

Givetian and early Frasnian conodonts from the Compte section (Middle–Upper Devonian, Spanish Central Pyrenees)

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The Givetian and Frasnian conodont succession investigated in the Compte section (Spanish Pyrenees) is subdivided into nine Givetian standard conodont zones and two Frasnian zones (MN zones). This succession allows precise identification of the lower/middle Givetian, middle/upper Givetian and of the Givetian–Frasnian boundaries by means of index conodonts. The joint entry of *Mesotaxis falsiovalis* and *Skeletognathus norrisi* in the same bed shows local isochroneity of the beginning of the *falsiovalis* and *norrisi* zones in the latest Givetian. In the earliest Frasnian the sequence of *Ancyrodella pristina*, *A. soluta* and *A. rotundiloba* is observed whilst *A. binodosa* is lacking. The conodont assemblages consist of key species of the following nine genera: *Polygnathus*, *Icriodus*, *Tortodus*, *"Ozarkodina"*, *Schnidtognathus*, *Klapperina*, *Mesotaxis*, *Skeletognathus* and *Ancyrodella*. This is the first conodont report from the Pyrenees showing such a detailed succession of enormous correlation potential.

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INTRODUCTION

One of the major efforts of the international Subcommission on Devonian Stratigraphy (SDS) during the last years has been the subdivision of the Givetian Stage. Several proposals were examined and finally, last year, SDS approved an official subdivision into substages based on the beginning of two conodont zones. In this sense, the middle Givetian Substage starts at the base of the *rhenanus/varcus* Zone and the upper Givetian Substage at the base of the hermanni Zone. The official Givetian-Frasnian boundary (GSSP) is defined as the lowermost occurrence of Ancyrodella rotundiloba, which also indicates the base of the Lower asymmetricus conodont zone in section Col du Puech de la Suque, Montaigne Noire (France) (Klapper et al., 1987). However, most authors place this boundary at the first entry of the genus Ancyrodella. In this paper we will not discuss historical details of this presumably slight heterochroneity, but rather we will describe the succession of local first entries of Ancyrodella species in the Compte section and relate it to other relevant sections worldwide.

Givetian rocks are widespread in the Spanish Central Pyrenees, but detailed studies are rare so far. The better-known area is the so-called "Compte subfacies area" (Hartevelt, 1970; Boersma, 1973; Valenzuela-Ríos and Liao, 2006) that belongs to the larger "Southern facies area" of Mey (1967). Several authors have carried out conodont studies of this "subfacies", but the most relevant report was the one presented by Boersma (1973). He surveyed several selected sections and provided their condont content; unfortunately, lack of illustrations precludes testing his taxonomic work. In his paper, he included the Compte section that, according to his data, spans the Givetian to the Carboniferous (Boersma, 1973, p. 323, 348, 377). He also studied three other Givetian sections: La Guàrdia d'Ares and Villech in the Compte subfacies area, and Sahún in the Renanué subfacies area. In other Givetian sections, he did not find any Givetian conodonts (e.g. Renanué section, compare Liao et al., 2001; Liao and Valenzuela-Ríos, 2005). Before Boersma's study, Ziegler (1959, p. 298-299) collected some conodont samples in the Compte section, which he called "Section in the Pallaresa valley south of Sort". He mentioned the presence of the Lower, Middle and Upper Devonian and Carboniferous, but regarding the Middle Devonian, only conodonts of questionable Eifelian age were reported from Ziegler's sample 1 (1959, p. 299). Most of his samples contained Upper Devonian conodonts.

In recent years we have conducted a comprehensive conodont research of the Givetian and early Frasnian part of the Compte section, but results have been presented only during professional meetings (Liao *et al.*, 2002; Liao and Valenzuela-Ríos, 2006). The main purpose of this paper is to present a detailed conodont succession for most of the Givetian and lower Frasnian at Compte section that serves as a basis for bio- and chronostratigraphical interpretations.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Compte section is located near the former national road N-260 between the localities of La Pobla de Segur and Sort, on the right bank of the Noguera Pallaresa River, roughly 1.4 km



Fig. 1. General (A) and detailed (B) geographical setting of the Compte section (CP)

Numbers -6 and 65 in Figure 1B refer to position of lowest (-6) and highest (65) section beds; pattern in the sketch map of Iberian Peninsula represents Palaeozoic outcrops

north of Gerri de la Sal (Fig. 1). Due to partly covered intervals, initial sampling was focused on outcrops along the road and on the hill, which were afterwards correlated, and a section was compiled (Liao et al., 2002). Biostratigraphical uncertainties, however, forced us to uncover some intervals, and the results presented herein come from the section along the road. It corresponds to a part of the A-member of the Compte Fm. at section Compte (03) of Boersma (1973, p. 307) that approximately correlates with the Comabella Fm. of Sanz-López (in: Montesinos and Sanz-López, 1999, p. 106). The studied part of the section comprises about 30 metres of variegated (pink, red, blue and green) nodular limestones and bedded limestones, with beds up to 90 cm thick. Decimetric layers of marly limestone appear in the upper part (Fig. 2). Texturally these are mostly wackestones and packstones with abundant dacryoconarids; other common fossils are crinoid ossicles, ostracods and trilobites.

The position of samples in the section is shown in Figure 2, together with ranges of conodont taxa and stratigraphy. Table 1 provides quantitative details including number of conodonts, sample weight and location in centimetres above the section base.

SYSTEMATIC PALAEONTOLOGY

Specimens are deposited at the Museum of Geology of University of València (MGUV) as indicated in the plate explanations. Only biostratigraphically relevant conodonts are briefly discussed and (or) ilustrated (Figs. 3–6).

