The Middle and Upper Devonian conodont sequence from La Guardia D’Àres Sections (Spanish Central Pyrenees)

JAU-CHYN LIAO & JOSÉ I. VALENZUELA-RÍOS

The analysis of conodont faunas from the Comabella Formation at La Guardia d’Àres in the Spanish Central Pyrenees improves the biostratigraphical characterization of this stratum. Forty-seven taxa spanning from the Eifelian through the Lower Frasnian are identified and described. The lower part of the formation starts in the Eifelian kockelianus Zone. The Eifelian/Givetian boundary can be identified by the entry of the index taxon Polygnathus hemiansatus. The Givetian part of the section is tectonically disturbed, affecting mostly the confident recognition of the rhenanus/varcus and the Upper varcus zones. All other Givetian zones are identified either by the defining index taxa or by the characterizing taxa. The Ancyrodella sequence permits recognition of Lower Frasnian MN1–MN3 zones. Direct comparison with Boersma’s data shows a strong chronostratigraphical discrepancy and their data are reinterpreted. • Key words: Middle Devonian, Lower Frasnian, conodont biostratigraphy, Spanish Central Pyrenees.


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Detailed work on Middle and early Upper Devonian strata from the Spanish Central Pyrenees carried out in the last decade has provided a detailed, conodont-based, Givetian and early Frasnian biozonation that can be correlated worldwide (Liao et al. 2001; Liao et al. 2008; Liao & Valenzuela-Ríos 2008, 2012; Gouwy et al. 2013). This biozonation is based in sections from three different subfacies areas (in the sense of Mey 1967): Section Renanué from Subfacies Renanué (Liao et al. 2001, 2008); Section Compte (Liao & Valenzuela-Ríos 2008) and Section Villech (Gouwy et al. 2013) from Subfacies Compte, and Section Ampriú from Subfacies Sierra Negra (Liao & Valenzuela-Ríos 2012). In spite of the general wealth of the conodont record, each section shows intervals that are not as well characterized as desirable for fine biostratigraphical correlation. A solution to such problems is detailed analysis of as many sections as possible and to integrate the data into the Pyrenean and global networks. Additionally, a detailed study of the Givetian/Frasnian boundary is also pursued.

Geological setting

The La Guardia d’Àres outcrop area is located about 1.5 km east of the La Guardia d’Àres village, on the recently paved road connecting the valleys of the Segre and Noguera Pallaresa rivers between Navas de Segre and Gerri de la Sal (Fig. 1).

Boersma (1973) described this area for first time; he established the stratigraphical sequence and partially dated these rocks. He recognized the upper part of the Basibé Fm. (Lower Devonian), the Villech Fm. (Lower to Middle Devonian), the three Members (A–C) of the Compte Fm. (Middle Devonian–Carboniferous) and the lowermost part of the overlying Bellver Fm. (Carboniferous).
The lower part of the section (Basibé and Villech formations) has already been studied (Martínez-Pérez et al. 2011). Herein, we will focus in the part corresponding to the Member A of the Compte Fm. that in current stratigraphic nomenclature is the Comabella Fm. According to Boersma (1973) this stratigraphical interval comprises from the Polygnathus kockelianus Zone (Eifelian) to the P. asymmetricus Zone (Frasnian). He was able to identify the Givetian Icriodus obliquimarginatus and P. varcus zones, but he failed in recognizing the Upper Givetian hermanni and cristatus zones, even though he identified Schmidtognathus hermanni in sample 132 (Boersma 1973, p. 318); he considered this record as belonging to the P. varcus Zone (Boersma, op. cit.)

We have been able to identify some of Boersma’s sample numbers and they can be directly correlated with our sampling for data comparison and subsequent bio-and chronostratigraphical interpretation.

The studied part (Fig. 2) measures about 40 m thick and is composed of reddish-pinkish and light grey nodular and platy limestone; the lower beds are platy; beds in the middle parts are thicker and massive with wavy surfaces; in the upper part the limestone beds are thin again, but thicker than the lower part.

The detailed fieldwork carried out in the area shows that this section is tectonically affected and several minor faults and a fold hinder a continuous record. The detailed sampling was needed for checking the tectonically affected intervals.

Besides the main section (LGA), we have sampled an auxiliary parallel section (LGA-I) for better characterizing the Givetian-Frasnian interval. The relative position of these two sections is documented in Figs 1 and 2.

Results

The conodont sequence allows assignation of the studied strata to a time span from the Eifelian to the Lower Frasnian and the identification of many of the main global conodont zones for this interval. Most data come from LGA section, but for the interval around the Givetian/Frasnian boundary an auxiliary section (LGA-I) was also studied.

LGA section

Eifelian (Fig. 3A)

The lower part of the LGA section is Eifelian in age, but a precise zonation cannot be established (Beds 167–179; Fig. 3A). The dominant taxon is Polygnathus linguiiformis linguiiformis that has an ample range spanning from the lower part of the Eifelian (costatus Zone) through the Middle Frasnian (MN 7 Zone). The presence of P. l. klapperi in the basal Bed (167) limits the age to the upper Eifelian kockelianus Zone. The last local records of P. costatus and P. oblongus in the Bed 168 correspond to the upper part of their ranges (kockelianus Zone). Another common taxon of the Eifelian part in LGA is P. angustipennatus, which records here correspond to the upper part of its range (costatus-base of hemiansatus zones). The related taxon P. angusticostatus that according to Walliser & Bultynck (2011) is almost restricted to the Eifelian (costatus-base of hemiansatus zones), appears

Figure 1. General (A) and detailed geographical setting of the La Guardia d’Àres section (LGA) in the Spanish Central Pyrenees (B). Numbers indicate the position of the lower (167) and the upper (227) Beds in LGA section. Section LGA-I is less than 2 m higher in the same hill at the position of the upper part of LGA.

Figure 2. Lithological columns of LGA and LGA-I sections with indication of the stratigraphy at the eastern limb of the fold, the conodont samples (arrows), the conodont distribution and the chronostratigraphical interpretation.
in sample 178a. *Icriodus struvei* (Bed 178b) mirrors the range of *P. angustipennatus*. The presence in sample 178a of *I. obliquimarginatus*, which ranges in Morocco from the base of the *hemiansatus* Zone (Walliser & Bultynck 2011, p. 17) suggests tentatively assignation of this Bed to the base of the *hemiansatus* Zone, and therefore, the beginning of the Givetian.

In brief, the Eifelian is represented in Beds 167–177 and they belong to the two upper Eifelian conodont zones, *kockelianus* and *ensensis*, but the position of the boundary cannot be recognized. Therefore, we grouped all these beds under the comprehensive *kockelianus-ensensis* term.

### Givetian

**Lower Givetian: hemiansatus Zone** (Fig. 3A). – The Givetian starts with the entry of *I. obliquimarginatus* in sample 178a. The lowest record of the index taxon *P. hemiansatus* is delayed (Bed 180). *P. pseudofoliatus* is also recorded from this bed. The upper part of this bed is tectonically disrupted by a normal fault. The rocks outcropping above this fault depict a fold that comprises strata from the Lower *varcus* to the Lower *hermanni* zones. Due to the biostratigraphical interest of this section and the tectonical disruption at this point, both limbs of the fold were sampled for a detailed checking of the strata age. The results are grouped into west and east limbs respectively (Fig. 3). The sample numbering of the western limb comprises Beds 195 to 201, while those from the eastern limb are, in stratigraphical order, from Bed 193 (older) to 181 (younger; the fold limb is not inverted, just the numbering is reversed).

#### Western limb:

**Middle Givetian: ansatus Zone** (Fig. 3A). – Bed 195 does not have a definitive age, as the only record is the long-ranging taxon *P. l. linguiformis*. Bed 196 yielded *P. rhenanus* and *P. beckmanni*; the former starts in the *rhenanus/varcus* Zone, but the latter does not appear before the *ansatus* Zone; consequently these records are interpreted as belonging to the Middle Givetian *ansatus* Zone. The index of this zone (*P. ansatus*) enters in the overlying bed (197); samples 196 and 197 are separated by only 4 cm. *Polygnathus l. linguiformis*, *P. l. klapperi* and the lowest local record of *P. l. weddigei* complete the conodont diversity of Bed 197.

**Upper Givetian: hermanni Zone** (Fig. 3A). – The association of *Tortodus trispinatus* and *P. limitaris* in sample 200c suggests that it belongs to the Lower *hermanni* Zone as the upper known range of the former does reach beyond the Lower *hermanni* Zone and the range of the latter starts at the *hermanni* Zone. The association of *P. l. macronatus* and “*Ozarkodina*” sannemanni adventa in the overlying bed (201), permits assignation of this bed to the Lower *hermanni* Zone, as well. The uppermost range of the former taxon is known from the *hermanni* Zone and the latter starts in this zone. Other taxa from this bed, *P. l. linguiformis*, *P. l. klapperi* and *P. varcus*, have longer ranges.

In summary, Beds 195 to 201 in the west limb of the fold cover an interval from the Middle Givetian *ansatus* Zone to the Upper Givetian *hermanni* Zone, but only these two zones are identified. The *semialternans-latiffossatus* Zone that shall be located between them has not been identified and has to be found in some place between samples containing the index and characterizing conodonts mentioned above (197 and 200c respectively).

#### Eastern limb:

**Middle-Upper Givetian: ansatus-Upper varcus-hermanni zones** (Fig. 3B). – *Polygnathus l. linguiformis* is present in all samples of this limb. The lowest sample (193) yielded *P. rhenanus*, which has a restricted range from the *rhenanus/varcus* Zone to the uppermost part of the *ansatus* Zone; but Aboussalam (2003) extends its range into the *semialternans-latiffossatus* Zone. Lack of definitive records from Beds 192–191 does not allow greater precision. However, the identification of the *hermanni* Zone (see below) in Bed 189, which lays 60 cm above Bed 193, hints at a tentatively position of Bed 193 within the upper part of the *P. rhenanus* range, probably in the *ansatus* Zone, but definitive evidence is pending.

The *hermanni* Zone could be identified in Bed 189 by the presence of “*O." sannemanni adventa*, which globally starts in this zone. However, there are records of two taxa that do not fit well with this interpretation. Also in Bed 189 *P. hemiansatus* and *P. rhenanus* are recorded; both taxa normally disappear within the Upper *varcus* Zone or earlier (*P. rhenanus*, see above); therefore, their joint occurrence with conodonts indicative of the younger *hermanni* Zone is puzzling. Records of the overlying beds (188–181) do not help to sort out this uncertainty.

