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Emsian (Lower Devonian) Polygnathids (Conodont) succession in the Spanish Central Pyrenees

Sucesión de Polygnátidos (Conodontos) del Emsiense (Devónico Inferior) en los Pirineos Centrales Españoles

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Abstract

A comprehensive conodont study of five sections of Emsian age, carried out in the Spanish Central Pyrenees, has revealed an important succession of polygnathids that can be used for identifying basal boundaries of globally recognized biozones.

This succession consists of *Polygnathus excavatus excavatus*, *Po. gronbergi*, *Po. nothoperbonus*, *Po. mashkovae*, *Po. laticostatus*, and the new species *Polygnathus luciae* that allows the identification of the *excavatus*, *nothoperbonus* and *laticostatus* Zones. The *nothoperbonus* Zone is further subdivided into Lower and Upper *nothoperbonus* subzones, relying upon the lowest occurrence of *Po. mashkovae*. These biostratigraphic data from the Spanish Central Pyrenees corroborate the succession of conodont indexes in other regions of Europe (north-western France and southern Italy), North Africa (Morocco), Central Asia, Australia, and North America (Alaska, Nevada and Canada).

Keywords: Conodonts; Lower Devonian; Emsian; *nothoperbonus* Zone; Spanish Central Pyrenees

Resumen

El estudio exhaustivo de cinco secciones de edad Emsiense en el Pirineo Central Español ha proporcionado una importante sucesión de especies de conodontos del género *Polygnathus* que puede usarse para reconocer los límites de diferentes biozonas de aplicación global.

Esta sucesión consiste en *Polygnathus excavatus excavatus*, *Po. gronbergi*, *Po. nothoperbonus*, *Po. mashkovae*, *Po. laticostatus* y la nueva especie *Polygnathus luciae*, lo que permite identificar las biozonas *excavatus*, *nothoperbonus* y *laticostatus*. Además, el primer registro de *Po. mashkovae* se usa para subdividir la Zona *nothoperbonus* en las Subzonas *nothoperbonus* Inferior y Superior.

Estos datos corroboran la sucesión de los índices de conodontos registrada en otras regiones de Europa (noroeste de Francia y sur de Italia), norte de África (Marruecos), Asia central, Australia y Norte América (Alaska, Nevada y Canadá).

Palabras clave: Conodontos; Devónico Inferior; Emsiense; Zona *nothoperbonus*; Pirineos Centrales Españoles

1. Introduction

Conodonts have been widely used to subdivide the Devonian rocks into short intervals (or biozones) that can be identified globally. According to this, the boundaries and biozones of the Emsian Stage are based essentially upon the successive occurrence of, phylogenetically related, species of the genus *Polygnathus* (see for example Klapper and Johnson, 1975; Klapper, 1977; Weddige and Ziegler, 1977; Lane and Ormiston, 1979; Yolkin *et al*., 1994; Bardashev *et al.*, 2002). Nevertheless, although the phylogeny of the Early Devonian polygnathids has been accepted as the basis for the conodont zonation of the Emsian Stage, this subdivision has been extensively discussed and diverse proposals have been put forward over recent decades (see discussion below and Mawson, 1995 for a historical review). Here we follow the zonal scheme for the Lower Emsian proposed by Yolkin *et al*. (1994), which includes the *kitabicus*, *excavatus* and *nothoperbonus* zones, although we consider the last one of these zones basically equivalent to the *gronbergi* Zone (see Mawson, 1995 and discussion below).

The *gronbergi* Zone was originally defined by Klapper and Johnson (1975) on the basis of the Early Devonian *Polygnathus*-bearing sequences found at Lone Mountain, Nevada (USA). This zone was subsequently subdivided into the Lower and Upper *gronbergi* subzones by Bultynck (1989), according to the polygnathid succession found in the La Grange Limestone of the Armorican Massif (north-western France), identifying the lower boundary of the Upper *gronbergi* subzone with the first occurrence of a new species, *Polygnathus catherinae*. However, some problems have since arisen over the definition of this new species, and consequently the proposed subdivision itself.

In the Pyrenees, the Devonian outcrops are relatively common and widespread. These Devonian rocks have been subdivided into four main facies-areas (the southern, central, western and northern facies-areas) (see Mey 1967a, b, 1968; Hartevelt 1970). The material studied herein comes exclusively from the southern facies-area and, more precisely, from the Compte and Baliera subfacies-area of Mey (1967b) (Fig. 1).

Emsian rocks are abundant and well exposed on both sub-facies, although strong tectonics precludes continuity and, therefore, the Emsian column has to be compiled from various sections that can be precisely correlated by means of conodonts. Within this context, we have begun a comprehensive study of several sections that yielded, relatively, abundant conodont faunas in these subfacies (Compte and Baliera). Therefore, the main purposes of this paper are to present this polygnathid assemblage, to describe a new species of the genus *Polygnathus*, and to propose the subdivision of the *nothoperbonus* Zone on the basis of the conodont distribution found in the Pyrenees and other regions.

2. Material provenance

Emsian outcrops are numerous in the Spanish Central Pyrenees but detailed studies of them are scarce. The better-known Emsian areas are included in the so-called Baliera and Compte Subfacies-areas (Mey, 1968; Habermehl, 1970; Hartevelt, 1970; Boersma, 1973a; Valenzuela-Ríos and Liao, 2006), which belong to the larger Southern Facies-area of Mey (1967) (see above). Emsian conodonts of this extensive area have been investigated by few authors; Ziegler (1959: p 299) was the first in recognizing the Emsian age by means of conodonts in one sample (“Probe 2”) in his section of the Pallaresa Valley, which corresponds to our section Compte I Top. Subsequently, Boersma (1973) identified Emsian conodonts from several sections, including La Guardia d’Àres and Villech sections. After Boersma’s pioneering and comprehensive work, only few Emsian conodont studies have been accomplished in the last 20 years (García-López *et al*., 1990; Sanz-López, 2002; Valenzuela-Ríos 1994, 2001; Martínez-Pérez and Valenzuela-Ríos, 2005; Martínez-Pérez *et al*., 2010).

All the material in this study came from five sections that have been described within the more extensive Southern Facies-area of Mey (1967). Four of these sections belong to the Compte Subfacies-area (Hartevelt, 1970) (see Fig. 1): the La Guardia d’Àres sections (LGA and LGA-XI), located in the proximity of the village of La Guardia d’Ares; the Compte-I top section (CP-I top),

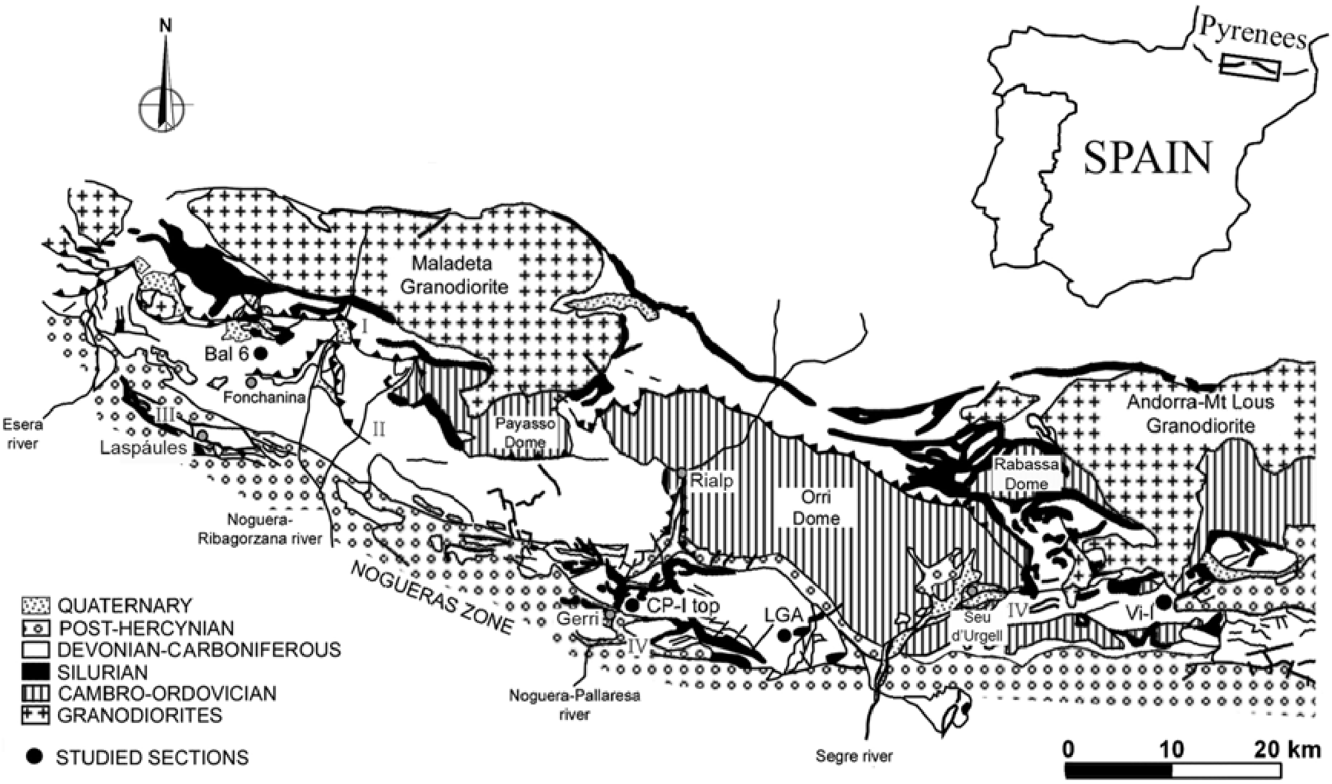


Fig. 1.- Geological scheme of the study area in the Central Spanish Pyrenees, indicating the four Subfacies areas contained in the Palaeozoic outcrops of the extensive Southern Facies-area of Mey (1967): I) Sierra Negra Subfacies, II) Baliera Subfacies, III) Renanué Subfacies and IV) Compte Subfacies; together with the location of the five sections studied: Baliera 6 section (Bal), the LGA sections (LGA), Compte-I top section. (CP-I top) and Villech sections (Vi-I) (Modified from Valenzuela-Ríos, 1994).