Genus Ancyrodella Ulrich and Bassler 1926 Ancyrodella pristina Khalymbadzha and Chernysheva, 1970 (Fig. 6I, J)

- *1970 Ancyrodella pristina sp. nov. Khalymbadzha and Chernysheva, p. 89, 90, pl. 1, figs. 3–8;
- 1989 Ancyrodella pristina Khalymbadzha and Chernysheva; Sandberg et al., p. 210, pl. 1, figs. 3, 4, 9, 10, 13, 14; text-fig. 2, figs. 2–4 (includes synonymy);
- 1992 Ancyrodella rotundiloba early form (Bryant); Norris et al., p. 73, pl. 15, figs. 7, 8;
- 1992 Ancyrodella pristina Khalymbadzha and Chernysheva; Bardashev, pl. 11, fig. 31;
- 1993 Ancyrodella pristina Khalymbadzha and Chernysheva; Ji and Ziegler, p. 53, pl. 1, figs. 7–9; text-fig. 7, fig. 6;
- 1993 Ancyrodella pristina Khalymbadzha and Chernysheva; Racki and Bultynck, pl. 6, fig. 2; pl. 7, figs. 5, 6;
- 1993 Ancyrodella soluta Sandberg et al.; Racki and Bultynck, pl. 7, figs. 1, 2, 8, 9;
- 1994 *Ancyrodella pristina* Khalymbadzha and Chernysheva; Bai *et al.*, p. 162, pl.1, figs. 2, 3 (non 4 = *Ancyrodella soluta*);
- 1994 *Ancyrodella rotundiloba* (Bryant); Weary and Harris, pl. 2, figs. 3–6; text-figs. 5–8;
- 1994 Ancyrodella rotundiloba early form (Bryant); Kirchgasser, pl. 1, figs. A–F, H, I;



Fig. 2. Lithology and stratigraphy of the Compte section showing locations of conodont samples (arrows) and ranges of conodont taxa for the interval between the Lower *varcus* Zone to the MN 2 Zone

- 1995 Ancyrodella pristina Khalymbadzha and Chernysheva; Iudina, text-fig. 2, figs. 3, 7;
- 1995 Ancyrodella pristina Khalymbadzha and Chernysheva; Hünecke, pl. 2, fig. 5;
- 1995 Ancyrodella rotundiloba (Bryant); Sanz-López, p. 454, 455, pl. 33, figs. 1–4;
- 1998 Ancyrodella pristina Khalymbadzha and Chernysheva; Spalleta and Perri, p. 192, pl. 2.1.1, fig. 6;
- 1999 Ancyrodella pristina Khalymbadzha and Chernysheva; Lazreq, p. 60, pl. 3, figs. 8, 9, 13.
- R e m a r k s. In accordance with Sandberg *et al.* (1989)
- A. pristina can be distinguished from A. binodosa by having a

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Distribution and number of conodont species at the lower part of the Compte section, Central Pyrenees

Question mark (e.g. ?1) indicates a questionable identification and Bo(XX) corresponds to Boersma (1973) sampling numbers; between beds 27b and 39 there is a short covered interval; because of that, section measurements have been splitted in two parts, from Bed -6 up to 29b and from Bed 39 upwards

Table 1A

Table 1B

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	Conodont biozonation	Bed/Sample	Centimeters in section	Samples weight [Kg]	I. b. brevis	I. symmetricus	Sch. hermanni	Sch. pietzneri	Sch. wittekindti	Sch. peracutus	P. limitaris	Oz. sannemanni	P. dubius	P. pennatus	P. c. cristatus	P. c. ectypus	P. dengleri	Kl. ovalis	Kl. disparilis	Kl. disparalvea	Kl. unilabius	M. falsiovalis	M asymmetricus	Sk. norrisi (Pa)	Sk. norrisi (Pb)	P. ordinatus	P. angustidiscus	P. webbi	A. pristina M2	A. pristina M3	A. soluta M1	A. soluta M2	A. soluta M3	A. isabelae	A. rotundiloba	A. triangulata	A. alata	Number of conodont

For explanations see Table 1A

Table 1C

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longer, more ovate rather than rounded platform, and larger marginal nodes; it has also a smaller basal cavity. Following Sandberg *et al.* (1989) the presence of additional nodes inserted between marginal nodes and a carina, and a smaller basal cavity distinguish *A. soluta* from *A. pristina*. Additionally, the former has a heart-shaped platform. Basing on a shape of lateral lobe margins, the morphotypes 2 and 3 of *A. pristina* of Sandberg *et al.* (1989) are recognized in our material. Morphotype 2 is characterized by a development of straight lateral lobe margins (Fig. 6J). Morphotype 3 has one straight lateral lobe margin and another one rounded (Fig. 6I).

S tr a t i g r a p h i c a l d i s tr i b u t i o n. — A. pristina ranges from the Early falsiovalis Zone into the Middle falsiovalis Zone (Ji and Ziegler, 1993); but Sandberg et al. (1989) restricted its range to the upper half of the lower part of the falsiovalis Zone. Here, we have considered that the first occurrence of A. pristina marks the beginning of the Upper Devonian. In terms of the Montagne Noire conodont zonation (Klapper, 1988), it ranges from MN1 to MN2 zones.

Ancyrodella rotundiloba (Bryant, 1921) (Fig. 6Q, R)

- *1921 Polygnathus rotundilobus sp. nov. Bryant, p. 26, 27, pl. 12, figs. 1–6;
- 1989 *Ancyrodella rotundiloba* (Bryant); Sandberg *et al.* p. 212, 213, pl. 2, figs. 5, 6, 9, 10; pl. 3, figs. 1–9; text-fig. 2, figs. 8–10 (includes synonymy).

R e m a r k s. — According to Sandberg et al. (1989) A. rotundiloba developed from A. soluta by transforming a basal cavity into a small pit and by increasing number of nodes on an upper platform surface. A. rotundiloba is distinguished from A. alata by height of the anterior blade, development of the strongly alate platform, and by a presence and orientation of secondary keels; inner keel is lateral-anteriorly directed, but the outer one is laterally or latero-posteriorly directed. The specimen illustrated herein (Fig. 6Q, R) exhibits some characteristics that might resemble A. recta, such as the straight, almost parallel to the carina, inner lobe margin which is also narrower than the outer one. This gives the platform a characteristic asymmetrical outline as in A. recta. However, the lack of an anteriorly-directed inner keel leads us to consider that this specimen can be a form intermediate between A. rotundiloba and A. recta whereas the other specimens from the same sample clearly belong to A. rotundiloba. A. rotundiloba, as considered herein, falls within the concept of A. rotundiloba late form of Klapper (1985).