**Upper Givetian: hermanni-norrisi Zones** (Figs 4, 5). – *hermanni* Zone (Fig. 4). The LGA section continues from the western limb upward, and consequently the numbering follows this order, being the next sample from Bed 202. The yields of the next 8 m thick set of beds (202–214b) is dominated by *P. l. linguiformis*, and *P. l. klapperi*, the upper range of the later, which last occurs in Bed 204, ends either in the *hermanni* Zone or in the succeeding *disparalis* Zone. Other common taxa in this interval, *P. xylus xylus*, *P. varcus*, and *P. timorensis*, have larger ranges that hinder further precision. The spotty occurrences of taxa with more restricted ranges, such as *P. l. macronatus* (Bed 214b) and “*O." semialternans* (Bed 212), only
indicates that Bed 214b is not younger than the hermanni Zone.

disparilis Zone (Figs 4, 5A). The record of Klappen- 
rina disparilis in Bed 214c identifies the base of the dispa-
rilis Zone. In the lower part of the zone, specimens of this 
taxon in several beds, and of P. dubius and P. cristatus 
cristatus, are common. In this part of the section is the 
lowest local (delayed) record of P. limitaris in the basal part 
of Bed 218. The entry of P. d. dengleri in the middle part 
of Bed 218 permits identification of the Upper disparilis 
Zone, and therefore the recognition of the twofold Lower and Up-
per subdivision of the disparilis Zone. In the upper part of 
Bed 218 is noteworthy the local entry of Schmidthognathus 
seitekindti. In the lower part of the overlying bed (219) the 
single occurrence of “O.” s. proxima is registered.
norrisi Zone (Fig. 5A, B). The uppermost Givetian norrisi Zone cannot be definitively identified by means of the index taxon at the LGA section. However, the physical continuity of strata with the nearby LGA-I section, which contains Skeletognathus norrisi, permits tentative assignation of the lower part of Bed 221 (lower 51 cm of a 200 cm thick bed), and probably the upper half of Bed 220 (the upper 17 cm of a 42 cm thick bed) to the norrisi Zone.

The record of P. alveliposticus in the uppermost 15 cm of Bed 219 can either belong to the disparilis or to the norrisi Zone as proposed by Bardashev (1992). The record of P. d. dengleri in the middle part of Bed 218 indicates the Upper disparilis Zone, which also supports the extension of P. alveoliposticus higher than the Lower disparilis Zone, but whether or not the LGA record belongs to the Upper disparilis or to the norrisi Zone cannot be tested by means of critical conodonts.

Frasnian (Fig. 5A)

Lower Frasnian: MN1–MN3 zones (Fig. 5A). – The beginning of the Frasnian, and therefore of the Upper Devonian Series, is placed 122 cm above the base of Bed 221 with the lowest record of Ancyrodella pristina, corresponding to MN Zone 1. The sequential entries of Ancyrodella taxa permit recognition of the three lower zones (MN 1–MN 3) according to the Montaigne Noire zonation (Klapper 1989). MN Zone 2 starts 195 cm above the base of Bed 221 with the entry of A. rotundiloba. The entry of A. r. alata late form at the top of Bed 225 identifies the base of MN Zone 3. Within this zone is the entry of A. africana in Bed 226.

LGA-I section

The adjacent very short auxiliary section LGA-I (220 cm) was sampled in order to better characterize the Givetian/Frasnian boundary. As this section shows some physical continuity with the LGA section, the projection of data would help in location of the G/F boundary in the LGA section.

Uppermost Givetian: norrisi Zone (Fig. 5B)

The lowest sample (1a) yielded Sk. norrisi together with P. pennatus that has narrow stratigraphical ranges around the G/F interval as well as P. dubius. The following sample...
(1b) yielded *P. limitaris*, a taxon that also has an upper range limited to the *norrisi* Zone or perhaps into the basal Frasnian.

**Lower Frasnian: MN1–MN3 zones (Fig. 5B)**

The Frasnian is identified in sample 1c by the presence of *A. pristina*; this sample belongs to MN Zone 1. MN Zone 2 starts in Bed 2, which yielded the entry of *A. rotundiloba*. The sequence of entries of the genus Ancyrodella continues with the record of *A. r. alata* late form in sample 6b, which indicates the beginning of MN Zone 3. This record matches the previous sequence described for LGA section, but the lithological correlation between both sections suggests that the taxon enters slightly earlier in LGA-I, as the Bed 6b equivalent is placed below the top of Bed LGA 225.

**Comparison with Boersma’s results**

In his pioneering work, Boersma (1973) studied with certain detail the section La Guardia d’Àres, a long section spanning from the Lower Devonian through the Lower Carboniferous; the interval between his samples 118 and 133 (Boersma 1973, fig. 8, table 2) largely corresponds with our LGA section. Boersma assigned the strata where samples 118–125 were taken to the Villech Fm.; however, we include these beds in the overlying Comabella Fm., which is the equivalent of his Compte A Member (see Montesinos & Sanz-López 1999, Valenzuela-Ríos & Sanz-López 2002). Therefore, the boundary between the Villech and Comabella Fms is shifted down about 20 m according to thicknesses inferred from his lithological column (Boersma 1973, fig. 8). Many of his field numbers were recognised, and therefore a direct comparison with our results is possible. Boersma dated the interval we studied herein as Eifelian–Upper Givetian, we correlated the sequence described for LGA section, but the lithological correlation between both sections suggests that the taxon enters slightly earlier in LGA-I, as the Bed 6b equivalent is placed below the top of Bed LGA 225.

Our yields lowered the lowest record of this taxon by about 1 m. The next number recognized in the field was 124, that corresponds to Bed 187 on the eastern limb of the fold. Boersma placed this sample in the *kockelianus* Zone, but our records indicate the *hermanni* Zone. This is a major discrepancy with his interpretations; the next record also reproduces this discrepancy. His number 125 corresponds to Bed 198 in the western limb of the fold. Sample 125 was also placed within the Eifelian *kockelianus* Zone; however, our records indicate the *ansatus* Zone for Bed 198. Number 126 was not identified, but numbers 127 and 128 were. Boersma placed these three samples within the Eifelian *kockelianus* Zone. Sample 127 corresponds to our Bed 204 and sample 128 to Bed 207; both beds are within the *hermanni* Zone. Sample 129 was not identified. Sample 130, the lowest sample considered by Boersma as Lower Givetian (*Ic. obliquimarginatus* Zone) corresponds to Bed 218, which is Upper *disparilis* Zone. Sample 131 was also assigned to the *Ic. obliquimarginatus* Zone; its corresponding bed in our section (Bed 219) is *norrisi* Zone. The last two Boersma samples recognized in our LGA section (132 and 133) were placed in the Givetian *P. varcus* Zone. Sample 132 correlates with our Bed 221, which is Lower Frasnian MN Zone 2; sample 133 correlates with Bed 226 that belongs to MN Zone 3.

**Summary**

The detailed sampling of La Guardia d’Àres sections yielded a conodont record of 47 taxa that encompasses a late Eifelian–Early Frasnian age for this part of the Comabella Formation, permitting the recognition of most of the Givetian and the lower three Frasnian zones. Furthermore, a direct comparison with the pioneer Boersma’s sampling shows discrepancy with his interpretations.

The lowest biostratigraphical unit belongs to the Eifelian *kockelianus* Zone; its upper boundary (*ensensis* Zone) could not be identified. This lower part, termed *kockelianus-ensensis*, is represented in Beds 169–177. The base of the Givetian is correlated with a level situated between 20–33 cm above the base of Bed 178, which yielded the entry of *I. obliquimarginatus*. The delayed entry of the defining taxon, *P. hemiansatus*, is at the base of Bed 180. The sequence on the western limb of the fold comprises up to the Lower *hermanni* Zone, but only the *ansatus* Zone and the Lower *hermanni* Zone can be identified by means of conodonts. The conodont sequence on the eastern limb does not provide better information, as records are still puzzling and the Middle Givetian zones cannot be discriminated. The beginning of the *hermanni* Zone is identified in the uppermost 10 cm of Bed 200 (sample 200c) with the presence of *P. limitaris*; this zone extends to the Bed 214b. The base of the overlying *disparilis* Zone starts at Bed 214c with the entry of the defining taxon *Klapperina disparilis*. The entry of *P. d. dengleri* in the middle part of Bed 218
allows recognition of the twofold subdivision (Lower and Upper) of the *disparilis* Zone. Basal beds (1a and 1b) of section LGA-I yielded *Skeletognathus norrisi* below the first *Ancyrodella*, characterizing the uppermost Givetian *norrisi* Zone. In section LGA, the physical continuity of strata combined with conodont yields pointed at a position of this zone between the upper half of Bed 220 and the lower part of Bed 221 (up to 51 cm above the base). The entry of *A. pristina* 122 cm above the base of Bed 221 (section LGA) and in Bed 1c (section LGA-1) indicates the beginning of the Frasnian; this taxon also serves to recognize MN Zone 1. The successive occurrences of *A. rotundiloba* and *A. r. alata* late form permit identification of MN2 and MN3 zones.

Direct comparison with Boersma’s data allows some modifications of his interpretations. The most important are: 1) shifting downwards, by about 20 m, the boundary between the Villech and Comabella Fms.; 2) including his samples 118–121 in the Villech and Comabella Fms.; 3) most of the *kockelianus* Zone; 4) the samples 130 and 131 that were assigned by Boersma to the Lower Givetian *norrisi* zones; 5) the samples 132 and 133 that Boersma assigned to the *disparilis* and *norrisi* zones; 6) the samples 132 limestone conodont samples were collected (Figs 3–5); 7) the samples 130 and 131 that were assigned by Boersma to the Villech and Comabella Fms.; 8) combining modifications of his interpretations. The most important are: 1) shifting downwards, by about 20 m, the boundary between the Villech and Comabella Fms.; 2) including his samples 118–121 in the Villech and Comabella Fms.; 3) most of the *kockelianus* Zone; 4) the samples 130 and 131 that were assigned by Boersma to the Lower Givetian *norrisi* zones; 5) the samples 132 and 133 that Boersma assigned to the *disparilis* and *norrisi* zones; 6) the samples 132 limestone conodont samples were collected (Figs 3–5); 7) the samples 130 and 131 that were assigned by Boersma to the Lower Givetian *norrisi* zones; 8) combining modifications of his interpretations. The most important are: 1) shifting downwards, by about 20 m, the boundary between the Villech and Comabella Fms.; 2) including his samples 118–121 in the Villech and Comabella Fms.; 3) most of the *kockelianus* Zone; 4) the samples 130 and 131 that were assigned by Boersma to the Lower Givetian *norrisi* zones; 5) the samples 132 and 133 that Boersma assigned to the *disparilis* and *norrisi* zones; 6) the samples 132 limestone conodont samples were collected (Figs 3–5); 7) the samples 130 and 131 that were assigned by Boersma to the Lower Givetian *norrisi* zones; 8) combining modifications of his interpretations.