Fig. 1.- Esquema geológico de los afloramientos paleozoicos en área de estudio en los Pirineos Centrales Españoles, con indicación de las cuatro subfacies pertenecientes al Área de Facies Sur de Mey (1967): I) Subfacies Sierra Negra, II) Subfacies Baliera, III) Subfacies Renanué y IV) Subfacies Compte; junto con la localización de las cinco secciones estudiadas: Baliera 6 (Bal), LGA (LGA), Compte-I top (CP-I top) y Villech (Vi-I) (Modificado de Valenzuela-Ríos, 1994).

situated near the village of Gerri de la Sal; and the Villech-IB section (Vi-IB), close to the hamlet of Villech. Finally, the Baliera 6 section (Bal 6), located in the Baliera valley area, described and studied originally by Valenzuela-Ríos (1994, 2001), belongs to the Baliera Subfacies-area of Mey (1968) (Fig. 1). This last section has been described from strata of the Llaviero Mbr. of the Basibé Fm. characterized by blue-grey, platy limestone with thick bedded limestone and shale intercalations (see Valenzuela-Ríos, 1994 for a detailed description and geographical setting of the section). The LGA, LGA-XI, CP-I top and Vi-IB sections include rocks from the top of the Castanesa Fm., characterized by dark-grey, platy limestones, to the mid layers of the Villech Fm. (made up of red and green nodular limestones with intercalated red carbonaceous shales); they include the local Castells Beds Mbr., which is characterized by brownish, platy limestones with numerous millimetric to centimetric intercalations of brown shales at the lower part of the Villech Fm. (for a detailed description of the sections see Martínez-Pérez, 2010). All the sections were sampled for conodonts. The positions of the samples in these five sections are shown in Figures 2 to 5 (black dots) together with the stratigraphical ranges of the conodont taxa selected.

3. Systematic Palaeontology

All the conodonts studied appear as isolated elements after the dissolution of carbonate rocks with formic acid (5–10%). The material recovered is housed in the Museum of Geology at the University of Valencia and is identified by the MGUV initials followed by their museum number. It is important to remark that only those important biostratigraphic conodonts around the *nothoperbonus* Zone are discussed (briefly) and/or illustrated (Figs. 6–8).

In the Materials section we have used different abbreviations to indicate the section and bed of the material studied, and number of specimens from each bed. Thus, Bal 6, CP-I top, Vi-IB, LGA and LGA XI indicate the

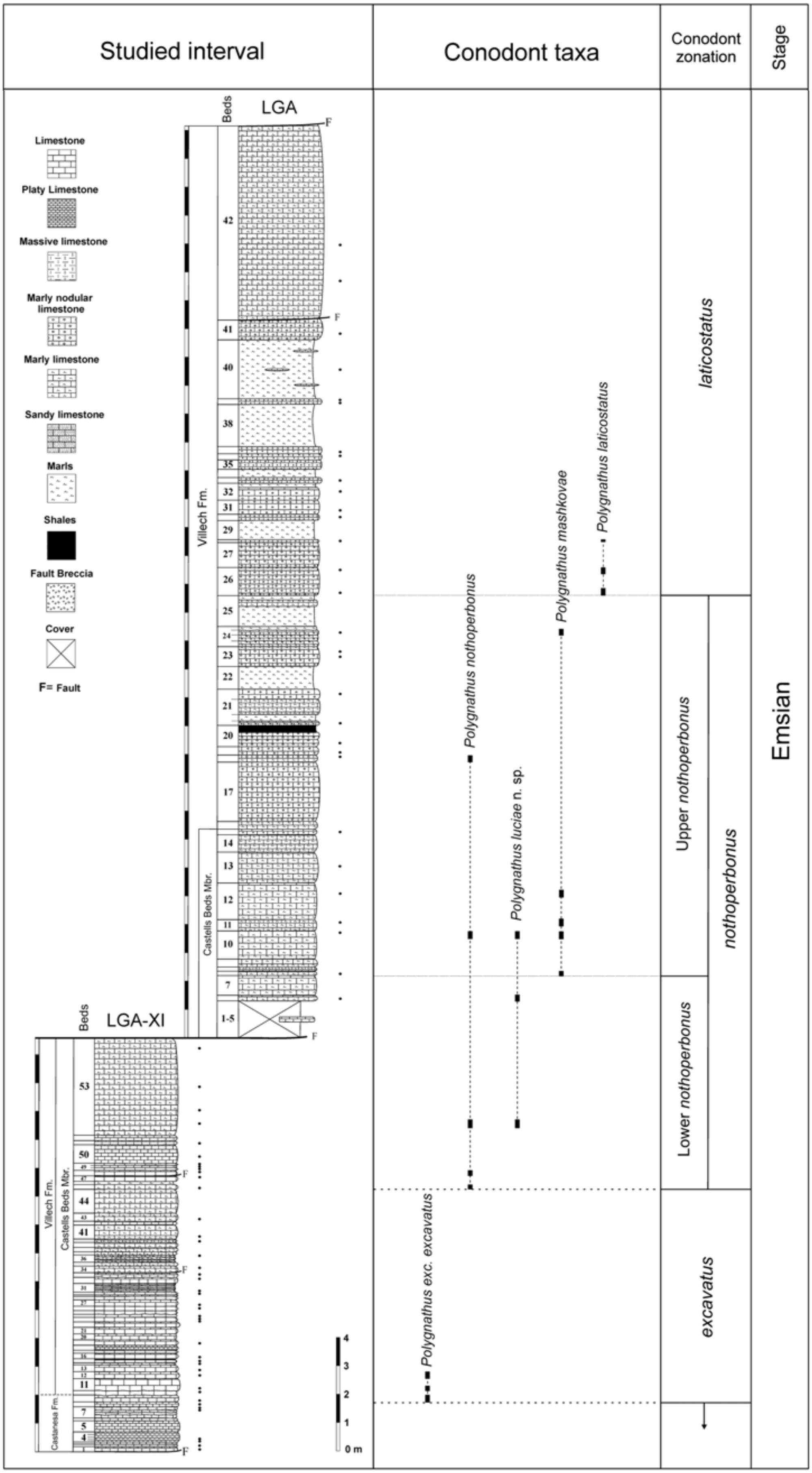


Fig. 2.- Stratigraphic column of the LGA and LGA-XI sections showing the location of the levels sampled for conodonts (black dots) and ranges of selected conodont taxa of biostratigraphic relevance around of the *nothoperbonus* Zone.

Fig. 2.- Columna estratigráfica de las secciones LGA y LGA-XI mostrando la localización de los niveles muestreados para conodontos (puntos negros) y los rangos de los taxones seleccionados con importancia bioestratigráfica alrededor de la Zona *nothoperbonus*.

sections, the following number separated by a slash ("/") indicates the bed, and the numbers in parentheses correspond to the numbers of elements. For example, LGA XI/53(3) indicates three specimens from Bed 53 of La Guardia d'Àres XI section.

Class Conodonta Eichenberg, 1930
Order Ozarkodinida Dzik, 1976
Family Polygnathidae Bassler, 1925
Genus *Polygnathus* Hinde, 1879

Polygnathus excavatus excavatus Carls and Gandl, 1969
Figure 6a

1969 *Polygnathus linguiformis* Hinde – Flood: plate 2, figures 1–2, 5–6.
*1969 *Polygnathus webbi excavata* n. ssp. Carls and Gandl: plate 18, figures 9–13, 14–19.
1971 *Polygnathus dehiscens* Philip and Jackson – Fahraeus: plate 77, figures 1–9.
1973a *Polygnathus foveolatus* Philip and Jackson – Boersma: plate 1, figures 1–6.
1975 *Polygnathus dehiscens* Philip and Jackson – Klapper and Johnson: plate 1, figures 1–2, 15–16.
1977 *Polygnathus dehiscens* Philip and Jackson – Klapper in Ziegler (ed.): plate 8, figures 7, 8.
1980 *Polygnathus dehiscens* Philip and Jackson – Chlupáč *et al*.: plate 21, figures 2–4, 6, 8–17; plate 22, figures 10, 14, 15.
1985 *Polygnathus dehiscens* Philip and Jackson – Schönlaub: plate 3, figures 8–10.
1992 *Polygnathus dehiscens dehiscens* Philip and Jackson – Mawson *et al*.: figures 7, I–K.
1994 *Polygnathus dehiscens* Philip and Jackson – Valenzuela-Ríos: plate 8, figures 17–18.
1994 *Polygnathus dehiscens "excavatus*" Carls and Gandl – García-López and Alonso-Menéndez: plate 3, figures 7–8.
2002 *Eocostapolygnathus excavatus* Carls and Gandl – Bardashev *et al*.: text-figures 14.10, 14.11.
2002a *Polygnathus excavatus excavatus* Carls and Gandl – García-López and Sanz-López: plate 1, figures 11–12.
2004 *Polygnathus excavatus* Carls and Gandl – Slavík: figures 11, 26–29.
2005 *Polygnathus excavatus* Carls and Gandl – Martínez-Pérez and Valenzuela-Ríos: plate 1, figures 7, 8, 10.

Material

18 elements from the following sections and beds: Bal 6/3(1), Bal 6/14(1), Bal 6/37(1), Bal 6/43a(1), Bal 6/47(2), Bal 6/49(3), Bal 6/50 (1), LGA X/36(3), LGA X/42(1), LGA XI/9(1), LGA XI/11(1) and LGA XI/12(2). Material referred: MGUV-20.882, MGUV-20.884, MGUV-20.887 to MGUV-20.892 and MGUV-20.894 to MGUV-20.903.

