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New Lower Devonian Polygnathids (Conodonta) from the Spanish Central Pyrenees, with comments on the early radiation of the group

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Abstract

The comprehensive study of six Pragian-lower Emsian (Lower Devonian) sections from the Spanish Central Pyrenees has yielded a rich assemblage of conodont faunas, highlighting an important succession of *Polygnathus* species. Among them, the presence of the biostratigraphical markers *P. pireneae*, *P. kitabicus, P. excavatus excavatus* and *P. exc.* 114 stands out. This conodont succession allows the identification of the Pragian/Emsian boundary and the early Emsian zones and subzones: the *kitabicus* Zone and the Lower and Middle *excavatus* subzones. It is also remarkable the presence of three new polygnathid species: *P. aragonensis* n. sp., *P. carlsi* n. sp. and *P. ramoni* n. sp. Additionally, *P. pannonicus* and *P. sokolovi* are also reported for first time in the Iberian Peninsula. According to all these records, the abundance and diversity of these species suggest that during this time interval an evolutionary radiation of the group took place, identifying two pulses during the early radiation of the group. The first one during the *pireneae-kitabicus* Zone, and a second one during the Lower *excavatus* Zone. The new data presented herein increase considerably the known paleobiodiversity of the genus during the Pragian-early Emsian interval in the Spanish Central Pyrenees and corroborates the presences of the most important early Emsian conodont markers used in other regions such us Europe, North Africa, Central Asia, Australia, and North America.

Keywords: Conodonts, *Polygnathus,* Emsian, Paleobiodiversity, Spanish Central Pyrenees

Resumen

El estudio en profundidad de seis secciones de edad Emsiense (Devónico Inferior) del Pirineo Central español ha proporcionado una rica asociación de conodontos, destacando una importante sucesión de especies del género *Polygnathus*. Entre ellos, resalta la presencia de los marcadores bioestratigráficos *P. pireneae*, *P. kitabicus*, *P. excavatus excavatus* y *P. exc*. 114. Esta sucesión de conodontos permite la identificación del límite Praguiense/Emsiense, así como de las principales zonas del Emsiense temprano: la Zona *kitabicus* y las subzonas *excavatus* Inferior y Media. También es destacable la presencia de tres nuevas especies de polygnátidos: *P. aragonensis* n. sp., *P. carlsi* n. sp. y *P. ramoni* n. sp.; junto con la primera referencia en la Península Ibérica de las especies *P. pannonicus* y *P. sokolovi*. De acuerdo con estos resultados, la abundancia y diversidad de estas especies sugiere que durante este intervalo temporal se produjo una radiación evolutiva del grupo, identificando dos momentos de la misma durante la evolución temprana del grupo. El primero durante el intervalo *pireneae-kitabicus*, y el segundo durante la Zona *excavatus* Inferior. Los nuevos datos presentados en este trabajo incrementan considerablemente la paleobiodiversidad conocida del género durante el Praguiense final y comienzos del Emsiense en el Pirineo Central español, y corrobora la presencia de los principales marcadores biostratigráficos del Emsiense inferior registrados en otras regiones como Europa, norte de África, Asia Central, Australia y América del Norte.

Palabras clave: Conodontos, *Polygnathus*, Emsiense, Paleobiodiversidad, Pirineos Centrales Españoles

1. Introduction

Conodonts, owing to their wide geographical distribution and their fast morphological evolution have been applied with great success for dating and correlating marine rocks from the Cambrian to the Triassic Periods. For specific time intervals, some groups of conodonts have demonstrated to be extremely good biomarkers. In that sense, Devonian polygnathid species have been extensively used in establishing boundaries between different stages and substages, being especially useful for the Emsian conodont-based zonal subdivision (see for example Klapper and Johnson, 1975; Klapper, 1977; Weddige and Ziegler, 1977; Lane and Ormiston, 1979; Yolkin *et al*., 1994; Mawson, 1995; Bardashev *et al*., 2002, Martínez-Pérez *et al.,* 2011).