S tratigraphical distribution. — From the beginning of the Middle *falsiovalis* Zone into the *punctata* Zone (Ji and Ziegler, 1993). As considered herein, *A. rotundiloba* ranges from the base of MN2 to the lower half of MN3. *1989 Ancyrodella soluta n. sp. Sandberg *et al*; p. 211, pl. 1, figs. 5, 6, 11, 12; pl. 2, figs. 1–4; text-fig. 2, figs. 5–7 (includes synonymy);

1992 Ancyrodella rotundiloba early form (Bryant); Norris et al., p. 73, pl. 15, figs. 15, 16.

R e m a r k s. — According to Sandberg *et al.* (1989) *A. soluta* is considered as the intermediate form between *A. pristina* and *A. rotundiloba*. A denser upper platform ornamentation and smaller basal cavity distinguish *A. soluta* from *A. pristina*. More pronounced ornamentation and reduction of basal cavity, which forms a small rhomb-shaped pit leads to *A. rotundiloba*, and these criteria are used by Sandberg *et al.* (1989) to separate both taxa.

In our collection, the three morphotypes of Sandberg *et al.* (1989) can be recognized:

 morphotype 1 has rounded lateral margin lobes and ornamentation consisting of irregular few nodes (Fig. 6M, N);

— morphotype 2 has both straight lateral margin lobes, and nodes of secondary carinas are aligned perpendicular to anterior and posterior ones (Fig. 6O, P);

— morphotype 3 is an intermediate form, with one straight margin and the other rounded and its platform bears more nodes than the other two morphotypes (Fig. 6K, L).

Stratigraphical distribution. — A. soluta ranges from the Early falsiovalis Zone into the transitans Zone (Sandberg et al., 1989), which corresponds to MN1–MN4.

Genus Icriodus Branson and Mehl, 1938 Icriodus difficilis Ziegler and Klapper, 1976 (Fig. 4C, D)

*1976 *Icriodus difficilis* n. sp; Ziegler and Klapper, pp. 117, 118, pl. 1, figs. 1–7, 17;

2001 *Icriodus difficilis* Ziegler and Klapper; Liao *et al.*, p. 17, 18, pl. 1, figs. 1–7 (includes synonymy).

R e m a r k s. — Diagnostic features include the presence of a conspicuous anteriorly projected spur and an associated moderately developed sinus, together with a posterior part bearing two or three aligned denticles conceded by a longitudinal ridge, the last one being the highest. Anterior transversal rows are widely spaced. Anterior carina varies from straight to slightly curved. Lateral denticles are rounded and connected to a smaller middle row denticles by weak transverse ridges; cusp varies from straight to reclined.

S tr a ti g r a p hi c a l distribution. — This species ranges from the Givetian to lower Frasnian. According to Bultynck (1987), the entry of this taxon, defines the *I. difficilis* Zone, which correlates with the upper part of the *P. rhenanus/var-cus* Zone. The upper range is in the *transitans* Zone.

Ancyrodella soluta Sandberg, Ziegler and Bultynck, 1989 (Fig. 6K–P) Icriodus obliquimarginatus Bischoff and Ziegler, 1957 (Fig. 3G, J)

- *1957 *Icriodus obliquimarginatus* n. sp; Bischoff and Ziegler, p. 62, 63, pl. 6, fig. 14;
- 1987 *Icriodus obliquimarginatus* Bischoff and Ziegler; Bultynck, p. 160, pl. 4, figs. 7–10, 12–16;
- 1989 *Icriodus obliquimarginatus* Bischoff and Ziegler; Bultynck, p. 102, 103, pl. 2, figs. 22, 23.

R e m a r k s. — Denticles (6-8) of a lateral row are located in lower position than those of the middle row, and in some specimens they are connected by weak transverse ridges; the posterior denticles (3-4) are connected by a longitudinal ridge; a cusp is reclined.

S tr a ti g r a p hi c a l distribution. — This taxon ranges from the *ensensis* Zone (Weddige, 1977) to the Middle *varcus* Zone (Ziegler *et al.*, 1976; Lazreq, 1999); but it has also been reported from the Upper *varcus* Zone (Broken River — Mawson and Talent, 1989) and even in the upper Givetian (Portilla Formation, Cantabrian Mountains — García-Alcalde *et al.*, 1979).

Genus *Klapperina* Lane, Müller and Ziegler, 1979 *Klapperina disparilis* (Ziegler and Klapper, 1976) (Fig. 5K, L, Q, R)

1976 Palmatolepis disparilis n. sp. Ziegler et al., p. 119, pl. 1, figs. 18–22, 24–31;

1982 *Palmatolepis disparilis* Ziegler *et al.*; Ziegler and Klapper, p. 467, 468, pl. 3, figs. 5, 7–15 (includes synonymy).

R e m a r k s. — This species shares with *Kl. disparalvea* a distinctive L-shaped cavity but *Kl. disparalvea* has a distinct outer lobe and coarser nodes on an upper side. *Kl. disparilis* differs from *Palmatolepis transitans* in having a straight carina that generally does not extend to a posterior end; the former also has a distinctive coarser node in a posterior part of a carina. A pit on the lower side varies from small to large.

The specimen MGUV5998 (Fig. 5K, L) represents a transitional form between *P. cristatus* and *Kl. disparilis* (see also Ziegler and Klapper 1982, pl. 3, figs. 5, 12). The characteristic L-shaped basal cavity leads us to include it in *Kl. disparilis*.

Stratigraphical distribution. — The earliest occurrence of this species defines the base of the *disparilis* Zone and it ranges into the *norrisi* Zone according to Ziegler and Wang (1985), whereas Wang (1994) extended its uppermost range to the Middle *transitans* Zone. Our specimens are restricted to the *disparilis* Zone.

Genus Mesotaxis Klapper and Philip, 1972 Mesotaxis falsiovalis Sandberg, Ziegler and Bultynck, 1989 (Fig. 6A, B)

- 1986 *Polygnathus asymmetricus* Bischoff and Ziegler; Bultynck, pl. 2, figs. 1, 2;
- 1989 *Mesotaxis falsiovalis* n. sp. Sandberg *et al.*, p. 213 (includes synonymy);

- 1992 *Mesotaxis falsiovalis* Sandberg *et al.*; Bardashev, pl. 10, figs. 14, 20;
- 1992 *Mesotaxis falsiovalis* Sandberg *et al.*; Carls and Gong, p. 206, pl. 3, figs. 6, 7;

1993 *Mesotaxis falsiovalis* Sandberg *et al.*; Ji and Ziegler, p. 58, pl. 32, figs. 7–13; text-fig. 7, fig.1 (includes synonymy);

1993 *Mesotaxis falsiovalis* Sandberg *et al.*; Racki and Bultynck, pl. 6, fig. 5;

1999 *Mesotaxis falsiovalis* Sandberg *et al.*; Lazreq, p. 67, pl. 3, fig. 3;

2004 *Mesotaxis falsiovalis* Sandberg *et al.*; Izokh *et al.*, pl. 1, fig. 1.