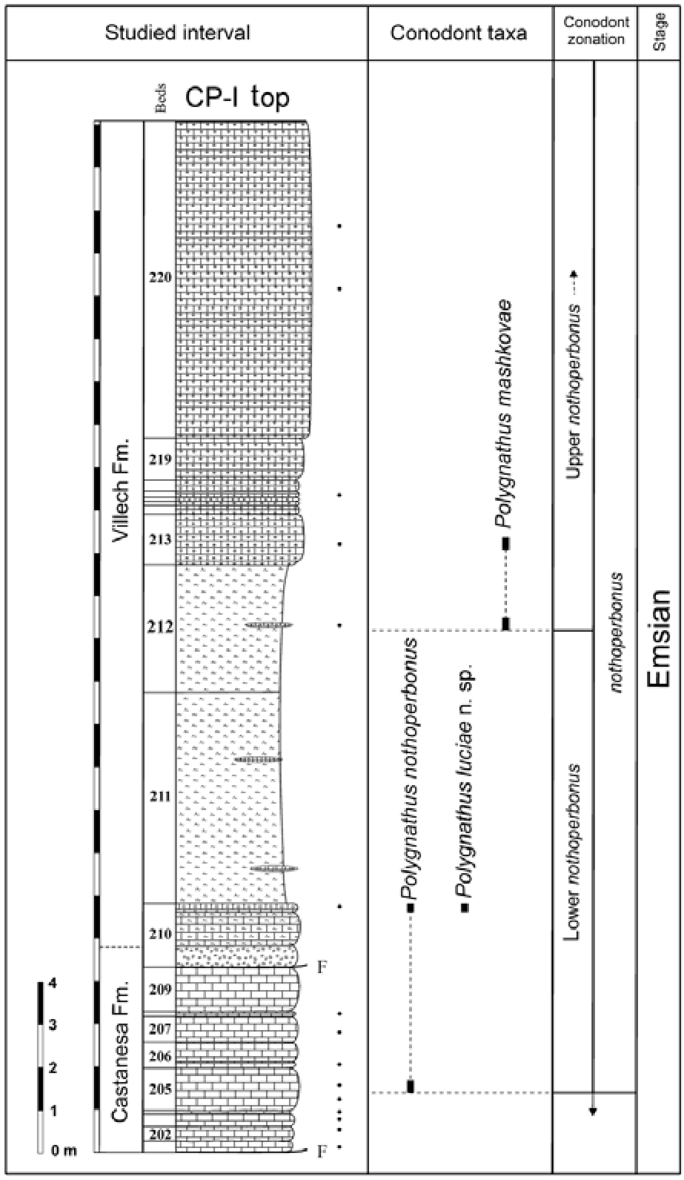


Fig. 3.- Stratigraphic column of the CP-I top section showing the location of the levels sampled for conodonts (black dots) and ranges of selected conodont taxa of biostratigraphic relevance around of the *nothoperbonus* Zone.

Fig. 3.- Columna estratigráfica de la sección CP-I top mostrando la localización de los niveles muestreados para conodontos (puntos negros) y los rangos de los taxones seleccionados con importancia bioestratigráfica alrededor de la Zona *nothoperbonus*.

Remarks

Po. exc. excavatus is characterized by a narrow platform with well developed but unequal adcarinal troughs, the outer one being more excavated and longer than the inner one; the carina is displaced towards the inner platform; platform surface ornamented by short ribs. Short tongue ornamented by interrupted transversal ridges. The elements present a relatively deep and open basal cavity, which occupies more than half of the length of the platform in lower view. This species is distinguished from its ancestors *Po. pireneae* and *Po. kitabicus* by the lanceolate shape of its platform (slightly curved internally), by a more restricted basal cavity, and by the development of clear adcarinal troughs.

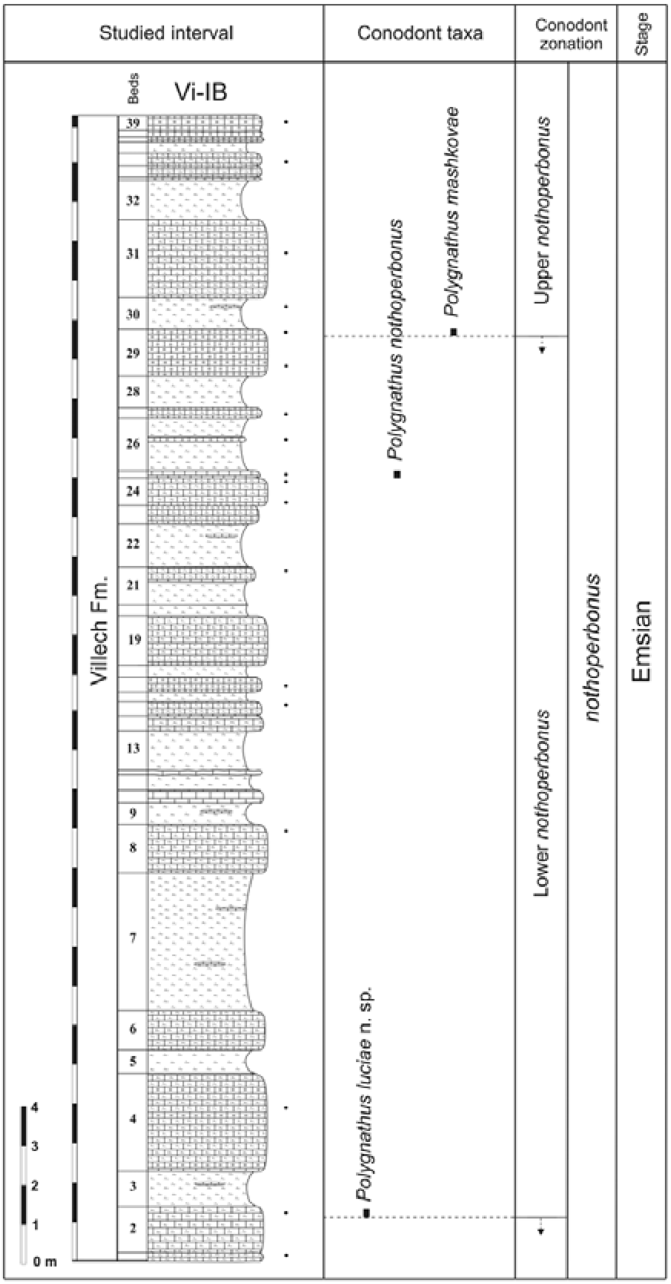


Fig. 4.- Stratigraphic column of the Vi-IB section showing the location of the levels sampled for conodonts (black dots) and ranges of selected conodont taxa of biostratigraphic relevance around of the *nothoperbonus* Zone.

Fig. 4.- Columna estratigráfica de la sección Vi-IB mostrando la localización de los niveles muestreados para conodontos (puntos negros) y los rangos de los taxones seleccionados con importancia bioestratigráfica alrededor de la Zona *nothoperbonus*.

Stratigraphical and geographical distribution

This taxon is the index for the Lower *excavatus* Subzone of Yolkin *et al.* (1994), and is recorded from the base of the *excavatus* Zone to lower parts of the *nothoperbonus* Zone. It is distributed worldwide and has been recorded in Spain from the Iberian Chains (Carls and Gandl, 1969), the Pyrenees (Boersma, 1973b; Valenzuela-Ríos, 1994; Martínez-Pérez and Valenzuela-Ríos, 2005) and the Cantabrian Mountains (García-López and Alonso-Menéndez, 1994; García-López and Sanz-López, 2002a); in Bohemia in the Czech Republic (Chlupáč *et al*., 1980; Slavík, 2004); in the Carnic Alps in Austria (Schönlaub, 1985); in Nevada in the USA (Klapper, 1969; Klapper and Johnson, 1975); in Canada (Fahraeus, 1971); in Zinzilban (Uzbekistan, central Asia) (Yolkin *et al*., 1994) and in Australia (Flood, 1969; Mawson *et al*., 1992).

Polygnathus gronbergi Klapper and Johnson, 1975
Figure 6b

1969 *Polygnathus lenzi* n. sp. Klapper: plate 6, figures 12–13?.
*1975 *Polygnathus gronbergi* n. sp. Klapper and Johnson: plate 1, figures 17–18, 21–24, 27–28 (non 19–20, 25–26).
1975 *Polygnathus foveolata* Philip and Jackson – Snigireva: plate 4, figure 6.
1977 *Polygnathus gronbergi* Klapper and Johnson – Klapper in Ziegler (ed): plate 8, figures 1, 5.
1978 *Polygnathus gronbergi* Klapper and Johnson – Apekina and Mashkova: plate 74, figures 6, 8; plate 75, figures 4–6.
1978 *Polygnathus gronbergi* Klapper and Johnson – Klapper *et al*.: plate 1, figures 2–3.
1979 *Polygnathus gronbergi* Klapper and Johnson – Lane and Ormiston: plate 6, figures 6–7, 13.
1980 *Polygnathus gronbergi* Klapper and Johnson – Chlupáč *et al*.: plate 21, figures 18, 21; plate 24, figures 5, 15.
1985 *Polygnathus gronbergi* Klapper and Johnson – Bultynck: plate 5, figures 15, 16.
1985 *Polygnathus gronbergi* Klapper and Johnson – Schönlaub: plate 3, figure 16.
1992 *Polygnathus gronbergi* Klapper and Johnson – Bardashev and Ziegler: plate 2, figures 28–32, 38, 39.
2002 *Polygnathus gronbergi* Klapper and Johnson – García-López *et al*.: plate 5, figures 15, 16.
2002 *Eocostapolygnathus gronbergi* Klapper and Johnson – Bardashev *et al*.: text–figures 14.14, 14.15.

Material

Four elements from the following sections and beds: Bal 6/48(1) (MGUV-20.919) and Bal 6/49(3) (MGUV-20.920 to 20.922).

Remarks

Diagnostic features of *Po. gronbergi* include a relatively large basal cavity, in lower view occupying most of the platform, which is flat or slightly inverted at the posterior end, and showing in upper view a short and moderately deflected posterior platform ornamented by few and short interrupted ridges. The specimens studied here are very similar to the holotype and paratypes of Klapper and Johnson (1975: pl. 1, figs. 1–18, 21–24, 27–28), as well as other specimens described in the literature (see for example Lane and Ormiston, 1979: pl. 6, figs. 6–7, 13 or Apekina and Mashkova, 1978: pl. 75, fig. 6). This species is clearly discernible from other taxa of the *Po. excavatus* group, differing mainly in the incipient inversion of the basal cavity at the posterior end of *Po. gronbergi*.

Stratigraphical and geographical distribution

The stratigraphical distribution of *Po. gronbergi* is restricted to the *gronbergi* Zone, or *nothoperbonus* Zone (*sensu* Mawson, 1995). In the Pyrenees, *Po. gronbergi* is very scarce and occurs slightly before the first record of *Po. nothoperbonus* (Fig. 5). It has been found in several Spanish regions: in the Pyrenees, Celtiberia (Carls and Valenzuela-Ríos, 2002) and Cantabrian Mountains (García-López *et al.*, 2002); but also in the Barrandian area of the Czech Republic (Klapper *et al.*, 1978); in the Ural Mountains in Russia (Snigireva, 1975); in Uzbekistan (Apekina and Mashkova, 1978); in Morocco (Bultynck, 1985); in Nevada (Klapper and Johnson, 1975) and Alaska (Lane and Ormiston 1979) in USA; and in Canada (Klapper, 1969).