The genus *Polygnathus* evolved during the Pragian (early Pragian in traditional sense, Valenzuela-Ríos, 1997) from the *Eognathodus* group (Klapper and Philip, 1972; Cooper, 1973; Klapper and Johnson, 1975). For decades, the earliest *Polygnathus* species was *P. pireneae* from the Lower Devonian strata of the Spanish Central Pyrenees (Boersma, 1973). However, more recently some authors have included two Pragian *Eognathodus* species, *Eognathodus trilinearis zeravshanicus* (Bardashev and Ziegler, 1992) and *Eognathodus trilinearis* (Cooper, 1973) as primitve *Polygnathus* (*P. zeravshanicus* and *P. trilinearis* respectively) (see Mawson *et al*., 1992; Mawson, 1998). All these basal *Polygnathus* species appeared during the early Pragian (Valenzuela-Ríos, 1997), but they underwent their great diversification during the early Emsian, becoming in important components of the conodont fauna during this time interval. This diversification has been described by Yolkin *et al*. (1994, 2008) and Izokh *et al.* (2011) in the Emsian stratotype area (Zinzilban, Uzbekistan, Central Asia), showing an important radiation of the species of the genus during the *kitabicus* and *excavatus* zones; this diversification, until now, had been exclusively recorded there.

During the last years, we have conducted an exhaustive research of the lower Emsian rocks from the Spanish Central Pyrenees. This study has yielded a significant assemblage of conodont faunas, which allows the recognition of an important *Polygnathus* radiation in the region, with the presence of different cosmopolitan and endemic species. Therefore, the main purposes of this paper are to describe this pyrenean lower Emsian polygnathid assemblage including the description of three new species of the genus *Polygnathus*, and to discuss the radiation this genus underwent during its early evolutionary stage.

2. Material Provenance

All the studied material comes from six sections that belong to the extensive Southern Facies-area of the Spanish Central Pyrenees defined by Mey (1967a) (Fig. 1). This Facies-area can be further subdivided into four smaller "subfacies-areas": Sierra Negra, Baliera, Renanué and Compte (Mey, 1967a, b, 1968; Hartevelt, 1970; Valenzuela-Ríos and Liao, 2006); the six sections herein studied belong exclusively to the Baliera and Compte subfacies-areas. Two sections belong to the Baliera Subfacies-area of Mey (1967a, 1968): the Baliera 6 section (Bal-6) and the Isábena 1 section (Isb-1), located in the Baliera and Isábena valleys respectively (Fig. 1). These sections were studied originally by Valenzuela-Ríos (1994, 2001) and both have been described from strata of the Llaviero Mbr. of the Basibé Fm., characterized by dominant blue-grey, platy limestone with few thicker bedded limestone and shale intercalations.

Other four sections have been described within the Compte Subfacies-area (Mey, 1967a; Hartevelt, 1970) (see Fig. 1): La Guardia d'Àres sections (LGA-X and LGA-XI) located in the proximity of La Guardia d'Ares; the upper part of Compte-I section (CP-I top) situated near the village of Gerri de la Sal; and the Villech-IA section (Vi-IA) close to the hamlet of Villech. These sections include rocks from the top of the Castanesa Fm., characterized by dark-grey, platy limestones, and the lower part of the Villech Fm. (made up of red and green nodular limestones with intercalated red carbonaceous shales). The sections LGA-X, LGA-XI and Vi-IA also expose the local Castells Beds unit in the lower part of the Villech Fm., which is characterized by brownish, platy limestones with numerous millimetric to centimetric intercalations of brown shales (see Martínez-Pérez, 2010a for a detailed stratigraphical and geographical descriptions). All the sections were sampled for conodonts. The positions of the samples in these six sections are shown in figures 2 to 7 (black dots) together with the stratigraphical ranges of the conodont taxa studied.

3. Systematic Palaeontology

Conodonts are characterized by a complex oral apparatus commonly composed of 13-17 individual elements. This apparatus is divided into an anterior set of structurally similar elements designated as S elements, a related set with a different structure called the M elements, and a posterior and more robust P elements (Pa and Pb respectively). Our work is entirely focused in the Pa elements, which rapid evolution has become in the base for the systematic of the group, including the genus *Polygnathus*.

