right above (sample V1/2) with the first occurrence of *P. ovatinodosus* (Klapper & Johnson 1980, Gouwy & Bultynck 2003), followed by the entry of *P. ansatus* (sample V502) and the first occurrence of *P. linguiformis weddigei* (sample Vi-I/19). Halfway this zone, *P. timorensis*, *I. brevis*, *I. difficilis*, *P. linguiformis mucronatus* and *P. varcus* appear for the first time in the section. The level formed by samples Vi-I/23A and V610 seems to mark a higher diversity of species (samples Vi-I/22 and V600 are almost barren). These are all species that normally have their first appearance in the Lower *varcus* Zone and are making a delayed entry here.

The basis of the *semialternans* Zone (uppermost part of the Middle *varcus* Zone) is indicated by the appearance of “O.” *semialternans* in sample Vi-I/26, coinciding with the entry of “O.” *brevis*.

The narrow but distinct layer of black limestone and shales is positioned between samples Q-1\1 and Vi-I/29 within this Zone.

In the upper part of the section, the *hermanni*, *disparilis* and *norrissi* zones are recognized, all indicated by their respective index species. The appearance of *Schmidtognathus hermanni* pinpoints the base of the *hermanni* Zone at sample Vi-I/33. *Polygnathus aff. cristatus cristatus* enters together with *K. disparilis* (sample Q-1\2). *Polygnathus dengleri dengleri* marks the base of the upper *disparilis* subzone in sample Vi-I/34. The appearance of *Sk. norrisi* marks the base of the *norrissi* Zone, the uppermost conodont zone of the Givetian at sample Vi-I/35. The base of that zone normally coincides with the base of the *falsiovalis* Zone although *Mesotaxis falsiovalis-ovalis* only appears here in sample Vi-I/35A, right beneath the appearance of *Ancyrodella cf. pristina* in sample Vi-I/36A.

The Givetian-Frasnian boundary is positioned in the uppermost part of the studied section, between samples Vi-I/35A and Vi-I/36A. In the field, a small fault was



**Figure 3.** Lithology and conodont distribution of the Villech section. Two possible faults are indicated (F). The Boersma limit between the Villech Formation and the Compte A Member starts at the base of sample Vi-I/12 (grey arrow). The black arrow indicates the position of the black limestone/shale deposit. Samples 1 to 36 are indicated in the text with Vi-I/1 to Vi-I/36. The sample names are shortened in the figure to save space. Samples from an earlier study by Valenzuela-Ríos are indicated on the right side of the lithologic column. The Villech Formation is indicated with the abbreviation V.

inferred between those samples. The occurrence of *Ad. pristina* in the latter indicates the base of the Frasnian (within the *falsiovalis* Zone). Sample 36 shows the joint entry of *Ad. rotundiloba* s.s. and *Ad. binodosa*. These first Frasnian beds correspond to the Montagne Noire 1 Zone (MN1, Klapper 1989).

### Comparison with another section from the Compte “subfacies area”

One other section from the Compte “subfacies area” of the Spanish Central Pyrenees was recently studied for its conodont biostratigraphy: the Compte section (Liao &

**Table 1.** Distribution and number of conodonts in the Villech section (part 1).

**Table 1.** Distribution and number of conodonts in the Villech section (part 2).

**Table 1.** Distribution and number of conodonts in the Villech section (part 3).

Valenzuela-Ríos 2008) located in the Compte “subfacies area” (about 50 km west of the Villech section). The detailed conodont biostratigraphic zonation scheme of this section allows a comparison with the biostratigraphic results of Villech section. The Compte section comprises the Givetian and the lowermost part of the Frasnian. The section shows a higher diversity in conodont taxa compared to the Villech section and comprises several stratigraphically important taxa absent in Villech (*I. lindensis*, *P. latifossatus*, *P. cristatus ectypus*, *Schn. peracutus*, *K. ovalis*, *K. unilobius* a.o.). It is considered the reference section for the Givetian of the Spanish Central Pyrenees.

In the Compte section the conodont fauna retrieved from the lowermost part of the section does not allow a distinction between the *hemiansatus* and *timorensis* zones; in the Villech section the lowermost sample containing a Givetian fauna (sample right above a covered interval) is assigned to the *timorensis-rhenanus/varcus* zones. The sample below the covered interval is placed in the *eifflius* Zone, indicating that the *ensensis* and *hemiansatus* zones are covered or maybe missing. So far, in the Compte “subfacies area”, no deposits can be with certainty assigned to the *ensensis* and *hemiansatus* zones. The *timorensis-rhenanus/varcus* zones interval and the *ansatus* Zone have been identified in both sections and demonstrate a considerable variation in thickness of the deposits assigned to those zones. The difference in thickness is also observed in the *latifossatus-semialternans* Zone in the sections. While reaching only one half meter in the Compte section, the deposits of the *semialternans* Zone are 10 m thick in the Villech section. The thickness varies less in the *hermanni*, *disparilis* and *norrissi* zones. In both sections, the base of the Frasnian is marked by the appearance of the first early ancyrodellids.

The inconsistent thickness variation of the deposits in the two sections and/or the possible absence of certain conodont zones suggest synsedimentary tectonic activity in the area in the Middle Devonian (also indicated by the presence of slumps in the Villech section, Fig. 2H).

## Systematic palaeontology

The conodont species discussed and illustrated here are the biostratigraphically most relevant ones or conodont specimens with a more problematic identification due to the bad preservation. The specimens of the Villech section are deposited in the conodont collection at the University of Valencia (Spain) and indicated by the according Museum collection numbers (MGUV).

*Ozarkodina* species in this paper are mentioned as “*Ozarkodina*” following the reviewed diagnosis of the genus by Murphy *et al.* (2004). In this reviewed diagnosis the genus name *Ozarkodina* is restricted to apparatus with Pa

element characterised by (Murphy *et al.* 2004) a high sail-like or fan-like set of denticles of the anteriormost part of the blade that are separated from the rest of the denticle row by a slight offset, a space or a distinct change in denticulation style. The Pa element has small basal platform lobes and a small basal cavity of which the anterior margin is situated in the anterior half of the blade. A stepped lower profile of the element is common. Species that were formerly classified under this genus but that do not show all these characteristics are here indicated by “*Ozarkodina*”.

### Genus *Ancyrodella* Ulrich & Bassler, 1926

Type species. – *Ancyrodella nodosa* Ulrich & Bassler, 1926.

#### *Ancyrodella binodosa* Uyeno, 1967

Figure 6F, G

- 1967 *Ancyrodella rotundiloba binodosa* n. subsp.; Uyeno, pp. 4, 5, pl. 1, figs 2, 4, 5.  
1980 *Ancyrodella binodosa* Uyeno. – Bultynck & Hollard, p. 28, pl. 10, fig. 4.  
1981 *Ancyrodella binodosa* δ morphotype. – Bultynck & Jacobs, pl. 9, figs 4, 5, 7, 8 (only).  
1989 *Ancyrodella binodosa* Uyeno. – Sandberg, Ziegler & Bultynck, p. 209, pl. 1, figs 1, 2, text-fig. 2, fig. 1.  
2007 *Ancyrodella binodosa* Uyeno. – Aboussalam & Becker, figs 9I, J.

Remarks. – In the original concept of *Ad. binodosa* (Uyeno, 1967), only specimens with an ornamentation on the upper surface that is confined to just two large nodes, one on each platform lobe, were included. Bultynck & Jacobs (1981) extended the concept by emphasising the importance of the basal pit size as the main criterion in the distinction with *Ad. rotundiloba* and by this included in *Ad. binodosa* specimens with upper platform surfaces covered with numerous large nodes. The latter were included in the early morphotypes of *Ad. rotundiloba* by Klapper (1985).

In upper view, the figured specimen shows two distinct rounded platform lobes, each one bearing one node. The carina is straight and consists of a row of small distinct denticles. The free blade is straight and consists, besides small denticles, of two markedly larger and higher denticles immediately behind the anteriormost smaller denticle. The basal pit is large and cruciform. The platform lobes are situated just posterior of the midlength of the element. Posterior of the lobes, the platform is very narrow and does not reach the posterior end.

The specimen can be distinguished from *Ad. pristina* by the shape of the platform that shows two distinct rounded

platform lobes and differs from the more triangular platform shape of *Ad. pristina*, by the absence of marginal nodes next to the single large node on each platform half, the absence of small secondary keels and by the larger basal pit.

In the Villech section, *Ad. binodosa* does not precede *Ad. pristina*, but its lowest occurrence takes place above the first appearance of *Ad. pristina* in sample Vi-I/36A. In sample Vi-I/36 several specimens are found that resemble *Ad. binodosa* in shape, but do not have any nodes (or at most a slight start of a node) on the platform. Their basal pit extends under the entire element, while in *Ad. binodosa*, the basal pit is cruciform or T-shaped. These specimens are considered juvenile forms. The smallest forms of most species of *Ancyrodella* generally have similar morphology. They are mentioned in this study as *Ancyrodella binodosa* juvenile form. (Fig. 6D, E). Similar forms were figured from Blauer Bruch (Germany) by Sandberg *et al.* (1989, pl. 1, figs 7, 8). A similar form was also illustrated as part of the ontogenetic series 2 of *Ancyrodella* by Miller (2007, figs 3U, V). The specimen illustrated in Fig. 6I, J can be seen as a transitional form between *Ad. binodosa* and *Ad. pristina* or a more advanced specimen of *Ad. binodosa*. The specimen still bears the two distinctively rounded platform lobes characteristic for *Ad. binodosa* but marginal nodes are already present on the platform around the two large nodes and aside of the carina. The basal pit is cruciform and smaller than the one typical for specimens of *Ad. binodosa*. One lateral keel, which does not reach the platform edge, is developed.