Polygnathus laticostatus Klapper and Johnson, 1975
Figure 6c

*1975 *Polygnathus laticostatus* n. sp. Klapper and Johnson: plate 2, figures 20–33.
1976 *Polygnathus laticostatus* Klapper and Johnson – Glenister *et al.*: figures 1H, I.
1978 *Polygnathus gronbergi–laticostatus* Klapper *et al.*: plate 1, figures 4–7.
1979 *Polygnathus laticostatus* Klapper and Johnson – Bultynck and Morzadec: plate 1, figures 21–24.
1980 *Polygnathus* n. sp. B Klapper – Klapper and Johnson: plate 4, figures 13, 14, 17, 18.
1992 *Polygnathus laticostatus* Klapper and Johnson – Bardashev and Ziegler: plate 5, figures 3–4.
2002 *Eocostapolygnathus laticostatus* Klapper and Johnson – Bardashev *et al.*: text-figure 14.23.
2003 *Polygnathus laticostatus* Klapper and Johnson – Pyle *et al.*: plate 2, figures 7–8.

Material

Four elements from the LGA section in the following levels: LGA/26(3) (MGUV-20.928 to MGUV-20.930) and LGA/28(1) (MGUV-20.931).

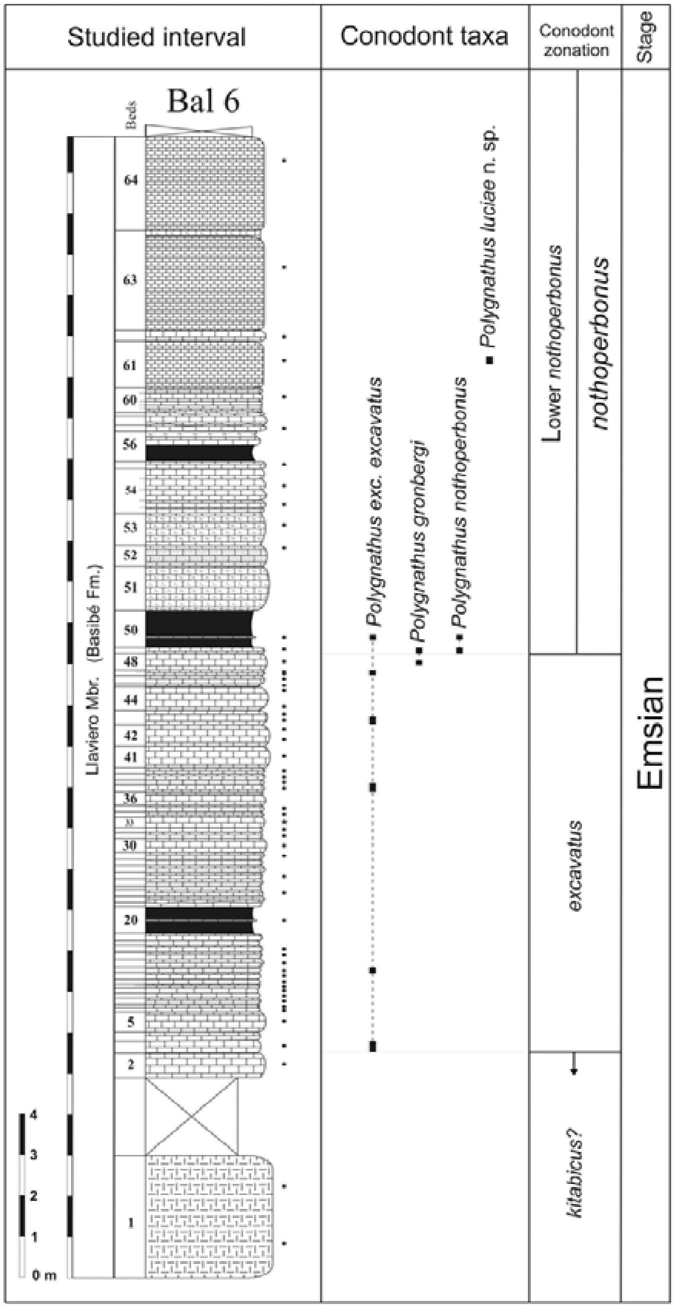


Fig. 5.- Stratigraphic column of the Baliera 6 sections showing the location of the levels sampled for conodonts (black dots) and ranges of selected conodont taxa of biostratigraphic relevance around of the *nothoperbonus* Zone.

Fig. 5.- Columna estratigráfica de la sección Bal-6 mostrando la localización de los niveles muestreados para conodontos (puntos negros) y los rangos seleccionados de taxones de conodontos de relevancia estratigrafíca en torno a la Zona *nothoperbonus.*

Remarks

Po. laticostatus has a broad, straight platform that curves inwards in the posterior third and develops a large triangular tongue. The upper surface is ornamented by numerous short transverse ridges; central carina and narrow, equally developed adcarinal troughs. The specimens studied have a completely inverted basal cavity with a relatively large, asymmetrical basal pit (with a more developed outer lip) located just before the inward deflection of the keel. This species is close in shape and ornamentation to *Po. gilberti* and *Po. linguiformis*, but the presence of an asymmetrical basal cavity, located more anteriorly in *Po. laticostatus*, and the morphological differences of their platforms, semicircular in *Po. gilberti*, and with a more developed tongue in *Po. linguiformis*, renders both taxa clearly distinguishable from *Po. laticostatus*.

Stratigraphical and geographical distribution

Po. laticostatus is an important biostratigraphic marker that has been used, together with *Po. inversus*, to indicate the lower/upper Emsian boundary and the base of the *laticostatus* Zone. Its stratigraphical distribution seems to be restricted to the *laticostatus* Zone. It has been found in the Pyrenees and Celtiberia (Carls and Valenzuela-Ríos, 2002) in Spain; in the Armorican Massif in France (Bultynck and Morzadec, 1979); in the Barrandian area in the Czech Republic (Klapper *et al*., 1978; Weddige and Ziegler, 1977); in Tajikistan (Bardashev and Ziegler, 1992) in central Asia; in Nevada (Klapper and Johnson, 1975; Johnson *et al*., 1980; Klapper and Johnson, 1980) in the USA; and in British Columbia (Pyle *et al.,* 2003) in Canada.

Polygnathus luciae n. sp.
Martínez-Pérez and Valenzuela-Ríos
Figures 7a–f

1975 *Polygnathus foveolata* Philip and Jackson – Snigireva: plate 4, figure 6.
1980 *Polygnathus gronbergi* Klapper and Jackson – Mashkova and Snigireva: plate 1, figures 5–6.
1987 *Polygnathus mashkovae* Bardashev – Aksenova: plate 27, figures 2, 3.
1989 *Polygnathus mashkovae* Bardashev – Bultynck: plate 1, figures 11, 14–15.
1989 *Polygnathus deshiscesns dehiscens* Philip and Jackson – Bultynck: plate 1, figures 1, 4–8.
1989 *Polygnathus gronbergi* Klapper and Jackson – Bultynck: plate 1, figures 9–10, 12.
2002 *Polygnathus excavatus* ssp. 114 Carls and Valenzuela-Ríos – García-López *et al*.: plate 4, figures 25–29.
2002 *Polygnathus mashkovae* Bardashev – García-López *et al*.: plate 5, figures 21, 22.
2002b *Polygnathus mashkovae* Bardashev – García-López and Sanz-López: plate 1, figures 13–14.

Derivatio nominis

The species is dedicated to Lucía Martínez Lara.

Material

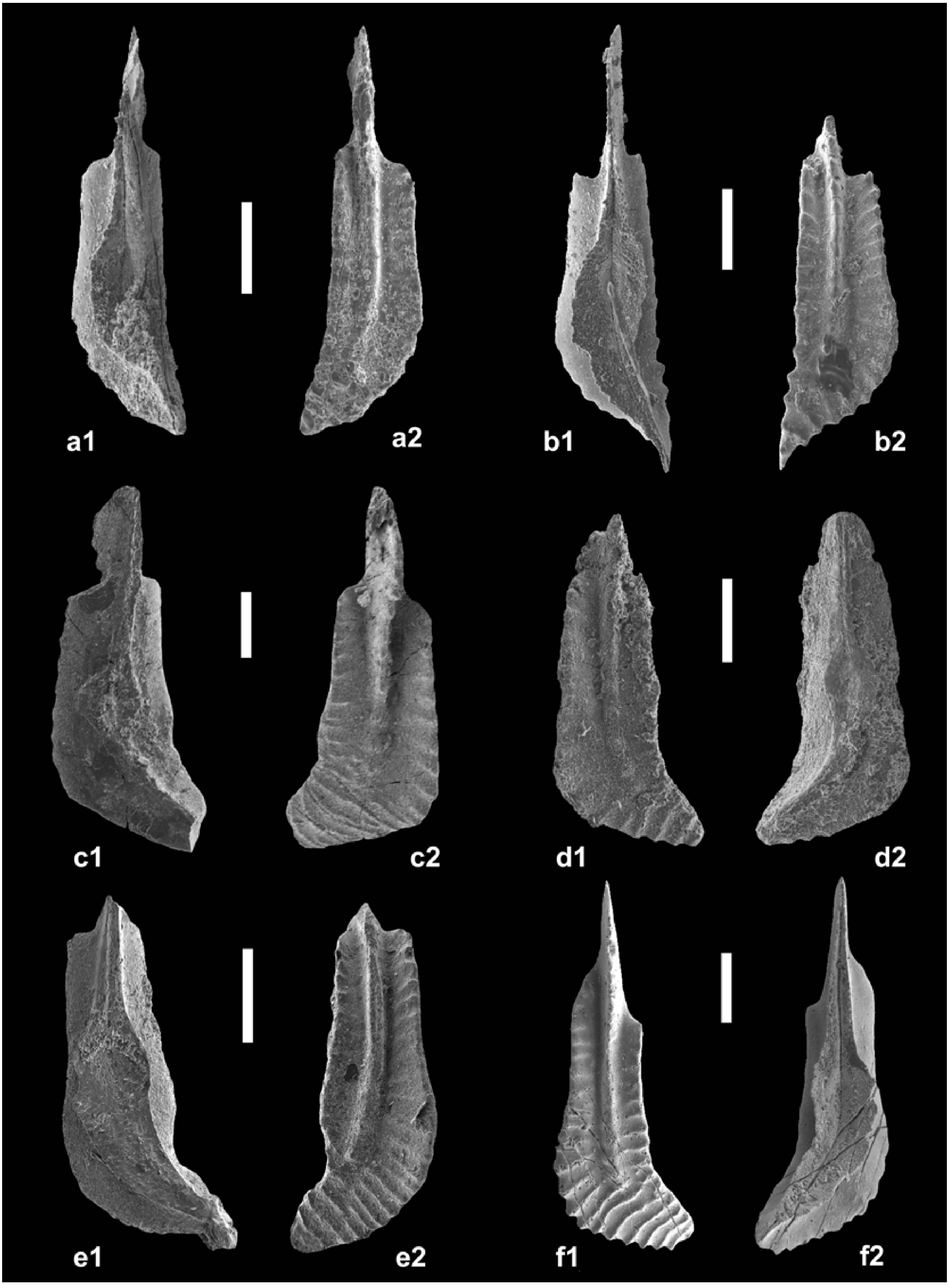
Holotype: MGUV-20.939. Element illustrated in Figure 7d.