All specimens discussed herein appear as isolated elements after the dissolution of carbonate rocks with formic acid (5–10%), and they are deposited at the Museum of Geology of University of Valencia (MGUV).

The abbreviations used indicate the section, bed and number of specimens of the material studied. Thus, Bal-6, Isb-1, CP-I top, Vi-IA, LGA-X and LGA-XI indicate the sections (see abbreviations in the Material Provenance section), the following number separated by a slash ("/") indicates the bed, and the numbers in parentheses correspond to the numbers of elements in this bed. The synonym list just shows the most important references.

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

Polygnathus aragonensis n. sp.
(Figs. 8a-d)

Derivatio nominis

Named after the Crown of Aragón, Spain, as the horizon and type locality of the species are near the origin-town of the Aragón Kingdom.

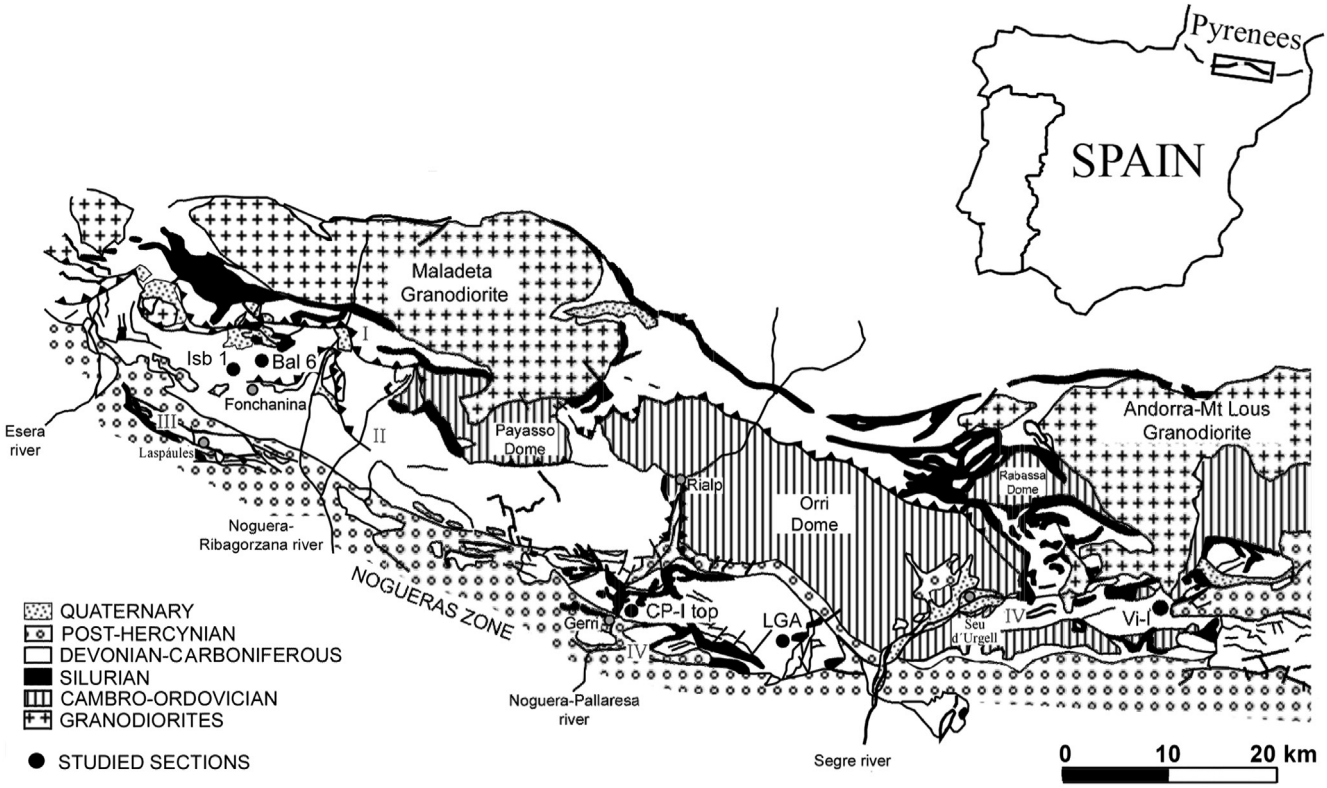


Fig. 1.- Geological scheme of the study area in the Central Spanish Pyrenees, indicating the four Subfacies areas contained in the Palaeozoic outcrops in the Southern Facies-area of Mey (1967): I) Sierra Negra Subfacies, II) Baliera Subfacies, III) Renanué Subfacies and IV) Compte Subfacies; together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

Material

Holotype: MGUV-20.854, element illustrated in figure 8a.

Paratypes: MGUV-20.849, MGUV-20.853 and MGUV-20.856. Elements illustrated in Figures 8b-d.

19 Pa elements from the following sections and beds: Isb-1/10M(10), Bal-6/23(1), Bal-6/34(1), Bal-6/43a(1), Bal-6/49(3), Bal-6/60d(1), Bal-6/62(1) and LGA-XI/6(1). Referred material: MGUV-20.849 to MGUV-20.867.

Type locality

Isábena 1 section, in the Isábena Valley (Huesca, Aragonian Pyrenees).

Type horizon

Bed 10M, described in the Llaviero Member of the Basibé Fm. from the Basibé Sufacies-area (Southern-facies area, Aragonian Pyrenees).

Diagnosis

Pa element with the following combination of characters: flat platform with poorly developed adcarinal troughs in the anterior half; marked inner inflexion on platform posterior half; platform ornamented by rounded nodes; inner anterior platform margin joints the free blade in a markedly posterior position with respect to the outer margin; and always with angles greater than 90º.

Description