*Stratigraphical distribution.* – Lower *falsiovalis* Zone (Sandberg *et al.* 1989); MN 1 Zone (Aboussalam & Becker 2007, Narkiewicz & Bultynck 2011), within the Lower *falsiovalis* Zone to the base of the *punctata* Zone (MN 1–4) (Gouwy *et al.* 2007), within MN 1, 2 zones (Narkiewicz & Bultynck 2010).

*Material.* – 4 specimens from sample Vi-I/36.

#### ***Ancyrodella pristina* Khalymbadzha & Chernysheva, 1970**

Figure 6L, M

- 1970 *Ancyrodella pristina* n. sp.; Khalymbadzha & Chernysheva, pp. 88, 89, pl. 1, figs 3–8.
- 1981 *Ancyrodella binodosa* Uyeno. – Bultynck & Jacobs, pp. 16, 17, pl. VIII, figs 1–10, 13, 14; pl. IX, figs 1–3, 6.
- 1985 *Ancyrodella rotundiloba* (Bryant). – Klapper, pl. 1, figs 1–14; pl. 2, figs 1–5, 2–8; pl. 3, figs 7, 8.
- 1989 *Ancyrodella pristina* Khalymbadzha & Chernysheva. – Sandberg, Ziegler & Bultynck, pp. 210, 211, text-

figs 2.2–2.4, pl. 1, figs 3, 4, 13, 14 [non figs 9, 10 = *Ad. soluta*].

- 2007 *Ancyrodella rotundiloba pristina* Khalymbadzha & Chernysheva. – Aboussalam & Becker, pp. 364, 365, figs 9K, L, O–R.
- 2007 *Ancyrodella pristina* Khalymbadzha & Chernysheva. – Miller, p. 445, figs 2A–2Y.
- 2008 *Ancyrodella pristina* Khalymbadzha & Chernysheva. – Liao & Valenzuela-Ríos, pp. 2, 3, 7, fig. 6J [only].

*Remarks.* – The concept of *Ad. pristina* used here follows the definition of the early morphotype of *Ad. rotundiloba* by Klapper (1985) and is also according to the interpretation of Aboussalam (2003). The most important features to distinguish this species are the subtriangular platform outline and the size of the basal pit which is about half of the platform width. The Villech population contains simple ontogenetic stages with a slight lanceolate platform shape, very few marginal nodes and two straight anterior platform margins (Fig. 6L, M, *Ad. pristina* morphotype 2 of Sandberg *et al.* 1989) and the more advanced ontogenetic stages with more secondary nodes and rounded anterior platform on one side (*Ad. pristina* morphotype 3 of Sandberg *et al.* 1989).

*Stratigraphical distribution.* – MN 1 Zone (Aboussalam & Becker 2007), within the Lower *falsiovalis* Zone (Sandberg *et al.* 1989, Gouwy *et al.* 2007), MN 1, 2 (Liao & Valenzuela-Ríos 2008).

*Material.* – 17 specimens in samples Vi-I/36A (1 cf.), Vi-I/36 (16).

#### ***Ancyrodella rotundiloba* (Bryant, 1921)**

Figure 6P, Q

- 1921 *Polygnathus rotundilobus* sp. nov.; Bryant, pp. 26, 27, pl. 12, figs 1–6.
- 1980 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Bultynck & Hollard, p. 38, pl. 10, fig. 7.
- 1981 *Ancyrodella binodosa* Uyeno. – Bultynck & Jacobs, pp. 16, 17, pl. VIII, figs 11, 12.
- 1981 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Bultynck & Jacobs, pp. 17, 18, pl. X, figs 5, 8, 9.
- 1985 *Ancyrodella rotundiloba* (Bryant). – Klapper, pp. 24–27, pl. 1, figs 15–20; pl. 2, figs 9–12; pl. 3, figs 5, 6; pl. 4, figs 9–12.
- 1989 *Ancyrodella soluta* n. sp. – Sandberg, Ziegler & Bultynck, pp. 211, 212, pl. 1, figs 5, 6; pl. 2, figs 1–4; text-fig. 2, figs 5–7.
- 1994 *Ancyrodella rotundiloba* (Bryant). – Kralick, figs 3.21 to 3.24.
- 2007 *Ancyrodella rotundiloba soluta* Sandberg, Ziegler & Bultynck. – Aboussalam, p. 364.

- 2007 *Ancyrodella rotundiloba* (Bryant). – Miller, pp. 445, 446, figs 3A–G, 3K–P, S–V.  
2008 *Ancyrodella soluta* Sandberg, Ziegler & Bultynck. – Liao & Valenzuela-Ríos, p. 7, figs 6K–P.

**Remarks.** – The figured specimen shows a lanceolate to triangular shaped platform ornamented with nodes. Two slightly larger nodes are situated in the middle part of the anterior half of the platform, one on each side of the carina. They are surrounded by marginal nodes and nodes situated in between the two larger nodes and the marginal nodes. On the lower platform side, the basal pit is rather small and cruciform. Small keels are developed as extensions of the pit, but do not reach the platform margins.

The taxonomy of the early ancyrodellids has been the topic of many discussions in the last few decades, especially when it concerns the validity of the *Ad. soluta* species. The authors here follow the opinion of Kralick (1994), Klapper (2000) and Miller (2007) in that *Ad. soluta* is not a valid species. Most of the original type specimen of Sandberg *et al.* (1989) cannot be distinguished from *Ad. pristina* and the holotype itself is a good representative of *Ad. rotundiloba* s.s. (late form of Klapper 1985). Kralick (1994) and Klapper (2000) suggested that *Ad. soluta* and *Ad. pristina* are not sufficiently distinguishable from each other to exist as separate species. Miller (2007) studied the ontogenetic series of early ancyrodellids amongst which *Ad. pristina* and *Ad. rotundiloba* and concluded that, after comparing several morphological trends, that the platform width to basal pit width ratio and platform shape are not such good criteria to distinguish between the species since they are observed to change within the ontogenetic series of both species. *Ancyrodella rotundiloba* s.s. is distinguished from *Ad. pristina* by more and denser nodes on the platform (one to several nodes inserted between the marginal nodes and the carina). The figured specimen Fig. 6N, O is a more evolved form of *Ad. pristina* compared to Fig. 6L, M (more platform nodes and smaller basal pit) and can be a transitional form with *Ad. rotundiloba* s.s. based on the platform ornamentation. Only two specimens of *Ad. rotundiloba* s.s. have been recovered, both found in sample Vi-I/36.

**Stratigraphical distribution.** – From within the Lower *falsiovalis* Zone till into the *transitans* Zone (Sandberg *et al.* 1989; MN 1–4).

**Material.** – 2 specimens in sample Vi-I/36.

#### Genus *Klapperina* Lane, Müller & Ziegler, 1979

**Type species.** – *Klapperina disparalvea* (Orr & Klapper, 1968).

#### *Klapperina cf. K. disparalvea* (Orr & Klapper, 1968)

Figure 5O, P

- 1968 *Palmatolepis? disparalvea* n. sp.; Orr & Klapper, pl. 140, fig. 1–11.  
1976 *Palmatolepis disparalvea* Orr & Klapper. – Ziegler, Klapper & Johnson, p. 119, pl. 1, fig. 23.  
1980 *Palmatolepis disparalvea* Orr & Klapper. – Bultynck & Hollard, p. 41, pl. VIII, figs 20a, b.  
2007 *Klapperina disparalvea* (Orr & Klapper). – Over, figs 10.21–10.22.

**Remarks.** – The figured specimen has the characteristic asymmetric platform with a broad outer lobe, located anterior to the position of the distinctive central node and delimited by a faint anterior sinus. A posterior sinus is not visible since the platform margin is missing in that position. The platform surface is covered with rather coarse irregularly placed nodes. The broad L-shaped basal pit is large, shallow and situated in the posterior half of the platform, covering ¾ of the posterior platform length.

*K. disparalvea* can be distinguished from *K. disparilis* by the presence of a well-differentiated outer platform lobe, a larger basal pit and the coarser nodes on the upper platform.

**Stratigraphical distribution.** – The species first occurs at the base of the *disparilis* Zone and ranges up to the top of the *norrissi* Zone (Aboussalam 2003).

**Material.** – 2 specimens from samples Vi-I/34A (1aff), Vi-I/ 35 (1cf).

#### *Klapperina cf. K. disparilis* (Ziegler & Klapper, 1976)

Figure 5S, T

- 1976 *Palmatolepis disparilis* n. sp.; Ziegler, Klapper & Johnson, p. 119, pl. 1, figs 18–22, 24–31.  
1982 *Palmatolepis disparilis* Ziegler & Klapper. – Ziegler & Klapper, p. 467, pl. 3, figs 5, 7–15.  
2003 *Klapperina disparilis* Ziegler & Klapper. – Aboussalam, p. 170, pl. 19, figs 13–14.  
2007 *Klapperina disparilis* Ziegler & Klapper. – Aboussalam & Becker, fig. 9e.  
2008 *Klapperina disparilis* Ziegler & Klapper. – Liao & Valenzuela-Ríos, p. 8, figs 5K, L (transitional form between *P. cristatus* and *K. disparilis*), 5Q, R.