Paratypes: MGUV-20.937, MGUV-20.938 and MGUV-20.941 to MGUV-20.943 (Figs 7a–c, 7e–7f).

20 elements from the following sections and beds: CP-I top/2008-210(13), LGA XI/53(3), LGA 6(1), LGA 10(1), Vi-IB/2(1) and Bal 6/61(1). Material referred: MGUV-20.937 to MGUV-20.949 and MGUV-21.300A-G.

Fig. 6.(opposite page) - Emsian conodonts from the Spanish Central Pyrenees. a1-a2) *Polygnathus exc. excavatus* Carls and Gandl, 1969 MGUV-20.889; a1, lower view; a2, upper view; Baliera 6 section Bed 49. b1-b2) *Polygnathus gronbergi* Klapper and Johnson, 1975 MGUV-20.920; b1, lower view; b2, upper view; Baliera 6 section Bed 49. c1-c2) *Polygnathus laticostatus* Klapper and Johnson, 1975 MGUV-20.931; c1, lower view; c2, upper view; LGA section Bed 28. d1-d2) *Polygnathus nothoperbonus* Mawson, 1987 MGUV-20.968; d1, upper view; d2, lower view; LGA section Bed 18. e1-e2) *Polygnathus nothoperbonus* Mawson, 1987 MGUV-20.966; e1, lower view; e2, upper view; CP-I top section Bed 210. f1-f2) *Polygnathus nothoperbonus* Mawson, 1987 MGUV-20.972.; f1, upper view; f2, lower view; Baliera 6 section Bed 50. All scale bars represent 200 µm.

Fig. 6.(página opuesta)- Conodontos del Emsiense de los Pirineos Centrales Españoles. a1-a2) *Polygnathus exc. excavatus* Carls y Gandl, 1969 MGUV-20.889; a1, vista aboral; a2, vista oral; sección Baliera 6 nivel 49. b1-b2) *Polygnathus gronbergi* Klapper y Johnson, 1975 MGUV-20.920; b1, vista aboral; b2, vista oral; sección Baliera 6 nivel 49. c1-c2) *Polygnathus laticostatus* Klapper y Johnson, 1975 MGUV-20.931; c1, vista aboral; c2, vista oral; sección LGA nivel 28. d1-d2) *Polygnathus nothoperbonus* Mawson, 1987 MGUV-20.968; d1, vista oral; d2, vista aboral; sección LGA nivel 18. e1-e2) *Polygnathus nothoperbonus* Mawson, 1987 MGUV-20.966; e1, vista aboral; e2, vista oral; sección CP-I top nivel 210. f1-f2) *Polygnathus nothoperbonus* Mawson, 1987 MGUV-20.972.; f1, vista oral; f2, vista aboral; sección Baliera 6 nivel 50. Todas las escalas representan 200 µm.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Type locality

CP-I top section, in the Noguera-Pallaresa valley (Lérida, Spanish Central Pyrenees).

Type horizon

Bed 210, described in the Villech Fm. of the Compte Subfacies (Spanish Central Pyrenees). Lower Emsian (*nothoperbonus* Zone).

Diagnosis

Pa elements with the following combination of characters: L-shaped platform, with a nearly rectilinear outer edge just before the sharply inward deflection at its posterior third; outer platform more developed in its posterior half; slightly asymmetrical and inverted basal cavity centrally located.

Description

Short free blade, representing approximately one fifth of the total length of the element (Fig. 7d), although in some specimens it may be slightly longer (Fig. 7e). The platform is relatively long and straight, with more or less rectilinear outer edges. The element is slightly asymmetric, with a narrow platform in the anterior region and broadly expanded in the posterior two-thirds. Both platform edges turn sharply inwards at the posterior end, with the outer margin forming an angle of almost 90º (although in some specimens this angle is slightly wider), giving their characteristic L-shape to the element (see, for example, Figs 7d–e), and developing a triangular tongue ornamented by numerous and continuous transversal ridges. The lateral flanks are slightly raised compared to the central part of the element but do not develop a parapet-like structure. The inner and the outer anterior platform edges join the free blade at the same positions with angles close to 90°.

The carina is slightly displaced towards the inner edge and composed by 4-5 rounded denticles laterally compressed. The edges of the platform are ornamented by ribs arranged perpendicular to the carina; some specimens show that several of these ribs are made up of aligned rounded denticles (Fig. 7f1). The ribs at the outer margin are more numerous. The adcarinal troughs are narrow and well developed, being the external slightly wider and longer than the inner one, running both up to the beginning of the tongue ornamentation. In lateral view the platform is practically straight, but slightly bent aborally in the posterior region.

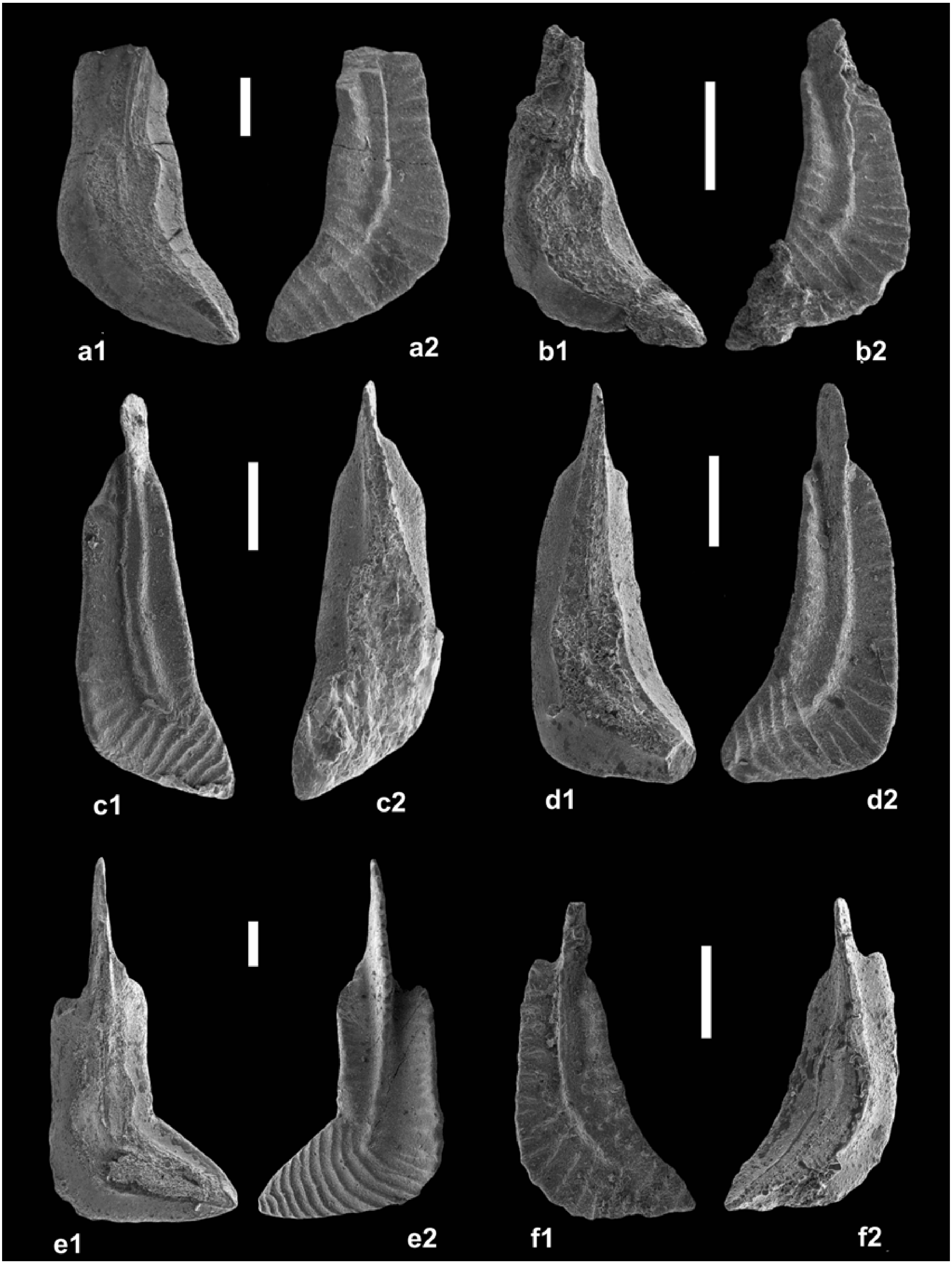
In lower view the shallow basal pit is located centrally just before the inward deflection of the platform. The rest of the basal cavity is inverted and slightly asymmetrical, with strongly marked bands of lamellae on the inverted area.

Discussion

Po. luciae n. sp. is characterized by: its elongated L-shaped platform, having a more developed outer platform in its posterior region; and by a slightly asymmetrical and inverted basal cavity. Numerous specimens with these features have been described in the literature (see list of synonyms), and some of them have been identified as *Po. mashkovae*, probably because the morphological characteristics of *Po. luciae* n. sp. are very similar to *Po. mashkovae* (see Fig. 8). However, *Po. luciae* n. sp. differs clearly from *Po. mashkovae* in that the latter has a marked constriction in the anterior region of the platform, a wider outer platform at the posterior two-thirds and a well developed parapet-like structure, features that are absent or at an early stage of development in *Po. luciae* n. sp. Despite these clear morphological differences, Bultynck (1989) identified many specimens of *Po. luciae* n. sp. at La Grange (Armorican Massif) that he assigned to *Po. mashkovae* (see list of synonyms), even though the

Fig. 7.(next páge)- *Polygnathus luciae* n. sp. Martínez-Pérez and Valenzuela-Ríos from the Spanish Central Pyrenees. a1-a2) *Polygnathus luciae* n. sp.; paratype MGUV-20.937. a1, lower view; a2, upper view; LGA XI section Bed 53; b1-b2). *Polygnathus luciae* n. sp.; paratype MGUV-20.938; b1, lower view; b2, upper view; LGA XI section Bed 53; c1-c2) *Polygnathus luciae* n. sp.; paratype MGUV-20.942; c1, upper view; c2, lower view; CP-I top section Bed 210; d1-d2) *Polygnathus luciae* n. sp.; holotype MGUV-20.939; d1, lower view; d2, upper view, CP-I top section Bed 210; e1-e2) *Polygnathus luciae* n. sp.; paratype MGUV-20.943; e1, lower view; e2, upper view; CP-I top section Bed 210; f1-f2) *Polygnathus luciae* n. sp.; paratype MGUV-20.941; f1, upper view; f2, lower view; CP-I top section Bed 210. All scale bars represent 200 µm.