R e m a r k s. — This species is close in shape and ornamentation to *Kl. ovalis*, but as stated by Sandberg *et al.* (1989), the presence of an asymmetrical, and more centrally located basal cavity distinguishes both taxa. In lower view, the pit of *M. falsiovalis* is also smaller.

S t r a t i g r a p h i c a l d i s t r i b u t i o n. — This taxon ranges from the beginning of the Early *falsiovalis* Zone to the Late *hassi* Zone according to Ji and Ziegler (1993), but Sandberg *et al.* (1989) extended its range up to the oldest part of the *Ancyrognathus triangularis* Zone. Our material comes from the *norrisi* Zone.

Genus Polygnathus Hinde, 1879 Polygnathus ansatus Ziegler and Klapper, 1976 (Fig. 3K, L)

*1976 *Polygnathus ansatus* n. sp. Ziegler and Klapper (in Ziegler *et al.*), p. 119, 120, figs. 11–26;

- 1985 *Polygnathus ansatus* Ziegler and Klapper; Ziegler and Wang, pl. 1, fig. 28;
- 1998 Polygnathus ansatus Ziegler and Klapper; Uyeno, p.161, pl. 12, fig. 28; pl. 15, figs. 7, 8.

R e m a r k s. — A combination of the three following characters is distinctive of *P. ansatus*:

---- anterior through margins are bowing outwards (the outer stronger),

- geniculation points are situated in almost opposite positions,

— anterior trough margins meet the blade at the same position. *P. hemiansatus* has a crenulation on inner side of an anterior trough margin and none of the three features mentioned above (compare Fig. 4B).

Stratigraphical distribution. — This species ranges from the base of the *ansatus* Zone to the lower part of the *disparilis* Zone (Bardashev, 1992). Our specimens are restricted to the Upper *varcus* Zone.

Polygnathus cristatus cristatus, Hinde 1879 (Fig. 5M, N)

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

R e m a r k s. — *P. c. cristatus* differs from *Kl. ovalis* in the presence of a weak ornamentation, absence of anterior trough margins and a smaller basal cavity that does not exhibit the characteristic "L" shape. There is an ongoing discussion regarding identification of the two subspecies, *P. c. cristatus* and *P. c. ectypus*. The former has commonly discrete nodes arranged in longitudinal rows parallel to a carina and a relatively large basal cavity that varies from symmetrical to slightly asymmetrical. Some nodes can be fused forming transverse ridges.

S r a t i g r a p h i c a l d i s t r i b u t i o n. — Klapper and Ziegler (1977) consider that this subspecies ranges from the Upper *hermanni* to the *punctata* zones, however, Klapper and Johnson (1990) indicated its disappearance in the Upper *disparilis* Zone. Our specimens range from the *disparilis* to *falsiovalis* (MN 1 to MN 2) zones.

Polygnathus cristatus ectypus Huddle 1934

*1934 Polygnathus ectypus, Huddle, p. 103, pl. 8, fig. 38;

- 1957 *Polygnathus cristata* Hinde; Bischoff and Ziegler, p. 86, 87, pl.15, figs. 1, 2–13, 16; pl. 17, figs. 12, 13;
- 1971 Polygnathus cristatus Hinde; Orr, p. 48, pl. 6, figs. 1, 2;
- 1992 Polygnathus cristatus Hinde; Bardashev, pl. 8, figs. 22–24;
- 1994 *Polygnathus cristatus* Hinde; Bai *et al.*, p. 176, 177, pl. 24, fig. 3;

1999 *Polygnathus cristatus* Hinde; Lazreq, p. 86, pl. 2, fig. 1; 2003 *Polygnathus cristatus ectypus* Huddle, Aboussalam, p. 177 pl 19 figs 7 9 (includes synonymy)

177, pl.19, figs. 7-9 (includes synonymy).

R e m a r k s. — P. c. ectypus differs from P. c. cristatus by having a more chaotic arrangement of nodes on a platform (lack of arrangement of nodes parallel to the carina), and in having a very small basal cavity on top of a sharp and thin keel. In same specimens nodes show a pinnate distribution.

The non-figured specimen from the Bed 46g (Table 1B) is fragmentary but a characteristic small and symmetrical basal cavity, and the lack of visible alingment of nodes in rows parallel to the carina, suggest its tentative determination as *P. c. ectypus*.

Stratigraphical distribution. — The subspecies ranges from the base of the Upper *hermanni* to the upper part of *transitans* zones (Sandberg *et al.*, 1994); our specimens represent the interval between the Upper *hermanni* and the *disparilis* zones.

Polygnathus latifossatus Wirth, 1967 (Fig. 40–T)

*1967 *Polygnathus latifossata* n. sp. Wirth, p. 227, pl. 22, figs. 17–19; text-figs. 14g–k.

R e m a r k s. — This species is characterized by a development of an incipient narrow platform, which can be accompanied by lateral denticle rows or by 1–3 individual denticles located on both sides of a posterior carina; some specimens have a relatively open basal cavity, which is located in a posterior third of the unit. *P. latifossatus* differs from *Schmidtognathus pieztneri* in having a narrower platform and a slightly nodose ornamentation.

S tratigraphical distribution. — This species defines the base of the Upper *varcus* Zone and ranges to the *norrisi* Zone (Kleinebrinker, 1992). Bardashev (1992) restricted its upper range to the *disparilis* Zone. Our specimens are from the base of the Upper *varcus* to the Upper *hermanni* zones.

Polygnathus rhenanus Klapper, Philip and Jackson, 1970 (Fig. 3M–P)

*1970 Polygnathus rhenanus sp. nov.; Klapper et al., p. 654, pl. 2, figs. 13–15, 19, 22.

R e m a r k s. — *P. rhenanus* is distinguished from *P. timorensis* by a longer free blade, a narrower and shorter platform, and a more anterior position of a basal cavity. Asymmetrical platform, a markedly arched blade and a more posterior position of the outer geniculation point distinguish *P. rhenanus* from *P. varcus*.