**Remarks.** – Only the posterior half of the platform, carrying the basal pit and part of the anterior half of the platform were preserved from the specimen found in sample Vi-I/34. The preserved part has an oval-shaped platform margin without lobe and bears moderate size nodes in a

chaotic arrangement on its upper side. The central node is not markedly larger than the nodes of the posterior part of the carina. The carina does not reach the posterior tip of the platform. A medium size L-shaped basal pit is developed on the lower side of the platform, covering slightly less than half of the posterior platform length.

The broken specimen in sample Q-1/2 (Fig. 5M, N) shows a rather straight carina with large central node and moderate sized nodes on the upper platform. The carina does not reach the posterior end. The basal pit is large and L-shaped. Part of the basal plate is still attached to the lower surface. Although the specimen is broken, an initiation of a platform lobe can be seen on the lower view. A weak sinus in the platform margin is situated immediately posterior of the missing part. Showing characteristics of *K. disparalvea* (large L-shaped basal pit and large central node) but missing a well-developed outer platform lobe, this specimen can be seen as transitional between *K. disparilis* and *K. disparalvea*.

The species differs from *K. disparata* by the distinct L-shape of the basal pit in the former.

*Stratigraphical distribution.* – The species defines the base of the *disparilis* Zone (Klapper & Johnson 1990) and its range is restricted to this Zone (Narkiewicz & Bultynck 2010).

*Material.* – 2 specimens from samples Vi-I/34 (1), Q-1/2 (1).

### Genus *Ozarkodina* Branson & Mehl, 1933

*Type species.* – *Ozarkodina typica* Branson & Mehl, 1933.

#### “*Ozarkodina*” *brevis* (Bischoff & Ziegler, 1957)

Figure 4P

- 1957 *Spathognathodus brevis* n. sp.; Bischoff & Ziegler, p. 116, pl. 19, figs 24, 27–29.
- 1976 *Ozarkodina brevis* (Bischoff & Ziegler). – Ziegler et al., pl. 3, figs 14–16.
- 1985 *Ozarkodina brevis* (Bischoff & Ziegler). – Olivieri, pl. 2, figs 9–11.
- 2003 *Ozarkodina brevis* (Bischoff & Ziegler). – Abousalam, p. 171, pl. 28, fig. 18.

*Remarks.* – The figured specimen is an “*Ozarkodina*” species with a short denticulated (11 denticles) blade. The blade is two times as long as it is high with a small deep rectangular-shaped basal cavity covering the posterior third of the blade and situated at its posterior end. The denticles of the blade (partially fused at their bases) are of equal size and height in the middle part of the blade and decline in height to the anterior end. The posteriormost

denticle is the broadest and is slightly inclined posteriorward.

*Stratigraphical distribution.* – The species is found from the upper part of the Lower *varcus* Zone (Weddige 1977) till up to the *norrisi* Zone (Klapper in Ziegler 1977).

*Material.* – 2 specimens in sample Vi-I/26.

#### “*Ozarkodina*” *sannemannii proxima* Pollock, 1968

Figure 5H

- 1968 *Spathognathodus sannemannii proxima* n. subsp.; Pollock, pp. 439, 440, pl. 63, figs 8, 9, 12, 13, 18, 19.
- 2003 *Ozarkodina sannemannii proxima* Pollock. – Abousalam, p. 173, pl. 24, figs 11, 12.
- 2007 *Ozarkodina sannemannii proxima* Pollock. – Abousalam & Becker, fig. 8P.

*Remarks.* – The figured specimen has a distinct outward bended anterior part of the blade. The denticles on the blade, partially fused at their bases, are larger on the anterior part of the blade. The basal cavity, situated in the posterior middle part of the blade, shows two lateral platform-like rounded expansions of which the inner one is only weakly developed and has a smooth upper surface. The outer lateral expansion carries one large node. The specimen can be distinguished from “*O.*” *sannemannii sannemannii* by the only weak development of the inner lateral expansion of the basal cavity and by the presence of only one node on only the outer lateral expansion. “*O.*” *sannemannii sannemannii* is characterised by at least one node on both well-developed lateral expansions.

*Stratigraphical distribution.* – The species appears at the base of the *hermanni* Zone and goes up into the *transitans* Zone (Pollock 1968). In the Villech section the species has been found in the *norrisi* Zone.

*Material.* – 2 specimens in sample Vi-I/35.

#### “*Ozarkodina*” *semialternans* (Wirth, 1967)

Figure 4Q

- 1967 *Spathognathodus semialternans* n. sp.; Wirth, text-figs 14a, b, pl. 23, figs 6–10.
- 1976 *Ozarkodina semialternans* (Wirth). – Ziegler, Klapper & Johnson, pp. 118, 119, pl. 3, figs 22–24.
- 1980 *Polygnathus semialternans* (Wirth). – Bultynck & Hollard, p. 45, pl. VIII, figs 5, 6.
- 1987 *Polygnathus semialternans* (Wirth). – Bultynck, p. 162.

2003 *Ozarkodina semialternans* (Wirth). – Aboussalam, pp. 173, 174, pl. 24, figs 1–7.

**Remarks.** – The figured specimen has a long blade, with anterior denticles that are somewhat broader than the posterior ones. An alternation of broad and narrower denticles is present only in the middle part of the blade immediately anterior of the basal cavity. This feature is mentioned in the revised description of Ziegler *et al.* (1976) as possibly present in the anterior part of the blade but usually absent in larger specimens. Some of the specimens illustrated by Aboussalam (2003) lack this alternation.

The denticles of the figured specimen decrease in height in the posterior third of the blade. The basal cavity is situated in the posterior third of the unit. The anterior lower margin of the blade is convex, is slightly turning upwards under the basal cavity and is bending down again behind the cavity in the posterior part of the blade.

**Stratigraphical distribution.** – The species first appears in the uppermost part of the Middle *varcus* Zone and goes up into the *norrissi* Zone (Norris & Uyeno 1982, Aboussalam 2003). The species defines the base of the *semialternans/latifossatus* Zone (Bultynck 1987).

**Material.** – 2 specimens from samples Vi-I/26 (1), Vi-I/34 (1).

### Genus *Polygnathus* Hinde, 1879

**Type species.** – *Polygnathus dubius* Hinde, 1879.

#### *Polygnathus angusticostatus* Wittekindt, 1966

Figure 4N

1966 *Polygnathus angusticostata* n. sp.; Wittekindt, p. 631, pl. 1, figs 15–18.

1971 *Polygnathus angusticostatus* Wittekindt. – Klapper, p. 65, pl. 3, figs 21–25.

1980 *Polygnathus angusticostatus* Wittekindt. – Bultynck & Hollard, p. 41, pl. 3, figs 10a, b, 17.

1988 *Polygnathus angusticostatus* Wittekindt. – Sparling, fig. 15.6.

**Remarks.** – The figured specimen has a small platform with short transverse ridges separated from the carina by wide adcarinal grooves. The small platform is triangular. The platform margins are subparallel to the carina in the anterior part of the platform. The carina extends posterior of the platform by two nodes. The pit is located between the mid-length and the anterior end of the platform and is of moderate size.

The species can be distinguished from *P. robusticostatus* by its posterior extension of the carina beyond the platform.

**Stratigraphical distribution.** – The species appears at the base of the *costatus* Zone (Belka *et al.* 1997) and the upper part of the zone in the Ardennes and the Eifel area (Weddige 1977). It ranges up to the base of the *ensensis* Zone in the Anti-Atlas (Belka *et al.* 1997) and to the lower part of the *hemiansatus* Zone in the Ardennes (Gouwy & Bultynck 2003).

**Material.** – 5 specimens from samples Vi-I/5 (2), Vi-I/17 (1), V502 (2).

#### *Polygnathus angustipennatus* Bischoff & Ziegler, 1957 Figure 4M

1957 *Polygnathus angustipennatus* n. sp.; Bischoff & Ziegler, p. 85, pl. 2, fig. 16; pl. 3, figs 1–3.

1971 *Polygnathus angustipennatus* Bischoff & Ziegler. – Klapper, p. 65, pl. 3, fig. 27.