Fig. 7 (página siguiente).- *Polygnathus luciae* n. sp. Martínez-Pérez y Valenzuela-Ríos de los Pirineos Centrales Españoles. a1-a2) *Polygnathus luciae* n. sp.; paratipo MGUV-20.937. a1, vista aboral; a2, vista oral; sección LGA XI nivel 53; b1-b2). *Polygnathus luciae* n. sp.; paratipo MGUV-20.938; b1, vista aboral; b2, vista oral; sección LGA XI nivel 53; c1-c2) *Polygnathus luciae* n. sp.; paratipo MGUV-20.942; c1, vista oral; c2, vista aboral; sección CP-I top nivel 210; d1-d2) *Polygnathus luciae* n. sp.; holotipo MGUV-20.939; d1 vista aboral; d2, vista oral, sección CP-I top nivel 210; e1-e2) *Polygnathus luciae* n. sp.; paratipo MGUV-20.943; e1 vista aboral; e2, vista oral; sección CP-I top nivel 210; f1-f2) *Polygnathus luciae* n. sp.; paratipo MGUV-20.941; f1, vista oral; f2, vista aboral; sección CP-I top nivel 210. Todas las escalas representan 200 µm.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elements that Bultynck (1989) identified as *Po. mashkovae* do not exhibit the characteristic constriction of their platforms in the anterior region, a feature that differs clearly between the two related species.

As far as the phylogenetic relationships of the new species is concerned, several phylogenetic lineages for Emsian polygnathids have been proposed in the second half of the twentieth century (see e.g., Bardashev, 1986; Bultynck, 1989; Yolkin *et al*., 1994). These lineages are based mainly on stratigraphic and morphological criteria such as the type of ornamentation, the basal cavity size, the development stage of the platform or the adcarinal troughs depth. In accordance with these criteria, *Po. luciae* n. sp. can be included at the base of the lateral branch *Po. luciae* n. sp. – *Po. mashkovae* – *Po. apekinae/Po. vigierei* – *Po. serotinus*, which has already been proposed by previous authors (see Bardashev, 1986; Bultynck, 1989; Yolkin *et al*., 1994) (Fig. 9). Thus, *Po. luciae* n. sp. would be the ancestor of *Po. mashkovae*. This lineage derives from the main stock of the *Po. excavatus* group and is characterized by very asymmetric platforms, with a broad outer platform with a characteristic outline and a high flange-like margin. In addition, the Pa elements of the different taxa belonging to this branch have a well developed tongue ornamented by continuous or interrupted transversal ridges.

Stratigraphical and geographical distribution

Po. luciae n. sp. is recorded within the *nothoperbonus* Zone, its upper range overlaps with the first record of *Po. mashkovae* in the Pyrenees, although according to Bultynck (1989), this taxon could reach the *inversus/laticostatus* Zone.

It has been found in the Pyrenees and Cantabrian Mountains in Spain (García-López and Sanz-López, 2002b; García-López *et al*., 2002); in the Armorican Massif in France (Bultynck and Morzadec, 1979); in the Peloritani Mountains in Sicily (Italy) (Navas-Parejo pers. obs.); in the Urals (Snigireva, 1975; Mashkova and Snigireva, 1980), and in Siberia in Russia (Aksenova, 1987).

Polygnathus mashkovae Bardashev, 1986
Figures 8a–f

1966 *Polygnathus linguiformis* Philip: plate 1, figures 12–14.
1977 *Polygnathus linguiformis faveolata* Philip and Jackson – Al-Rawi: plate 6, figures 56a, b.
1977 *Polygnathus lenzi* Klapper – Al-Rawi: plate 6, figures 62a, b.
?1978 *Polygnathus perbonus* subsp. D Pickett: plate 1, figures 23–25; plate 2, figure 18.
*1986 *Polygnathus mashkovae* n. sp. Bardashev: plate 1, figures 4–11.
1989 *Polygnathus catharinae* n. sp. Bultynck: plate 2, figures 1–12.
1992 *Polygnathus mashkovae* Bardashev – Bardashev and Ziegler: plate 4, figure 33.
2002 *Eolinguipolygnathus mashkovae* Bardashev – Bardashev *et al*.: text-figures 15: 15, 16.
2002 *Eolinguipolygnathus catharinae* Bultynck – Bardashev *et al*.: text-figure 15.27.
2002 *Polygnathus mashkovae* Bardashev transitional to *Polygnathus viegerei* Bultynck – García-López *et al*.: plate 5, figures 23, 24.

Material

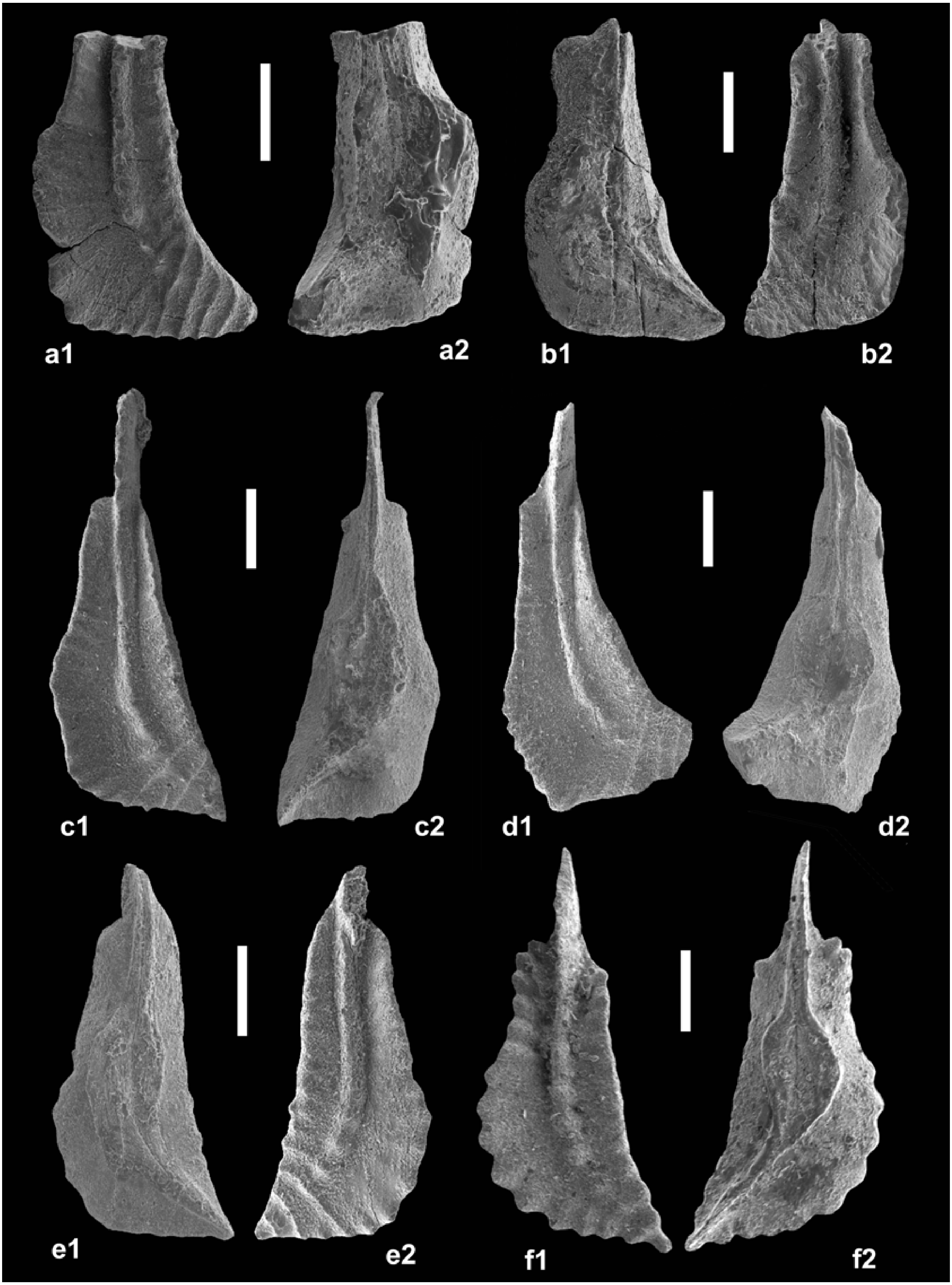
22 elements from the following sections and beds: CP-I top/212(1), CP-I top/213(1), LGA/8(2), LGA/10(10), LGA/11(1), LGA/12(1), LGA/24c(5) and Vi-IB/29(1). Material referred: MGUV-20.950 to MGUV-20.964, MGUV-21.306A-D and MGUV-21.307A-B.

Remarks

Specimens from the Pyrenees assigned to *Po. mashkovae* have a characteristic asymmetric platform, with a narrow anterior third and a broadly expanded platform at the posterior two-thirds. In addition, the edge of the outer platform develops a constriction in the anterior half and a high, flange-like structure at the outer edge of its posterior half. The tongue, with continuous transverse ridges, is markedly deflected inwards. In lower view, the basal cavity is expanded beneath the platform, before the rounded

Fig. 8 (next page).- *Polygnathus mashkovae* from the Spanish Central Pyrenees. a1-a2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.950; a1, upper view; a2, lower view; CP-I top section Bed 212. b1-b2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.951; b1, lower view; b2, upper view; CP-I top section Bed 213. c1-c2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.954; c1, upper view; c2, lower view; LGA section Bed 10. d1-d2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.955; d1, upper view; d2, lower view; LGA section Bed 10. e1-e2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.956; e1, lower view; e2, upper view, LGA section Bed 10. f1-f2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.957; f1, upper view; f2, lower view; Vi-IB section Bed 29. All scale bars represent 200 μm.

