

# Graphic correlation of the upper Eifelian to lower Frasnian (Middle-Upper Devonian) conodont sequences in the Spanish Central Pyrenees and comparison with composite standards from other areas

S. Gouwy, J.-C. Liao, and J.I. Valenzuela-Ríos

# ABSTRACT

Through graphic correlation of Eifelian-Givetian sections from different facies settings in the Spanish Central Pyrenees, a local composite standard based on conodonts, is established to which new data from the Pyrenees can be related. This local conodont database is compared and correlated with the Middle Devonian composite standard already containing data from the Anti-Atlas (Morocco), the Ardenne (Belgium), and the composite standard of the Montagne Noire. The correlation project comprises three Pyrenean sections (Compte, Villech and La Guàrdia d'Ares) belonging to the same paleogeographical setting tectonically located in the southern part of the European Variscan Chain. The Compte section, yielding the most complete and detailed conodont succession for the Givetian, is selected as reference for the correlation project. The combination of data from these sections permits identification, by means of the index taxa, of all Givetian standard conodont zones and subzones. The high resolution correlation and comparison of these sections shows thickness differences in several intervals. This study is an important step in the construction of the Pyrenean high resolution composite standard that, integrated into the Anti-Atlas, Montagne Noire and Ardenne composite standard, will contribute to the construction of a global Middle Devonian conodont database and the improvement of chronostratigraphy and accuracy in intercontinental correlations for the Eifelian and Givetian stages.

S. Gouwy. (present address) Paleontology Section, Geological Survey of Canada (Calgary), 3303, 33<sup>rd</sup> Street, NW Calgary, Alberta, T2L 2A7 Canada. sofie.gouwy@canada.ca and Paleontology Department, Royal Belgian Institute of Natural Sciences, Vautierstraat 29, 3000 Brussels J.-C. Liao. Department of Geology, University of Valencia, E-46100, Burjasot, Spain. jau.liao@uv.es J.I. Valenzuela-Ríos. Department of Geology, University of Valencia, E-46100, Burjasot, Spain.

Jose.I.Valenzuela@uv.es

Keywords: Graphic correlation; conodont biostratigraphy; Middle Devonian; Armorican Terrane Assemblage; Peri-Gondwana; Spanish Central Pyrenees

Submission: 15 January 2016 Acceptance: 22 August 2016

Gouwy, S., Liao, J.-C., and Valenzuela-Ríos, J.I. 2016. Graphic correlation of the upper Eifelian to lower Frasnian (Middle-Upper Devonian) conodont sequences in the Spanish Central Pyrenees and comparison with composite standards from other areas. *Palaeontologia Electronica* 19.3.39A: 1-18

palaeo-electronica.org/content/2016/1620-pyrenean-givetian-correlation

Copyright: Her Majesty the Queen in right of Canada October 2016

# INTRODUCTION

Middle Devonian rocks are widespread in the Spanish Central Pyrenees (SCP), but few studies of these strata have focused on their paleontology and sedimentology. Only in the last 40 years has the research been intensified (Mey, 1967a,b; Hartevelt, 1970; Boersma, 1973; Zwart, 1979; Valenzuela-Ríos and Carls, 1994; Sanz-López, 1995, 2002; Valenzuela-Ríos and Blieck, 1996; Liao et al., 2001, 2007, 2008; Valenzuela-Ríos and Liao, 2006; Ginter et al., 2008; Liao and Valenzuela-Ríos, 2008, 2012, 2013; Gouwy et al., 2013). One of the relevant earliest works for conodont studies was Boersma (1973), which was the initial study of several important Middle and Upper Devonian sections. A few of those sections were recently resampled at a higher resolution and studied in detail: Compte section (Liao and Valenzuela-Ríos, 2008), Villech section (Gouwy et al., 2013), Renanué section (Liao et al., 2001, 2008) and La Guàrdia d'Ares section (Liao and Valenzuela-Ríos, 2013). In spite of the abundance of conodonts, each section had intervals in which the biostratigraphic detail was not sufficient for correlation. In a case like this, the use of the graphic correlation method can be a solution for the high resolution correlation problem. This method (Shaw's method; Shaw, 1964) has the advantage that it uses first and last occurrences of all fossil taxa present and is not limited to the index taxa as is the case in most biozonal classifications and correlations. Shaw's method offers a higher resolution than can ever be attained with many biozonal correlations. Moreover, the method does not assume that the entries of zone-defining species are synchronous everywhere and emphasizes they can only be considered isochronous or nearly so through demonstration of their position on or very close to the Line of Correlation (Shaw, 1964).

Graphic correlation of Middle Devonian sections began with Belka et al. (1997) on Eifelian and lower Givetian sections of the eastern Anti-Atlas (Morocco). Six well-studied sections were correlated with the Jebel Ou Driss section as standard reference to form the basis of the Middle Devonian graphic correlation project. Gouwy and Bultynck (2002, 2003) added Middle Devonian sections from the Ardenne (Belgium) to the database and Gouwy, et al. (2007) enriched the database with upper Givetian data from the eastern Anti-Atlas.

The aim of this paper is to increase the resolution power of biozonal correlations in the Middle Devonian of the Spanish Central Pyrenees by using regional graphic correlation of sections from the Compte subfacies area. Three well-studied sections from this area will be included: Compte, Villech and La Guàrdia d'Ares. The resulting range chart will be compared to the current Middle Devonian database. In the future, sections from this and from other subfacies areas might be added to this regional project.

The relevance of the selected region rests on the importance of sound data from the Armorica Terrane in the context of Devonian paleogeography and the position and interrelation of the terranes of the perigondwanan regions around the north margin of Gondwana. Our data will help to calibrate current, and divergent, ideas and proposals on the position and evolution of this array of terranes that are referred to as perigondwanan terranes [Armorica, Perunica, Alpine fragments (compare Cocks and Torsvik, 2006)].

# GEOLOGICAL BACKGROUND

# Paleogeographic Setting

The Variscan terranes that later formed the Spanish Central Pyrenees were situated in the southern hemisphere, at about 30-40° latitude during the Middle Devonian. They were part of an extensive shelf area formed at the northwestern margin of Gondwana (Figure 1.1) (Golonka, 2000; Robardet, 2003 and references therein) included in the Armorican Terrane Assemblage (Cocks and Torsvik, 2006). Their collision with Eurasia between the Late Cretaceous and the Early Miocene led to the formation of the Pyrenees. The Pyrenean Paleozoic rocks now belong to the south flank of the European Variscan Chain where south-verging structures prevail, south of the North Pyrenean Fault Zone (Figure 2.1).

# **Devonian Deposits and Their Lateral Variations**

The Devonian lithologies from the central Pyrenees change laterally and are grouped into four different large "facies areas" (Mey, 1967a; Zwart, 1979). The concept of subfacies in the southern facies area was introduced by Mey (1967a) who distinguished the Sierra Negra, Baliera, Renanué and Compte subfacies based on the grouping of similar Devonian sequences (Figure 2). Subsequent authors (Boersma, 1973; Zwart, 1979) regrouped the stratigraphic units. Since the work of Valenzuela-Ríos and Liao (2006), who reappraised Mey's subdivision, enough data have been accumulated to support the initial four-fold subdivision (Liao and Valenzuela-Ríos, 2012, 2013; Gouwy et al., 2013).

PALAEO-ELECTRONICA.ORG



**FIGURE 1.** 1. Middle Devonian paleogeographic situation with indication of the study area (courtesy of R. Blakey, NAU Geology), 2. Map of Paleozoic rocks on the Iberian Peninsula and position of figure 1.3, 3. Location of the studied Devonian outcrops.

The current study focusses on the Compte Subfacies, part of the southern facies area. In this subfacies, the upper part of the Emsian, the Middle Devonian and the Frasnian are represented by the Villech and Comabella formations. Age assignment of these two formations and position of the Givetian-Frasnian boundary were discussed and updated in Valenzuela-Ríos and Liao (2006). According to these authors, and taking into account previous results of Montesinos and Sanz-López (1999), the Villech Formation ends in most sections within the *serotinus* Zone, but in one section (Serra Comabella, Montesinos and Sanz-López, 1999) this formation can extend into the overlying *patulus* Zone. These data suggest a slightly diachronic boundary for the base of the Comabella Formation in the upper Emsian (Lower Devonian).

#### DATA

Three sections belonging to the Compte Subfacies: Compte (Liao and Valenzuela-Ríos, 2008), La Guàrdia d'Ares (Liao and Valenzuela-Ríos, 2013) and Villech (Gouwy et al., 2013), (Figures



**FIGURE 2.** 1. Map of Paleozoic rocks on the Iberian Peninsula and position of Figure 2.2 (black square), 2. Structural geological map of the Spanish Pyrenees with indication of the studied area (white square) and 2. Structural geological map of the Spanish Pyrenees with indication of the studied area (red square) and the most important faults and thrust faults, FNP: North Pyrenean Fault, CPP: Petites Pyrénées thrust fault, CFN: Frontal North Pyrenean thrust fault [modified from Barnolas and Pujalte (2004)], 3. Map of the Devonian facies areas and subdivision of the southern facies area in the southern Spanish Pyrenees [modified from Zwart (1979)], studied area in black square, location of the sections indicated by black stars.