Stratigraphical distribution. — According to Bultynck (1987) this species is recorded in the Ardennes from the upper part of the Lower *varcus* Zone (*rhenanus/varcus* Subzone) to the upper part of the *ansatus* Zone which agrees with our data.

Polygnathus timorensis Klapper, Philip and Jackson, 1970 (Fig. 3E, F)

*1970 *Polygnathus timorensis* sp. nov.; Klapper, Philip and Jackson, p. 655, text-fig. 2a–d, pl. 1, figs. 1–3, 7–10 (includes synonymy).

R e m a r k s. — The outer anterior trough margin of *P*. *timorensis* is strongly developed and this feature distinguishes it from *P. ansatus* which displays symmetrical anterior trough margins (see also description of *P. ansatus*).

Stratigraphical distribution. — This species is recorded from the base of the Lower *varcus* (the *timorensis* Subzone) to the *disparilis* Zone (Aboussalam, 2003). Our specimens range to the upper part of the *ansatus* Zone (Middle *varcus* Zone).

Genus Schmidtognathus Ziegler, 1965 Schmidtognathus hermanni Ziegler, 1965 (Fig. 5B, C)

*1965 Schmidtognathus hermanni n. sp. Ziegler, p. 664, pl. 3, figs. 5–26.



Fig. 3. Conodonts from the Compte section

A — Polygnathus linguiformis weddigei Leuteritz and Ziegler, 1979; upper view of MGUV5970, Bed CP/-1, timorensis? Subzone; B — Polygnathus linguiformis klapperi Clausen, Leuteritz and Ziegler 1979; upper view of MGUV5971; Bed CP/8base, rhenanus/varcus Subzone; C, D — Polygnathus linguiformis linguiformis Hinde 1879; upper (C) and lower (D) views of MGUV5972; Bed CP/7, rhenanus/varcus Subzone; E, F — Polygnathus timorensis Klapper, Philip and Jackson 1970; upper (E) and lower (F) views of MGUV5973; Bed CP/6, rhenanus/varcus Subzone; G–J — Icriodus obliquimarginatus Bischoff and Ziegler 1957 upper (G) and lateral (H) views of MGUV5974; Bed CP/-2, timorensis? Subzone; upper (I) and lateral (J) views of MGUV5975; Bed CP/20, ansatus (Middle varcus) Zone; K, L — Polygnathus ansatus Ziegler and Klapper, 1976; upper (K) and lower (L) views of MGUV5977; Bed CP/5; rhenanus/varcus Subzone; Q, R — Polygnathus eiflius Bischoff and Ziegler 1957; upper (Q) and lower (P) views of MGUV5978; Bed CP/14; rhenanus/varcus Subzone; Q, R — Polygnathus eiflius Bischoff and Ziegler 1957; upper (Q) and lower (R) views of MGUV5979; Bed CP/1; rhenanus/varcus Subzone; S, T — Icriodus regularicrescens Bultynck 1970; upper (S) and lateral (T) views of MGUV5980; Bed CP/6; rhenanus/varcus Subzone; L — Polygnathus eiflius Bischoff and Ziegler 1957; upper (Q) and lower (R) views of MGUV5979; Bed CP/7; rhenanus/varcus Subzone; S, T — Icriodus regularicrescens Bultynck 1970; upper (S) and lateral (T) views of MGUV5980; Bed CP/6; rhenanus/varcus Subzone; L — Polygnathus eiflius Bischoff is per (S) and lateral (T) views of MGUV5980; Bed CP/6; rhenanus/varcus Subzone; C, R — Polygnathus 1976; upper view of MGUV5981; Bed CP/7(70-90); rhenanus/varcus Subzone; all scale bars = 200 mm, except U (=500 mm)



Fig. 4. Conodonts from the Compte section

A, B — Polygnathus hemiansatus Bultynck 1987; lower (A) and upper (B) views of MGUV5982, Bed CP/18b, ansatus (Middle varcus) Zone; C, D — Icriodus difficilis Ziegler and Klapper, 1976; lower (C) and upper (D) views of MGUV5983; Bed CP/18b, ansatus Zone; E, F — Polygnathus linguiformis mucronatus Wittekindt 1966, E — upper view of MGUV5984; Bed CP/41a, ansatus Zone, F — upper view of MGUV5985; Bed CP/41b, ansatus Zone; G, H — Tortodus weddigei Aboussalam 2003 = Tortodus sp. A, "γ" morphotype Sparling 1999; upper (G) and lower (H) views of MGUV5986; Bed CP/41b, ansatus Zone; I-K — Tortodus trispinatus Aboussalam 2003 = Tort. sp. B, "α" morphotype Sparling 1999; upper (I), lateral (J) and lower (K) views of MGUV5987; Bed CP/45b, uppermost part of the ansatus Zone; L-N — Tortodus aff. bultyncki; upper (L), lateral (M) and lower (N) views of MGUV5988; Bed CP/46a; Lower hermanni Zone; O-T — Polygnathus latifossatus Wirth 1967; upper (O), lateral (P) and lower (Q) views of MGUV5989; bed CP/45c; latifossatus (Upper varcus) Zone; upper (R), lateral (S) and lower (T) views, MGUV5990; Bed CP/45c; latifossatus Zone; U, V — Schmidtognathus aff. pietzneri Ziegler 1965; upper (V) and lower (U) views of MGUV5991; Bed CP/45c; latifossatus Zone; all scale bars = 200 mm, except E (=500 mm)