Fig. 8 (página siguiente).- *Polygnathus mashkovae* de los Pirineos Centrales Españoles. a1-a2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.950; a1, vista oral; a2, vista aboral; sección CP-I top nivel 212. b1-b2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.951; b1, vista aboral; b2, vista oral; sección CP-I top nivel 213. c1-c2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.954; c1, vista oral; c2, vista aboral; sección LGA nivel 10. d1-d2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.955; d1, vista oral; d2, vista aboral; sección LGA nivel 10. e1-e2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.956; e1, vista aboral; e2, vista oral, sección LGA nivel 10. f1-f2) *Polygnathus mashkovae* Bardashev, 1986 MGUV-20.957; f1, vista oral; f2, vista aboral; sección Vi-IB nivel 29. Todas las escalas representan 200 μm..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or sharp inward deflection of the posterior platform, and is clearly inverted.

Our specimens are very similar to the original material described by Bardashev (1986: pl. 1, figs. 4–11). On the other hand, Bultynck (1989: pl. 2, figs. 1–12), described the new species *Po. catharinae* on the basis of material from La Grange (Armorican Massif) and, as he commented (Bultynck, 1989: p. 183), *Po. catharinae* resembles *Po. mashkovae* very closely. Both taxa present a characteristic asymmetric platform, with a broadly expanded platform at the posterior two-thirds, high flange-like structure at the outer edge and a well developed constriction in the anterior region of the platform. In the light of all the above, we believe that the forms that Bultynck (1989) identified as *Po. catharinae* belong in fact to *Po. mashkovae*, and therefore *Po. catharinae* is a junior synonym of this latter species. Furthermore, and after studying the material from the Pyrenees, we believe that the specimens that Bultynck (1989) identified as *Po. mashkovae* are actually the new species described here as *Po. luciae* n. sp., which is easily distinguishable from *Po. mashkovae* (see *Po. luciae* n. sp. discussion).

Stratigraphical and geographical distribution

Po. mashkovae is recorded from the mid *nothoperbonus* Zone to the *inversus/laticostatus* Zone. This taxon is used here to subdivide the *nothoperbonus* Zone into the Lower and Upper *nothoperbonus* subzones, indicating the first record of *Po. mashkovae* the base of the Upper *nothoperbonus* subzone (see the Discussion section below).

This species has been found in the Pyrenees and Cantabrian Mountains in Spain (García-López *et al.*, 2002); in the Armorican Massif in France (Bultynck, 1989); in Frankenwald in Germany (Al-Rawi, 1977); in the Peloritani Mountains in Sicily (Italy) (Navas-Parejo pers. obs.) and in Tajikistan, Central Asia (Bardashev, 1986; Bardashev and Ziegler, 1992).

Polygnathus nothoperbonus Mawson, 1987
Figures 6d–f

1974 *Polygnathus foveolata* Philip and Jackson – Lütke: text–figure 4, figures 1–3.
1975 *Polygnathus foveolata* Philip and Jackson – Snigireva: plate 4, figure 6.
1975 *Polygnathus* aff. *Po. perbonus* Klapper and Johnson: plate 2, figures 1–10.
?1979 *Polygnathus* aff. *perbonus* Klapper and Johnson – Lane and Ormiston: plate 8, figures 26, 27.
1980 *Polygnathus* aff. *perbonus* Klapper and Johnson – Uyeno and Klapper: plate 8.1, figures 5, 6; plate 8.3, figures 11, 12.
1985 *Polygnathus* aff. *perbonus* Klapper and Johnson – Ziegler and Wang: plate 1, figure 6.
*1987 *Polygnathus nothoperbonus* n. sp. Mawson: text-figures 8 A and B; plate 32, figures 11–15; plate 33, figures 1, 2; plate 36, figure 7.
1987 *Polygnathus dehiscens* Philip and Jackson – *Po. nothoperbonus* Mawson – Mawson: plate 32, figures 8–10.
1989 *Polygnathus nothoperbonus* Mawson – Bultynck: plate 1, figure 13; plate 4, figures 1–5.
1992 *Polygnathus perbonus* Philip – Bonceva: plate 4, figures 4–6.
1992 *Polygnathus nothoperbonus* Mawson – Mawson *et al*.: figures 7 O–P, figures 8 B–D.
1992 *Polygnathus dehiscens* Philip and Jackson – *nothoperbonus* Mawson – Mawson *et al*.: figure 8A.
v1994 *Polygnathus nothoperbonus* Mawson – Yolkin *et al*.: plate 1, figures 16–17 (with synonymy list).
1995 *Polygnathus nothoperbonus* Mawson – Colquhoun: plate 1, figures 7, 8.
2002 *Eolinguipolygnathus nothoperbonus* Mawson – Bardashev *et al*.: text–figure 15.19.
2002 *Polygnathus nothoperbonus* Mawson – García-López *et al*.: plate 5, figures 25, 26.
?2002b *Polygnathus nothoperbonus* Mawson; García-López and Sanz-López: pl. 1, figs. 15–16.
2003 *Polygnathus nothoperbonus* Mawson – Mawson and Talent: plate 1, figures 1–4.

Material

25 elements from the following sections and beds: Bal 6/49(4), Bal 6/50(8), LGA XI/45a(1), LGA XI/48(1), LGA XI/53(1), LGA/10(1), LGA/18(2), CP-I top/205b(2), CP-I top/210(2) and Vi-IB/25(3). Material referred: MGUV-20.965 to MGUV-20.989.

Remarks

Po. nothoperbonus has a long, narrow platform, with its outer and inner edges running more or less parallel in the anterior two-thirds, where there is no high flange-like development of the outer edge, and a short tongue deflected inwards and bearing either interrupted or continuous ridges. The platform surface is ornamented by short transverse ridges distributed perpendicularly to the platform edges. The basal cavity is variable in size, though the posterior end is always inverted or flattened.

Mawson (1987) described *Po. nothoperbonus* as a new species on the basis of material from Victoria (Australia) and Lone Mountain in Nevada (USA). According to Mawson, *Po. nothoperbonus* is distinguishable from *Po. perbonus* mainly by the beginning of the inversion of the basal cavity in *Po. nothoperbonus* and the extra depth of this structure in *Po. perbonus*. In addition, *Po. nothoperbonus* differs from *Po. luciae* n. sp. and *Po. mashkovae* in the characteristic asymmetric platforms of these spe-

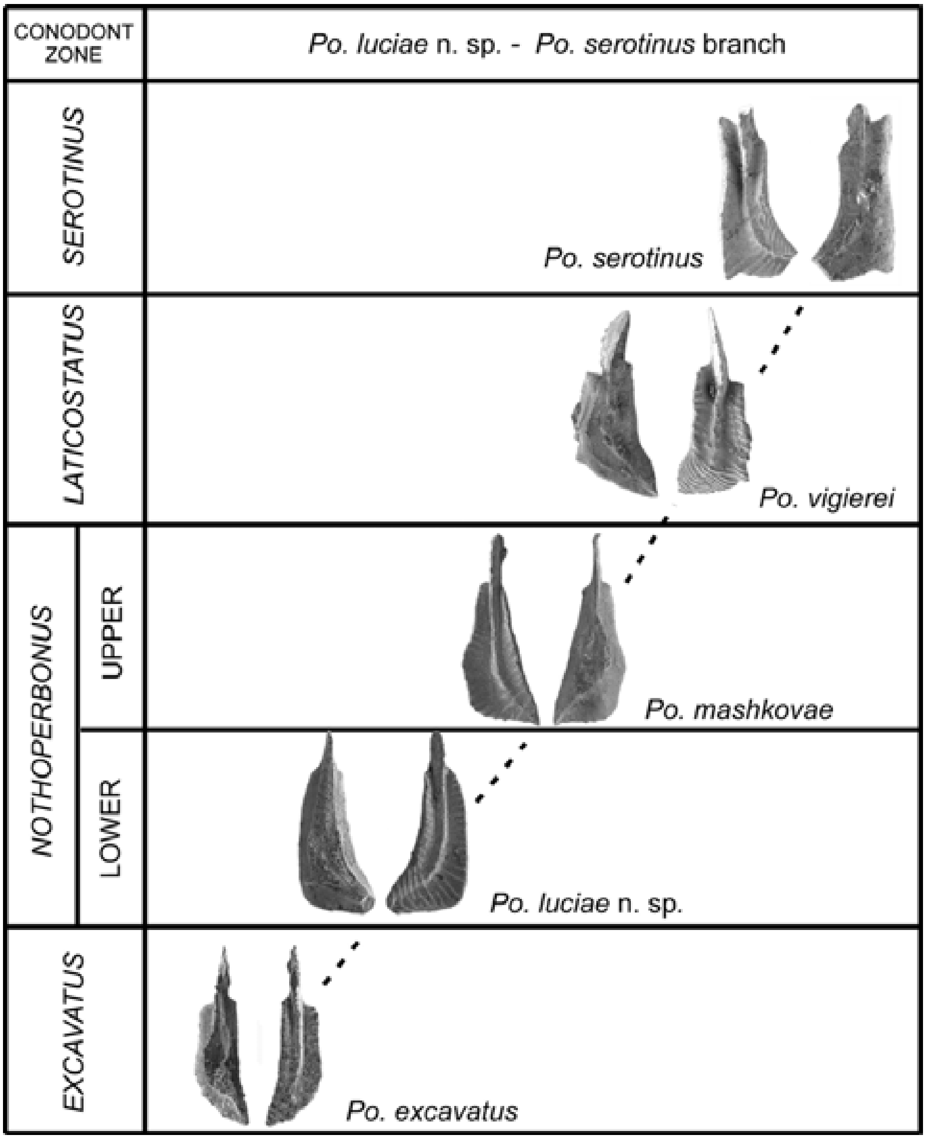

Fig. 9.- *Po. luciae* n. sp.– *Po. mashkovae – Po. apekinae/Po. vigierei – Po. serotinus* linage (see Bardashev, 1986; Bultynck, 1989; Yolkin *et al.*, 1994). This lateral branch derives from the main stock of the *Po. excavatus* group and is characterized by very asymmetric platforms with a well developed tongue ornamented either by continuous or interrupted tranversal ridges. Elements figured: *Po. exc. excavatus* (MGUV-20.889), *Po. luciae* n. sp. (MGUV-20.939), *Po. mashkovae* (MGUV-20.954), *Po. vigierei* (MGUV-21.087) and *Po. serotinus* (MGUV-21.084) from the Spanish Central Pyrenees.