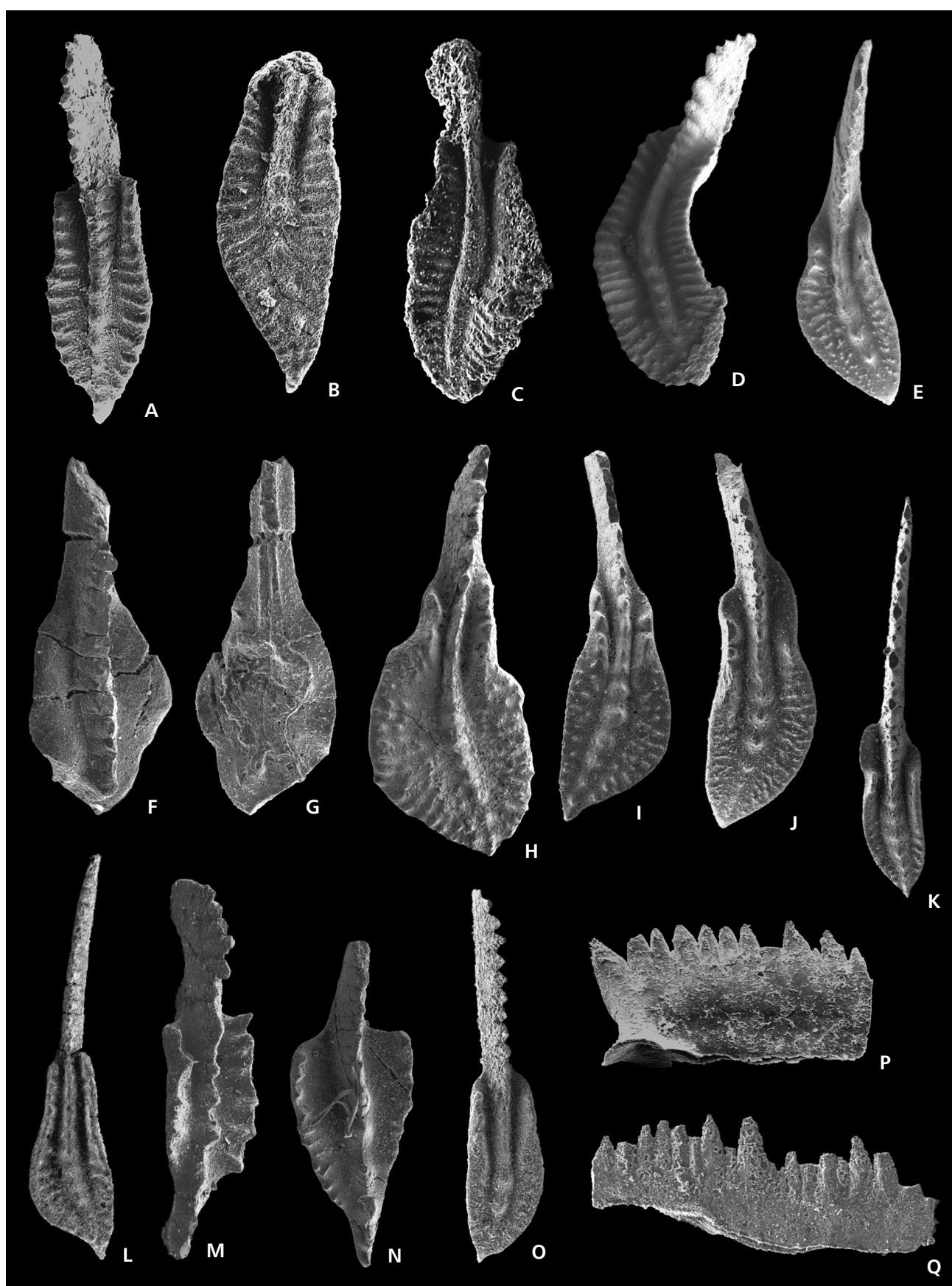
1980 *Polygnathus angustipennatus* Bischoff & Ziegler. – Bultynck & Hollard, p. 41, pl. 3, figs 9a, b.

1987 *Polygnathus angustipennatus* Bischoff & Ziegler. – Bultynck, pl. 9, fig. 15.

1988 *Polygnathus angustipennatus* Bischoff & Ziegler. – Sparling, fig. 15.5.

**Remarks.** – The figured specimen shows a small platform that occupies one third of the total length of the unit. The

**Figure 4.** A – *Polygnathus* sp. A, upper view, Vi-I/8 MGUV6002,  $\times 80$ . • B – *Polygnathus partitus* Klapper, Ziegler & Mashkova, 1978, upper view, Vi-I/8 MGUV6003,  $\times 63$ . • C, D – *Polygnathus costatus* Klapper, 1971, upper views, 3: Vi-I/3, MGUV6004,  $\times 37$ ; 4: Vi-I/5, MGUV6005,  $\times 42$ . • E – *Polygnathus pseudofoliatus* Wittekindt, 1966, α morphotype Walliser & Bultynck, 2011, upper view, Vi-I/18 MGUV6011,  $\times 41$ . • F, G – *Tortodus cf. T. kockelianus kockelianus* (Bischoff & Ziegler, 1957), upper and lower views, Vi-I/15 MGUV6006,  $\times 61$ . • H – *Polygnathus pseudoeifflius* Walliser & Bultynck, 2011, upper view, Vi-I/20 MGUV6012,  $\times 57$ . • I – *Polygnathus eifflius* Bischoff & Ziegler, 1957, upper view, Vi-I/19 MGUV6015,  $\times 59$ . • J – *Polygnathus hemiansatus* Bultynck, 1987, upper view, Vi-I/18 MGUV6016,  $\times 56$ . • K – *Polygnathus aff. P. ansatus* Ziegler & Klapper, 1976, upper view, Vi-I/32 MGUV6014,  $\times 54$ . • L – *Polygnathus denisbriceae* Bultynck, 1979, upper view, Vi-I/25 MGUV6013,  $\times 37$ . • M – *Polygnathus angustipennatus* Bischoff & Ziegler, 1957, upper view, V500 MGUV6001,  $\times 80$ . • N – *Polygnathus angusticostatus* Wittekindt, 1966, upper view, Vi-I/5 MGUV6022,  $\times 58$ . • O – *Polygnathus ensensis* Ziegler & Klapper, 1976; upper view, Vi-I/18, MGUV6021,  $\times 67$ . • P – “*Ozarkodina*” brevis (Bischoff & Ziegler, 1957), lateral view, Vi-I/26 MGUV6017,  $\times 100$ . • Q – “*Ozarkodina*” *semialternans* (Wirth, 1967), lateral view, Vi-I/34 MGUV6019,  $\times 75$ .



high platform margins are more or less parallel and are ornamented with strong marginal ridges. The carina extends beyond the platform by three carina denticles.

*P. angustipennatus* can be distinguished from *P. angusticostatus* by the more restricted platform development and a longer and higher free blade.

*Stratigraphical distribution.* – The species appears from the lowermost part of the *costatus* Zone (Belka *et al.* 1997). Bultynck & Hollard (1980) report a *P. aff. P. angustipennatus* from the upper part of the *partitus* Zone. *P. angustipennatus* ranges up till the lowermost part of the *hemiansatus* Zone (Bultynck 1987, Gouwy & Bultynck 2002).

*Material.* – 1 specimen from samples V 500.

#### *Polygnathus aff. P. ansatus* Ziegler & Klapper, 1976

Figures 4K, 5F

*Remarks.* – Both figured specimens show a long, slender and slightly sideward bowed platform ornamented with thin transverse ridges separated from the carina by adcarinal grooves. The wide carina reaches the posterior tip and continues slightly beyond the margins of the platform. Both anterior trough margins are bowed; the inner one only slightly. The small basal pit is situated in the anterior part of the platform. Both specimens resemble *P. ansatus* in the bowing of the anterior through margins but are distinguished from the typical specimens by the broader carina consisting of almost completely fused nodes, the somewhat wider platform and the less deep adcarinal grooves. Moreover, the Fig. 4K specimen differs from *P. ansatus* by the anterior ends of the anterior through margins meeting the blade at different positions; the Fig. 5F specimen differs by the non-opposite geniculation points.

*Stratigraphical distribution.* – Base of the *disparilis* Zone.

*Material.* – 2 specimens from samples Q-1/2 (1) and Vi-I/32 (1).

#### *Polygnathus costatus* Klapper, 1971

Figure 4C, D

- 1971 *Polygnathus costatus costatus* subsp. nov. – Klapper, p. 63, pl. 1, figs 30–36; pl. 2, figs 1–7.
- 1978 *Polygnathus costatus costatus* Klapper. – Klapper *et al.*, pl. 2, figs ?10, ?11, 12.
- 1983 *Polygnathus costatus costatus* Klapper. – Sparling, pl. 10, figs AB, AC; pl. 11, figs AB, AC, AF, AG.
- 1985 *Polygnathus costatus costatus* Klapper. – Bultynck, p. 270, pl. 8, figs 13–17.

2009 *Polygnathus costatus costatus* Klapper. – Berková, pp. 676, 678, pl. 6I–L.

2011 *Polygnathus costatus* Klapper. – Vodrážková, Klapper & Murphy, p. 742, figs 6A–I, K, L.

*Remarks.* – Specimens have a platform with an outer platform side that is slightly wider than the inner platform side. The platform is curved, long and narrow. The anterior platform margins are constricted, the platform is widest in its posterior third. The platform is ornamented with thin, long, densely spaced ridges, separated from the carina by deep, narrow grooves. The grooves become less deep, but are still narrow, closer to the posterior end of the platform. The carina reaches the posterior end. The pit is situated more or less at the first third of the platform.

*P. costatus* can be distinguished from *P. patulus* and *P. partitus* by the width of the platform, which is largest in its posterior third. The platform bears more densely spaced transverse ridges compared with the other two subspecies. *P. costatus* has a more constricted anterior platform than *P. patulus* and has more rounded posterior margins compared to *P. partitus*.

*Stratigraphical distribution.* – The first appearance of the species defines the base of the *costatus* Zone. *Polygnathus costatus* ranges up till halfway the *australis* Zone in Morocco (Belka *et al.* 1997) and up to the *kockelianus* Zone in the Eifel region (Weddige 1977).

*Material.* – 16 specimens from samples Vi-I/3 (2), Vi-I/5 (9), Vi-I/6 (2), Vi-I/8A (2), Vi-I/12 (1).

#### *Polygnathus cf. P. cristatus cristatus* Hinde, 1879

Figure 5Q, R

- 1879 *Polygnathus cristata* n. sp.; Hinde, p. 366, pl. 7, fig. 11.
- 2008 *Polygnathus cristatus cristatus* Hinde. – Liao & Valenzuela-Ríos, pp. 8, 9, figs 5M, N.

*Remarks.* – The specimen found in sample Q-1/2 is fragmentary. The fragment is rather thick and is ornamented with coarse nodes that are arranged in rows parallel to the carina. The platform is broken right through the basal pit.