Fig. 5. Conodonts from the Compte section

A — Polygnathus dubius Hinde 1879; upper view of MGUV5992, Bed CP/45c, latifossatus Zone; **B**, **C** — Schmidtognathus hermanni Ziegler 1965; lower (B) and upper (C) views of MGUV5993; Bed CP/46a, Lower hermanni Zone; **D** — Polygnathus limitaris Ziegler, Klapper and Johnson 1976; upper (D) view of MGUV5994; Bed CP/46a, Lower hermanni Zone; **E**, **F** — Schmidtognathus aff. pietzneri Ziegler 1965; upper (E) and lower (F) views of MGUV5995; Bed CP/46b, Lower hermanni Zone; **G**, **H** — Schmidtognathus pietzneri Ziegler 1965; upper (G) and lower (H) views of MGUV5996; Bed CP/46b, Lower hermanni Zone; **I**, **J** — Ozarkodina sannemanni sannemanni Bischoff and Ziegler 1957; lateral (I) and lower (J) views of MGUV5997; Bed CP/46b, Lower hermanni Zone; **K**, **L** — Polygnathus cristatus \rightarrow Klapperina disparilis; lower (K) and upper (L) views of MGUV5998; Bed CP/46(190-200), Upper hermanni Zone; This specimen represents a transitional form; note regular distribution of coarse nodes in upper view and L-shaped basal cavity in central position in lower view; **M**, **N** — Polygnathus cristatus cristatus Hinde 1879; upper (M) and lower (N) views of MGUV5090; Bed CP/49; disparilis Zone; **O**, **P** — Klapperina cf. Kl. disparilis Ziegler and Klapper 1976; lower (Q) and upper (P) views of MGUV6000; Bed CP/47; disparilis Zone; **Q**, **R** — Klapperina disparilis Ziegler and Klapper 1976; lower (Q) and upper (R) views of MGUV6001; Bed CP/51; disparilis Zone; **S** — Klapperina ovalis (Ziegler and Klapper) 1964; upper-lateral view of MGUV6002; Bed CP/59⁴⁴; MN 1 Zone;



Fig. 6. Conodonts from the Compte section

A, **B** — *Mesotaxis falsiovalis* Sandberg, Ziegler and Bultynck 1989; A — lower view of MGUV6003; Bed CP/59; *norrisi* Zone; B — Upper view of MGUV6004; Bed CP/58b; *norrisi* Zone; **C**–**F** — *Skeletognathus norrisi* (Uyeno 1967); upper (C) and lower (D) views of the "Pa" element, MGUV6005; Bed CP/58b; *norrisi* Zone; upper (E) and lateral (F) views of the "Pb" element, MGUV6006; Bed CP/58b; *norrisi* Zone; **G**, **H** — *Polygnathus pennatus* Hinde 1879; lower (G) and upper (H) views of MGUV6007; Bed CP/58b; *norrisi* Zone; **I**, **J** — *Ancyrodella pristina* Khalymbadzha and Chernysheva 1970; I — upper view of morphotype 3 (Sandberg *et al.*, 1989), MGUV6008; Bed CP/59⁰⁴; MN 1 Zone; **J** — upper view of morphotype 2 (Sandberg *et al.*, 1989), MGUV6009; Bed CP/59⁰⁴; MN 1 Zone; **L** — *Ancyrodella soluta* Sandberg, Ziegler and Bultynck 1989; upper (K) and lower (L) views of morphotype 3, MGUV6010; Bed CP/60b; MN 1 Zone; upper (M) and lower (N) views of morphotype 1, MGUV6011; Bed CP/60c; MN 1 Zone; upper (O) and lower (P) views of morphotype 2, MGUV6012; Bed CP/61⁰⁴; MN 1 Zone; **Q**, **R** — *Ancyrodella rotundiloba–Ancyrodella recta*; upper (Q) and lower (R) views of MGUV6013; Bed CP/64; MN 2 Zone; all scale bars = 200 mm, except K (=500 mm)

R e m a r k s. — Sch. hermanni differs from Sch. wittekindti in the presence of a short and low blade composed of denticles which are similar in size. Sch. wittekindti has denticles of different size with a conspicuous cusp in the middle part of a blade. Outline of a platform of Sch. hermanni is rather rhombic, and not triangular as in Sch. wittekindti, and therefore the maximum width is located in the middle length of the platform of Sch. hermanni but in the anterior part in Sch. wittekindti. The platform of Sch. wittekindti is also narrower bearing a rather regular ornamentation.

The different proportion of blade to platform distinguishes *Sch. hermanni* from *Sch. pietzneri*; in the former species, the platform composes two-thirds of the entire length whilst in the latter it occupies half of the length. Basal cavity of *Sch. hermanni* is asymmetric.

S tr a ti g r a p h i c a l d i s tr i b u ti o n. — Ziegler (1965, 1971) considered the range of *Sch. hermanni* from the *hermanni* to the Early *falsiovalis* Zones. Klapper and Johnson (1990) restricted its higher range to the upper part of the Upper *disparilis* Subzone.

Schmidtognathus pietzneri Ziegler, 1965 (Fig. 5G, H)

*1965 Schmidtognathus pietzneri n. sp. Ziegler, p. 666, 667, pl. 2, fig. 11–25.

R e m a r k s. — *Sch. pietzneri* is closely related to *Sch. peracutus* by a nodose ornamentation and a flat platform but the latter has a wider platform and ornamentation composed of chaotic nodes.

Stratigraphical distribution. — This species ranges from the Lower *hermanni* to the Early *falsiovalis* Zones.

Genus Skeletognathus Sandberg, Ziegler and Bultynck, 1989 Skeletognathus norrisi (Uyeno, 1967) (Fig. 6C–F)

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

1989 *Skeletognathus norrisi* (Uyeno); Sandberg *et al.* p. 214, pl. 5, figs. 1–12 (includes synonymy);

1994 Skeletognathus norrisi (Uyeno); Kirchgasser, pl. 3, figs. C, K, M–O;

2001 Skeletognathus norrisi (Uyeno); Liao et al. p. 41, 42, pl. 4, figs. 22–24 (includes synonymy).

R e m a r k s. — This species has a platform consisting of severals thin needle shaped plates or denticles organized in a "chevron" pattern. Based on the margin outline, two different morphological types can be recognized in our specimens: parallel and triangular. The ornamentation is variable because the thin plates can be fused thus forming transversal ridges. The lower side bears a very small pit. Some specimens have a wrinkled ornamentation consisting of few ridges perpendicular to the elevated keels that do not reach the margins of the element. S tr a ti g r a p hi c a l distribution. — This species is restricted to a narrow interval around the Givetian–Frasnian boundary. Its first appearance is in the *norrisi* Zone and it ranges into the *transitans* Zone (Sandberg *et al.*, 1989). However, Klapper and Johnson (1990) restrict its upper range to the MN 2 Zone (still within the *falsiovalis* Zone). Our material comes from the *norrisi* Zone (Givetian) and the MN1 Zone (Frasnian).