### Systematic palaeontology

132 limestone conodont samples were collected (Figs 3–5); they were dissolved in dilute formic acid (6–8 %). The insoluble residue was then, decanted and only a sieve of 1.25 mm was used to separate larger fragments from the finer fraction. The residue smaller than 1.25 mm was dried and hand-picked utilizing a microscope. Selected specimens were photographed with a Philips 30XL Scanning Electron Microscope; photographs were digitally produced and saved.

All specimens are deposited at the Museum of Geology, University of Valencia MGUV. Only “Pa” and “I” elements are described.

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

*Ancyrodella pristina* Khalymbadzha & Chernysheva, 1970

Figure 6A, B

2002 *Ancyrodella pristina* Khalymbadzha & Chernysheva, 1970. – García-López & Sanz-López, pl. 2, figs 21, 22 (renamed from the holotype of *Ac. isabelae*)


2007 *Ancyrodella rotundiloba binodosa* Khalymbadzha & Chernysheva, 1970. – Aboussalam & Becker, fig. 9M, N.

2007 *Ancyrodella rotundiloba* Khalymbadzha & Chernysheva, 1970. – Over, fig. 11.18.

2008 *Ancyrodella pristina* Khalymbadzha & Chernysheva, 1970. – Liao & Valenzuela-Ríos, pp. 2, 3 and 7; tab. 1C; fig. 6J (further synonymy).

2008 *Ancyrodella binodosa* Uyeno, 1967. – Ovnatanova & Kononova, p. 1080, pl. 26, fig. 3.

2010 *Ancyrodella pristina* Khalymbadzha & Chernysheva, 1970. – Gouwy, pp. 113, 114, pl. 10, figs 6a, b (see further synonymy).


**Description.** – *Pa* element upper side: asymmetrical platform with triangular outline; acute, straight to sub-rounded lobes. Platform length equal or slightly longer than the blade. Anterior carina with 5–7 elliptic denticles, wide spaced and decreasing in size anteriorly. Slightly curved posterior carina, composed of 4–5 rounded oval nodes, close spaced; some of them, fused. Posterior lobe ornamented by one row, one each side, of aligned nodes, which are sub-parallel to the carina and small nodes disposed close to the margins that are less numerous. Secondary lobes, with straight or rounded anterior margins; the outer is slightly asymmetrical. *Pa* element lower side: moderate basal pit, cross-shaped slightly stretched, located on the anterior part of the platform; it has projected flanges as in *A. binodosa*. Straight and narrow anterior keel and slightly bent posterior keel, which is wider (near to the pit) than the anterior one. Secondary keels poor to well developed, forming an angle close to 180°, that do not reach the ends of the lobe margins.

**Remarks.** – Traditionally, the species is considered as one of the early ancyrodellids forms. In the 1980’s, Klapper (1985) named it as *A. rotundiloba* early form and, subsequently, Sandberg et al. (1989) re-used the name *A. pristina*, which previously was coined by Khalymbadzha & Chernysheva (1970). Both concepts are used herein. The main characteristics of *A. pristina* are: 1) a lanceolate to sub-triangular platform-outline with rounded or straight anterior margins; 2) a simple ornamentation consisting of two large nodes, one on each side of the carina and few small nodes in the margins; 3) a longer free blade and 4) medium size, “T” shaped, basal cavity. Sandberg et al. (1989: 211) distinguished three morphotypes on the bases of the lateral lobe margins shape. Our specimens show only two forms: M1 and M2.
Both specimens illustrated here are considered as mature forms of *A. pristina*; but one of them (Fig. 6A) is characterized by having a sub-rectangular shaped basal cavity, somewhat stretched; the angle formed by the outer secondary and main carinae is approximately 110°.

**Stratigraphical distribution.** – *A. pristina* is restricted to the Lower falsiovalis Zone; in terms of the Montagne Noire conodont zonation (Klapper 1989), it ranges from MN 1 to MN 2 zones (Lower Frasnian).

*Ancyrodella rotundiloba alata* Glenister & Klapper 1966

Figure 6C, D

*1966 Ancyrodella rotundiloba alata n. sp., Glenister & Klapper, pp. 799, 800, pl. 85, figs 1–8; pl. 86, figs 1–4.
* 1968 *Ancyrodella rotundiloba alata* Glenister & Klapper, 1966. – Pollock, p. 420, pl. 61, figs 2, 3.
* 1985 *Ancyrodella alata* Glenister & Klapper, 1966. – Klap- per, p. 27, pl. 4, figs 1–8; pl. 5, figs 1–16; pl. 6, figs 1–12; pl. 7, figs 1–11; pl. 8, fig. 8; text-fig. 3K, L, O–R.
* 1989 *Ancyrodella alata* Glenister & Klapper, 1966. – Bar- dashev & Ziegler, p. 76, pl. 2, fig. 27.
* 1986 *Ancyrodella alata* Glenister & Klapper, 1966. – Bul- tynck, pp. 276, 277, pl. 1, figs 10, 11.
* 1989 *Ancyrodella alata* Glenister & Klapper, 1966. – Sand- berg et al., p. 222, pl. 2, figs 7, 8; pp. 226, pl. 4, figs 8, 10, 11.
* 1989 *Ancyrodella alata* Glenister & Klapper, 1966. – Van- delae et al., p. 239, pl. 1, figs 2a, b.
* 2003 *Ancyrodella alata* Glenister & Klapper, 1966. – Over et al., p. 222, pl. 1, figs 16, 17.

**Material.** – Eight specimens from beds LGA225top(2), LGA226(1), LGA227b(4), LGA-1/b(1). Figured specimens: LGA225top(2), MGUV6152–6153.

**Description.** – Pa element upper side: Slightly asymmetrical, alate platform outline. Rounded to straight lobes. Platform length half to two thirds of blade length. Slightly inclined anterior carina, composed of 6–7 oval to rounded denticles, which are partly fused at their bases, free tips, and connected by a weak ridge; straight posterior carina with 4–6 oval to rounded nodes, partly fused or single, and wide spaced; the carina decreases in size posteriorly. Secondary carina with 2–4 rounded nodes, separated or partly fused, decreasing in size to the margins. Outer secondary carina longer than inner. Platform ornamented by 2 or 3 rows of rounded nodes, decreasing in size to the margins and running sub-parallel to the carina. Pa element lower side: medium size, rhombic basal pit; anterior keel slightly bent and posterior straight. Fine secondary keels moderately well developed, ending before the crimp. Inner keel, curved anteriorly; outer, straight laterally to slightly curved posteriorly. Anterior and inner keels form an acute angle; secondary keels angle, about 100 to 120°.

**Remarks.** – *A. rotundiloba alata* is characterized by a strongly alate platform outline and by the typical development of secondary keels, where the inner keel is lateral-anteriorly directed, but the outer one is latero-posteriorly directed. The figured specimens (Fig. 6C, D) show typical features of this species, fine and well developed secondary keels with straight and asymmetrical anterior margins, and the high number of nodes. The presence of relatively numerous nodes, small basal pit, and non-cruiciform aspect of our specimen suggest close relation to the “stratigraphically higher forms” of the Montagne Noire (see Klapper 1981, p. 27). All our specimens belong to Klapper’s late form. The specimens figured by Uyeno (1974, pl. 1, figs 3, 7; 1991, pl. 4, fig. 4) show a shorter development of the keels, specially the outer one that does not reach beyond the middle of the lobe. Also these Canadian specimens have comparatively larger secondary lobes with more marked “alate” development.

**Stratigraphical distribution.** – This species ranges from the falsiovalis to the transitans zones (Sandberg et al. 1989). In terms of MN zones, this taxon ranges from MN 2 to MN 4 zones.

*Ancyrodella rotundiloba rotundiloba* (Bryant, 1921)

Figures 6E, F

1921 *Polygnathus rotundilobus* sp. nov. Bryant, pp. 26, 27, pl. 12, figs 1–6.

1986 *Ancyrodella rotundiloba* (Bryant, 1921). – García-

Remarks. – The presence of an ornamentation gap between the blade and the carina is a typical feature of A. rotundiloba, A. rugosa and A. r. alata “early” form.

Description. – The secondary keels of A. rugosa are more anteriorly directed, forming an angle of about 100–120° and the platform bears more nodes.

The sub-triangular platform outline and the incipient development (or even lacking) of secondary keels in A. rotundiloba contrast with alate platform and clear secondary keels of A. r. alata.

The high number of nodes on the platform of the partly broken specimen (Fig. 6E) resembles A. rugosa. However, because of the poor development of the anteriorly directed inner- and laterally directed outer secondary keels, this specimen is included in A. rotundiloba “late” form. The rest of specimens from LGA can clearly be classified as A. rotundiloba “late” form.

Stratigraphical distribution. – From the beginning of the Middle falsiovalis Zone into the punctata Zone (Ji & Ziegler 1993). In our material An. rotundiloba ranges from the base of MN Zone 2 to the lower half of MN Zone 3.

Genus Icriodus Branson & Mehl, 1938

Icriodus struvei Weddige, 1977

Figure 6G

1977 Icriodus struvei Weddige sp. nov., pp. 296, 297, pl. 2, figs 21, 22.
2010 Icriodus struvei Weddige, 1977. – Gouwy, pp. 118, 119, pl. 4, fig. 11.

Material. – Two specimen from bed LGA178b, 33–47; fig. text-fig. 7, fig. 8; text-fig. 8, fig. 2.

Description. – “I” element upper side: slightly biconvex, tear-shaped spindle, with narrow margins anteriorly and wide posteriorly. Straight to curved middle row consisting of 9–10 elliptic to rounded denticles of different sizes and connected by a weak longitudinal ridge; the two more anterior denticles are higher and partly fused at the base, and their free tips are either rounded or sharp. The two more posterior middle rows denticles increase slightly in size with reclined cusp and convex posterior margin. Lateral rows consists of 6–7 denticles; last row denticles connected by a weak transversal ridge; denticles of the two anterior lateral rows are slightly posterior to corresponding middle row denticles. Two anterior transversal rows more spaced than...
posterior ones. I element lateral side: both ends of the unit higher than the central part. Middle row row higher than lateral rows. I element lower side: symmetrical basal cavity, narrow at the anterior half and wide posteriorly. Rounded and broad posterior margin.

Remarks. – The spindle of I. struvei, I. obliquimargina-tus and I. difficilis are slightly tear shaped; the lower number of denticles on the posterior middle row and the absence of the inner spur distinguish I. struvei from the other two.

Stratigraphical distribution. – According to Weddige (1977, p. 297), this species ranges from the middle part of the costatus Zone through the lower half of the ensensis Zone. Other authors, Belka et al. (1997), Mawson & Talent (1989), extend the lower range to the base of the costatus Zone, and Bultynck (2003, p. 297) extends the range up to the upper part of the partitus Zone. According to Gouwy & Bultynck (2003, p. 327), the range of I. struvei starts in the upper part of the partitus Zone and reaches the base of the ensensis Zone.

The specimens from Bed LGA178b-33–47 belong to the uppermost Eifelian.