1–2) were correlated in this study. All three sections expose the lower part of the Comabella Formation and are composed of variegated, bedded and nodular limestones. These limestones show similar microfacies and a diversity of conodonts belonging to an offshore marine or deep water marine facies. This set of sections comprises one of the richest Middle Devonian conodont sequences in the area and stretches from the lower Eifelian to the lower Frasnian (Valenzuela-Ríos and Liao, 2006; Liao and Valenzuela-Ríos, 2008, 2013; Gouwy et al., 2013).

#### **Compte Section**

The Compte section is exposed along the road approximately 15 km north of La Pobla de Segur on the right bank of the Noguera Pallaresa River (Figure 1.3) and was sampled for biostratigraphic study by Liao and Valenzuela-Ríos (2008). The studied section covers the lower part of the Givetian to the lower Frasnian and is part of a larger outcrop comprising Lochkovian to Famennian deposits. This section has the highest sample resolution of the three correlated sections: 142 samples in a 29 m thick section within the Comabella Formation and consists of an alternation of dark and light grey and sometimes pinkish, thick bedded, massive limestone and nodular limestone. In the middle part of the section, several small covered intervals interrupt the succession. The base of the studied interval is tentatively positioned within the hemiansatus Zone. The conodonts are not diagnostic and do not allow a precise positioning of the lowermost part of the section. The lowest conodont zone that can be accurately identified is the rhenanus/varcus Zone, in the lower third of the section. The middle third is recognized as the ansatus and semialternans/latifossatus zones. The upper third of the section comprises all upper Givetian conodont zones and the Frasnian zones 1-3 (Liao and Valenzuela-Ríos, 2008; new terminology of the Frasnian conodont zonation by Gilbert Klapper and William T. Kirchgasser [Klapper and Kirchgasser, 2016]).

#### La Guàrdia d'Ares Section

The La Guàrdia d'Ares section used for the graphic correlation is located in between the Compte and Villech sections (Figure 1.3), about 1.5 km east of the village of La Guàrdia d'Ares. The study of this section based on 129 samples revealed upper Eifelian to lower Frasnian deposits (Liao and Valenzuela-Ríos, 2013). The succession in La Guàrdia d'Ares consists of massive and nodular grey, thin bedded limestone with near vertical inclination, interrupted by a fault and followed by thick limestone beds in an anticlinal fold structure. The lowermost part of the studied section is positioned within the kockelianus Zone and kockelianus-ensensis zones interval. For several of the Givetian conodont zones, the zone-defining taxa have a delayed first occurrence. The Frasnian zones 1-3 and all Givetian conodont zones, except for the *rhenanus/varcus* and Upper varcus zones, can be positively identified, some based on associated taxa. The position of the bases of the hemiansatus, ansatus, semialternans-latifossatus and

Upper *hermanni* zones is still uncertain (Liao and Valenzuela-Ríos, 2013).

#### **Villech Section**

The Villech section is located about 18 km east of La Seu d'Urgell (Figure 1.3) and 3.5 km southwest of Martinet. The 54 m thick section is exposed on the eastern slope of the hill and in an abandoned quarry along the narrow road going from Martinet to the village of Villech. It shows the lower part of the Comabella Formation, consisting of nodular limestones and condensed red beds in the lowermost part of the section followed by condensed, pinkish-grevish limestones with hardground development, especially in the upper part of the section. The Villech section is part of a series of almost continuous outcrops and was the subject of a biostratigraphic study by Gouwy et al. (2013) based on 52 conodont samples. The section starts at the base of the Comabella Formation, which is positioned in the costatus Zone (lower Eifelian) as indicated by the lowest local record of Polygnathus angustipennatus. The kockelianus and eiflius zones are recognized in the lower part of the section. The ensensis and hemiansatus zones (uppermost Eifelian and lowermost Givetian) have not been found. A covered interval in the section hindered sampling around the expected position of the Eifelian-Givetian boundary. All other Givetian biozones were recognized in the upper part of the section followed by the Frasnian Zone 1 in the lowermost Frasnian (Gouwy et al., 2013). The disparilis Zone in the section was subsequently subdivided into a lower and upper subzone by Liao (2014). A narrow interval of black shale and black limestone in the upper part of the section could be the local signature of the global Taghanic Crisis (Liao et al., 2010).

#### **GRAPHIC CORRELATION METHOD**

For graphic correlation, the Compte section was chosen as the standard reference section, since it contained the most detailed Givetian conodont range chart (Liao and Valenzuela–Rios, 2008). The Compte section was preferred over the Villech section as reference, because although the latter has thicker Givetian deposits, the section is interrupted by two faults and it does not provide the high biostratigraphic resolution given by the study of the Compte section. The first occurrence datum (FOD) and last occurrence datum (LOD) of conodont taxa plotted in the field of the graphs (Figures 3–4) allow the construction of the line of correlation that represents the point-by-point time-equivalence



**FIGURE 3.** Graphic correlation between the Villech section and the composite standard for the Spanish Central Pyrenees (third round). The numbers represent the taxa listed in the range chart (Figures 5 and 6), the error boxes indicate the sampling intervals. (*sem./lat.: semialternans/latifossatus*).

of the sections. Since graphic correlation uses first and last occurrences of all taxa present, it is not affected by the assumed isochronous nature of zone-defining taxa of biozonal correlations. This key characteristic of the method is especially useful in areas where delayed FODs of zone-defining taxa have been demonstrated, as for some Givetian taxa here in the SCP: *Polygnathus hemiansatus, P. timorensis* and *P. varcus* in all three sections, *P. rhenanus* in the Villech section, and "Ozarkodina" semialternans in the La Guàrdia d'Ares section (Figure 5). Diachrony of FODs of important conodont taxa was already demonstrated through graphic correlation for the Middle Devonian of the eastern Anti-Atlas (Belka et al., 1997) and the Frasnian of the Montagne Noire and western Canada (Klapper, 1997). The line of correlation (LOC) is positioned in a way to cause the least disruption or changes to the first and last occurrences of taxa in the reference section. Ideal plots have all the FODs to the left and LODs to the right side. Through LOC, data from the Villech and La Guàrdia d'Ares sections are projected onto the reference section initiating the construction of a composite standard (CS) for the SCP.

# **CORRELATION GRAPHS**

The third round correlation graphs (Figures 3–4) both show multi-segment lines of correlation with variable segment slope. As is typical for the



**FIGURE 4.** Graphic correlation between the La Guàrdia d'Ares section and the composite standard (third round). The numbers represent the taxa listed in the range chart (Figures 5 and 6), error boxes indicate the sampling intervals.

early stage of a graphic correlation project, the clouds formed by the correlation points are rather wide. Since only three sections have been used to build the Composite Standard (CS) so far, the CS cannot yet be considered 'mature'; each newly-added section, therefore, might still adjust first (FOD) and last occurrence data (LOD) in the CS and extend the regional conodont ranges.

The correlation graph of the Villech section (Figure 3) shows a line of correlation consisting of eight segments and intersecting with the FODs of *Polygnathus ansatus* (28), *Tortodus caelatus* (41), *Schmidtognathus hermanni* (48), *Klapperina disparilis* (54), *Skeletognathus norrisi* (64), *Ancyrodella pristina* (69) and *Ad. rotundiloba* (73) and the LODs of *P. costatus* (6) and *Icriodus obliquimarginatus* (17). The Eifelian part of the graph is based on the cross-correlation between the Villech and La Guàrdia d'Ares sections. The lower part of

the LOC is not well constrained by correlation points, and the illustrated position of the LOC is one of several possibilities (dashed lines on Figure 3). This one is preferred because of its intersection with the LOD of P. costatus. For the Eifelian, the Villech section contains longer taxa ranges than the CS, the FODs plotting to the right of the line of correlation. These ranges are extended in the CS by projection of the correlation points onto the CS through the LOC. Continued research on the lower Eifelian part of the Villech and La Guàrdia d'Ares sections will allow more accurate positioning of the lowermost part of the LOC. The upper Givetian correlation points form a narrow channel in which a tightly controlled LOC can be drawn. The closer the points are to the LOC, the slighter the diachrony is between the occurrences in the Villech section and in the CS.

The La Guàrdia d'Ares correlation graph (Figure 4) shows a broader cloud of FODs and LODs for the Eifelian compared to the Villech correlation graph, indicating that the taxa ranges in the La Guàrdia d'Ares section are less 'mature' than the taxa ranges in the CS. The LOC, built of nine segments, runs through the FODs of Icriodus obliquimarginatus (17), Polygnathus hemiansatus (19), P. ansatus (28), P. limitaris (47), Klapperina disparilis (54), P. dengleri (56), Skeletognathus norrisi (64), Ancyrodella pristina (69), Ad. rotundiloba (73) and Ad. alata (80). In this section the FOD of P. hemiansatus is delayed and coincides with the base of the timorensis Zone. The base of the Givetian is here indicated by the FOD of *I. obliquimarginatus*. The position of the lowermost segment of the LOC is suggested by the LOD of P. costatus (6). Future sampling and extension of the study interval downward will give extra data points for the positioning of this segment. The subhorizontal second segment of the LOC suggests that deposits of the upper part of the kockelianus-ensensis zones interval are very condensed or missing in this section. The correlation graph shows three levels in the section at which FODs are grouped. Sampling intervals are small around these levels. They are found at 8 m, 12.5 m and 15 m from the base of the section. These levels coincide with the bases of the hemiansatus, ansatus and hermanni zones. The position of several LODs on the left side of the LOC in the upper right part of the graph indicates younger LODs in the La Guàrdia d'Ares section compared to the CS and ranges will be extended through the correlation. Both LOCs consist of multiple segments with strongly varying slopes. This indicates rather strong differences in sediment accumulation rates in the Villech and La Guàrdia d'Ares sections compared to the Compte section (reference section) especially in the semialternans/ latifossatus and hermanni zones.