Pa element upper view: free blade about 1/4 of the element total length (Fig. 8d). Anterior carina formed by at least 9 rounded denticles, laterally compressed and partially fused in the anterior part of the platform (Fig. 8d). Posterior carina located at the centre of the platform with 4-7 rounded denticles that reaches the end of the element. Platform clearly bent inward with a sharp angle in the outer platform margin (Figs. 8a-c). The platform anterior margins meet the free blade at angles clearly greater than 90°. Inner margin always meets free blade in a position markedly anterior than the outer one. Oral surface platform margins ornamented by rounded nodules vaguely thicker than those of the central carina (Figs. 8a1, b1, c2); in some specimens are slightly compressed laterally (Fig. 8d2). Weak adcarinal troughs only in the most anterior region of the platform. Pa element lateral view: element predominantly straight, bent aborally in the posterior region. Pa element lower side: slightly asymmetrical and deep basal cavity, occupying most of the lower surface, being the outer lip more developed than the inner. Basal cavity margins do not protrude the platform margins in most specimens; but in some specimens show slightly protrusion (Fig. 8b). Basal cavity continues anterior and posteriorly by narrow and deep

furrows, with the tip of the basal cavity sited in the anterior part of the element.

Discussion

The morphological features above described placed *P. aragonensis* n. sp. within the stock of primitive species within the genus, very close to other taxa such as *P. pireneae, P. kitabicus* and *P. sokolovi,* all characterized by the absence or poorly development of adcarinal troughs, by the position and angles of the margins-platform junction, by its ornamentation represented basically by individual nodes, and by the great development of the basal cavity, being fully expanded.

P. aragonensis is close to *P. pireneae*. However, the former has a stronger inner bent, and smaller basal cavity with no protrusion of basal margins.

P. sokolovi and *P. kitabicus* have better developed adcarinal troughs and more restricted basal cavities than *P. aragonensis* n. sp. Besides, *P. kitabicus* bears well individualized rounded nodules, in contrast with the small ridges of *P. aragonensis* n. sp.

Stratigraphical and geographical distribution

P. aragonensis n. sp. ranges from the Lower *excavatus* Subzone to the *nothoperbonus* Zone (lower Emsian). It has been only found in the Spanish Central Pyrenees.