Genus Klapperina Lane, Müller & Ziegler, 1979

Klapperina disparilis (Ziegler & Klapper, 1976)

Figure 6H, I

1985 Palmatolepis disparilis Ziegler & Klapper, 1976. – Ziegler & Wang, p. 20, tab. 1, pl. 2, fig. 20; pl. 3, figs 1, 3, 4.
1989 Klapperina disparilis (Ziegler & Klapper, 1976). – Wang, p. 73, pl. 37, fig. 4.
1993 Klapperina disparilis (Ziegler & Klapper, 1976). – Racki & Bultynck, pl. 6, figs 6a, b.
1999 Klapperina disparilis (Ziegler & Klapper, 1976). – Lazreq, p. 66, pl. 2, figs 6, 7, 10, 11.
2008 Klapperina disparilis (Ziegler & Klapper, 1976). – Liao & Valenzuela-Ríos, p. 8, figs 5K, L, Q, R.
2010 Klapperina disparilis (Ziegler & Klapper, 1976). – Lazreq, p. 120, 121, pl. 9, figs 7a, b (see further synonomy).

Material. – 13 specimens from beds LGA214c(3), LGA216a(2), LGA216b(2), LGA217a(2), LGA218(2), LGA19d5(1) and LGA219(2). Figured specimens: LGA218(1), MGUV6157 and LGA219(1), MGUV 6158.

Description. – Pa element upper side: asymmetrical, oval-shaped platform with rounded anterior and sharp posterior margins. Maximum width between the end of the first third and the anterior half. Blade/platform ratio 1 : 5. Short free blade, consists of 3–4 oval denticles of similar height, partly fused at the bases and free at the tips. Carina straight anteriorly and slightly curved posteriorly, bears 7–10 oval to rounded denticles, partly fused (most anterior) and increasing in size posteriorly. Common ornamentation consists of transversal rows of fine nodes; some specimens with wider platform develop elongated nodes at the margins. Outer platform wider than inner. Shallow and wide anterior throughs. Pa element lateral side: most of the flat specimens show a high carina and a free blade. A few specimens exhibit slightly higher platform margins. Pa element lower side: medium size, L-shaped basal pit located near the mid point. Outer flange more developed than inner. Anterior keel, narrow close to the basal pit, but wider anteriorly, posterior keel wide near the basal pit that narrows posteriorly.

Remarks. – Both figured specimens are broken (Fig. 6H, I); however, the combination of an ornamentation pattern consisting of random arrangement of the fine nodes in the central part and coarser nodes in the anterior margins, a slightly curved carina with an increasing denticles size and a distinctive L-shaped basal cavity permits assignment to K. disparilis.

Klapperina disparilis has a poor development of the platform lobe and fine nodes on the upper side in contrast with that of K. dispersalvea, which is characterized by greater platform development and coarser nodes; furthermore, the outer flange of Kl. dispersalvea is considerably larger.

Stratigraphical distribution. – According to Ziegler & Wang (1985) the highest range of this species reaches to the norrisi Zone, but Wang (1994) expands its range up to the lower half of the transitans Zone. Our specimens range from the base of the dispersilis Zone to the top of the Upper dispersilis Zone.
**Klapperina ovalis** (Ziegler & Klapper, 1964)

*Figure 6J*

1957 *Polygnathus dubia dubia sensu* Bischoff & Ziegler, pl. 1, figs 1, 2.
1985 *Polygnathus asymmetricus ovalis* Ziegler & Klapper, 1964. – Ziegler & Wang, p. 20, table 1, pl. 3, fig. 6.
2004 *Mesotaxis falsiovalis* Sandberg *et al.*, 1989. – Izokh *et al.*, p. 94, text-fig. 3; pl. 1, fig. 2.
2008 *Klapperina ovalis* (Ziegler & Klapper, 1964). – Liao & Valenzuela-Rios, p. 6, tab. 1C, fig. 5S.

**Material.** – Seven specimens from beds LGA22017cm sup(1), LGA226(1) and LGA227b(5). Figured specimen: LGA226, MGUV6159.

**Description.** – Pa element upper side: symmetrical to slightly asymmetrical platform, oval to leaf shape with rounded to sharp anterior margins. Maximum width located between the end of the first third and the anterior half. Pointed posterior end. Blade/platform ratio 1 : 5. Short free blade, consists of 3 oval denticles, partly fused at their bases, the two anterior denticles are higher. Carina is slightly bent at the anterior and straight at the posterior end; composed of 7–10 oval denticles, partly fused (most anterior) at their bases, sharp free tips; their size and spacing increase posteriorly. Platform ornamented by transversal rows or irregular arrangement of fine nodes, which can cover total or partly the oral surface; some specimens show fused nodes at the platform margins. Shallow and wide anterior troughs. Pa element lateral side: all specimens are flat and downwards arched; high free blade. Pa element lower side: slightly asymmetrical, medium size, oval to tear shaped basal pit, located near between the end of the first anterior third and the anterior half. Outer flange more developed than inner. Slightly bent and narrow anterior keel; wide posterior keel near to the pit that narrows posteriorly.

**Remarks.** – The oval outline, the distribution of fine nodes in the external part, and symmetrical basal pit near the half length of the platform are typical characteristics of *K. ovalis*.

The broken specimen (Fig. 6J) has a short free blade, a straight carina that reaches the posterior end, and well developed keels; the unit is slightly arched in lateral view. *K. ovalis* has a smaller basal pit and more symmetrical labial expansions than *K. unilabius*.

In contrast with *M. falsiovalis*, the basal pit of *K. ovalis* is located in a more posterior position.

Our material is closer to the North-African and European forms and differ clearly from Asiatic specimens, which have a markedly larger basal cavity.

**Stratigraphical distribution.** – According to Ziegler & Sandberg (1990), *K. ovalis* appears in the *disparilis* Zone and extends to the *hassi* Zone.

**Genus Ozarkodina** Branson & Mehl, 1934

We use the concept of *Ozarkodina* according to the restricted sense of Murphy *et al.* 2004; in order to avoid creation of new genera at this state of knowledge, we use quotation marks for the specimens referred herein to *Ozarkodina* to stress that they are not true *Ozarkodina* and that in future works new genera will have to be established for them.

"Ozarkodina" *sannemanni adventa* (Pollock, 1968)

*Figure 6K*


**Material.** – Two specimens from beds LGA20115cm inf. and LGA189top. Figured specimen: LGA189top, MGUV6160.

**Description.** – Pa element upper side: elongated and laterally compressed unit. Anterior blade higher than posterior. Only the outer platform is developed. Carina straight or slightly bent to the anterior and slightly bent posteriorly; it consists of 15–16 rounded to oval denticles, fused at their
bases and sharp or partly fragment at their tips. The most anterior three to four denticles are slightly larger than the posterior ones. Outer platform lobe has an ear-shaped outline. Pa element lateral side: palisade denticles decrease in size posteriorly. Pa element lower side: asymmetrical basal cavity, with only one incipient lateral expansion. Open, wide and deep grooves, parallel-sided that narrow to both ends.

**Remarks.** – “Ozarkodina” sannemanni adventa is characterised by a lateral incipient lobe on one or both sides with sub-rounded and symmetrical outline, and an anterior or posterior inflexion. Our specimens develop only an outer lateral lobe without denticles as in Fig. 6K, but specimens from Morocco may have two symmetrical lateral lobes.

**Stratigraphical distribution.** – According to Bardashev (1992), the first occurrence of this subspecies is within the *disparilis* Zone and ranges to the basal Frasnian; but Aboussalam & Becker (2007) extend the range from the base of the *hermanni* to MN Zone 2 Zone; Narkiewicz & Bultynck (2010), extended the range up to the *punctata* Zone (which corresponds to MN Zone 5).

“Ozarkodina” sannemanni proxima (Pollock, 1968) Figure 6L

1968 *Spathognathodus sannemanni proximus* n. subsp.; Pollock, pp. 439–440, pl. 63, figs 8, 9, 12, 13, 18, 19.
2007 *Ozarkodina sannemanni proxima* (Pollock, 1968). – Aboussalam & Becker, tables 1, 2, 4, 5; figs 8P, Q.
2010 “Ozarkodina” sannemanni proxima (Pollock, 1968). – Gouwy, p. 125, pl. 9, fig. 4.

**Material.** – Only one specimen from sample LGA219(225–240), MGUV6162.

**Description.** – Pa element upper side: Oval shaped and slightly asymmetrical platform. Total length double the width. Free blade absent or very short. Sharp anterior and posterior ends. Anterior part of carina slightly sigmoidal consisting of five oval denticles, which are close spaced. Posterior part, carina slightly curved with seven rounded and wide spaced denticles. Platform covered by coarser and rounded nodes, which are mainly situated in the posterior half, and thinner and rounded nodes or short transversal ridges at the margins. Pa element lateral side: the unit is flat-convex. Pa element lower side: basal pit partly covered by matrix; approximately located at the middle half.

**Remarks.** – This species is characterised by its oval shaped outline, a very short free blade, a slightly curved carina and two longitudinal row of nodes, on each side, at the posterior part and transversal nodes situated at the inner and anterior part of the platform. The figured specimen (Fig. 6M)
has a carina consisting of oval narrow denticles at the anterior part and rounded and spaced denticles at the posterior part; the platform of specimen MGUV6162 has fewer nodes than the holotype. The unit is slightly arched downwards.

The basal pit of *M. falsiovalis* is located more anteriorly (at the first third part of the unit); in comparison the nodes are larger and regularly arranged in *P. alveoliposticus*.

**Stratigraphical distribution** – According to Klug (1982), this species is recorded from the middle part of the Lower Zone to the Lower *disparilis* Zone. Our specimen corresponds to the *norrisi* Zone.

**Polygnathus angusticostatus** Wittekindt, 1966

*Figure 7B*

\*1966 Polygnathus angusticostata n. sp. Wittekindt, p. 631, pl. 1, figs 15–18.
1983 Polygnathus angusticostatus Wittekindt, 1966. – Sparling, p. 854, fig. 13Z.
1984 Polygnathus angusticostatus Wittekindt, 1966. – Kim et al., pp. 75, 76, pl. 23, fig. 8.
1985 Polygnathus angusticostatus Wittekindt, 1966. – Schönlaub, p. 361, pl. 5, figs 9, 10.
1990 Polygnathus angusticostatus Wittekindt, 1966. – Bardashev, pp. 34, 35, pl. 5, figs 13, 14, 21, 24.
1995 Polygnathus angusticostatus Wittekindt, 1966. – Sanz-López, pp. 483, 484, pl. 21, figs 10, 11; pl. 24, fig. 3.
2003 Polygnathus angusticostatus Wittekindt, 1966. – Benfríka & Bultynck, p. 212, pl. 1, fig. 11.
2003 Polygnathus angusticostatus Wittekindt, 1966. – Pyle et al., pp. 106, 107, tables 1, 2, pl. 2.
2004 Polygnathus angusticostatus Wittekindt, 1966. – Gouwy, p. 90, pl. 3, fig. 7.
2010 Polygnathus angusticostatus Wittekindt, 1966. – Gouwy, p. 133, pl. 4, figs 6, 7, 9 (further synonymy).