The specimen fragment differs from specimens of *K. disparilis* or *P. cristatus ectypus* by the orderly arranged platform nodes. Aboussalam & Becker (2007) restrict the definition of the subspecies and assign only specimens with partly fused platform nodes to it.

*Stratigraphical and geographical distribution.* – The subspecies has its first appearance in the *hermanni* Zone and ranges up within the Upper *disparilis* Zone (Klapper & Johnson 1990).

*Material.* – One specimen from sample Q-1/2.

***Polygnathus aff. P. dengleri sagitta* Aboussalam & Becker, 2007**

Figure 6B, C

*Remarks.* – The figured specimen does not show the typical subtriangular, sagittate platform but a subtriangular to somewhat oval shaped platform ornamented by strong transverse ridges that are separated from the carina by shallow adcarinal grooves. The short free blade consists of a few fused denticles. The anterior part of the carina is straight and formed by fused nodes; the posterior carina is formed by slightly merged nodes and reaches the pointed tip of the platform. The small basal pit is elongated and is located in the middle of the anterior half of the platform. The keel is slightly curved.

The specimen differs from *P. dengleri dengleri* by the shape of the platform and the more anterior position of the basal pit.

*Stratigraphical distribution.* – From the base of the *dengleri sagitta* Subzone (Aboussalam & Becker 2007) up to MN 3.

*Material.* – 1 specimen in sample Vi-I/34.

***Polygnathus eiflius* Bischoff & Ziegler, 1957**

Figure 4I

- 1957 *Polygnathus eiflia* n. sp.; Bischoff & Ziegler, pp. 89, 90, pl. 4, figs 5–7.
- 1977 *Polygnathus eiflius* Bischoff & Ziegler. – Weddige, p. 311, pl. 4, fig. 66.
- 2001 *Polygnathus eiflius* Bischoff & Ziegler. – Liao *et al.*, pp. 27, 28, pl. 3, figs 6, 8–9, 13.
- 2011 *Polygnathus eiflius* Bischoff & Ziegler. – Walliser & Bultynck, p. 11, pl. 1, fig. 6.

*Remarks.* – The modified description by Walliser & Bultynck (2011) is followed here, indicating *P. eiflius* by a platform with the typical short anterior symmetric rostrum with relatively high and mostly serrated margins that continue as diagonal ridges or rows of nodes. The platform is widest in the posterior half and shows a distinct convex curve in the outer platform margin. The inner platform margin is only slightly curved. The platform is ornamented with small rounded or elongated nodes.

*Stratigraphical distribution.* – The species ranges from the base of the *eiflius* Zone up to within the lower part of the *timorensis* Zone (Walliser & Bultynck 2011).

*Material.* – 26 specimens from samples Vi-I/17 (3), Vi-I/17t (1), Vi-I/18A (3), Vi-I/18 (1), Vi-I/19 (1), Vi-I/20 (14), Vi-I/21 (1), V502 (2).

***Polygnathus ensensis* Ziegler & Klapper, 1976**

Figures 4O, 5A (aff.)

- 1976 *Polygnathus xylus ensensis* n. sp.; Ziegler & Klapper, pp. 125–127, pl. 3, figs 4–9.
- 1987 *Polygnathus ensensis* Ziegler & Klapper. – Bultynck, p. 161, pl. 7, figs 1–6.
- 1989 *Polygnathus ensensis* Ziegler & Klapper. – Bultynck, pp. 97–99, pl. 2, figs 12–21.
- 2001 *Polygnathus xylus ensensis* Ziegler & Klapper. – Liao *et al.*, p. 40, pl. 3, fig. 23.

*Remarks.* – The figured specimen has distinctly serrated anterior platform margins, straight to steeply downward declined anterior trough margins joining the free blade at the same position and a posteriorly down-arched platform. The platform surface is smooth and has deep adcarinal troughs in the anterior part and shallow troughs in the posterior part. In lateral view the platform is down-arched (not figured). *Polygnathus aff. P. ensensis* in Fig. 5A, misses the down-arching of the platform typical for *P. ensensis* specimens but shows serrations on the inner anterior platform margin.

*Polygnathus ensensis* can be distinguished from *P. xyloides* by the distinctly serrated anterior platform margins and the distinctly down-arched posterior platform.

*Stratigraphical distribution.* – *P. ensensis* ranges from the base of the *ensensis* Zone up to the uppermost part of the Middle *varcus* Zone (Liao & Valenzuela-Ríos 2008).

*Material.* – 21 specimens from samples Vi-I/18A (3), Vi-I/18 (5), Vi-I/19 (7), Vi-I/20 (3), Vi-I/21 (1), Vi-I/23A (1), Vi-I/26 (1 aff.).

***Polygnathus hemiansatus* Bultynck, 1987**

Figure 4J

- 1980 *Polygnathus aff. P. ansatus* Ziegler & Klapper. – Bultynck & Hollard, p. 42, pl. 5, fig. 18; pl. 6, figs 2–4.
- 1985 *Polygnathus ansatus* Ziegler & Klapper. – Bultynck, p. 269, pl. 6, figs 19, 20.
- 1987 *Polygnathus hemiansatus* n. sp.; Bultynck, pp. 161, 162, pl. 7, figs 16–27; pl. 8, figs 1–7.
- 2008 *Polygnathus hemiansatus* Bultynck. – Liao & Valenzuela-Ríos, figs 4A, B.
- 2011 *Polygnathus hemiansatus* Bultynck. – Walliser & Bultynck, p. 12, pl. 1, figs 11–17.

**Remarks.** – The figured specimen shows the main characteristic of *P. hemiansatus*: outward bowing of the outer anterior trough margin, a straight inner anterior platform margin, a strong constriction posterior of the outer geniculation point. The inner anterior platform margin is serrated. The platform is ornamented with small nodes and small interrupted ridges. This specimen belongs to the  $\beta$  morphotype of Walliser & Bultynck (2011).

The species is distinguished from *P. ansatus* by the straight inner platform margin instead of the outward bowing of the inner margin in the latter. It is different from *P. timorensis* in the wider shape of the posterior platform and the shallow adcarinal grooves of the former.

**Stratigraphical distribution.** – The species defines the base of the *hemiansatus* Zone and ranges into the *ansatus* Zone (Walliser & Bultynck 2011).

**Material.** – 15 specimens from samples Vi-I/18A (4), Vi-I/18 (6), V1/2 (3), Vi-I/23A (1), Vi-I/28 (1).

***Polygnathus partitus* Klapper, Ziegler & Mashkova, 1978**

Figure 4B

- 1978 *Polygnathus costatus partitus* subsp. nov.; Klapper et al., p. 109, pl. 2, figs 1–5, 13.  
1985 *Polygnathus costatus partitus* Klapper, Ziegler & Mashkova. – Bultynck, p. 270, pl. 8, figs 19, 20.  
1999 *Polygnathus costatus partitus* Klapper, Ziegler & Mashkova. – Gouwy et al., pl. 1, fig. 6, table.  
2009 *Polygnathus costatus partitus* Klapper, Ziegler & Mashkova. – Berková, pp. 675, 676, figs 5D–I.

**Remarks.** – Specimen has a slender, narrow, suboval platform with an outer platform that is slightly larger than the inner platform. The anterior platform margins are constricted. The inner and outer posterior margins tend to be straight and meet the posterior end of the platform to form a sagittate outline. The upper platform bears narrow, long trans-

verse ridges separated from the carina by adcarinal grooves that are relatively deep in the anterior part of the platform and shallow to flat in the posterior half. In some specimens the tip is slightly curved.

*Polygnathus partitus* can be distinguished from *P. costatus* by the wider platform at midlength, the straight inner and outer posterior margins, converging to form a sagittate outline, the less constricted or parallel anterior trough margins and less the densely spaced transverse ridges as ornamentation on the platform surface.

**Stratigraphical distribution.** – The first appearance of the species indicates the base of the *partitus* Zone. The species ranges up into the *costatus* Zone (Belka et al. 1997).

**Material.** – 7 specimens from samples Vi-I/2 (1), Vi-I/3A (2), Vi-I/4 (1), V501 (1), Vi-I/8 (1), Vi-I/10 (1).

***Polygnathus pseudoeifflius* Walliser & Bultynck, 2011**  
Figure 4H

- 2010 *Polygnathus* aff. *P. eifflius* Bischoff & Ziegler. – Gouwy, p. 141, pl. 5, fig. 6.  
2011 *Polygnathus pseudoeifflius* n. sp.; Walliser & Bultynck, p. 11, pl. 1, figs 3–5.

**Remarks.** – The specimen shows strongly constricted parallel anterior platform margins and a posterior outer and inner platform expansion in a strong convex curve. The inner anterior margin is serrated. The platform is ornamented with small nodes.