Polygnathus carlsi n. sp.
(Figs. 8e-h)

v1994 *Polygnathus dehiscens* Philip and Jackson – Valenzuela-Ríos: plate 8, figure 36.

1995 *Polygnathus kitabicus* Yolkin *et al*. – Kalvoda: plate 2, figure 9.

v2005 *Polygnathus kitabicus* Yolkin *et al*. – Martínez-Pérez and Valenzuela-Ríos: plate 1, figure 6.

Derivatio nominis

To honor Prof. Dr. Peter Carls (Technische Universität Braunschweig, Germany) for his outstanding work in increasing the knowledge about the Devonian System and to foster cooperation.

Material

Holotype: MGUV-20.868. Element illustrated in figure 8e.

Paratypes: MGUV-20.869 and MGUV-20.872. Elements illustrated in figure 8f-h.

15 Pa elements from the following sections and beds: Isb-1/10M(2), Isb-1/13C(2), Bal-6/6(1), Bal-6/9(1), Bal-6/14(1), Bal-6/16(2), Bal-6/32(1), Bal-6/49(2) and LGA-X/36(3). Referred material: MGUV-5.285, MGUV-20.868 to MGUV-20.881.

Type locality

Isábena 1 section, in the Isábena Valley (Huesca, Aragonian Pyrenees).

Type horizon

Bed 10M, described in the Llaviero Member of the Basibé Fm. from the Basibé Sufacies-area (Southern-facies area, Aragonian Pyrenees).

Diagnosis

Based on Pa elements with a characteristic platform outline: straight inner margin and sinuous outer margin, with its edge slightly concave in the anterior region and convex in the mid-posterior region. The carina is positioned closer to the inner side on the tongue.

Description

Pa element upper side: short free blade, representing approximately between 1/4 and 1/5 of the element total length. Anterior carina with, at least, 8 denticles strongly compressed laterally, even forming a ridge in the platform area. Main body slightly lanceolate, asymmetrical, with great development of the outer platform, especially in the posterior half. The element has a characteristic outline, with a straight inner margin, which is turned slightly inwards at its most posterior end, and an outer sinuous margin, slightly concave in the anterior part and convex in the middle-posterior area, ending in a sharp tongue bearing interrupted ridges (Fig. 8e1, f1, h2, g2). Anterior platform region narrower than the middle part of the element; anterior margins joint the free blade approximately at the same height, with angles greater than 90º, although in some specimens this angle is close to 90° (Fig. 8e1). Posterior carina formed by, at least, 8 rounded denticles situated in a central position, but gradually approaching the inner margin in the posterior region; in some specimens they reach the inner edge. Platform upper surface ornamented with small ridges arranged perpendicular to the margins. These ridges are more or less aligned with the carina denticles, being more numerous in the outer platform. Adcarinal troughs well developed, being the outer slightly deeper and longer.

Pa element lateral side: straight main body, bending aboraly in the posterior region.

Pa element lower side: deep and asymmetrical basal cavity, occupying most of the lower surface, the tip of the basal cavity is located approximately in the middle of the element; asymmetrical lips, being more developed the outer one, but without protruding beyond the platform margins; basal cavity extends toward the anterior and posterior ends of the element in open, deep furrows.

Discussion

The great basal cavity development and the shape of the anterior region of the platform indicate that *P. carlsi* n. sp. is a primitive species within the genus. *P. carlsi* n. sp. differs from *P. kitabicus* for the further development of the adcarinal troughs. Besides, the carina in *P. kitabicus* is positioned in the centre while in *P. carlsi* n. sp. it is closer to the inner side, even contacting with the inner edge in the most posterior region of the platform of some specimens. The minor development of adcarinal troughs and the characteristic platform outline separate *P. carlsi* n. sp. from *P. exc. excavatus*. Some specimens of *P. aragonensis* n. sp. have morphologies similar to those of *P. carlsi* n. sp. (Fig. 8d). However, *P. carlsi* n. sp. has ridges and well developed adcarinal troughs, in contrast with the hemispherical nodules and poor developed or absent adcarinal troughs of *P. aragonensis* n. sp.