BIOSTRATIGRAPHY

LOWER GIVETIAN

The lower quarter of the section (beds –6 to 4b) is unsatisfactorily characterized by means of diagnostic conodonts, and most probably belongs to the lower Givetian, but a latest Eifelian age cannot be excluded. The joint occurrence of *I. lindensis* and *I. brevis* in Bed 4b immediately below the lowermost record of *P. rhenanus* (Bed 5), correlates Bed 4b with upper parts of the *timorensis* Subzone in accordance with the entry of *I. brevis* within the latter subzone. Below the Bed 4b, the conodont record does not allow tracing the *hemiansatus–timorensis* boundary.

In spite of the proposed appearance of *I. obliquimarginatus* in the uppermost Eifelian of Western Europe and Morocco (Bultynck, 2003, fig. 1), this taxon has been traditionally considered as a Givetian one. Such age is also demonstrated for North America (Bultynck, 2003, fig. 2) and for the Ardennes (Gouwy and Bultynck, 2003; Gouwy, 2004). Stratigraphic ranges were established in these latter publications by setting up the Middle Devonian Composite Standard based on graphic correlation. Thus, we consider that the lowest occurrence of *I. obliquimarginatus* in the Bed –2 indicates still the Givetian *hemiansatus* Zone.

MIDDLE GIVETIAN

The base of the rhenanus/varcus Subzone and, consequently, of the middle Givetian is defined as the lowest occurrence of P. rhenanus, which first occurs in Bed 5 in the Compte section. P. varcus is recorded more than 3.5 m higher (Bed 10). Last observed records of I. regularicrescens within the lower part of the rhenanus/varcus Subzone (beds 5 and 6) are in agreement with most ranges observed elsewhere (Bultynck, 2003, figs. 1, 2). The joint occurrence of P. rhenanus and I. regularicrescens in Compte contrasts with the reported range of the latter in the Ardennes (Gouwy and Bultynck, 2003; Gouwy, 2004), where its highest range is positioned within the Lower Givetian timorensis Subzone (below Ardenne regional composite CSU 2000, whilst the middle Givetian starts at CSU 2129). P. eiflius mostly does not reach the upper part of the timorensis Subzone and even in the Ardennes it is restricted to the lower part of the Eifelian eiflius Zone (Gouwy and Bultynck, 2003, fig. 10b; Gouwy, 2004, fig. 4-2.12b). However, the table compiled by Aboussalam (2003, text-fig. 4a) shows an extended range, at least to the lower part of the ansatus Zone (Middle varcus Zone) and a range questionably extended to the top of the latifossatus Zone (late Upper varcus

Zone). This latter record refers to the sample 146 of the section SD 15 in Queensland (Mawson and Talent, 1989) and it is considered by Aboussalam (2003, p. 313) as a possible reworked conodont. In any case, it seems that the range of *P. eiflius* can reach higher than the *timorensis* Subzone, at least in Morocco and in North Queensland, and now in the Pyrenees as well (Fig. 3Q, R). The highest occurrence of the taxon in the Compte section is in Bed 18b together with *P. ansatus*, in the Middle *varcus* Zone (see below). Long-ranging polygnathids such as *P. timorensis*, *P. linguiformis linguiformis*, *P. ling. klapperi* and *P. ling. weddigei* are common in many samples of the interval (Fig. 2 and Table 1).

The entry of P. ansatus in the Bed 9 (Fig. 3K, L) defines the base of the ansatus Zone and of the Middle varcus Zone. The Bed 18b contains the highest record of P. eiflius together with the local delayed entries of P. hemiansatus and I. difficilis, which in other places enter already in the preceding zone (Fig. 2). I. obliquimarginatus ranges to the top of the Middle varcus Zone except for the Ardennes where it does not reach the Middle varcus Zone (Gouwy and Bultynck, 2003; Gouwy, 2004). However, in Compte the last observed record is in the lower half of the Middle varcus Zone (Bed 20). Other icriodids that are almost restricted to the lower half of the zone in the Compte section are I. brevis and I. eslaensis (apart from two specimens of the former in the basal Frasnian MN1 Zone, Table 1C). P. rhenanus and P. x. ensensis disappeared, as elsewhere, in the upper part of the zone. P. ling. mucronatus is restricted in Compte to the upper half of the Middle varcus Zone (beds 41a-43f; Table 1B). P. hemiansatus becomes locally extinct at the upper part of the Zone (Bed 44; Table 1B).

The presence of up to six species of *Tortodus* in the upper part of the zone (beds 41a-45b; Fig. 2, Table 1B) is remarkable. They represent the first Givetian Pyrenean record of the genus. Local ranges of *T. caelatus*, *T. bultyncki* and *T. trispinatus* are restricted to the Middle *varcus* Zone, whilst *T. weddigei* ranges higher (Fig. 2). The record of *T.* aff. *bultyncki* (Fig. 4L–N) in the Lower *hermanni* Zone (Bed 46a, Table 1B) is noteworthy, too.

The entry of *P. latifossatus* in the Bed 45c identifies the base of the Upper varcus Zone. *P. dubius* (Fig. 5A) also appears in the same bed, whereas elsewhere it enters in the overlying Lower *hermanni* Zone. The conodont succession at Compte (see also below) leads us to believe that this record of *P. dubius* can be attributed to the Upper varcus Zone, and therefore it evidences a downward extension of its global range. The Bed 45f marks the last local occurrence of *P. ansatus* and *I. difficilis*. The appearance of *I. symmetricus* in the Bed 45f (Table 1B) would also notably extend its range downward; elsewhere it appears in the *disparilis* Zone (Aboussalam, 2003) or even in the lowermost Frasnian (Bultynck, 2003).

UPPER GIVETIAN

The base of the Lower *hermanni* Zone, and accordingly of the upper Givetian, is identified by the entry of *Schmidtognathus hermanni* in the Bed 46a. This bed contains the first record of *P. limitaris* and the local last record of *T. weddigei*. The latter extends the geographical and stratigraphical range of the species that previously was known only from the "pre-taghanic" *ansatus* Zone in Southern Morocco (Aboussalam, 2003) and from the Middle *varcus* Zone of the basal Prout Dolomite, Ohio (Sparling, 1999). The slightly delayed first *Sch. pietzneri* is recorded above the base of the Lower *hermanni* Zone in the Bed 46b.