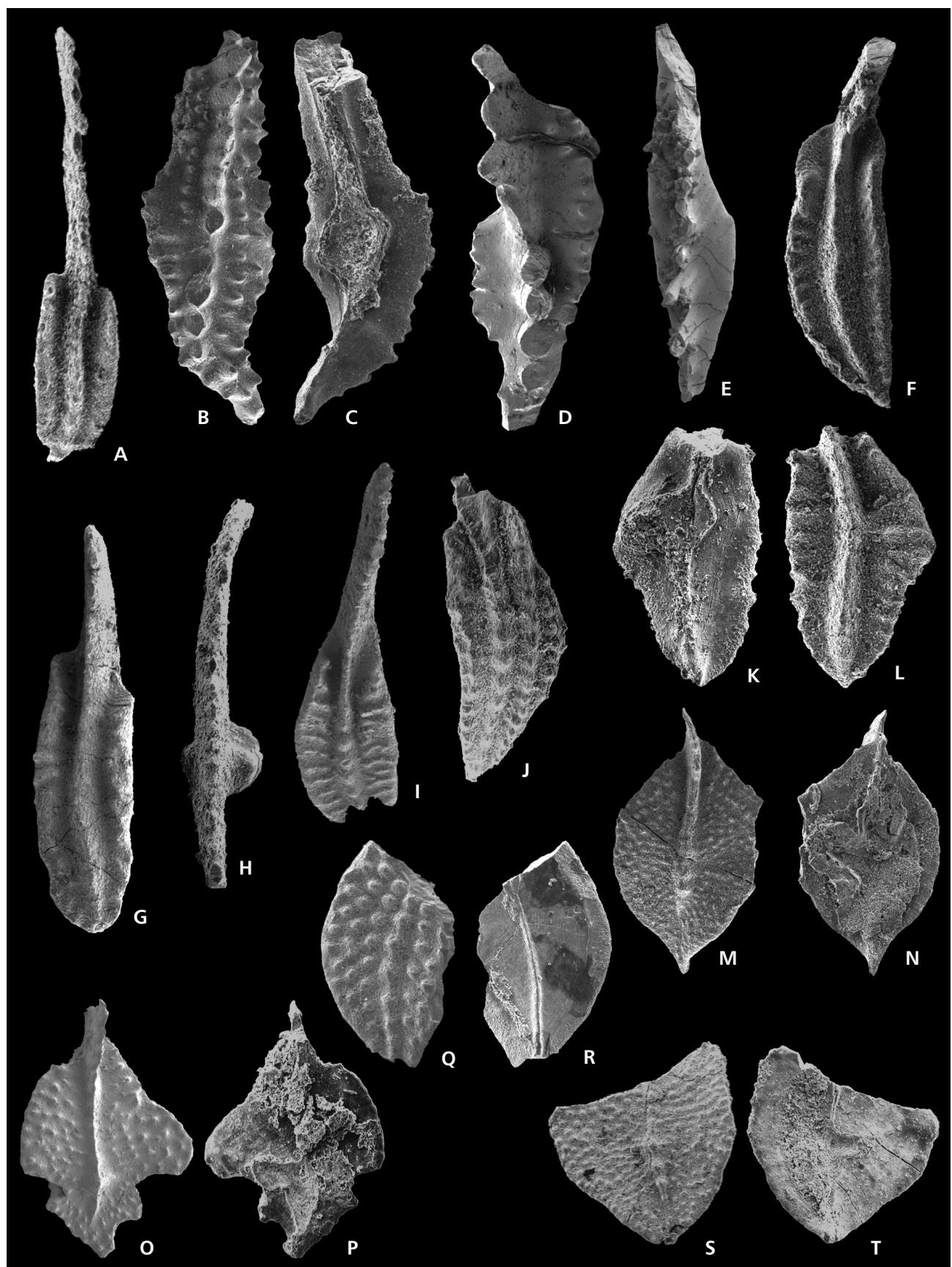
The specimen lacks the diagonal rostral ridges that are typical for *P. eifflius*.

**Stratigraphical distribution.** – Walliser & Bultynck (2011) situate the species from within the *kockelianus* Zone up to within the *timorensis* Zone. It is found in the lower part of the *ansatus* Zone in the Villech section.

**Material.** – 1 specimen from sample Vi-I/20.

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**Figure 5.** A – *Polygnathus* aff. *P. ensensis* Ziegler & Klapper, 1976, upper view, Vi-I/26 MGUV6027,  $\times 65$ . • B, C – *Tortodus caelatus* (Bryant, 1921), upper and lower views, Vi-I/30 MGUV6028,  $\times 45$ . • D – *Tortodus* aff. *T. schultzei* Aboussalam, 2003, upper view, Vi-I/29 MGUV6029,  $\times 49$ . • E – *Tortodus bultyncki* Aboussalam, 2003, upper view, Vi-I/33A MGUV6030,  $\times 45$ . • F – *Polygnathus* aff. *P. ansatus* Ziegler & Klapper, 1976; upper view, Q-1/2, MGUV6023,  $\times 24$ . • G – *Schmidtognathus pietzneri* Ziegler, 1966, upper view, Vi-I/33 MGUV6037,  $\times 63$ . • H – Ozarkodina sannemannii proxima Pollock, 1968, upper view, Vi-I/35 MGUV6038,  $\times 62$ . • I – *Polygnathus* cf. *P. tafilensis* Aboussalam & Becker, 2007, upper view, Vi-I/33 MGUV6036,  $\times 57$ . • J – *Schmidtognathus wittekindti* Ziegler, 1966, upper view, Vi-I/35 MGUV6039,  $\times 65$ . • K, L – *Schmidtognathus* aff. *Schmidtognathus hermanni* Ziegler, 1965, lower and upper views, Vi-I/33 MGUV6041,  $\times 52$ . • M, N – transitional form between *Klapperina disparilis* (Ziegler & Klapper, 1976) and *Klapperina disparalvea* (Orr & Klapper, 1968), upper and lower views, Q-1/2, MGUV6035,  $\times 44$ . • O, P – *Klapperina* cf. *K. disparalvea* (Orr & Klapper, 1968), upper and lower views, Vi-I/35 MGUV6032,  $\times 56$ . • Q, R – *Polygnathus* cf. *P. cristatus* Hinde, 1879; upper and lower views, Q-1/2, MGUV6034,  $\times 44$ . • S, T – *Klapperina* cf. *K. disparilis* (Ziegler & Klapper, 1976), upper and lower views, Vi-I/34 MGUV6033,  $\times 37$ .



***Polygnathus pseudofoliatus* Wittekindt, 1966,  
α morphotype Walliser & Bultynck, 2011**

Figure 4E

- 1966 *Polygnathus pseudofoliatus* n. sp.; Wittekindt, pp. 637, 638, pl. 2, figs 19–23.  
2011 *Polygnathus pseudofoliatus* Wittekindt, morpho-type α. – Walliser & Bultynck, p. 11, pl. 1, figs 1, 2.

**Remarks.** – The figured specimen has a slightly asymmetric platform that is constricted anteriorly (more constriction on the outer anterior side) and is covered with transverse ridges and small nodes, separated from the carina by adcarinal grooves. The platform is widest near its mid-length. The inner anterior platform margin bears some small marginal nodes. The free blade is slightly less than ½ of the total length of the unit.

The species differs from *P. eiflius* by the absence of diagonal rostral ridges, and from *P. pseudoeiflius* by the greater constriction of the anterior platform in the latter. The α morphotype is distinguished from the β morphotype by its less distinct rostrum and broader platform with a predominant ornamentation of small nodes and irregular ribs.

**Stratigraphical distribution.** – *P. pseudofoliatus* morphotype α ranges from within the *kockelainus* Zone to the *an-satus* Zone (Walliser & Bultynck 2011).

**Material.** – 14 specimens from samples Vi-I/15 (2), Vi-I/17t (1), Vi-I/18A (8), Vi-I/18 (1), V1/2 (2).

***Polygnathus* cf. *P. tafilensis* Aboussalam & Becker,  
2007**

Figure 5I

- 2007 *Polygnathus tafilensis* n. sp.; Aboussalam & Becker, p. 370, figs 5P–T.

**Remarks.** – The specimen has an asymmetric, flat platform ornamented with transverse ridges that almost touch the carina, separated by very narrow anteriorly situated adcarinal grooves. The platform is widest in the anterior half. The free blade seems shorter than the platform (posteriormost

part of the platform is missing). The posterior tip of the specimen is broken. The platform is constricted anteriorly.

The specimen differs from *P. pennatus* by having weaker ribs.

**Stratigraphical distribution.** – The *dengeri* to MN1 zones in the Anti-Atlas (Aboussalam & Becker 2007).

**Material.** – One specimen from sample Vi-I/33.

***Polygnathus* sp. A**

Figure 4A

**Remarks.** – The specimens show an almost symmetrical short and broad platform bearing rather coarse transverse ribs separated from the carina by rather deep and narrow adcarinal grooves. They are deeper anteriorly and flatten posteriorly. The platform margins are slightly constricted in the anterior half of the platform. The platform is widest near midlength. The posterior margins are slightly curved, reaching the carina anterior of the posteriormost denticle. The short free blade is high and consists of narrow partially fused denticles. The straight carina reaches the tip of the platform and continues with one denticle beyond the platform margin.