Stratigraphical and geographical distribution

The stratigraphical distribution of *P. carlsi* n. sp. in the Spanish Central Pyrenees is restricted from the Lower *exca-*

vatus to the Lower *nothoperbonus* subzones (lower Emsian). It has been identified in the Spanish Central Pyrenees (Valenzuela-Ríos, 1994; Martínez-Pérez and Valenzuela-Ríos, 2005) and in Bohemia (Kalvoda, 1995).

Polygnathus excavatus excavatus Carls and Gandl, 1969
(Figs. 9m-n)

*1969 *Polygnathus webbi excavata* n. ssp. Carls and Gandl: plate 18, figures 9–13, 14–19.
2011 *Polygnathus excavatus* Carls and Gandl – Martínez-Pérez *et al*.: figure 6a (with synonymy list).

Material

18 Pa 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). Referred material: MGUV-20.882, MGUV- 20.884, MGUV-20.887 to MGUV-20.892 and MGUV-20.894 to MGUV-20.903.

Remarks

P. exc. excavatus shows a lanceolated narrow platform with well developed adcarinal troughs, being the outer more excavated and longer than the inner; carina displaced towards the inner margin; platform surface bears short ribs; short tongue with interrupted transversal ridges; relatively deep and open basal cavity, which occupies more than half of the platform length.

This species is distinguished from other early polygnathids such as *P. pireneae, P. aragonensis* n. sp. and *P. kitabicus* by the lanceolate-shaped platform (slightly curved internally), by a more restricted basal cavity, and by the development of clear adcarinal troughs, being the external one more excavated. It also differs from *P. carlsi* n. sp. by the characteristic outline of the later (see above).

Stratigraphical and geographical distribution

This taxon is the conodont index of the Lower *excavatus* Subzone of Yolkin *et al*. (1994), and is recorded from the base of the *excavatus* Zone to the Lower *nothoperbonus* Zone. It is worldwide distributed (see Martínez-Pérez *et al*., 2011 for a recent list of occurrences).

Polygnathus excavatus 114 Carls and Valenzuela-Ríos, 2002
(Figs. 9o-p).

1990 *Polygnathus dehiscens* Philip and Jackson – Olivieri and Serpagli: plate 3, figures 7-10.
v1994 *Polygnathus excavatus gronbergi* Carls and Gandl – Yolkin *et al*.: text-figure. 1c (with synonymy list).2002 *Polygnathus excavatus* ssp. 114 Carls and Valenzuela-Ríos: plate 4, figures 19-24.
2004 *Polygnathus excavatus* Carls and Gandl, – Slavík: figs. 11.28 and 11.29 (only).