# COMPOSITE STANDARD UNITS AND CONODONT BIOZONATION

Projection of the conodont data from the Villech and La Guàrdia d'Ares sections onto the CS allowed the construction of a taxa range chart for most of the Eifelian, the entire Givetian and the early Frasnian (Figures 5–6). Subdivided into 51 Composite Standard Units (CSU) based on the thickness of the reference section, the chart provides a high resolution conodont biostratigraphy based on 82 taxa for this interval in the Compte subfacies area. Projection of the CSUs onto the Villech and the La Guàrdia d'Ares sections confirms the correlation of the sections based on the conodont zonation (Figure 7) and additionally allows a precise correlation and projection of levels within the conodont zones. A complete list of the taxa with the CSU values for first and last occurrences per section is given in Appendix.

The oldest strata treated in this correlation project (which are also the base of the Comabella Formation) are placed within the lower part of the Eifelian and are only found in the Villech section. The combined occurrence of Polygnathus angustipennatus, P. partitus, P. bultyncki and P. robusticostatus positions the lowermost part of the studied sequence in the costatus Zone. The correlation with the La Guàrdia d'Ares section suggests the lowermost part (lowermost 5 m) of this section would be placed within the costatus Zone (Figure 4). Since the position of the lowermost LOC seqment in the La Guàrdia d'Ares graph is not well constrained and the taxa identifications are not conclusive, the zonal position of the lowermost part of the La Guàrdia d'Ares section is left open for further sampling and investigation (Figures 4 and 6). The australis Zone has not yet been identified in the studied sections; the zone defining taxon Tortodus k. australis was not found. The base of the kockelianus Zone is indicated by the FOD of T. k. kockelianus (14) in the Villech section at 16.35 CSU. It coincides with the FOD of P. pseudofoliatus (13) in the same section. The base of the ensensis Zone cannot be located. Although P. ensensis was identified in the Villech and Compte sections, both FODs are delayed. The base of the alternative eiflius Zone (Bultynck, 1987) was defined by the FOD of P. eiflius (15) in the Villech section at 21.40 CSU (Figure 8).

The graphic correlation with the Guardia d'Ares section suggests this zone is very narrow or missing in this section (subhorizontal segment in the LOC). The lowest base in the CS of Icriodus obliquimarginatus (17) is in the Compte section. It places the base of the hemiansatus Zone at 23.07 CSU. The FOD of Polygnathus hemiansatus is found higher within this zone. The base of P. timorensis (25), the defining species for the timorensis Zone, is situated several CSUs above the base of P. xylus (21), which is used as an auxiliary index species for the base of this zone (Ziegler and Klapper, 1976). The lowest base in the CS of P. xylus is at the Villech section. It is found right above a covered interval, which implies that the base of the timorensis Zone might be situated within the covered interval, somewhat lower than the indicated position. Polygnathus ansatus (28), the defining



PALAEO-ELECTRONICA.ORG

**FIGURE 5.** Conodont range chart based on the Spanish Central Pyrenean sections. Precise CSU values are given in the Appendix.

species for the base of the *ansatus* Zone (=Middle *varcus* Zone), has the lowest occurrence at 30.27 CSU based on data from the Compte section. This zone contains the FODs of 16 species. In our CS, the FODs of *"Ozarkodina" semialternans* (39) and *P. latifossatus* (44) are about 1 CSU apart. They

appear together in the same sample in the Compte section, but only "O." semialternans (39) was found in the Villech and La Guàrdia d'Ares sections. On the correlation graph with the Villech section (Figure 3), the FOD correlation point of "O." semialternans falls on the wrong side of the LOC and



FIGURE 6. Conodont range chart based on the Spanish Central Pyrenean sections (continued). Precise CSU values are given in the Appendix.

causes the FOD of the species to be lowered in the CS. For this reason the base of the semialternans/ latifossatus Zone shows a discrepancy in our composite range chart (Figure 5). Several Tortodus species have their CS ranges limited within the uppermost part of the ansatus Zone and the entire semialternans/latifossatus Zone and could be useful as marker species for this interval. The Compte section established the lowest bases of Schmidtognathus hermanni (48) and Klapperina disparilis (54), defining species for the hermanni and disparilis zones, respectively. The former has a delayed occurrence at La Guàrdia d'Ares and appears there within the upper part of the *disparilis* Zone; the latter only shows minor diachrony among the sections (Figure 8). Similarly the Compte section also establishes the subdivisions of both zones into a lower and upper part, based on the FODs of Polygnathus c. ectypus (53) and P. dengleri (56), respectively. Polygnathus c. cristatus (55) appears higher in the section, at the base of the *disparilis* Zone. The base in the CS of Skeletognathus norrisi (64), the defining species for the norrisi Zone, is provided by the Compte section and is well-constrained in both correlation graphs. The lowermost Frasnian species in the range chart is Ancyrodella pristina (69), positioning the base of the Frasnian (and Frasnian Zone 1) at 47.7 CSU. The lowest base of Ad. rotundiloba (73) in the CS, pinpointing the base of Frasnian Zone 2, is settled by the Compte section data. The base of Frasnian Zone 3 is approached by the joint FODs of Ad. alata (80) and Ad. triangulata (81). In the original Frasnian

(Klapper, 1997) they are located only 0.1 CSU below and above, respectively, the FOD of *Ad. rugosa*, the defining species for the base of Frasnian Zone 3 (Klapper, 1997) that was not found in our studied sections.

Montagne Noire graphic correlation range chart

# CORRELATION WITH THE MIDDLE DEVONIAN COMPOSITE STANDARD

The Pyrenean CS can be correlated with the Middle Devonian CS as a next step in the construction of a global composite standard for the Middle Devonian. So far the Middle Devonian CS consists of Ardenne and Anti-Atlas ranges [Gouwy and Bultynck (2002) updated with information from Aboussalam (2003), Aboussalam and Becker (2007) and Walliser and Bultynck (2011)]. It contains data from six sections in the eastern Anti-Atlas and nine sections in the Ardenne. The correlation shows a very dense cloud of data points in the upper Givetian making it a straightforward correlation in that part of the graph (Figure 9); in the Eifelian to Middle Givetian portion, less data points are available.

The line of correlation passes through a few important data points; it intersects with the FODs of *Tortodus k. kockelianus* (14), *Polygnathus eiflius* (15), *Icriodus obliquimarginatus* (17), *P. ansatus* (28), *P. latifossatus* (44), *Klapperina disparilis* (54), *Skeletognathus norrisi* (64) and *Ancyrodella bino-dosa* (75). The FODs of several zone defining taxa fall to the left of the LOC which indicates their delayed first occurrence in the SCP compared to the Middle Devonian CS [*P. costatus* (6), *P. ensen-*



FIGURE 7. Correlation of the three sections based on the results of the graphic correlation method.

sis (20), *P. hemiansatus* (19), *P. timorensis* (25) and *P. varcus* (29)]. Numerous FODs are located to the right side of the LOC [*Polygnathus I. klapperi* (10), *P. parawebbi* (12), *P. I. weddigei* (18), *P. beckmanni* (27) and *I. symmetricus* (45)]. Projection of these data points onto the LOC and the CS will lower the bases of these conodont ranges in the Middle Devonian CS. A few LODs are found to the left of the LOC; projection of these data points onto the se data points onto the LOC and the CS will expand the range of these taxa into higher CSU values [*P. pseudofoliatus* (13), *P. angusticostatus* (7), *P. denisbriceae* (36), *P. ensensis* (20), *P. pseudoeiflius* (31) and *I. struvei* 

(9)]. The correlation with the Pyrenean database also adds new taxa to the Middle Devonian database: *Ad.* sp. A Liao, 2014, *Ad.* sp. B Liao, 2014, *P. oblongus, Tortodus bultyncki, "Ozarkodina" s. adventa* and *P. alveoliposticus.* 

#### COMPARISON WITH COMPOSITE STANDARDS OF OTHER AREAS

The Pyrenean CS was also correlated with and compared to the separate CSs of the Ardenne, Anti-Atlas and the Montagne Noire to test the FOD diachrony of the zonal defining taxa. Projection of



**FIGURE 8.** Graphic correlation of the three Compte subfacies area sections. The columns show the observed first occurrences of important taxa in the studied sections, indicated by their projected position on the Pyrenean CS. The numbers represent the taxa listed in the range chart (Figures 5 and 6) and in the Appendix. (CSU: Composite Standard Unit).

those FODs from the CS of the different areas onto the Middle Devonian CS, allows a direct comparison in CSU values (Figure 10), which clearly demonstrates that several FODs are diachronous between the areas. It is most remarkable in the lower and middle Givetian where the FODs of *Polygnathus timorensis* (25), *P. rhenanus* (24), *P. xylus* (21), *P. hemiansatus* (19) and *Icriodus obliquimarginatus* (17) are delayed in several areas. Klapper (1997) and Belka et al. (1997) have already emphasized that diachrony of important first appearances can be substantial and our results confirm this finding.