Fig. 9.- Linaje *Po. luciae* n. sp.– *Po. mashkovae – Po. apekinae/Po. vigierei – Po. serotinus* (ver Bardashev, 1986; Bultynck, 1989; Yolkin *et al.*, 1994). Esta rama lateral deriva del stock principal del grupo *Po. excavatus* (Yolkin *et al.*, 1994), y está caracterizado por plataformas muy asimétricas con una lengüeta muy bien desarrollada, la cual está ornamentada por crestas transversales continuas o interrumpidas. Elementos figurados: *Po. exc. excavatus* (MGUV-20.889), *Po. luciae* n. sp. (MGUV-20.939), *Po. mashkovae* (MGUV-20.954), *Po. vigierei* (MGUV-21.087) y *Po. serotinus* (MGUV-21.084) de los Pirineos Centrales Españoles.

cies compared to the straight and narrow platform of *Po. nothoperbonus*.

Stratigraphical and geographical distribution

Po. nothoperbonus is the conodont index of the *nothoperbonus* Zone, *sensu* Yolkin *et al.* (1994). It is recorded from the base of the *nothoperbonus* Zone to the *inversus/laticostatus* Zone.

Po. nothoperbonus has a wide geographical distribution. It has been found in the Pyrenees and Cantabrian Mountains in Spain (García-López *et al.*, 2002; García-López and Sanz-López, 2002b); in the Armorican Massif in France (Bultynck, 1989); in Bulgaria (Bonceva, 1992); in the Urals in Russia (Snigireva, 1975; Mashkova and Snigireva, 1980); in eastern (Guangxi, China) (Ziegler and Wang, 1985) and central Asia (Zinzilban, Uzbekistan) (Yolkin *et al*., 1994); in Nevada (Klapper and Johnson, 1975) and Alaska in USA (Lane and Ormiston, 1976); in Canada (Uyeno and Klapper, 1980); and in several Australian localities (Mawson, 1987; Mawson *et al.*, 1992; Colquhoun, 1995).

4. Discussion

4.1. Emsian Zonal Scheme.

Among the diverse Emsian zonations, the one based on the successive occurrence of different species of the genus *Polygnathus* is the most commonly used for biostratigraphical subdivisions and world-wide correlations (see, for example, Klapper and Johnson, 1975; Klapper, 1977; Weddige and Ziegler, 1977; Lane and Ormiston, 1979; Yolkin *et al.*, 1994, Bardashev *et al*., 2002). The phylogeny of the Early Devonian polygnathids has been accepted as the basis for this conodont zonation, however, this subdivision has been hotly debated and several proposals have been put forward by various authors over recent years (see Mawson, 1995 for a historical review).

Since the original proposal of Klapper and Johnson (1975), the most important and problematic changes in the Emsian zonal scheme have been suggested by Yolkin *et al*. (1994) and Bardashev *et al*. (2002). On the basis of the polygnathid sequences found in Zinzilban (central Asia), Yolkin *et al*. (1994) proposed a new zonation for the Early Emsian. This proposal substantially changed the lower Emsian zones, replacing the former *dehiscens* and *gronbergi* zones with the *kitabicus*, *excavatus*, and *nothoperbonus* zones. However, the most controversial proposal was that of Bardashev *et al.* (2002). On the basis of new polymorphogenetic lineages introduced by themselves, these authors suggested up to three alternative conodont-based zonations for the Pragian and Emsian stages. Their correlation bears big mistakes and conceptual errors that produced misleading results and impracticability. As a consequence, these zonations have been questioned by several authors (Mawson and Talent, 2003; Murphy, 2005; Slavík *et al*., 2007), who pointed out serious discrepancies in their concept of taxonomy and zonation. All these authors criticised the procedure of Bardashev *et al.* (2002), who chose only single-figured specimens from the literature without any biostratigraphic control, introducing, as a consequence, important errors into the stratigraphic position of some individual taxa. We agree with these criticisms and prefer to follow the scheme of Yolkin *et al.* (1994) to subdivide the lower Emsian in the Spanish Central Pyrenees.

This report is focused almost exclusively on the *nothoperbonus* Zone, which was defined by Yolkin *et al*. (1989, 1994) to replace partially the previous *gronbergi* Zone of Klapper and Johnson (1975). Mawson (1995) pointed out, however, that these two zones were virtually equivalent, a proposal upheld by the almost simultaneous occurrence of *Po. gronbergi* and *Po. nothoperbonus* in several regions and sections: both taxa appear for the first time at level 55 in locality 1 of Salmontrout (Alaska, USA) (Lane and Ormiston, 1979). In section A of the La Grange Limestone in the Armorican Massif in France, Bultynck (1989) described the first occurrence of *Po. gronbergi* in sample 0, and slightly above (15 cm), the first record of *Po. nothoperbonus* in sample 1, although, as he commented, the sequence is markedly condensed. The almost synchronicity of both taxa is also observed in the Pyrenean section Baliera-6, there, *Po. gronbergi* appears in Bed 48, and *Po. nothoperbonus* is registered slightly above (40 cm), in Bed 49 (Fig. 5). Additionally, as Mawson (1995) discusses, these two zones (*gronbergi* and *nothoperbonus*) are also equivalent to the *perbonus* Zone. *Po. perbonus* (the index of the *perbonus* Zone or Upper *exacatus* Subzone of Yolin *et al*., 1994) is registered together with *Po. nothoperbonus* in Australia (Mawson, 1987) and the Zeravshan Range in Asia (Apekina and Mashkova, 1978). In addition, the co-occurrence of *Po. perbonus* and *Po. gronbergi* has been documented as well in correlative strata in Bohemia (Czech Republic) (Klapper, 1977; Klapper *et al.*, 1978) and China (Bardashev and Ziegler, 1992).

In the Pyrenees, due to the apparent lack of *Po. perbonus,* the scarcity of *Po. gronbergi* and the relative abundance of *Po. nothoperbonus* in the different sections studied, we use the *nothoperbonus* Zone to identify the interval between the *excavatus* and the *laticostatus* zones, including the Upper *excavatus* Subzone of Yolkin *et al.* (1994) within the *nothoperbonus* Zone (see also Mawson, 1995).

4.2. The nothoperbonus *Zone Subdivision.*

As commented above, the *nothoperbonus* Zone was defined by Yolkin *et al*. (1989, 1994) to replace partially the previous *gronbergi* Zone of Klapper and Johnson (1975). Additionally, Bultynck (1989) recognised the *gronbergi* Zone in section A at La Grange in the Armorican Massif, a biozone which he subdivided into the Upper and Lower *gronbergi* subzones, identifying the boundary between the two subzones with the first record of *Polygnathus catherinae*. Following the original idea of Bultynck (1989), we use *Po. mashkovae s. s.* (but not *Po. catherinae* or *Po. mashkovae sensu* Bultynck, 1989) for subdividing the *nothoperbonus* Zone into the Lower and Upper *nothoperbonus* subzones.

This subdivision is supported by the biostratigraphic dates from the Spanish Central Pyrenees (see Figs. 2–5). Among these records, we draw attention to the occurrence of different *Polygnathus* species (*Po. excavatus excavatus, Po. gronbergi, Po. laticostatus, Po. mashkovae, Po. nothoperbonus* and the new species described here, *Po. luciae* n. sp.), all of which, are important biostratigraphic markers (see the ranges of the conodont taxa selected for the interval studied in Figs. 2–5). According to these records, *Po. nothoperbonus* has been registered in all five sections studied, marking in LGA-XI, CP-I top, and Bal 6 sections (Figs. 2, 3 and 5), the base of the Lower *nothoperbonus* Subzone. In the lower part of this subzone, in all the sections studied, *Po. luciae* n. sp. appears slightly above the first record of *Po. nothoperbonus*, so the lowest record of that taxon took place in the lower part of the *nothoperbonus* Zone. *Po. mashkovae* is first registered in the middle parts of the *nothoperbonus*

Zone in LGA, CP-I top and Vi-IB sections (see Figs. 2, 3 and 4), and always above the first records of *Po. luciae* n. sp., although both taxa briefly overlap (see Fig. 2). This consistent distribution has already been reported in other regions such as France (Bultynck, 1989), Morocco (Bultynck and Hollard, 1980) and Italy (Navas-Parejo pers. obs.) and strongly supports the *nothoperbonus* Zone subdivision proposed here. In the Pyrenees, the top of this zone has been identified only in the middle parts of the LGA section with the first record of *Po. laticostatus*, the index of the overlying conodont zone (Fig. 2).

5. Concluding remarks

We have recovered a significant conodont assemblage from five Pyrenean Lower Devonian (Emsian) sections (LGA, LGA-XI, CP-I top, Vi-IB and Bal 6), but only those conodonts with biostratigraphic relevance around the *nothoperbonus* Zone are discussed herein. Among these conodonts, the occurrence of different *Polygnathus* species, such as *Po. excavatus excavatus*, *Po. gronbergi*, *Po. nothoperbonus*, *Po. mashkovae*, *Po. laticostatus* and *Po. luciae* n. sp., stand out. According to these records, we have identified the Emsian *excavatus*, *nothoperbonus* and *laticostatus* zones and, subdivided the *nothoperbonus* Zone into the Lower and Upper *nothoperbonus* subzones by the entry of *Po. mashkovae s.s*. This subdivision is supported by the biostratigraphic data from the Spanish Central Pyrenees and corroborated by the consistent distribution of these conodont markers in other regions such as France (Bultynck, 1989), Morocco (Bultynck and Hollard, 1980) and Italy (Navas-Parejo pers. obs.).

In addition, the new species described in this paper, *Polygnathus luciae* n. sp., appears slightly above the first records of *Po. nothoperbonus* and, thus, the first record of that taxon would indicate a lower Emsian, early *nothoperbonus*, age. Moreover, *Po. luciae* n. sp. can be included at the base of the lateral branch of the following phylogenetically succession (Fig. 9): *Po. mashkovae – Po. apekinae/Po. vigierei – Po. serotinus* already proposed by previous authors (see Bardashev, 1986; Bultynck, 1989; Yolkin *et al*., 1994); all these conodonts are characterized by very asymmetric platforms.

Furthermore, all these data, revealing important widespread conodont markers, allow a close correlation of this Pyrenean conodont succession with other successions in Alaska (Lane and Ormiston 1979) and Nevada (Klapper and Johnson, 1975) in North America, north-western France (Bultynck, 1989), central Asia (Yolkin and Izokh, 1988; Yolkin *et al.*, 1994, Apekina and Mashkova, 1978) and in Australia (Mawson, 1987, 1995).

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