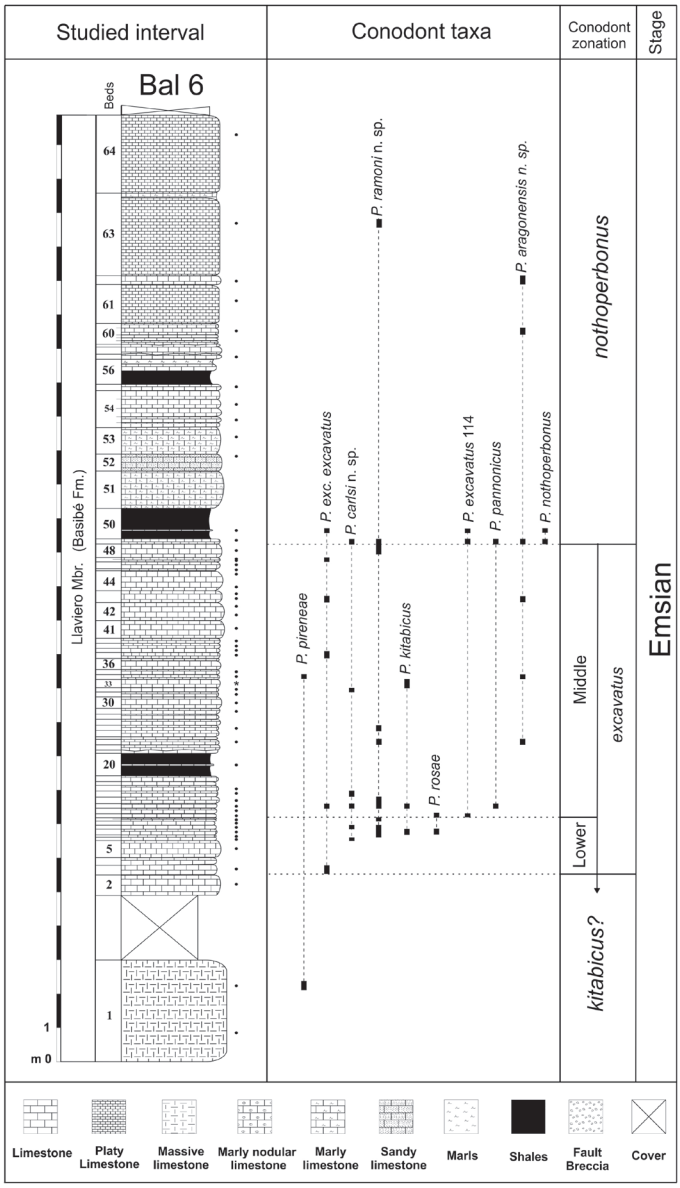


Fig. 2-. Stratigraphic column of the Baliera 6 section showing the location of the levels sampled for conodonts (black dots) and ranges of selected conodont taxa of biostratigraphic relevance. *Polygnathus nothoperbonus* is just figured to show the upper boundary of the Middle *excavatus* Zone.

Material

12 Pa elements from the following sections and beds: Isb-1/11(1), Bal-6/12(1), Bal-6/49(2), Bal-6/50(3), LGA-X/36(1), LGA-X/43(1), LGA-X/44(1) and LGA-XI/13(2). Referred material: MGUV-20.904 to MGUV-20.915.

Remarks

P. excavatus 114 has a smaller and shallower basal cavity and a tongue ornamented by semi-crossed instead of interrupted ridges, in contrast with that of *P. exc. excavatus*. The basal cavity of the closely related *P. gronbergi* shows a slight inverted basal cavity at its most posterior part as opposed to that of *P. excavatus* 114.

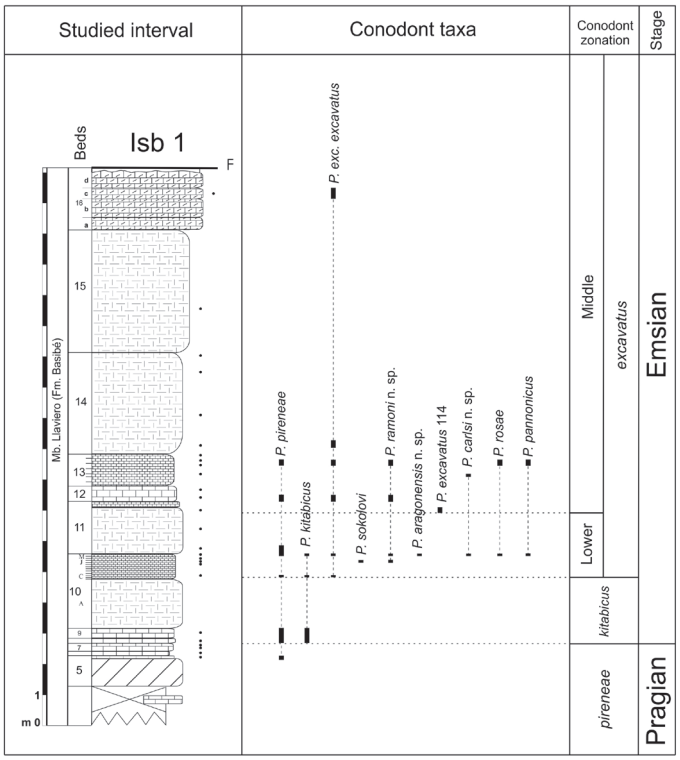


Fig. 3-. Stratigraphic column of the Isábena 1 section showing the location of the levels sampled for conodonts (black dots) and ranges of selected conodont taxa.