#### CONCLUSIONS

The graphic correlation of the Compte, Villech and La Guàrdia d'Ares sections allows the construction of a Middle Devonian conodont database for the Spanish Central Pyrenees containing 82 taxa. It should be emphasized that this is a result based on the correlation of only three sections, and



**FIGURE 9.** Correlation between the Pyrenean composite standard and the Middle Devonian composite standard. The numbers represent the taxa listed in the range chart (Figures 5 and 6) and Appendix. See also legend in Figure 4.

the addition of more sections will most likely increase the precision of the taxa ranges and modify the position of the LOCs as the ranges in the CS database cannot yet be assumed to be 'mature'. The resulting range chart from these sections confirms identification, by means of the index taxa, of all Givetian standard conodont zones and subzones (Liao and Valenzuela-Ríos, 2008; Gouwy et al., 2013; Liao and Valenzuela-Ríos, 2013). The high-resolution correlation confirms significant variations in thickness of the conodont biozones between the sections. This variation in thickness changes through time in the different sections. Possible explanations for this change can be tectonic activity and/or changes in sedimentation rate during the Givetian. Correlation with the Middle Devonian CS reveals that the CS of the SCP would provide important taxa range extension information and several new taxa when added to the Middle Devonian CS. The correlations also demonstrate the diachronic nature of first occurrence of several important zonal defining taxa, within the SCP as well as between different areas. Since graphic correlation is based on more than just the zone-defining taxa and allows correlation of sections from different paleoenvironments and biofacies, it is therefore an important tool for correlations alongside the more traditional way of correlating using conodont biozonation.



**FIGURE 10.** Graphic correlation of four composite standard (CS) databases, three from NW-Gondwana (Anti-Atlas, Pyrenees and Montagne Noire) and one from S-Laurussia (Ardenne) (Golonka, 2000). The standard reference section for the Middle Devonian CS and the Anti-Atlas CS is the Jebel Ou Driss section in the Eastern Anti-Atlas (Morocco) (Belka et al., 1997). The standard reference sections for the Ardenne and Montagne Noire CSs are the Couvin-Givet section and the Pic de Vissou section, respectively. The columns show the observed first occurrences of important taxa in the regional CS's, indicated by their projected position on the Middle Devonian CS. The numbers represent the taxa listed in the range chart (Figures 5–6) and in the Appendix.

#### ACKNOWLEDGEMENTS

This work has been supported by the Spanish Research Project CGL-2011-24775- MINECO, the M100131201 Hi-Res correlation Mid-Paleozoic Project and is a contribution to the UNESCO/ IGCP-596 project. Earlier research on these sections was supported by the DAAD (J-C L) and the Alexander von Humboldt-Stiftung (JIV-R). The authors also thank A.D. McCracken (GSC Calgary), D.J. Over (SUNY Geneseo) and two anonymous reviewers for their comments on an earlier version of the manuscript. This is a Geological Survey of Canada contribution # 20150480.

#### REFERENCES

- Aboussalam, S.Z. 2003. Das "Taghanic-Event" im höheren Mittel-Devon von West-Europa und Marokko. Münstersche Forschungen zur Geologie und Paläontologie, 97:1-332.
- Aboussalam, S.Z. and Becker, R.T. 2007. New Upper Givetian to basal Frasnian conodont faunas from the Tafilalt (Anti-Atlas, Southern Morocco). *Geological Quarterly*, 51(4):345-374.
- Barnolas, A. and Pujalte, V. 2004. La Cordillera Pirenaica, p. 233-343. In Vera, J.A. (ed.), *Geología de España*, SGE-IGME, Madrid.
- Belka, Z., Kaufmann, B., and Bultynck, P. 1997. Conodont-based quantitative biostratigraphy for the Eifelian of the eastern Anti-Atlas, Morocco. *Geological Society of America Bulletin*, 109(6):643-651.

- Boersma, K. Th.1973. Devonian and Lower Carboniferous conodont biostratigraphy, Spanish Central Pyrenees. *Leidse Geologische Mededelingen*, 49:303-377.
- Bultynck, P. 1987. Pelagic and neritic conodont successions from the Givetian of pre-Sahara Morocco and the Ardennes. *Bulletin van het Koninklijk Instituut voor Natuurwetenschappen, Aardwetenschappen*, 57:149-181.
- Cocks, L.R.M. and Torsvik, T.H. 2006. European geography in a global context from the Vendian to the end of the Palaeozoic. In Gee, D.G. and Stephenson, R.A. (eds.), *European Lithosphere Dynamics*. Geological Society, Memoirs, London, 32:83-95.
- Ginter, M., Liao, J.-C., and Valenzuela-Ríos, J.I. 2008. New data on chondrichthyan microremains from the Givetian of the Renanué section in the Aragonian Pyrenees (Spain). *Acta Geologica Polonica*, 58(2):165-172.
- Golonka, J. 2000. *Cambrian-Neogene Plate Tectonic Maps*. Wydawnictwa Uniwersytetu Jagielloñskiego, Kraków.
- Gouwy, S. and Bultynck, P. 2002. Graphic correlation of Middle Devonian sections in the Ardenne region (Belgium) and the Mader-Tafilalt (Morocco): development of a Middle Devonian composite standard. *Aardkundige Mededelingen*, 12:105-108.
- Gouwy, S. and Bultynck, P. 2003. Conodont based Graphic Correlation of the Middle Devonian Formations of the Ardenne (Belgium): implications for stratigraphy and construction of a regional composite. *Revista española de Micropaleontologia*, 35(3):315-344.
- Gouwy, S., Hayduckiewicz, J., and Bultynck, P. 2007. Conodont-based graphic correlation of upper Givetian-Frasnian sections of the Eastern Anti-Atlas (Morocco). *Geological Quarterly*, 51(4):375-392.
- Gouwy, S., Liao, J.-C., and Valenzuela-Ríos, J.I. 2013. Eifelian (Middle Devonian) to Lower Frasnian (Upper Devonian) conodont biostratigraphy in the Villech section (Spanish Central Pyrenees). *Bulletin of Geosciences*, 88(2):315-338.
- Hartevelt, J.J.A. 1970. Geology of the Upper Segre and Valira valleys, Central Pyrenees, Andorra/Spain. *Leidse Geologische Mededelingen*, 45:167-236.
- Klapper, G. 1997. Graphic correlation of Frasnian (Upper Devonian) sequences in Montagne Noire, France and western Canada, p. 113-129. In Klapper, G., Murphy, M.A., and Talent, J. A. (eds.), Paleozoic Sequences Stratigraphy, Biostratigraphy and Biogeography: Studies in Honor of J. Granville ("Jess") Johnson. GSA Special Paper 321, Boulder, Colorado.
- Klapper, G. and Kirchgasser, W.T. 2016. Frasnian Late Devonian conodont biostratigraphy in New York: graphic correlation and taxonomy. *Journal of Paleontology*, 90(3):525-554.
- Liao, J.-C. 2014. Middle Devonian conodont biostratigraphy from the Central Pynenees. Tesi doctoral

"Mención de Doctorado Europeo" Universidad Complutense de Madrid. Base Teseo.