**Material.** – Two specimens from Bed LGA178a(2). Figured specimen: MGUV6164.

**Description.** – Pa element upper side: oval to sub-triangular shield-shaped, symmetrical platform with rounded outline. Maximum width at the middle of the unit. Posterior end slightly sharp. Broken free blade. Straight carina with 8–10 rounded to oval denticles, decreasing in size to the posterior. The platform bears marginal nodes or short transversal ridge. Shallow and wide adcarinal troughs. Pa element lateral side: flat unit, downwards arched. Pa element lower side: Small oval-shaped basal pit located at the anterior part of the platform. Posterior keel straight.

**Remarks.** – The specimen MGUV6164 (Fig. 7B) is assigned to *P. angusticostatus* by the combination of short transversal ridges, shallow adcarinal troughs, a low carina and a small basal pit.

*Polygnathus angustipennatus* has shorter and marginal transversal ridges and shallower and wider adcarinal throughs than *P. robosticostatus*.

*Polygnathus angustipennatus* has a reduced platform, its maximum width is generally located at the anterior margin, long anterior blade and shorter posterior one, narrow and deep adcarinal throughs; high carina that decreases to the posterior and a large basal pit. All these characters permit distinction from the closely related species *P. angusticostatus*.

**Stratigraphical distribution.** – According to Walliser & Bultynck (2011), *P. angusticostatus* ranges from the *costatus* Zone and reaches to the base of the *hemiansatus* Zone.

**Polygnathus angustipennatus** Bischoff & Ziegler, 1957

*Figure 7A*

\*1957 Polygnathus angustipenna n. sp. Bischoff & Ziegler, p. 85, pl. 2, fig. 6; pl. 3, figs 1–3.
1970 Polygnathus angustipenna Bischoff & Ziegler, 1957. – Bultynck, p. 124, pl. 17, figs 3–6; pl. 18, fig. 1.
1992 *Polygnathus angustipennatus* Bischoff & Ziegler, 1957. – Bardashev, pp. 36, 44, 46, 47, tables 4.1, 6, 7, 9, 10; pl. 2, figs 18–24.


2010 *Polygnathus angustipennatus* Bischoff & Ziegler, 1957. – Gouwy, pp. 133, 134, pl. 4, figs 5, 8 (further synonymy).

2011 *Polygnathus angustipennatus* Bischoff & Ziegler, 1957. – Walliser & Bultynck, p. 13, pl. 2, figs 5a, b.

**Material.** – Nine Pa elements from beds LGA174, 178a, 179, 189, 197. The figured specimen belongs to Bed LGA197, MGUV6165.

**Description.** – Pa element upper side: oval to triangular-shaped, symmetrical and short platform. In complete specimens the length ratio between free blade and platform plus posterior end is about 2:5. Straight anterior free blade; sharp and slightly curved posterior end. High anterior carina with 5 or 6 oval denticles. Low posterior carina with 9 rounded denticles. Deep adcarinal throughs and fine nodes alternate with short transversal ridges on the lateral margins. Pa element lateral side: flat unit slightly arched. Pa element lower side: large basal pit located at the first third of the platform. Deep, parallel-sided, narrow posterior basal groove.

**Remarks.** – The broken figured specimen (Fig. 7A) mainly preserves the posterior part of the platform with a high carina, a narrow and long posterior end, and marginal nodes and short transversal ridges.

*Polygnathus angustipennatus* shares with *P. trigonicus* a sub-triangular platform outline, but the former has a very narrow and short platform with a simple ornamentation; in contrast, the latter, has larger platform that bears a well-developed ornamentation.

For a comparison with the closely similar *P. angusticostatus*, see under the latter.

**Stratigraphical distribution.** – According to Walliser & Bultynck (2011), *P. angustipennatus* ranges from *australis* to *ensensis* zones.

*Polygnathus ansatus* Ziegler & Klapper, 1976

Figure 7C


1984 *Polygnathus ansatus* Ziegler & Klapper, 1976. – Kim et al., pl. 24, fig. 4.

1986 *Polygnathus ansatus* Ziegler & Klapper, 1976. – Garcia-López, p. 87, pl. 11, fig. 23; pl. 12, figs 1–13 (see further synonymy).


1992 *Polygnathus ansatus* Ziegler & Klapper, 1976. – Bardashev, text-figs 5.4, 5.5, 5.8, pl. 5, figs 23, 27.

1994 *Polygnathus ansatus* Ziegler & Klapper, 1976. – Bai et al., p. 175, pp. 22, figs 11, 12.


1999 *Polygnathus ansatus* Ziegler & Klapper, 1976. – Lazreq, p. 75, pl. 1, fig. 17.


2008 *Polygnathus ansatus* Ziegler & Klapper, 1976. – Liao & Valenzuela-Ríos, p. 8, fig. 3K; L (with synonymy).

2010 *Polygnathus ansatus* Ziegler & Klapper, 1976. – Narkiewicz & Bultynck, table 2, 5, 6, figs 4A–E, G, K.

**Material.** – Two specimens from beds LGA189, 197. The figured specimen ranges from the base LGA197, MGUV6165.


**Remarks.** – The figured specimen, Fig. 7C, shows the typical features of *P. ansatus*: marked constriction at the anterior platform, and well-developed anterior through margins.

**Stratigraphical distribution.** – According to Liao & Valenzuela-Ríos (2008), Narkiewicz & Bultynck (2008, 2010) and Aboussalam (2003), this species ranges from the base...
of the ansatus Zone to the Upper hermanni Zone; but Bardashev (1992) extends the upper range to the Lower disparilis Zone.

**Polygnathus oblongus Weddige, 1977**

Figure 7F, G

*1977* Polygnathus costatus oblongus n. subspp. Weddige, pp. 309, 310, pl. 4, figs 71, 72.

1979 Polygnathus costatus oblongus Weddige, 1977. – Lane *et al.*, p. 218, pl. 1, fig. 16.


1989 Polygnathus costatus oblongus Weddige, 1977. –


1990 Polygnathus costatus oblongus Weddige, 1977. – Bardashev, p. 34, pl. 3, figs 18, 19, 25; pl. 11, fig. 19.

1992 Polygnathus costatus oblongus Weddige, 1977. –

Bardashev, p. 62, text-figs 7, 10, pl. 1, fig. 33.

**Material.** – Two specimens from bed LGA168. MGUV6166, 6167.

**Description.** – Pa element upper side: Sub-rectangular and elongate asymmetrical platform. The maximum width is approximately at the middle of the posterior part of the unit. Blade/platform ratio about 1 : 5. Anterior platform restricted by a "rostrum". Sub-rounded posterior margin of the platform, weakly or strongly bent to the inner side. Short and straight free blade, composed of 4–5, laterally compressed, oval denticles. Carina composed of 10–12 rounded denticles, partially fused at their bases; they decrease in size and wider their space posteriorly; it is straight anteriorly where narrows to a fine ridge; the posterior part is also straight at the beginning but bends posteriorly. The platform bears fine transversal ridges, which are replaced by simple fine nodes at both, anterior and inner posterior margins. Deep and slightly wide adcarinal throughs at the anterior part that shallow at the posterior part. Outer platform slightly wider than the inner. The outer anterior margin is lower than the inner. Pa element lateral side: slightly arched downwards. Pa element lower side: small basal pit located at the beginning of the anterior part of the platform. Straight, wide and deep anterior basal groove; bent posterior keel.

**Remarks.** – The figured specimen (Fig. 7F) has a moderate development of the outer platform and it has a lower outer anterior platform margin.

This species evolved from *P. costatus* by narrowing the anterior part of the platform and developing an inner-turn of the posterior platform.

*Polygnathus oblongus* differs from *P. costatus* by the development of a sinuous outer posterior platform.

**Stratigraphical distribution.** – According to Weddige (1977), *P. c. oblongus* is restricted to the kockelianus Zone; but Bardashev (1990, 1992), extends the range down to the australis Zone.

**Polygnathus cristatus cristatus Hinde, 1879**

Figure 7D, E

*1879* Polygnathus cristatus n. sp. Hinde, p. 366, pl. 17, fig. 11.

1964 Polygnathus cristata Hinde, 1879. – Orr, p. 13, pl. 3, figs 4–8; text-figs 4A–K.

1966 Polygnathus cristata Hinde, 1879. – Flajs, pl. 23, fig. 8.


1985 Polygnathus cristatus Hinde, 1879. – Bardashev & Ziegler, p. 76, pl. 2, figs 1, 3.


1992 Polygnathus cristatus Hinde, 1879. – Bardashev, p. 76, pl. 8, figs 17–21.

1994 Polygnathus cristatus Hinde, 1879. – Bai *et al.*, pp. 176, 177, pl. 24, fig. 1.


1999 Polygnathus cristatus Hinde, 1879. – Lazreq, p. 86, pl. 2, figs 2, 3.


2007 Polygnathus cristatus cristatus Hinde, 1879. – Aboussalam & Becker, p. 359, fig. 9H.

2008 Polygnathus cristatus cristatus Hinde, 1879. – Liao & Valenzuela-Ríos, table 1C, figs SM. N.

2010 Polygnathus cristatus cristatus Hinde, 1879. – Gouwy, pp. 139, 140, pl. 9, figs 8a, b.

**Material.** – 14 specimens from samples LGA214c/cm(1), LGA216a/cm(1), LGA216a/cm(2), LGA217b(1), LGA218a/cm(2), LGA219a/cm(1), LGA220a/cm(3), LGA221a/cm(2) and LGA223(1). Figured specimens: LGA216a/cm(6), MGUV6168 and LGA219a/cm(6) MGUV6169.

**Description.** – Pa element upper side: oval shaped and slightly asymmetrical platform, which widest part is at the anterior half. Blade/platform ratio about 1 : 5. Rounded or sharp posterior end. In complete specimens, the free blade is short and consists of 5–8 oval denticles; in some specimens the two anterior denticles are higher. Carina with 9–16 aligned, rounded denticles, of comparable size and height, slightly lower than denticles on the blade; posteriorly they are smaller and more elliptical; in the anterior third they are close spaced and, in some specimens, fused...
in a ridge; in the posterior part they are widely spaced. The platform has 2–3 rows of rounded nodes of variable size, arranged oblique in the anterior part and sub-parallel to the carina posteriorly. The anterior nodes are larger than the posterior ones. Rounded and smooth anterior platform margins. Incipient development of the anterior adcarinal through. Pa element lateral side: anterior part of the unit, slightly arched downwards. Pa element lower side: Small and asymmetrical basal pit, located anterior of the platform mid-length; it continues anteriorly and posteriorly with straight, narrow keels.