**Stratigraphical distribution.** – Both specimens are found in the *costatus* Zone.

**Material.** – 2 specimens from samples Vi-I/8 (2).

**Genus *Schmidtognathus* Ziegler, 1966**

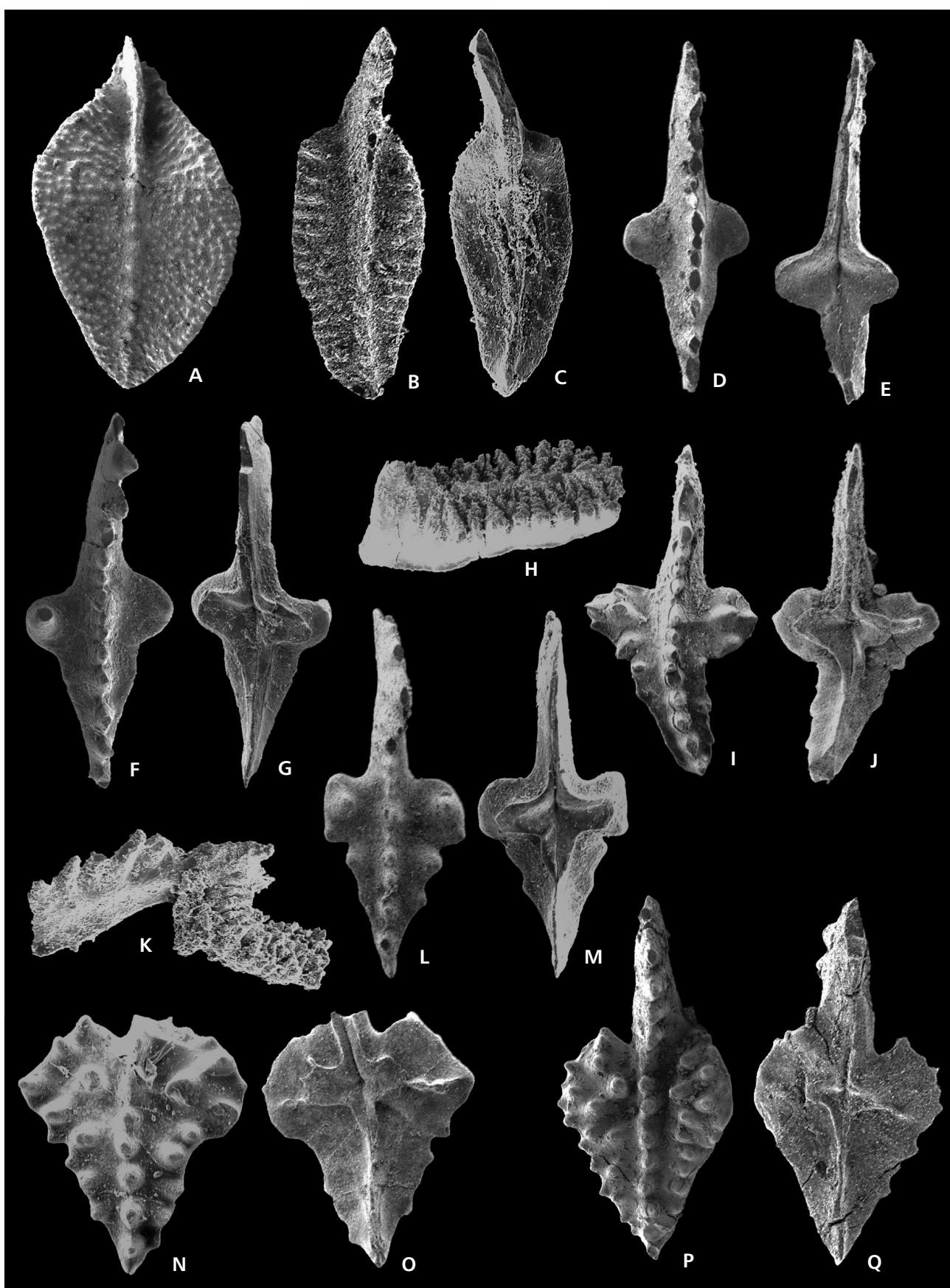
**Type species.** – *Schmidtognathus hermanni* Ziegler, 1966.

***Schmidtognathus* aff. *Schmidtognathus hermanni*  
Ziegler, 1966**

Figure 5K, L

- 1966 *Schmidtognathus hermanni* n. sp.; Ziegler, pp. 664, 665, pl. 3, figs 5–26.  
1973 *Schmidtognathus hermanni* Ziegler. – Ziegler, Catalogue of conodonts, vol. 1, pp. 425, 426, *Schmidtognathus*, pl. 1, fig. 3.

**Figure 6.** A – *Mesotaxis falsiovalis-ovalis*, upper view, Vi-I/36A MGUV6040, × 34. • B, C – *Polygnathus* aff. *P. dengleri* sagitta Aboussalam & Becker, 2007, upper and lower views, Vi-I/34 MGUV6043, × 45. • D, E – *Ancyrodella binodosa*; upper view of juvenile specimen MGUV6050, × 76 and lower view of juvenile specimen MGUV6052; Vi-I/36, × 77. • F, G – *Ancyrodella binodosa* Uyeno, 1967, upper and lower views, Vi-I/36 MGUV6049, × 65. • H, K – *Skeletognathus norrisi* (Uyeno, 1967); H – upper-lateral view of Pa-element MGUV6048, × 91; K – lateral view of Pb-element, MGUV6051, × 73, Vi-I/35. • I, J – transitional form between *Ancyrodella binodosa* Uyeno, 1967 and *Ancyrodella pristina* Khalymbadzha & Chernysheva, 1970; upper and lower views; Vi-I/36, MGUV6046, × 36. • L, M – *Ancyrodella pristina* Khalymbadzha & Chernysheva, 1970, morphotype 2 of Sandberg *et al.* (1989); upper and lower views, Vi-I/36 MGUV6047, × 52. • N, O – *Ancyrodella pristina*, transitional form with *Ad. rotundiloba* (Bryant, 1921), upper and lower views, Vi-I/36 MGUV6045, × 43. • P, Q – *Ancyrodella rotundiloba* (Bryant, 1921), late form of Klapper (1985), upper and lower views, Vi-I/36 MGUV6044, × 42.



- 2003 *Schmidtognathus hermanni* Ziegler. – Aboussalam, pl. 20, figs 11, 12; pl. 21, figs 13, 16, 17, pl. 22, figs 1–5.
- 2008 *Schmidtognathus hermanni* Ziegler. – Liao & Valenzuela-Ríos, pp. 9, 14, figs 5B, C.

**Remarks.** – The elongated asymmetric platform bears broad marginal ridges and is constricted in the anterior part. The outer anterior half of the platform is wider than the inner anterior half of the platform. The carina consists of completely fused nodes and is slightly curved. The anterioformost part of the platform and the free blade are missing. The large basal pit of Fig. 5K is clearly asymmetric, somewhat L-shaped and has raised margins.

The specimen differs from *Schm. pietzneri* by the more posterior position of the greatest platform width in the former.

**Stratigraphical distribution.** – The species ranges from the base of the *hermanni* Zone up to within the *norrissi* Zone (Aboussalam & Becker 2007).

**Material.** – 1 specimen from samples Vi-I/33 (1).

#### ***Schmidtognathus pietzneri* Ziegler, 1966**

Figure 5G

- 1966 *Schmidtognathus pietzneri* n. sp.; Ziegler, pp. 666, 667, pl. 2, figs 11–25.
- 1973 *Schmidtognathus pietzneri* Ziegler. – Ziegler (ed.), Catalogue of conodonts, Vol. I, p. 431, *Schmidtognathus*, pl. 1, fig. 2.
- 1980 *Schmidtognathus pietzneri* Ziegler. – Bultynck & Hollard, pl. 9, figs 7, 8.
- 2003 *Schmidtognathus pietzneri* Ziegler. – Aboussalam, p. 193, pl. 21, figs 5–21.
- 2008 *Schmidtognathus pietzneri* Ziegler. – Liao & Valenzuela-Ríos, figs 5G, H.

**Remarks.** – The long and narrow platform is slightly curved sideways. The platform margins bear nodes and are separated from the carina by adcarinal grooves. The outer adcarinal trough is deep and rather wide. The anterior platform margins join the free blade at different positions. The free blade is formed by almost completely fused denticles and continues into the slightly curved carina, consisting of completely fused nodes and reaching the posterior tip of the platform. The asymmetric basal pit is situated in the anterior half of the platform.

The species is distinguished from *Schm. wittekindti* by the pointed posterior part of the platform and the extra row of nodes parallel to the carina on both sides in the latter.

**Stratigraphical distribution.** – The species occurs from the

base of the *hermanni* Zone (Ziegler 1973) up into the Upper *disparilis* Zone (Bultynck & Hollard 1980, Narkiewicz & Bultynck 2010).

**Material.** – 1 specimen from sample Vi-I/33 (1).

#### ***Schmidtognathus wittekindti* Ziegler, 1966**

Figure 5J

- 1966 *Schmidtognathus wittekindti* n. sp.; Ziegler, pp. 665, 666, pl. 1, figs 11–16; pl. 2, figs 1–10.
- 1973 *Schmidtognathus wittekindti* Ziegler. – Ziegler, Catalogue of conodonts, vol. 1, pp. 433–434, *Schmidtognathus*, pl. 1, fig. 1.
- 2003 *Schmidtognathus wittekindti* Ziegler. – Aboussalam, pp. 193, 194, pl. 22, figs 6–10.

**Remarks.** – The specimen has a long, narrow and pointed platform ornamented with a row of very closely spaced nodes on both sides of the carina. In lateral view the specimen is markedly arched and shows a rather thick platform. The free blade is broken. The small asymmetric basal pit is situated in the anterior half of the platform.

The specimen differs from *Schm. pietzneri* and *Schm. hermanni* by the presence of the rows of nodes parallel to the carina, between the carina and the marginal platform nodes.

**Stratigraphical distribution.** – The species is found from the base of the *hermanni* Zone up to within the *norrissi* Zone (Ziegler 1973).