- Liao, J.-C., Ginter, M., and Valenzuela-Ríos, J.I. 2007. Chondrychthian microremains from the Givetian of the Aragonian Pyrenees. *Bulletin de la Société géologique de France*, 178 (3):171-178.
- Liao, J.-C., Königshof, P., Valenzuela-Ríos, J.I., and Schindler, E. 2008. Depositional environment interpretation and development of the Renanué section (Upper Eifelian–Lower Frasnian; Pyrenees, N. Spain. *Bulletin of Geosciences*, 83(4):481-490.
- Liao, J.-C. and Valenzuela-Ríos, J.I. 2008. Givetian and early Frasnian conodonts from the Compte section (Middle- Upper Devonian, Spanish Central Pyrenees). *Geological Quarterly*, 52(1):1-18.
- Liao, J.-C. and Valenzuela-Ríos, J.I. 2012. Upper Givetian and Frasnian (Middle and Upper Devonian) conodonts from Ampriú (Aragonian Pyrenees, Spain): global correlations and palaeogeographic relations. *Palaeontology*, 55(4):819-842.
- Liao, J.-C. and Valenzuela-Ríos, J.I. 2013. The Middle and Upper Devonian conodont sequence from the La Guàrdia d'Ares sections (Spanish Central Pyrenees). *Bulletin of Geosciences*, 88(2):339-368.
- Liao, J.-C., Valenzuela-Ríos, J.I., and Gouwy, S. 2010. Givetian (Middle Devonian) Geoevent at the Villech Section, p. 139-140. In Lamolda, M.A. (ed.), *Geoevents, Geological Heritage and the role of the IGCP*. Caravaca 15<sup>th</sup>-18<sup>th</sup> September 2010.
- Liao, J.-C., Valenzuela-Ríos, J.I., and Rodríguez, S. 2001. Descripción de los conodontos del Givetiense y Frasniense inferior (Devónico) de Renanué (Pirineos Aragoneses). *Coloquio Paleontología*, 52:13-45.
- Mey, P.H.W. 1967a. Evolution of the Pyrenean Basins during the Late Paleozoic, p. 1157-1166. In Oswald, D.H., (ed.), *International Symposium on the Devonian System*. Alberta Society of Petroleum Geologists, Calgary.
- Mey, P.H.W. 1967b. Geology of the upper Ribagorzana and Tor Valleys, Central Pyrenees, Spain. *Leidse Geologische Mededelingen*, 41:229-292.
- Montesinos, J.R. and Sanz-López, J. 1999. Ammonoideos del Devónico Inferior y Medio en el Pirineo oriental y central. Antecedentes históricos y nuevos hallazgos. *Revista Española de Paleontología, Homenaje al Prof. J. Trujols nº extraordinario*:97-108.
- Robardet, M. 2003. The Armorica 'microplate': fact or fiction? Critical review of the concept and contradictory palaeobiogeographical data. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 195:125-148.
- Sanz-López, J. 1995. Estratigrafía y bioestratigrafía (conodontos) del Silùrico superior-Carbonifero inferior del Pirineo oriental y central. Tesis doctoral Facultat de Geología, Univertitat de Barcelona, 1-717. Collecció de Tesis Doctorals Microfitxades nùm. 2840. Publicacions de la Universitat de Barcelona (1996), 1-9 and microfilms.

- Sanz-López, J. 2002. Devonian and Carboniferous pre-Stephanian rocks from the Pyrenees, p. 367-389. In García-López, S. and Bastida, F. (eds.), *Palaeozoic conodonts from Northern Spain*. Instituto Geológico y Minero de España, serie Cuadernos del Museo Geominero 1.
- Shaw, A.B. 1964. *Time in Stratigraphy*. New York, McGraw-Hill.
- Valenzuela-Ríos, J.I. and Blieck, A. 1996. Early Middle Devonian vertebrate micro remains from the Aragonian Pyrenees (Northern Spain). *Contes Rendues de l'Académie des Sciences de Paris*, 323(IIa):817-823.
- Valenzuela-Ríos, J.I. and Carls, P. 1994. Conodontos e Invertebrados del Devónico Medio del Valle de Tena (Pirineos Aragoneses). *Coloquios de Paleontología*, 46:43-59.

- Valenzuela-Ríos, J.I. and Liao, J.-C. 2006. Annotations to Devonian Correlation Table, R357-360 si-ds 06: Spanish Central Pyrenees, southern part. Senckenbergiana lethaea, 86(1):105-107.
- Walliser, O. and Bultynck, P. 2011. Extinctions, survival and innovations of conodont species during the Kačák Episode (Eifelian-Givetian) in south-eastern Morocco. Bulletin de l'Institut Royal des Sciences Naturelles de la Belgique, Sciences de la terre, 81:5-25.
- Ziegler, W. and Klapper, G. 1976. In Ziegler, W., Klapper, G., and Johnson, J.G. (eds.), Redefinition and subdivision of the *varcus*-Zone. (Conodonts, Middle– ?Upper Devonian in Europe and North America). *Geologica et Palaeontologica*, 10:109-140.
- Zwart, H.J. 1979. The Geology of the Central Pyrenees. *Leidse Geologische Mededelingen* 50:1-74.

# APPENDIX

First and last occurrences of the species in the different sections and in the resulting Composite Standard (CSU values). Compte : Compte section, LGA : La Guàrdia d'Ares section, Villech: Villech section, CS: Composite Standard. \*: first and last occurrence in the section that provided the first and last occurrence in the CS.

Species	Section	Base CSU	Top CSU	Species	Section	Base CSU	Top CSU
Ancyrodella	LGA	50.59	50.67	I. regularicrescens	Compte	20.93	27.62*
africana (82)	CS	50.59	50.67	(5)	Villech	2.19*	2.35
					CS	2.19	27.62
Ad. alata (80)	Compte	50.54*	50.88*				
	LGA	50.59	***	I. struvei (9)	LGA	23.41	23.44*
	CS	50.54	50.88		Villech	3.23*	3.38
					CS	3.23	23.44
Ad. binodosa (75)	Villech	48.27	48.49				
. ,	CS	48.27	48.49	I. symmetricus (45)	Compte	40.83*	50.88*
					Villech	25.42	25.73
Ad. pristina (69)	Compte	47.72*	50.88*		CS	40.83	50.88
	LGA	47.76	49.36				
	Villech	47.74	48.49	Klapperina	Compte	45.50	45.60
	CS	47.72	50.88	disparalvea (59)	CS	45.50	45.60
Ad. rotundiloba (73)	Compte	47.98*	50.88*	K. disparilis (54)	Compte	42.98*	46.80*
	LGA	48.29	50.63		LGA	42.99	46.78
	Villech	48.27	48.49		Villech	43.76	46.66
	CS	47.98	50.88		CS	42.98	46.80
Ad. rugosa (71)	LGA	47.76	48.29	K. ovalis (57)	Compte	44.90*	50.88*
	CS	47.76	48.29		LGA	47.50	***
					CS	44.90	50.88
Ad. sp. A (77)	Compte	49.43	49.48				
	CS	49.43	49.48	K. unilabius (58)	Compte	44.90	50.88
					CS	44.90	50.88
Ad. sp. B (79)	Compte	49.67	49.72				
	CS	49.67	49.72	Mesotaxis	Compte	49.33	49.38
				asymmetricus (75)	CS	49.33	49.38
Ad. triangulata (81)	Compte	50.54	50.55				
	CS	50.54	50.55	Mes. falsiovalis (68)	Compte	47.55	47.72
					CS	47.55	47.72
Icriodus brevis	Compte	26.81*	47.72*				
brevis (22)	Villech	34.15	34.27	"Ozarkodina" brevis	Villech	39.66	39.67
· · ·	CS	26.81	47.72	(38)	CS	39.66	39.67
I. b. eslaensis (30)	Compte	30.86	34.78*	"O." s. adventa (46)	Compte	41.08*	41.13*
	CS	30.86	34.78		LGA	41.08	41.08
					CS	41.08	41.13
I. difficilis (32)	Compte	33.38*	40.83*				
	Villech	34.15	34.27	"O." s. proxima (60)	LGA	45.84*	45.85
	CS	33.38	40.83		Villech	47.49	47.50*
					CS	45.84	47.50
I. expansus (33)	Villech	34.70	34.86		~		
	CS	34.70	34.86	"O." s. sannemanni	Compte	41.22*	47.55
				(50)	Villech	47.56	47.74*
I. l. latericrescens (72)	Compte	47.98	48.03		CS	41.22	47.74
<u> </u>	CS	47.98	48.03	"O." semialternans	Compte	40.64	47.55*
				(39)	LGA	42.37	42.38
I. lindensis (23)	Compte	26.81	26.81		Villech	39.66*	46.66
1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1	CS	26.81	26.81		CS	39.66	47.55
		20,01	20.01				
L obliguimarginatus	Compte	23.07*	34 38*	Polygnathus	LGA	46.78	46.81
(17)	LGA	23.07	23.12	alveoliposticus (62)	CS	46.78	46.81
(**)	Villech	23.12	34 27				
	CS	23.07	34.38				
		25.07	54.50	L	1	1	I