The base of the Upper *hermanni* Zone is identified in the Bed 46g with the entry of *P. cristatus ectypus*. The entry of *Sch. peracutus* in the overlying Bed 46h is consistent with the succession of entries within the Upper *hermanni* Zone (Klapper and Johnson, in: Johnson, 1990, fig. 52). The delayed entry of *Sch. wittekindti* is also recorded from the Bed 46h. Within this zone, we record the last local occurrence of *P. ling. linguiformis*, which ranges higher into the Frasnian in other locations. Also within the Upper *hermanni* Zone, the last record of *P. latifossatus* (Bed 46h) is documented.

The entry of Kl. disparilis (Fig. 5K, L) at the top of the thick Bed 46 (about 125 cm above the Bed 46h, Fig. 2) indicates the base of the disparilis Zone. This specimen is transitional with P. cristatus, which suggests that the early stage of the "disparilis branch" development according to the phylogenetic interpretation of Ziegler and Klapper (1982: text-fig. 1) is represented in the Pyrenees in Compte section, Bed 46 (190–200) (Figs. 2, Table 1B). The occurrence of an incomplete specimen assigned to P. dengleri in the Bed 47 might indicate the upper part of the *disparilis* Zone, but clear records of P. dengleri start in the Bed 51. On the other hand, the highest local record of Sch. wittekindti in the Bed 49 supports assignment of this bed to the Lower disparilis Zone because this taxon becomes extinct in the lower half of the Lower disparilis Zone (Klapper and Johnson, in: Johnson, 1990). Before establishing the exact boundary between the Lower and Upper disparilis zones, and extending the range of Sch. wittekindti, more research has to be done in the Compte section. Tentatively, we place the boundary at the Bed 47, and consequently we extend the range of Sch. wittekindti. The highest observed record of P. c. ectypus is in the Bed 51, still within the disparilis Zone. Within the upper part of the zone, the first appearance of Kl. unilabius (Bed 53), unique record of Kl. disparalvea (Bed 54) and last appearances of Sch. pietzneri (Bed 53) and of Kl. disparilis (Bed 57) were noted.

The base of the *norrisi* Zone (=lowermost *asymmetricus* Zone, = *falsiovalis* Zone) is recognized at the Bed 58b with the joint entry of the corresponding index species *Sk. norrisi* and *M. falsiovalis*. This joint record evidences, at least locally, the supposed isochronous appearance of these two taxa and strengthens the correlation potential of any of these index species for the base of the uppermost Givetian conodont zone. In the same bed, the last record of *Sch. peracutus* was noted; this record slightly extends up to the upper half of the Upper *disparilis* Subzone the range of the taxon documented by Klapper and Johnson (in: Johnson, 1990). However, Huddle (1981, tab. 2) had already shown that *Sch. peracutus* ranges into the Frasnian *punctata* Zone. The highest local record of "*Oz.*" sannemanni was also observed in Bed 58b.

GIVETIAN/FRASNIAN AND LOWER FRASNIAN

There is a discussion regarding taxonomy of early *Ancyrodella* forms in the context of defining the base of the Frasnian worldwide (compare Klapper, 1985, 1988; Sandberg

et al., 1989). Different taxonomic opinions need to be carefully evaluated but this is far beyond the aims of this paper and therefore it will not be discussed here. We tentatively use the entry of A. pristina morphotypes 2 and 3 (Figs. 6I, J) within the Bed 59 (sample 59^{,04}) to locate the base of the Frasnian and, accordingly, of the Upper Devonian in the Compte section. We stress the fact that our specimens morphologically fall within the concept of A. pristina by Sandberg et al. (1989). This concept includes the specimen SUI9085 figured by Klapper (1985, pl. 2, figs. 11, 12), which comes from the Bed 42b at Col du Puech de la Suque section (classified as A. rotundiloba early form). The GSSP is established in the Bed 42a' in this section. In the Compte section A. pristina is followed by A. soluta in the Bed 60b (35 cm above the entry of A. pristina). For the Frasnian part of the section we follow the Klapper's conodont zonation established in the Montagne Noire (Klapper, 1988). Accordingly, the first conodont zone, described above, will belong to the MN1 Zone.

The lowest occurrence of *A. rotundiloba* late form of Klapper (1985) in the Bed 62a identifies the base of the MN2 Zone in the Compte section. This bed has also yielded the lowest representatives of *A. isabelae*. As the early form of *A. alata* is limited to the MN2 Zone 2 (Klapper, 1988) its appearance in the Bed 64 confirms the presence of the upper part of this zone in the Compte section. Conodonts from the Bed 65 are not diagnostic.

CONCLUSIONS

The analysis of the Givetian and early Frasnian conodont sequence obtained from the Compte section (Spanish Pyrenees) allows its subdivision into nine Givetian standard conodont zones and two Frasnian zones (MN zones).

This section turns out to be one of the key sections worldwide for supporting the three- fold subdivision of the Givetian and for the future discussions on the Givetian–Frasnian boundary and on the evolution of the early species of *Ancyrodella*. Co-occurrence of conodonts from several biofacies augments the correlation potential of this section and reinforces the correlative potential for other sections. In this context, the isochronous entry of *Sk. norrisi* and *M. falsiovalis* is remarkable as these are two different index taxa defining *norrisi* and *falsiovalis* zones, respectively, encompassing the uppermost part of the Givetian in different sections around the world.

The conodont ranges established observed in the Compte section allow to expand total stratigraphical ranges of several taxa, while confirming and expanding also the geographical distribution of others. The range of I. regularicrescens is extended upwards into the P. rhenanus/varcus Subzone. P. dubius appears in the Upper varcus Zone below its lowest currently assumed range in the hermanni Zone while I. symmetricus ranges down to the Upper varcus Zone. Records of P. eiflius confirm its range up to the ansatus Zone. The record of transitional specimens between P. cristatus and Kl. disparilis, supports the phylogenetic concept of Ziegler and Klapper (1982) and permits precise identification of the beginning of the "disparilis branch", and therefore, of the nominal zone in the Compte succession. The highest record of Sch. peracutus in the norrisi Zone confirms that the taxon ranges higher than proposed by Klapper and Johnson (in: Johnson 1990, p. 941, fig. 52; see also Huddle, 1981, tab. 2). Finally, the notable presence of a high specific diversity of Tortodus in the upper part of the Middle varcus Zone also extends known ranges of particular taxa.

The Eifelian–Givetian boundary can not be currently identified in the Compte section.

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