**Material.** – 2 specimens in samples Vi-I/34A (1) and Vi-I/35 (1).

#### **Genus *Skeletognathus* Sandberg, Ziegler & Bultynck, 1989**

**Type species.** – *Polygnathus norrisi* Uyeno, 1967.

#### ***Skeletognathus norrisi* (Uyeno, 1967)**

Figure 6H, K

- 1967 *Polygnathus norrisi* Uyeno; pp. 10, 11, pl. 2, figs 4, 5.
- 1980 *Polygnathus norrisi* Uyeno. – Bultynck & Hollard, p. 44, pl. VIII, figs 12a, c.
- 1989 *Skeletognathus norrisi* (Uyeno). – Sandberg et al., p. 214, pl. 5, figs 1–12.
- 2001 *Skeletognathus norrisi* (Uyeno). – Liao et al., pp. 41, 42, pl. 4, figs 22–24.
- 2003 *Skeletognathus norrisi* (Uyeno). – Aboussalam, p. 194, pl. 9, fig. 6.

2008 *Skeletognathus norrisi* (Uyeno). – Liao & Valenzuela-Ríos, figs 6C–F.

**Remarks.** – The retrieved specimens show irregular plates on the upper side of the platform and subparallel platform margins. The posterior platform margin is rounded. The platform plates are merged together on the lower side of the platform. On the lower platform a forrowed keel is present. The free blade is missing. The Pb-element (Fig. 6H) has a high free blade with inclined posterior denticle. The platform is deformed and shows, similar to the Pa-element, irregular plates on its upper surface. The lower side of the platform is covered with sediment.

**Stratigraphical distribution.** – The species ranges from the base of the *norrisi* Zone up into the *transitans* Zone (MN 4) in the Lower Frasnian according to Sandberg *et al.* (1989). According to Klapper & Johnson (1990) the species has its upper range within the MN2 Zone.

**Material.** – 6 specimens from samples Vi-I/35 (1Pa, 2 Pb), Vi-I/35A (1 Pb), Vi-I/36A (2 Pb).

### Genus *Tortodus* Weddige, 1977

**Type species.** – *Polygnathus kockelianus* Bischoff & Ziegler, 1957.

#### *Tortodus bulytnicki* Aboussalam, 2003

Figure 5E

2003 *Tortodus bulytnicki* n. sp.; Aboussalam, p. 197, pl. 25, figs 1–3.

**Remarks.** – The long, narrow and smooth platform is slightly bent downwards in the posterior part and is widest in the middle part. The blade shows a light torsion and changes sides of the platform from the anterior to the posterior end. The blade consists of large denticles that are partially fused posterior of the pit and only fused at the base in the rest of the blade. The denticles are somewhat narrower in the middle part of the blade. The large basal pit is situated under the widest part of the platform.

The species differs from *T. weddigei* by the slender platform shape, the lack of ornamentation on the upper platform and by the different denticulation pattern of the blade (3–4 isolated large denticles in the posterior part of the blade in *T. weddigei*).

**Stratigraphical distribution.** – The species is found in the upper *ansatus* Zone (Sparling 1995) and ranges up into the upper part of the *disparilis* Zone (Aboussalam 2003).

**Material.** – 1 specimen from sample Vi-I/33A.

#### *Tortodus caelatus* (Bryant, 1921)

Figure 5B, C

- 1921 *Polygnathus caelatus* n. sp.; Bryant, p. 27, pl. 13, figs 5, 6, 8, 9, 11, 12, 13 (non pl. 13, figs 1–4, 7 = T. aff. *caelatus*).
- 1980 *Polygnathus beckmanni* Bischoff & Ziegler. – Bultynck & Hollard, p. 42, pl. 8, fig. 9.
- 1987 *Polygnathus beckmanni* Bischoff & Ziegler. – Bultynck, p. 181, pl. 9, fig. 18.
- 2003 *Tortodus caelatus* (Bryant, 1921). – Aboussalam, pp. 197, 198, pl. 26, figs 1–4.

**Remarks.** – The specimen has a long platform with a carina formed by two large and high nodes in its anteriormost part and continues into a row of partially fused decreasing nodes. Above the pit the carina nodes are again somewhat larger and less fused. The posteriormost part of the carina is formed by a row of small-aligned nodes and reaches the posterior tip of the platform. The carina is straight with the posterior part that is strongly curved. The widest part of the platform is located at midlength. The platform is ornamented with strong nodes, loosely aligned into wide rows parallel to the carina, in the middle part of the platform. The basal pit is large and located in the middle part of the platform.

The specimens differ from *T. schultzei* by the lack of strong torsion of the blade and the absence of four strong and separated denticles posterior of the basal pit.

**Stratigraphical distribution.** – The species is found from the base of the Middle *varcus (ansatus)* Zone till in the lower part of the Frasnian (Aboussalam 2003).

**Material.** – 1 specimen from sample Vi-I/30.

#### *Tortodus cf. T. kockelianus kockelianus* (Bischoff & Ziegler, 1957)

Figure 4F, G

- 1957 *Polygnathus kockelianana* n. sp.; Bischoff & Ziegler, p. 91, pl. 2, figs 1–12.
- 1977 *Tortodus kockelianus kockelianus* (Bischoff & Ziegler). – Weddige, pp. 328, 329, pl. 3, fig. 52.
- 1985 *Polygnathus kockelianus kockelianus* Bischoff & Ziegler. – Bultynck, pl. 7, fig. 19.
- 2009 *Tortodus kockelianus kockelianus* (Bischoff & Ziegler). – Berková, pp. 682–684, figs 6A–C, E–G.

**Remarks.** – The figured specimen has a smooth platform that is widest around the pit and decreasing in width anteriorly

and posteriorly. The platform is broken and cracked and missing the posterior part. The carina is formed by partially fused high denticles, decreasing in size posteriorward. The large pit is situated below the widest part of the platform. The keel is bent laterally (as far as the posterior platform is preserved), indicating the typical bent in the posterior platform of *T. k. kockelianus*.

The specimen differs from *T. intermedius* by the presence of a well-developed platform and from *T. variabilis* by the lack of ornamentation on the platform surface. It can be distinguished from *T. k. australis* by the denticles of the carina that remain high till the posterior end and the more restricted platform development in the latter.

**Stratigraphical distribution.** – The first appearance of the species indicates the base of the *kockelianus* Zone, ranges up to the lowermost part of the *ensensis* Zone (Weddige 1977, Belka *et al.* 1997).

**Material.** – 2 specimens from samples Vi-I/15 (1), Vi-I/16 (1).

#### ***Tortodus* aff. *T. schultzei* Aboussalam, 2003**

Figure 5D

2003 *Tortodus schultzei* n. sp.; Aboussalam, pp. 199, 200,  
fig. 51, pl. 25, figs 10–12.

**Remarks.** – The blade of the figured specimen shows torsion and bears large equal sized denticles. Because of the broken state of the platform denticles their height evolution on the platform is not clear. The platform is narrow at the posterior end and is widest halfway, where the outer platform abruptly finished. The inner platform side is ornamented with marginal nodes mostly situated in the anterior part; the outer platform bears some small marginal nodes. The posterior platform half bears four strong denticles. An inner platform that continues till the anterior end, only slightly narrowing compared to mid-length, is a characteristic that is not found in *T. schultzei*. In the latter the inner platform distinctly wedges out to the anterior end. Some specimens assigned to *T. caelatus* show this asymmetric platform, but differ from the figured specimen in having blade denticles that gradually decrease in size to the posterior part of the blade. Since so far only one specimen of *T. schultzei* has been found and described (holotype), the variability within the species is not known and the specimen figured here cannot be placed with certainty within the species.

**Stratigraphical distribution.** – The sample is situated in the *semialternans* Zone. *T. schultzei* is found in the upper part of the *ansatus* Zone and is reported from the Anti-Atlas (Aboussalam 2003).

**Material.** – 1 specimen in sample Vi-I/29.

## **Conclusions**

The conodont biostratigraphic study of a selected part of the Villech section in the Spanish Central Pyrenees reveals deposits of Eifelian, Givetian and lowermost Frasnian age, providing the first elaborated conodont biostratigraphic framework for the Eifelian in the Compte “subfacies area”. The Eifelian *costatus*, *kockelianus* and *eiflius* zones, the Givetian *rhenanus-varcus*, *ansatus*, *semialternans*, *hermanni*, *disparilis* and *norrisi* zones and the Frasnian MN1 Zone are identified. The *australis* Zone has not been recognized (*T. kockelianus australis* is not found in the section). The *ensensis* and *hemiansatus* zones have not been found either due to a covered interval in the section. Because of that the Eifelian- Givetian boundary can, so far, not be accurately positioned in the Villech section.

A thin black limestone/ black shale deposit, a hypoxic interval situated in the *semialternans* Zone in the Villech section, is possibly the local signature of the upper expression of the Taghanic event, one of the most important global extinction events in the Middle Paleozoic, which is recognized for the first time in the Spanish Central Pyrenees. The inconsistent thickness variation of the conodont zones in the Villech, Compte and Renanué sections and/or the possible absence of certain conodont zones suggest synsedimentary tectonic activity in the area in the Middle Devonian.

## **Acknowledgements**

The authors thank G. Klapper and K. Narkiewicz for their kindly provided constructive reviews. This work is a contribution to IGCP-596 and has been supported by the Spanish Research Project CGL2011-24775. The DAAD (J-CL) and the Alexander von Humboldt-Stiftung (JIV-R) supported earlier activities of this research. A UNESCO-German Committee (J-C. L & JIV-R) travel grant was used to attend at the IGCP 596 Opening Meeting in Graz, September 2011. We are grateful to the SCSIE (Servicio Central de Soporte a la Investigación Experimental) of the University of Valencia for technical support. C. Gentilini and M. Tonelli (Università di Modena e Reggio Emilia, Italy) are thanked for their help with the SEM imaging.

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