APPENDIX	(CONTINUED).
----------	--------------

Species	Section	Base CSU	Top CSU	Species	Section	Base CSU	Top CSU
P. angusticostatus	LGA	20.82	23.08	P. eiflius (15)	Compte	28.37	33.38*
(7)	Villech	3.16*	30.41*		Villech	21.40*	32.37
	CS	3.16	30.41		CS	21.40	33.38
P anoustidisous	Compte	47.64*	18 02*	P ansansis (20)	Compte	40.01	40.03*
(70)	Villech	47.04	48.92	T. ensensis (20)	Villech	25.88*	35.01
(70)	CS	47.74	48.49		CS	25.88	40.03
	0.5	47.04	40.92		0.5	25.00	40.05
P. angustipennatus	LGA	16.19	24.28*	P. furtivus (78)	Compte	49.43	49.67
(1)	Villech	0.00*	14.66		CS	49.43	49.67
	CS	0.00	24.28	D. I			20.01.1
D (20)	G i	20.27*	40.02	P. hemiansatus (19)	Compte	33.38	39.91*
P. ansatus (28)	Compte	30.27*	40.83		LGA	25.76*	39.90
	LUA Villach	30.39	30.51		Villech	25.88	37.71
	CS	30.32	43.70		Co	23.70	39.91
	0.5	30.27	45.70	P latifossatus (44)	Compte	40.64	41.66
P. beckmanni (27)	LGA	GA 30.18 30.22 P. langossatus (44) Com	CS	40.64	41.66		
1. 5000000000000000000000000000000000000	CS	30.18	30.22		0.5	10.01	11.00
				P. limitaris (47)	Compte	41.08*	47.72
P. bultyncki (3)	Villech	0.77	0.87		LGA	41.08	48.32*
· · ·	CS	0.77	0.87		CS	41.08	48.32
P. cristatus cristatus	Compte	43.63	49.48*	P. linguiformis	Compte	24.41	39.96
(55)	LGA	42.99*	49.20	klapperi (10)	LGA	10.81*	41.50*
	Villech	43.76	43.91		Villech	28.54	39.34
	CS	42.99	49.48		CS	10.81	41.50
<i>P. c. ectypus</i> (53)	Compte	41.58*	44.05	P. l. linguiformis (8)	Compte	30.39	42.98
	LGA	47.61	47.62*		LGA	10.81	44.49*
	CS	41.58	47.62		Villech	3.16*	41.54
					CS	3.16	44.49
P. collieri (67)	Compte	47.55	47.57*				
	LGA	47.50*	47.51	P. l. mucronatus	Compte	39.03	39.91
	CS	47.50	47.57	(34)	LGA	41.14	42.89*
D ( ( ( )	ICA	11.20	11.42		Villech	34.70*	35.01
P. costatus (6)	LGA	2.10*	11.42		CS	34.70	42.89
	CS	2.19	11.60	P 1 weddiaei (18)	Compte	23 71*	39.13
		2.17	11.00	1 . i. weddigei (10)	LGA	30.39	41.08*
P. dengleri (56)	Compte	44.05*	50.88*		Villech	30.62	39.71
	LGA	44.10	48.32		CS	23.71	41.08
	Villech	46.35	47.50				
	CS	44.05	50.88	P. oblongus (11)	LGA	11.39	11.42
					CS	11.39	11.42
P. decorosus (65)	LGA	47.76	***				
	Villech	47.49*	48.49*	P. ordinatus (66)	Compte	50.16	50.55*
	CS	47.49	48.49		Villech	49.49*	47.50
P. denisbriceae (36)	Villach	30.62	30.62		CS	47.49	50.55
	CS	39.02	39.02	P. ovatinodosus (26)	Compte	40.64	41.22
	US .	39.02	37.02	1 . ovannoaosus (20)	Villech	29.08*	41.22
P. dubius (43)	Compte	40.64*	50.88*		CS	29.08	47.06
1. aubius (45)	LGA	40.99	48.62			22.00	17.00
	Villech	46.35	47.06	P. parawebbi (12)	LGA	11.39*	11.42
	CS	40.64	50.88		Villech	33.10	33.16*

Species	Section	Base CSU	Top CSU	Species
P. partitus (2)	Villech	0.77	9.51	Schm. pera
	CS	0.77	9.51	(49)
P. pennatus (63)	Compte	47.55	50.88*	Schm. pietz
	LGA	46.78*	50.39	
	Villech	47.56	48.49	
	CS	46.78	50.88	
D 1 (21)	x 7.11 1	21.22#	21.20#	Schm. witte
P. pseudoeiflius (31)	Villech	31.23*	31.29*	(50)
	CS	31.23	31.29	
P. psaudofoliatus	IGA	25.76	43.01*	
(13)	Villech	16.35*	29.22	Skeletogna
(15)	CS	16.35	43.01	norrisi (64)
	0.5	10.35	45.01	1011131 (04)
P. rhenanus (24)	Compte	27 02*	39.91*	
1	LGA	30.18	39.90	
	Villech	33.75	39.90	Tortodus af
	CS	27.02	39.91	schultzei (4
				,
P. robusticostatus	LGA	12.56	13.82*	T. bultynck
(4)	Villech	0.77*	0.87	
	CS	0.77	13.82	
P. rugosa (71)	LGA	47.76	48.28	T. caelatus
	CS	47.76	48.28	
D 41 . (54)		10.001	10.001	
P. tafilensis (74)	Compte	48.22*	48.92*	
	LGA	48.24	48.33	I. kockeliai
	CS .	48.22	48.92	Kockellanus
P timorensis (25)	Compte	27.62*	39.91	
1. 111101 Ch313 (23)	LGA	41 14	42 37*	T trispinat
	Villech	34.7	39.67	1.1.1.5p.1.4
	CS	27.62	42.37	
P. trigonicus (16)	Villech	22.63	22.80	T. weddigei
	CS	22.63	22.80	
P. varcus (29)	Compte	30.77*	39.96	
	LGA	41.14	42.89*	
	Villech	34.15	39.90	
	CS	30.77	42.89	
D 11.((1)	<i>a</i> .	46.15%	45.50	
<i>P. webbi</i> (61)	Compte	46.15*	47.72	
	Villech	47.74	48.49*	
	CS	46.15	48.49	
$P_{\rm rv} lus(21)$	Compte	33.78	40.50	
1. Nyius (21)	I GA	42 34	43.53	
	Villech	25.88*	46 66*	
	CS	25.88	46.66	
		20.00	0.00	
Schmidtognathus	Compte	41.08*	44.90	
hermanni (48)	LGA	46.78	47.46*	
	Villech	41.54	41.76	
	CS	41.08	47.46	