**Remarks.**– The partially matrix-covered, broken specimen (Fig. 7E) shows the typical nodes arrangement and the asymmetrical basal pit. The “puzzle” specimen (Fig. 7D) shows a slightly sinuous carina with denticle-size decreasing posteriorly and the platform bears simple longitudinal rows of nodes, which are sub-parallel to the carina.

*Polygnathus c. cristatus* is similar to *M. falsiovalis* in the oval platform outline, location and size of the basal pit, but the former has a higher number of coarser nodes, which are arranged in longitudinal rows, while the platform of the latter is ornamented by fine nodes that have a transverse arrangement. Additionally, the asymmetrical basal pit of *P. c. cristatus* is larger and located more posteriorly.

The differences between *P. c. cristatus* and *P. c. ec- typus* are described below.

**Stratigraphical distribution.**– According to Klapper & Ziegler (1977), *P. c. cristatus* ranges from the Upper hermanni Zone to the punctata Zone; but Klapper & Johnson (1990) indicate the last occurrence of this subspecies in the Lower disparilis Zone.

Our specimens range from the base of the Lower disparilis Zone to the Upper falsiovalis Zone (MN Zone 2 of Klapper 1985).

*Polygnathus cristatus etypus* Huddle, 1934

Figure 7H

1934 *Polygnathus cristatus etypus* n. subsp. Huddle, p. 103, pl. 8, fig. 38.
1957 *Polygnathus cristatus* Hinde, 1879. – Bischoff & Ziegler, pp. 86, 87, pl. 15, figs 1, 2–12, 13, 16; pl. 17, figs 12, 13.
1971 *Polygnathus cristatus* Hinde, 1879. – Orr, p. 48, pl. 6, figs 1, 2.
1992 *Polygnathus cristatus* Hinde, 1879. – Bardashev, p. 76, pl. 8, figs 22–24.
1994 *Polygnathus cristatus* Hinde, 1879. – Bai et al., pp. 176, 177, pl. 24, fig. 3.
1999 *Polygnathus cristatus* Hinde, 1879. – Lazreq, p. 86, pl. 2, fig. 1.

2003 *Polygnathus cristatus etypus* Huddle, 1934. – Aboussalam, p. 177, pl. 19, figs 7–9.
2007 *Polygnathus cristatus* n. subsp. Huddle, 1934. – Aboussalam & Becker, p. 368, figs 9F, G.
2008 *Polygnathus cristatus etypus* Huddle, 1934. – Liao & Valenzuela-Ríos, p. 9, tables IB, C.
2010 *Polygnathus cristatus etypus* Huddle, 1934. – Narkiewicz & Bultanynck, p. 620, tables 2, 6, figs 17, 14, 15.

**Material.**– One specimen from Bed LGA22146–51, MGUV6170.

**Description.**– Pa element upper side: slightly asymmetrical, wide oval platform; broken – short? – free blade. Maximum width at the end of the anterior half. High carina with nearly complete fused denticles, but some free tips are observed. Platform ornamented by a chaotic arrangement of coarse nodes at the central part and thinner ones at the margins. Anterior part of the platform has few nodes; smooth anterior margins. Pa element lateral side: flat unit, anteriorly arched. Pa element lower side: Basal pit covered by matrix.

**Remarks.**– *P. c. cristatus* has a platform with less size-variability of nodes that are regularly arranged, in contrast with that of *P. c. etypus*.

**Stratigraphical distribution.**– The subspecies ranges from the base of the Upper hermanni to the transitsans Zone (Sandberg et al. 1994); our specimen comes from the top of the Lower falsiovalis Zone.

*Polygnathus dengleri dengleri* Bischoff & Ziegler, 1957

Figure 7I, J

1957 *Polygnathus dengleri* n. sp.; Bischoff & Ziegler, p. 103, pl. 8, figs 14, 15, 17–24; pl. 16, figs 1–4.
2001 *Polygnathus dengleri* Bischoff & Ziegler, 1957. – Liao et al., p. 26, pl. 4, figs 7–9, 12 (further synonymy).
2007 *Polygnathus dengleri dengleri* Bischoff & Ziegler, 1957. – Aboussalam & Becker, p. 356, fig. 6(C–F).

**Material.**– Eight specimens from samples LGA21845–52(1), LGA219108–120(1), LGA219225–240(1), LGA221610(1), LGA2216123–130(1), LGA22195–200(2), LGA-I/5(1) and LGA-I/6a(1). Figured specimens: MGUV6171 (Fig. 7I; LGA219225–240) and MGUV6172 (Fig. 7J; LGA221122–130).
Description. – Pa element upper side: oval to spear-shaped, symmetrical and narrow platform. Maximum width close to the anterior half; slender and elongate unit. Blade/platform ratio about 1 : 5. Short free blade with 4–5, anteriorly inclined denticles; the 2–3 more anterior denticles are higher and sharp. Anterior part of carina composed of fused denticles forming a ridge or of individual denticles; posterior part of carina with 7 rounded and wide spaced or oval denticles connected by a fine ridge. The height of the carina denticles decreases posteriorly. Variable platform ornamentation consists of fine nodes with random arrangement or thin transversal ridges on one side of the carina and small, thin and single nodes combined with fused nodes on the other side. Wide and shallow adcarinal throughs.

Pa element lateral side: flat unit slightly arched at both ends; in some specimens, the lateral margins are slightly higher than the carina. The combination of the anterior convex margin and the high and inclination of the denticles confers a wedge shape. Pa element lower side: small to medium size basal pit, with tear to oval-shaped smooth flange; continues to both ends with straight and narrow keels.

Remarks. – *P. d. dengleri* is probably one of the taxa from the Givetian-Frasnian interval with a high morphological variation. Traditionally, three morphotypes have been distinguished. Klapper (*in* Johnson *et al.* 1980, p. 102) distinguished two morphotypes from central Nevada: one form is characterised by a rather coarse and somewhat irregular transversal ridges and nodes and its range is limited to the *Lower disparilis* Zone (the former *Lower dengleri* Zone). The other form is characterised by a platform with fine nodes and fewer, weaker transversal ridges. It corresponds to the holotype, and appears in the *Upper disparilis* Zone (the former *Upper dengleri* Zone).

Bultynck & Jacobs (1981, p. 19) have recognised both morphotypes of Klapper (*in* Johnson *et al.* 1980) from south-eastern Morocco, which were named “β” and “γ” forms respectively, and a new one “α” form. The latter is characterised by a longer blade, a sub-triangular shaped platform, somewhat straight anterior margins and coarse and irregular ornamentation, which is restricted at the margins and considered as the earlier form.

Aboussalam & Becker (2007, p. 369) in Mdoura-East(Md-E) section, Tafifat Platform have recognised the characteristics of the “α” form described already by Bultynck & Jacobs (1981), and erected the new subspecies *Polygnathus dengleri sagitta*.

The figured specimen (Fig. 7I) is a typical “γ” form characterised by a platform ornamented by few nodes, a carina formed by oval to rounded denticles, which are widely spaced posteriorly and by a medium size basal pit, with smooth flange more developed posteriorly. The other specimen (Fig. 7J) is characterised by a narrower and longer platform, with one of the anterior margins lower. The carina consists of a ridge and denticles are distinguished only on the blade and in the posterior carina. Rather small basal pit, located at the end of the anterior platform. This form is considered as the “narrow” form by Klapper (1985).

Stratigraphical distribution. – According to Feist & Klapper (1985), Narkiewicz & Bultynck (2010): this taxon ranges from the Upper *disparilis* Zone to the top of the *transi* tans Zone (MN Zone 4 of Klapper 1985).

*Polygnathus hemiansatus* Bultynck, 1987

Figure 7K, L

1987 *Polygnathus hemiansatus* n. sp. Bultynck, pp. 161, 162, pl. 7, figs 16–27; pl. 8, figs 1–7.

2008 *Polygnathus hemiansatus* Bultynck, 1987. – Liao & Valenzuela-Ríos, p. 11, tabs 1A, B, figs 4A, B.

2010 *Polygnathus hemiansatus* Bultynck, 1987. – Gouwy, p. 142, pl. 5, figs 12, 13; pl. 6, fig. 1 (further synonymy).


Material. – Two specimens from samples LGA18010 cm inf., MGUV6173 and LGA18906, MGUV6184.

Description. – Pa element upper side: asymmetrical, elongated and somewhat slender platform, with maximum width at the posterior half. Partially broken free blade. Slightly straight carina, composed of 7–12 oval to rounded denticles; anterior denticles are closer and posterior ones are more spaced (Fig. 7L); denticles in specimen in Fig. 7K are fused in a ridge with only tips protruding. Denticles size increases at the central part of the platform. Platform ornamented by fine nodes and fine transversal ridges, with radial distribution. Marked constriction in the outer platform margin, just posterior to the geniculation point, that continues with a rounded platform margin. Less developed inner platform margin that is smooth (Fig. 7K) or serrated, posterior of the geniculation point (Fig. 7L). Outwards strongly bowed outer anterior through margin; less bowed inner one. Non-opposite geniculation points. Sharp posterior end, slightly reclined. Pa element lower side: due to breakage it is not easy to exactly locate the basal pit, but probably sits at the anterior half.

Remarks. – According to Bultynck (1987) and Walliser & Bultynck (2011), the main characteristics of *P. hemiansatus* are the strong constriction in the outer platform margin posterior to the geniculation point and the well developed outwards bowing of the outer anterior through margin. The
degree of development of these characteristics permitted these authors the recognition of three morphotypes: α, β and γ. For details, see comments in Walliser & Bultynck (2011, pp. 12, 13).

Our specimens from LGA section belong to the “γ” form. The figured specimens (Fig. 7K, L) show the typical morphological features: well-developed outer platform margin; bowed outer anterior through; serrated inner platform margin close to the geniculation point; ornamentation consisting of small nodes and fine and discontinued ridges. Our specimens are rather slender and narrow and can be distinguished from the Morocco material in the platform outline.

Stratigraphical distribution. – The range of *P. hemiansatus* starts at the base of the nominal zone, which is the base of the Givetian, and to the top of the *semialternans/latifossatus* Zone (the former Upper varcus Zone), the transition between Middle to Upper Givetian. According to Walliser & Bultynck (2011), the range of the three morphotypes is different. The α form is restricted to the lower part of the hemiansatus Zone, β and γ forms range into the ansatus Zone.

**Polygnathus linguiformis klapperi** Clausen, Leuteritz & Ziegler, 1979

Figure 7M

*1979* *Polygnathus linguiformis klapperi* n. ssp.; Clausen et al., p. 32, pl. 1, figs 7, 8.


2008 *Polygnathus linguiformis klapperi* Clausen et al., 1979. – Liao & Valenzuela-Rios, p. 10, tables 1a, 1b, fig. 3B. 