# APPENDIX (CONTINUED).

CSU         CSU         CSU           Schm. peracutus (49)         Compte         41.08         47.55           CS         41.08         47.55           CS         41.08         47.55           Schm. pietzneri (52)         Compte         41.22*         44.90           Villech         41.54         47.06*           Schm. wittekindti         CS         41.22         47.06           Schm. wittekindti         Compte         41.08*         43.63           (50)         LGA         44.65         47.51*           Schm. wittekindti         Compte         47.06         26.57           CS         41.08         47.61         26.57           CS         41.08         47.87           norrisi (64)         LGA         47.50         48.89*           Villech         47.48         47.87           norrisi (64)         LGA         47.50         48.89*           Villech         39.76         39.76         39.76           schultzei (40)         CS         39.63         39.68           Villech         39.63         40.28*         20.28*           CS         39.79*         40.50*           <	Species	Section	Base	Тор
Schm. peracutus (49)         Compte CS         41.08         47.55           (49)         CS         41.08         47.55           Schm. pietzneri (52)         Compte         41.22*         44.90           Villech         41.54         47.06*           CS         41.22         47.06           Schm. wittekindti         Compte         41.08*         43.63           (50)         LGA         44.65         47.51*           Schm. wittekindti         Compte         41.08*         43.63           (50)         LGA         44.65         47.51*           Villech         47.06         26.57           CS         41.08         47.87           norrisi (64)         LGA         47.50         48.89*           Villech         47.48*         47.87           norrisi (64)         LGA         47.50         48.89*           Villech         39.76         39.76         39.76           schultzei (40)         CS         39.63*         39.68           Villech         39.63         40.28*         20.28*           CS         39.63         39.81         20.50*           T. bultyncki (37)         Compte <td< th=""><th></th><th></th><th>CSU</th><th>CSU</th></td<>			CSU	CSU
(49)       CS $41.08$ $47.55$ Schm. pietzneri (52)       Compte $41.22^*$ $44.90$ Villech $41.54$ $47.06^*$ CS $41.22$ $47.06$ Schm. wittekindti       Compte $41.08^*$ $43.63$ (50)       LGA $44.65$ $47.51^*$ Villech $47.06$ $26.57$ Schm. wittekindti       Compte $41.08^*$ $47.61$ (50)       LGA $44.65$ $47.51^*$ Villech $47.06$ $26.57$ CS $41.08^*$ $47.87$ norrisi (64)       Compte $47.48^*$ $47.87$ norrisi (64)       LGA $47.50$ $48.89^*$ Villech $39.76$ $39.76$ $39.76$ schultzei (40)       CS $39.63^*$ $39.68$ Villech $39.63^*$ $39.68$ $40.28^*$ CS $39.63$ $40.28^*$ $40.50^*$ T. bultyncki (37)       Compte $39.63^*$ $39.68$ CS $39.79^*$ $40.50^*$ $40.50^*$	Schm. peracutus	Compte	41.08	47.55
Schm. pietzneri (52)         Compte         41.22*         44.90           Villech         41.54         47.06*           CS         41.22         47.06           CS         41.22         47.06           Schm. wittekindti         Compte         41.08*         43.63           (50)         LGA         44.65         47.51*           Villech         47.06         26.57           CS         41.08         47.51           Villech         47.06         26.57           CS         41.08         47.51           Skeletognathus         Compte         47.48*         47.87           norrisi (64)         LGA         47.50         48.89*           Villech         47.49         47.74           CS         47.48         48.89           Tortodus aff.         Villech         39.76         39.76           schultzei (40)         CS         39.76         39.76           T. bultyncki (37)         Compte         39.63*         39.68           Villech         40.20         40.28*         40.50*           T. caelatus (41)         Compte         39.79*         40.50*           Villech         39.80 </td <td>(49)</td> <td>CS</td> <td>41.08</td> <td>47.55</td>	(49)	CS	41.08	47.55
Schm. pietzneri (52)         Compte $41.22^*$ $44.90$ Villech $41.54$ $47.06^*$ CS $41.22$ $47.06$ Schm. wittekindti         Compte $41.08^*$ $43.63$ (50)         LGA $44.65$ $47.51^*$ Villech $47.06$ $26.57$ CS $41.08^*$ $47.51^*$ Villech $47.66$ $26.57$ CS $41.08^*$ $47.51^*$ Villech $47.48^*$ $47.87$ norrisi (64)         LGA $47.50$ $48.89^*$ Villech $47.48^*$ $47.74$ CS $47.48$ $48.89$ Villech $39.76$ $39.76$ schultzei (40)         CS $39.63^*$ $39.68$ Villech $39.63^*$ $39.68$ $40.28^*$ CS $39.63^*$ $39.68^*$ $39.68^*$ Villech $40.20^*$ $40.28^*$ $40.50^*$ CS $39.63^*$ $39.68^*$ $39.68^*$ <				
Villech       41.54       47.06*         CS       41.22       47.06         Schm. wittekindti       Compte       41.08*       43.63         (50)       LGA       44.65       47.51*         Villech       47.06       26.57         CS       41.08       47.51         Villech       47.06       26.57         CS       41.08       47.51         Skeletognathus       Compte       47.48*       47.87         norrisi (64)       LGA       47.50       48.89*         Villech       47.49       47.74         CS       47.48       48.89         Tortodus aff.       Villech       39.76         schultzei (40)       CS       39.76       39.76         Schultzei (40)       CS       39.63       40.28*         CS       39.63       40.28       40.28         CS       39.63       40.28       40.50*         T. caelatus (41)       Compte       39.79*       40.50*         Villech       39.80       39.81       50         CS       39.79       40.50       40.50         T. caelatus (41)       Compte       39.80       39.81	Schm. pietzneri (52)	Compte	41.22*	44.90
CS $41.22$ $47.06$ Schm. wittekindti         Compte $41.08^*$ $43.63$ (50)         LGA $44.65$ $47.51^*$ Villech $47.06$ $26.57$ CS $41.08$ $47.51^*$ Villech $47.06$ $26.57$ CS $41.08$ $47.51^*$ Skeletognathus         Compte $47.48^*$ $47.87^*$ norrisi (64)         LGA $47.50$ $48.89^*$ Villech $47.48^*$ $48.89^*$ Tortodus aff.         Villech $39.76^*$ $39.76^*$ schultzei (40)         CS $39.76^*$ $39.76^*$ T. bultyncki (37)         Compte $39.63^*$ $39.68^*$ Villech $40.20^*$ $40.28^*$ CS $39.63^*$ $39.68^*$ $39.68^*$ Villech $40.20^*$ $40.50^*$ $40.50^*$ T. caelatus (41)         Compte $39.79^*$ $40.50^*$ CS $39.79^*$ $40.50^*$ $50.8^*$		Villech	41.54	47.06*
Schm. wittekindti         Compte         41.08*         43.63           (50)         LGA         44.65         47.51*           Villech         47.06         26.57           CS         41.08         47.51           Villech         47.06         26.57           CS         41.08         47.51           Skeletognathus         Compte         47.48*         47.87           norrisi (64)         LGA         47.50         48.89*           Villech         47.49         47.74           CS         47.48         48.89           Tortodus aff.         Villech         39.76           schultzei (40)         CS         39.76         39.76           Schultzei (40)         CS         39.63*         39.68           Villech         40.20         40.28*           CS         39.63         40.28*           CS         39.63         40.28*           CS         39.79*         40.50*           Villech         39.80         39.81           CS         39.79         40.50*           Villech         39.80         39.81           CS         39.79         40.50		CS	41.22	47.06
Schm. wittekindti         Compte $41.08^*$ $43.63$ (50)         LGA $44.65$ $47.51^*$ Villech $47.06$ $26.57$ CS $41.08$ $47.51^*$ Skeletognathus         Compte $47.48^*$ $47.87^*$ norrisi (64)         LGA $47.50$ $48.89^*$ Villech $47.48^*$ $48.89^*$ Tortodus aff.         Villech $39.76^*$ $39.76^*$ Schultzei (40)         CS $39.76^*$ $39.76^*$ Tortodus aff.         Villech $39.76^*$ $39.76^*$ Schultzei (40)         CS $39.63^*$ $39.68^*$ Villech $40.20^*$ $40.28^*$ CS $39.63^*$ $39.68^*$ Villech $40.20^*$ $40.28^*$ CS $39.63^*$ $40.50^*$ T. caelatus (41)         Compte $39.81$ CS $39.79^*$ $40.50^*$ T. kockelianus         LGA $20.82^*$ kockelianus (14)         Compte $4$				
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Schm. wittekindti	Compte	41.08*	43.63
Villech       47.06       26.57         CS       41.08       47.51         Skeletognathus       Compte       47.48*       47.87         norrisi (64)       LGA       47.50       48.89*         Villech       47.49       47.74         CS       47.48       48.89         Tortodus aff.       Villech       39.76       39.76         schultzei (40)       CS       39.76       39.76         T. bultyncki (37)       Compte       39.63*       39.68         Villech       40.20       40.28*       40.28*         CS       39.76       39.76       39.76         T. bultyncki (37)       Compte       39.63*       39.68         Villech       40.20       40.28*       40.28*         CS       39.63       40.28*       40.28*         CS       39.79*       40.50*       40.50*         T. caelatus (41)       Compte       39.79*       40.50*         Villech       39.80       39.81       50*         T. kockelianus       LGA       20.82       20.82*         kockelianus (14)       Villech       16.35*       19.15         CS       39.90*       41	(50)	LGA	44.65	47.51*
CS $41.08$ $47.51$ Skeletognathus norrisi (64)       Compte $47.48^*$ $47.87$ LGA $47.50$ $48.89^*$ Villech $47.49$ $47.74$ CS $47.48$ $48.89^*$ Villech $47.49$ $47.74$ CS $47.48$ $48.89^*$ Tortodus aff.       Villech $39.76$ $39.76$ schultzei (40)       CS $39.63$ $39.68$ T. bultyncki (37)       Compte $39.63^*$ $39.68$ Villech $40.20$ $40.28^*$ CS $39.63$ $40.28$ T. bultyncki (37)       Compte $39.79^*$ $40.50^*$ T. caelatus (41)       Compte $39.79^*$ $40.50^*$ Villech $39.80$ $39.81$ $50^*$ T. kockelianus       LGA $20.82$ $20.82^*$ kockelianus (14)       Compte $40.50$ $40.50$ T. trispinatus (42)       Compte $40.50$ $40.50$ LGA $39.90^*$ $41.08^*$ T. weddigei (35)       Compte </td <td></td> <td>Villech</td> <td>47.06</td> <td>26.57</td>		Villech	47.06	26.57