2010 *Polygnathus linguiformis klapperi* Clausen et al., 1979. – Gouwy, p. 144, pl. 6, fig. 11.

2011 *Polygnathus linguiformis klapperi* Clausen et al., 1979. – Walliser & Bultynck, p. 15, pl. 3, figs 7, 8.

**Material.** – 29 specimens from the following beds: LGA167(1), LGA174(1), LGA175(2), LGA178b 56(3), LGA197(4), LGA199a(3), LGA199b(3), LGA200b(1), LGA200c(2), LGA201(2); LGA190(1), LGA189 56(2), LGA186 56(1), LGA184(1), LGA182(2). Figured specimen: LGA167, MGUV6175.

**Description.** – Pa element upper side: asymmetrical to slightly symmetrical platform with robust and convex margins. Outer platform more developed and higher than inner. A well developed, somewhat long, and narrow sub-triangular tongue at the platform posterior third. Carina formed by fused nodes that are connected by a strong ridge that ends within the tongue. Platform ornamented by transversal ridges or aligned fine nodes. Narrow and deep anterior adcarinal through. The last portion of the outer platform margin meets the tongue by an inflexion. Sharp posterior end of the tongue. Pa element lateral side: both ends of the unit are arched; outer margin higher than the inner. Pa element lower side: heart shaped small-sized basal pit located at the middle of the platform anterior half. Straight anterior keel; smoothly curved posterior keel.

**Remarks.** – *P. l. klapperi* is distinguished from *P. l. linguiformis* by several aspects: 1) rounded platform outline between the outer margin and the tongue; 2) more nodes on the inner platform margin; 3) bigger and robust tongue; 4) rounded posterior end of the tongue.

**Polygnathus linguiformis klapperi** because the latter, has concave-convex margins, asymmetrical platform, less strongly curved carina, more developed outer platform margins and a poorly development of the tongue.

Stratigraphical distribution. – Weddige (1977) cited its lower range starting from the hemiansatus Zone; but according to Bultynck (1987), Belka et al. (1997) and Walliser & Bultynck (2011) this taxon ranges from the kockelianus Zone to the semialternans/latifossatus Zone.
**Polygnathus linguiformis mucronatus**
Wittekindt, 1966

Figure 7N, O

2003 *Polygnathus linguiformis mucronatus* Wittekindt, 1966. – Aboussalam, pp. 182, 183, pl. 17, figs 11, 16, 17 (further synonymy).
2008 *Polygnathus linguiformis mucronatus* Wittekindt, 1966. – Liao & Valenzuela-Ríos, p. 11, fig. 4E, F.
?2010 *Polygnathus linguiformis mucronatus* Wittekindt, 1966. – Gouwy, pp. 144, 145, pl. 6, fig. 9 (further synonymy).

**Material.** – Two specimens from samples LGA201,15 cm inf. (MGUV6176) and LGA214b,10 cm sup. (MGUV6185).

**Description.** – Pa element upper side: nearly symmetrical and tiny sub-rectangular-shaped platform with parallel margins. Straight free blade with 7 oval and compressed denticles. Carina composed of 8 oval to rounded denticles, which can be fused in a ridge or individually connected. The carina is straight to the tongue and then deflects inward and disappears within the anterior part of the tongue. Narrow subtriangular and sharp tongue, which turns to the inner side and downwards; it bears thin wide spaced transversal ridges that in the anterior part are interrupted by the carina. Platform bears denticulated margins that continue in transversal ridges. Deep adcarinal throughs.

Pa element lower side: Small, symmetrical, round-shaped basal cavity located at the beginning of the tongue. Narrow subtriangular and sharp tongue, which turns to the inner side and downwards; it bears thin wide spaced transversal ridges that in the anterior part are interrupted by the carina. Platform bears denticulated margins that continue in transversal ridges. Deep adcarinal throughs.

Pa element lateral side: strongly arched unit. Denticles height decreases posteriorly. Pa element lower side: oval to heart shaped basal cavity, located at the beginning of the anterior half. Slightly straight anterior basal groove; posterior curved keel.

**Remarks.** – The main characteristics of this subspecies are the reduced development of the platform, the presence of a narrow tongue which is inwardly and downwards inclined and a basal cavity located in the most anterior part of the platform. According to the shape of the platform outer margin outline and the tongue, we have recognised two forms combining our material and figured specimens from literature. One form, has a straight outline as in Fig. 7N or the original specimen of Ziegler & Klapper (1976, pl. 4, fig. 21) and the other form, has a rounded outline, as in Fig. 7O or the original specimen of Ziegler & Klapper (1976, pl. 4, fig. 20).

**Stratigraphical distribution.** – This subspecies appears from the base of the *rhenanus/varcus* Zone and reaches to the middle part of the *semialternans/latifossatus* Zone (Weddige 1977).

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**Polygnathus linguiformis ssp.**

Figure 7P

**Material.** – Only one specimen from Bed LGA171, MGUV6177.

**Description.** – Pa element upper side: asymmetrical leaf-shaped platform with weak and short transverse ribs on the margins; outer platform almost double the width of the inner. Blade/platform ratio about 1 : 5. Short and straight free blade with 3–4 fused denticles forming a ridge. Straight anterior carina composed of 3–5 rounded denticles connected by a ridge; slightly curved posterior carina with 6–7 rounded distinct denticles decreasing in size posteriorly and ending at the beginning of the tongue. Small, triangular tongue with transverse ribs, bent to the inner side. Well developed outer margin with rounded and denticulated outline; posterior half inward turned and downwards arched. Anterior platform margins meet the blade at different points; the inner more to the anterior. Pa element lateral side: downwards arched unit, specially the more posterior part. Pa element lower side: Small, symmetrical, round-shaped basal pit with thin flanges. Straight and deep, parallel-sized anterior basal groove; curved, narrow, shallow and weak developed posterior groove.

**Remarks.** – The combination of outline and short tongue with transverse ribs that interrupt the carina separates our specimen from other known subspecies of *P. linguiformis*.

**Polygnathus tafilensis** Aboussalam & Becker, 2007

Figure 8A

2007 *Polygnathus tafilensis* n. sp. Aboussalam & Becker, p. 30, fig. 5P–T.
2010 *Polygnathus cf. tafilensis* Aboussalam & Becker, 2007. – Gouwy, p. 151, pl. 9, fig. 2.

**Material.** – One specimen from Bed LGA221,195–200 cm sup. MGUV6178.

**Description.** – Pa element upper side: Slightly asymmetrical and flat, leaf-shaped platform. The maximum width of the unit is at the posterior third. Free blade little shorter than the platform, with 10–12 stout denticles fused at the base. The most anterior four denticles are anteriorly oblique-inclined. The last 3–4 denticles of the blade are fused into a thin ridge. Slightly curved carina composed of, at least, 10 partially fused, round-oval denticles, which are connected by a ridge; the height of these denticles decreases to the posterior end. Platform ornamented by fine nodes, randomly distributed on each side of the carina and by short and weakly transverse ridges at the anterior part of the
platform. Anterior platform margins develop an incipient and short “rostrum”. Shallow, short and narrow anterior adcarinal troughs. Outer side of the posterior platform more developed than the inner. Pa element lower side: flat unit with downwards arched posterior end. Anterior margins higher than posterior ones. Pa element lateral side: tiny, heart-shaped basal pit with slightly asymmetrical flanges located at the anterior platform half. Both basal grooves are narrow and parallel-sided; the anterior one straight and anteriorly appressed; the posterior one slightly curved.

Remarks. – The blade/platform ratio distinguished P. tai-lensis (about 1 : 2) from P. dubius (1 : 3). Besides, P. du-bius has distinctive transverse ridges, a stronger carina, and develops a rostrum.

Our specimen, with the posterior end broken, is closer to the paratypes, than to the holotype.

Stratigraphical and geographical distribution. – According to Aboussalam & Becker (2007) this species ranges from the dengleri Zone to the top of the pristina Zone (MN Zone 1 of Klapper 1985). Our specimen comes from Bed LGA221195–200, that belongs to the soluta Zone (MN Zone 2 of Klapper 1985). This taxon has only been recognized in Morocco (Anti-Atlas) and in the Spanish Central Pyrenees.

Polygnathus timorensis Klapper, Philip & Jackson, 1970

Figure 8B

*1970 Polygnathus timorensis sp. nov.; Klapper et al., p. 655, figs 2a–d, pl. 1, figs 1–3, 7–10 (with synonymy).
1983 Polygnathus timorensis Klapper et al., 1970. – Raven, pl. 3, fig. 3.
1989 Polygnathus ansatus Ziegler & Klapper, 1970. – Wang, pl. 33, fig. 10.
2001 Polygnathus timorensis Klapper et al., 1970. – Liao et al., pp. 38, 39, pl. 4, figs 4–6 (with synonymy).
2008 Polygnathus timorensis Klapper et al., 1970. – Liao & Valenzuela-Ríos, p. 9, tables 1A, B, figs 3E, F.
2010 Polygnathus timorensis Klapper et al., 1970. – Gouwy, pp. 151, 152, pl. 6, figs 2, 3, 5 (with synonymy).

Material. – Five specimens from samples LGA189s–16(1), LGA184(1), LGA207, 10 cm sup(1), LGA210(1) and LGA212, 22 cm inf(1). Figured specimen: LGA184, MGUV6179.

Description. – Pa element upper side: Narrow, lanceolate-shaped, symmetrical platform posterior of anterior trough margins. Sharp posterior end. Free blade partially complete in some specimens shows that the blade is at least half of the total length; the free blade has five (or more) elliptical and laterally compressed denticles, free at their tips. Straight carina with 10–12 sub-elliptical to rounded denticles connected anteriorly by a ridge; posteriorly they are distinct. Denticles size increases and height decreases to the posterior end. Platform ornamented by denticulated margins that reach to the geniculation points. Outer anterior margin more developed than the inner. Smooth adcarinal troughs, deeper anteriorly, which can extend to the posterior end. Inner geniculation point distinctly higher than the outer. Pa element lateral side: Both ends downwards inclined. Platform margins and carina of similar height. Straight and concave inner margin of the anterior trough; strongly downwards inclined outer margin, which is in a more advanced position near the blade. Pa element lower side: Oval-shaped basal pit of medium to small size with symmetrical flanges and located at the most anterior platform. Slightly curved and narrow basal grooves.

Remarks. – The outer anterior trough margin of P. timorensis is strongly developed and this character distinguishes it from P. ansatus (symmetrical anterior trough margins). Our figured specimen, Fig. 8B has a typical development of the ear-flap structure at the outer anterior trough margin; the position of the basal pit is at the anteriormost part of the platform and the outer geniculation is clearly lower than the inner one.

Stratigraphical distribution. – This species ranges from the base of the timorensis Subzone (the Lower varcus Zone) to the disparilis Zone (Aboussalam 2003); but Aboussalam & Becker (2007) restricted its range to the ectypus Zone. Our specimens range within the hermanni Zone.