Skeletognathus norrisi (64)         Compte $47.48^*$ $47.87$ LGA $47.50$ $48.89^*$ Villech $47.49$ $47.74$ CS $47.48$ $48.89^*$ Villech $47.49$ $47.74$ CS $47.48$ $48.89^*$ Tortodus aff.         Villech $39.76$ $39.76$ schultzei (40)         CS $39.76$ $39.76$ T. bultyncki (37)         Compte $39.63^*$ $39.68$ Villech $40.20$ $40.28^*$ CS $39.63$ $40.28$ CS $39.63$ $40.28^*$ CS $39.63$ $40.28^*$ CS $39.63$ $40.28^*$ CS $39.79^*$ $40.50^*$ T. caelatus (41)         Compte $39.80$ $39.81$ CS $39.79^*$ $40.50^*$ $9.28^*$ Kockelianus         LGA $20.82^*$ $20.82^*$ kockelianus (14)         Villech $16.35^*$ $19.15^*$		CS	41.08	47.51
$\begin{array}{c c c c c c c c c c c c c c c c c c c $				
norrisi (64)         LGA         47.50         48.89*           Villech         47.49         47.74           CS         47.48         48.89           Tortodus aff.         Villech         39.76         39.76           schultzei (40)         CS         39.76         39.76           T. bultyncki (37)         Compte         39.63*         39.68           Villech         40.20         40.28*           CS         39.63         40.28           T. bultyncki (37)         Compte         39.63         40.28           CS         39.63         40.28         40.28           CS         39.63         40.28         40.50*           T. caelatus (41)         Compte         39.79*         40.50*           Villech         39.80         39.81         CS         39.79         40.50           T. kockelianus         LGA         20.82         20.82*         20.82*           kockelianus (14)         Villech         16.35*         19.15           CS         39.90*         41.08*         CS         39.90*         41.08*           T. trispinatus (42)         Compte         39.90*         41.08*         7.         weddigei (35) <td>Skeletognathus</td> <td>Compte</td> <td>47.48*</td> <td>47.87</td>	Skeletognathus	Compte	47.48*	47.87
Villech $47.49$ $47.74$ CS $47.48$ $48.89$ Tortodus aff. schultzei (40)Villech $39.76$ T. bultyncki (37)Compte $39.63^*$ $39.68$ Villech $40.20$ $40.28^*$ CS $39.63$ $40.28^*$ CS $39.63$ $40.28^*$ T. caelatus (41)Compte $39.79^*$ Villech $39.80$ $39.81$ CS $39.79^*$ $40.50^*$ Villech $39.80$ $39.81$ CS $39.79^*$ $40.50^*$ T. kockelianus kockelianus (14)LGA $20.82$ CS $16.35^*$ $19.15$ CS $16.35^*$ $19.15$ CS $39.90^*$ $41.08^*$ T. trispinatus (42)Compte $40.50$ LGA $39.90^*$ $41.08^*$ CS $39.13^*$ $41.08^*$ Villech $39.90^*$ $41.08^*$ Villech $39.90^*$ $41.08^*$	norrisi (64)	LGA	47.50	48.89*
CS $47.48$ $48.89$ Tortodus aff. schultzei (40)Villech $39.76$ $39.76$ T. bultyncki (37)Compte $39.63^*$ $39.68$ Villech $40.20$ $40.28^*$ CS $39.63$ $40.28^*$ CS $39.63$ $40.28^*$ T. caelatus (41)Compte $39.79^*$ Villech $39.80$ $39.81$ CS $39.79^*$ $40.50^*$ Villech $39.80$ $39.81$ CS $39.79^*$ $40.50^*$ T. kockelianus kockelianus (14)LGA $20.82$ CS $16.35^*$ $19.15$ CS $16.35$ $20.82$ T. trispinatus (42)Compte $40.50$ LGA $39.90^*$ $41.08^*$ CS $39.13^*$ $41.08^*$ T. weddigei (35)Compte $39.13^*$ Villech $39.90$ $40.28$		Villech	47.49	47.74
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		CS	47.48	48.89
$\begin{array}{c c c c c c c c c c c c c c c c c c c $				
schultzei (40)       CS $39.76$ $39.76$ T. bultyncki (37)       Compte $39.63^*$ $39.68$ Villech $40.20$ $40.28^*$ CS $39.63$ $40.28^*$ T. caelatus (41)       Compte $39.79^*$ $40.50^*$ Villech $39.80$ $39.81$ CS $39.79^*$ $40.50^*$ Villech $39.80$ $39.81$ CS $39.79^*$ $40.50^*$ Villech $39.80$ $39.81$ CS $39.79^*$ $40.50^*$ Villech $16.35^*$ $19.15$ CS $16.35$ $20.82^*$ Kockelianus (14)       Villech $16.35^*$ $20.82^*$ CS $16.35$ $20.82$ $-40.50^*$ T. trispinatus (42)       Compte $40.50^*$ $41.08^*$ CS $39.90^*$ $41.08^*$ $-41.08^*$ T. weddigei (35)       Compte $39.90^*$ $41.08^*$	Tortodus aff.	Villech	39.76	39.76
$T. bultyncki$ (37)       Compte $39.63^*$ $39.68$ Villech $40.20$ $40.28^*$ CS $39.63$ $40.28^*$ $T. caelatus$ (41)       Compte $39.79^*$ $40.50^*$ Villech $39.80$ $39.81$ CS $39.79^*$ $40.50^*$ Villech $39.79^*$ $40.50^*$ Villech $39.80$ $39.81$ CS $39.79^*$ $40.50^*$ $V$ illech $16.35^*$ $19.15^*$ CS $16.35^*$ $20.82^*$ $V$ illech $16.35^*$ $20.82^*$ $T. trispinatus$ (42)       Compte $40.50^*$ $CS$ $39.90^*$ $41.08^*$ $T. weddigei$ (35)       Compte $39.13^*$ $T. weddigei$ (35)       Compte $39.90^*$ $Villech$ $39.90^*$ $41.08^*$ $Villech$ $39.90^*$ $41.08^*$	schultzei (40)	CS	39.76	39.76
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$				
Villech $40.20$ $40.28*$ CS $39.63$ $40.28$ T. caelatus (41)       Compte $39.79*$ $40.50*$ Villech $39.80$ $39.81$ CS $39.79*$ $40.50*$ Villech $39.80$ $39.81$ CS $39.79*$ $40.50*$ T. kockelianus       LGA $20.82$ $20.82*$ Kockelianus (14)       Villech $16.35*$ $19.15$ CS $16.35$ $20.82$ T. trispinatus (42)       Compte $40.50$ $40.50$ LGA $39.90*$ $41.08*$ CS $39.13*$ $41.08*$ T. weddigei (35)       Compte $39.90$ $40.28$ $40.28$	T. bultyncki (37)	Compte	39.63*	39.68
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		Villech	40.20	40.28*
$T. \ caelatus$ (41)       Compte $39.79^*$ $40.50^*$ Villech $39.80$ $39.81$ CS $39.79$ $40.50^*$ $T. \ kockelianus$ LGA $20.82$ $20.82^*$ kockelianus (14)       Villech $16.35^*$ $19.15^*$ CS $16.35^*$ $20.82^*$ $T. \ trispinatus$ (42)       Compte $40.50^*$ $LGA$ $39.90^*$ $41.08^*$ CS $39.13^*$ $41.08^*$ $T. \ weddigei$ (35)       Compte $39.90^*$ $41.08^*$		CS	39.63	40.28
$\begin{array}{c ccccc} T. \ caelatus (41) & Compte & 39.79* & 40.50* \\ & Villech & 39.80 & 39.81 \\ & CS & 39.79 & 40.50 \\ \hline \\ T. \ kockelianus \\ kockelianus (14) & LGA & 20.82 & 20.82* \\ \hline \\ Kockelianus (14) & Villech & 16.35* & 19.15 \\ & CS & 16.35 & 20.82 \\ \hline \\ T. \ trispinatus (42) & Compte & 40.50 & 40.50 \\ & LGA & 39.90* & 41.08* \\ & CS & 39.90 & 41.08* \\ \hline \\ T. \ weddigei (35) & Compte & 39.13* & 41.08* \\ & Villech & 39.90 & 40.28 \\ \hline \\ \end{array}$				
Villech         39.80         39.81           CS         39.79         40.50           T. kockelianus         LGA         20.82         20.82*           kockelianus (14)         Villech         16.35*         19.15           CS         16.35         20.82           T. trispinatus (42)         Compte         40.50         40.50           LGA         39.90*         41.08*         CS         39.90         41.08*           T. weddigei (35)         Compte         39.13*         41.08*         Villech         39.90         40.28	T. caelatus (41)	Compte	39.79*	40.50*
CS         39.79         40.50           T. kockelianus         LGA         20.82         20.82*           kockelianus (14)         Villech         16.35*         19.15           CS         16.35         20.82           T. trispinatus (42)         Compte         40.50         40.50           LGA         39.90*         41.08*           CS         39.13*         41.08*           T. weddigei (35)         Compte         39.90         40.28           CS         39.13*         41.08         41.08		Villech	39.80	39.81
T. kockelianus         LGA         20.82         20.82*           kockelianus (14)         Villech         16.35*         19.15           CS         16.35         20.82           T. trispinatus (42)         Compte         40.50         40.50           LGA         39.90*         41.08*         CS         39.13*         41.08*           T. weddigei (35)         Compte         39.13*         41.08*         CS         39.13         41.08		CS	39.79	40.50
T. kockelianus kockelianus (14)         LGA         20.82         20.82*           Villech         16.35*         19.15         5           CS         16.35         20.82           T. trispinatus (42)         Compte         40.50         40.50           LGA         39.90*         41.08*           CS         39.90         41.08           T. weddigei (35)         Compte         39.13*         41.08*           Villech         39.90         40.28           CS         39.13         41.08				
kockelianus (14)         Villech         16.35*         19.15           CS         16.35         20.82           T. trispinatus (42)         Compte         40.50         40.50           LGA         39.90*         41.08*           CS         39.90         41.08           T. weddigei (35)         Compte         39.13*         41.08*           Villech         39.90         40.28           CS         39.13         41.08	T. kockelianus	LGA	20.82	20.82*
CS         16.35         20.82           T. trispinatus (42)         Compte         40.50         40.50           LGA         39.90*         41.08*           CS         39.90         41.08           T. weddigei (35)         Compte         39.13*         41.08*           Villech         39.90         40.28         41.08	kockelianus (14)	Villech	16.35*	19.15
T. trispinatus (42)         Compte         40.50         40.50           LGA         39.90*         41.08*           CS         39.90         41.08           T. weddigei (35)         Compte         39.13*         41.08*           Villech         39.90         40.28		CS	16.35	20.82
T. trispinatus (42)       Compte       40.50       40.50         LGA       39.90*       41.08*         CS       39.90       41.08         T. weddigei (35)       Compte       39.13*       41.08*         Villech       39.90       40.28       41.08				
LGA         39.90*         41.08*           CS         39.90         41.08           T. weddigei (35)         Compte         39.13*         41.08*           Villech         39.90         40.28         41.08	T. trispinatus (42)	Compte	40.50	40.50
CS         39.90         41.08           T. weddigei (35)         Compte         39.13*         41.08*           Villech         39.90         40.28         60.28           CS         39.13         41.08         41.08	· ` ` ´	LGA	39.90*	41.08*
T. weddigei (35)         Compte         39.13*         41.08*           Villech         39.90         40.28         60.28           CS         39.13         41.08         41.08		CS	39.90	41.08
T. weddigei (35)         Compte         39.13*         41.08*           Villech         39.90         40.28         60.28           CS         39.13         41.08         41.08				
Villech 39.90 40.28	T. weddigei (35)	Compte	39.13*	41.08*
CS 3913 41.08		Villech	39.90	40.28
0.5 57.15 41.06		CS	39.13	41.08