Genus Schmidtognathus Ziegler, 1965

Schmidtognathus hermanni Ziegler, 1965

Figure 8C

1976 Schmidtognathus hermanni Ziegler, 1965. – Ziegler et al., tables 6, 9, 13–15, pl. 3, figs 34, 35.
1985 Schmidtognathus hermanni Ziegler, 1965. – Bardashev & Ziegler, pp. 69, 74, pl. 1, figs 30, 31.
1986 Schmidtognathus hermanni Ziegler, 1965. – Hou et al., p. 49, pl. 15, figs 18, 19.
1994 *Schmidtognathus hermanni* Ziegler, 1965. – Bai et al., p. 185, pl. 29, fig. 4.
2010 *Schmidtognathus hermanni* Ziegler, 1965. – Gouwy, pp. 154, 155, pl. 8, figs 8, 9 (further synonymy).

**Material.** – Eight specimens from samples LGA219225–240(7), LGA22017cm sup.(1). Figured specimen: LGA219225–240, MGUV6180.

**Description.** – Pa element upper side: Symmetrical to asymmetrical, elongate, robust platform with wide-lanceolate shape. The maximum width is at the posterior third. The blade-platform ratio is about 1:4. Short and straight free blade composed of 7–8 oval denticles, the three anterior higher. Anterior carina consists of 3–4 oval distinct denticles followed by fused denticles connected by a ridge. Posterior carina with 8–10 individual rounded denticles, which decrease in size. Platform ornamented by two or three longitudinal rows of nodes subparallel to the carina and fine nodes at the margins. Oblique margin troughs on both sides of anterior platform. Pa element lateral side: slightly arched unit with both ends inclined downwards. Pa element lower side: medium to small-sized basal pit, with an anteriorly asymmetric development of the outer flange and a posterior small fold. It is located at the posterior third. Anterior basal groove deeper and wider than posterior.

**Remarks.** – *S. hermanni* is distinguished from *S. wittekindti* by the presence of a low and short free blade bearing similar sized denticles, while the latter has a higher cusp at the middle of the blade. Also, the platform outline in *S. hermanni* varies from rhomboidal to lanceolate shape, the platform outline of *S. wittekindti* is rather triangular. The maximum width in *S. hermanni* is located about the midlength of the unit, while in *S. wittekindti* is at the anterior third.

The blade-platform ratio in *S. hermanni* is about 1:4, while in *S. pietzneri* is about 1:2.

The figured specimen, Fig. 8C, has the typical characteristics of *S. hermanni*. The presence of two or three longitudinal rows of nodes, which are subparallel to the carina; small constriction at the anterior platform, and development of shallow anterior troughs. The basal pit is covered by matrix, but other specimens from the same bed exhibit a clearly asymmetrical basal pit.

**Stratigraphical distribution.** – According to Ziegler (1965, 1971), the range of this species starts in the base of the Lower *hermanni* Zone and goes up to the Lower falsiovalis Zone; but Klapper & Johnson (1990) have restricted its upper range to the top of the Upper falsiovalis Zone.

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**Schmidtognathus wittekindti** Ziegler, 1965

*Figure 8D*

1965 *Schmidtognathus wittekindti* n. sp. Ziegler, p. 665, pl. 1, fig. 11; pl. 2, figs 1–10.
1986 *Schmidtognathus peracutus* (Bryant), 1965. – *Schmidtognathus peracutus* (Bryant), 1965. – Orr, p. 56, pl. 6, fig. 9.
1985 *Schmidtognathus wittekindti* Ziegler, 1965. – Bardashev & Ziegler, p. 69, pl. 1, fig. 33.
1986 *Schmidtognathus wittekindti* Ziegler, 1965. – Hou et al., pp. 49, 50, pl. 16, figs 1, 2, 5–12.
1992 *Schmidtognathus wittekindti* Ziegler, 1965. – Bardashev, pp. 51, 52, pl. 6, figs 21–23, 35?.
1994 *Schmidtognathus wittekindti* Ziegler, 1965. – Bai et al., p. 185, pl. 29, figs 5, 6.

**Material.** – Twelve specimens from beds LGA219225–240(10), LGA22017cm sup.(1). Figured specimen: LGA219225–240, MGUV6181.

**Description.** – Pa element upper side: Symmetrical and elongated platform, sub-triangular to arrow-shaped. Maximum width is in the anterior third of the total length. Blade-platform ratio about 1:4. Very short free blade bearing 7–11 oval and fused denticles with their sharp ends.
connected by a fine ridge. Three denticles close to the anterior margin are the highest. Anterior carina formed by fused denticles connected by a ridge that continues from the free blade. Posterior carina with 10–11 partly fused denticles connected by a smooth ridge; posteriorly the spacing is greater. Platform ornamented by fine marginal nodes and two or three longitudinal rows of nodes parallel to the carina. Nodes decrease in size posteriorly. Incipient oblique anterior trough. Pa element lateral side: slightly arched downwards unit. Pa element lower side: Tiny rhomboidal basal pit with a slightly asymmetrical anterior outer flange; it is located at the anterior fourth of the platform. Straight, wide anterior basal groove; straight and high posterior keel.

Remarks. – *S. wittekindti* is distinguished from *S. peracutus* by the anterior margins and the length of the platform. *S. peracutus* has straight anterior margins and a short platform, while *S. wittekindti* has rounded margins and a longer platform.

**Stratigraphical distribution.** – According to Ziegler (1965, 1971) and Hou *et al.* (1985), the range of this species starts at the base of the Lower *hermanni* Zone; Klapper & Johnson (1990) restricted the upper range to the base of the Lower *disparilis* Zone, but Narkiewicz & Bultynck (2010) extended the upper range to the lower part of the Upper *disparilis* Zone.

Our material ranges from the Upper *disparilis* Zone to the lower part of the *falsiovalis* Zone.

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

**Skeletognathus norrisi** (Uyeno, 1967)

Figure 8E

1967 *Polygnathus norrisi* n. sp.; Uyeno, pp. 10, 11, pl. 2, figs 4, 5.

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and a concentric irregular arrangement of nodes. The “chevron” structure is due to an advanced development stage of the plates or laminae, which are radially distributed and fused. Pa element lateral side: unit smoothly arched downwards. Anterior platform margins somewhat higher than the carina. Pa element lower side: very tiny, oval-shaped, basal pit, located near the anterior part of the platform. Slightly curved, wide anterior keel; narrow posterior keel.

Remarks. – The typical “chevron” structure is a diagnostic characteristic for this species although ornamentation is variable. Our figured specimen differs from the figured specimens in literature by the presence of a longer free blade and more nodes.

Stratigraphical distribution. – This species is restricted to a narrow interval near the Givetian/Frasnian boundary. According to Sandberg et al. (1989), it ranges from the base of the norrisi Zone to the transitans Zone (MN Zone 4 of Klapper 1985); but Klapper & Johnson (1990) restricted the upper range to the MN Zone 2 of Klapper (1985). Our specimens range from the norrisi Zone (Givetian) to the MN Zone 2 (Lower Frasnian).

Genus Tortodus Weddige, 1977

Tortodus kockelianus kockelianus (Bischoff & Ziegler, 1957) Figure 8F

1957 *Polygnathus kockelianus* n. sp. Bischoff & Ziegler, p. 91, pl. 2, figs 1–10; 11, 12 (non).
1966 *Polygnathus kockelianus* Bischoff & Ziegler, 1957. – Wittekindt, p. 634, pl. 2, fig. 7.
1970 *Polygnathus kockelianus* Bischoff & Ziegler, 1957. – Seddom, p. 59, pl. 6, figs 1, 2.
1970 *Polygnathus kockelianus* Bischoff & Ziegler, 1957. – Bultynck, p. 125, pl. 15, fig. 4.
1984 *Tortodus kockelianus kockelianus* (Bischoff & Ziegler, 1957). – Kim et al., p. 86, pl. 23, fig. 10.

Material. – Two specimens form beds LGA-J/1a (figured specimen, MGUV6182) and LGA-J/6a.

Description. – Pa element upper side: symmetrical to asymmetrical platform with sub-triangular shape and sharp posterior end; maximum width of the unit at the posterior part. Blade-platform ratio about 1 : 2. Slightly curved free blade (partly broken) with, at least, four individual, elliptic denticles. The slightly curved carina is lower than the blade and consists of an anterior weak ridge that transforms into individual denticles, which decrease in size posteriorly. The two specimens have a different ornamentation showing two distinct morphological features: a subtle “chevron” structure and a concentric irregular arrangement of nodes. The “chevron” structure is due to an advanced development stage of the plates or laminae, which are radially distributed and fused. Pa element lateral side: unit smoothly arched downwards. Anterior platform margins somewhat higher than the carina. Pa element lower side: very tiny, oval-shaped, basal pit, located near the anterior part of the platform. Slightly curved, wide anterior keel; narrow posterior keel.

Stratigraphical distribution. – This species is restricted to a narrow interval near the Givetian/Frasnian boundary. According to Sandberg et al. (1989), it ranges from the base of the norrisi Zone to the transitans Zone (MN Zone 4 of Klapper 1985); but Klapper & Johnson (1990) restricted the upper range to the MN Zone 2 of Klapper (1985). Our specimens range from the norrisi Zone (Givetian) to the MN Zone 2 (Lower Frasnian).


2010 Tortodus kockelianus kockelianus (Bischoff & Ziegler, 1957). – Gouwy, pp. 159, 160, pl. 4, figs 10a, b (with synonymy).

**Material.** Only one specimen from Bed LGA178a, MGUV6183.

**Description.** Pa element upper side: element partly complete with sub-triangular shape. Platform outline varies from symmetrical in the anterior part to asymmetrical in the most posterior part. Maximum width of the platform is in the anterior third. Incomplete anterior blade bears at least four elliptic denticles. Slightly curved carina at the anterior end and sinuous at the posterior part. It is composed of seven elliptical to rounded denticles; their height decreases posteriorly. Smooth platform surface with a strong outwards torsion in the posterior third. Pa element lateral side: the posterior end of the unit is slightly arched downwards. Pa element lower side: large-sized slightly asymmetrical basal cavity located in the widest part of platform. The posterior basal groove is wider anteriorly and narrower and bent outwards.

**Remarks.** The figured specimen is close to the holotype and paratypes, but differs somewhat, in having a shorter platform-posterior-end than the holotype.

*Tortodus k. kockelianus* is distinguished from other species by the presence of elliptic to rounded denticles decreasing in height posteriorly, and by the strong platform inflexion in the posterior part.

**Stratigraphical distribution.** *T. k. kockelianus* ranges from the base of the *kockelianus* Zone to the *ensensis* Zone – the uppermost Eifelian part. Our specimen occurs at the top of the *ensensis* Zone.

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