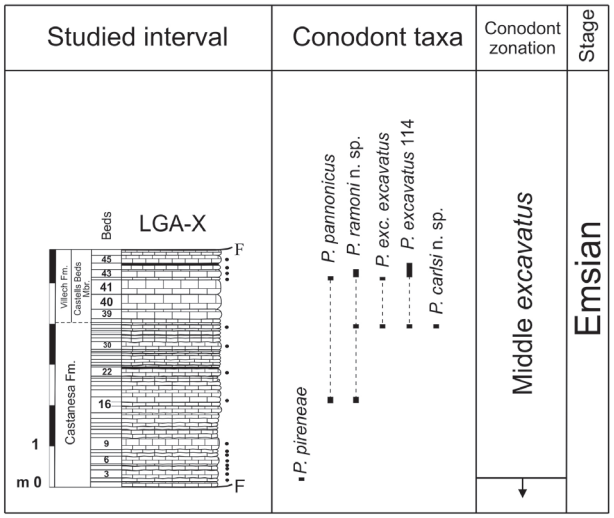


Fig. 4-. Stratigraphic column of the LGA X section showing the location of the levels sampled for conodonts (black dots) and ranges of selected conodont taxa. The age of the bottom of the section is given by unpublished data from the genus *Icriodus*.

Stratigraphical and geographical distribution

P. excavatus 114 (= *P. exc. gronbergi sensu* Yolkin *et al*., 1994), is the index taxon for the Middle *excavatus* Subzone of Yolkin *et al*. (1994), being also the proposed index for the redefinition of the Emsian Stage (see Carls *et al*., 2008). Its stratigraphical distribution is restricted to the Emsian (Lower Devonian), from the Middle *excavatus* Subzone to the base of the *nothoperbonus* Zone in Pyrenees, although Yolkin *et al*. (1994) extended its range to the *inversus* Zone. According to the synonym list given by Yolkin *et al*. (1994), *P. excavatus* 114 seems to have a worldwide distribution.

Polygnathus kitabicus Yolkin *et al.*, 1994
(Figs. 9e-g).

*v1994 *Polygnathus kitabicus* n. sp. Yolkin *et al.*: 149-150, text-figure 1, b; plate 1, figures 1-4 (with synonymy list).
v2005 *Polygnathus kitabicus* Yolkin *et al.* – Martínez-Pérez and Valenzuela-Ríos: plate 1, figure 5 (with synonymy list).
2011 *Polygnathus kitabicus* Yolkin *et al*. – Izokh *et al*.: plate I, figures 7-10 (with synomymy list).

Material

Six Pa elements from the following sections and beds: Isb-1/8(1), Isb-1/9(1), Bal-6/8(1), Bal-6/14(1), LGA-XI/12(1) and Vi-IA/11(1). Referred material: MGUV- 5.284, MGUV-20.923 to MGUV- 20.927.

Remarks

P. kitabicus has a narrow and elongated platform that slightly curves inwards in its posterior half. Upper surface bears transverse ribs, slightly more numerous in the outer margin; weakly developed and narrow adcarinal troughs, being slightly more excavated in the anterior region, both reach the platform posterior end. Asymmetrical, deep, and completely expanded basal cavity, occupying most of the lower surface. Basal cavity expansions reach the platform margins; in some specimens, slightly exceed their limits (Fig. 9e).

P. kitabicus differs from *P. pireneae* and *P. aragonensis* n. sp. by the clear development of adcarinal troughs and by its ornamentation composed of short ribs. *P. rosae* presents a more elongated platform with a characteristic constriction in the anterior region, in contrast with *P. kitabicus*. The platform marked inflexion in the posterior half and the presence of isolated nodes in the adcarinal space separates *P. sokolovi* from *P. kitabicus*.

Stratigraphical and geographical distribution

According to the current formal definition of the P/E bounday, this taxon is the index for the beginning of the Emsian (Yolkin *et al*., 1994). It has been recorded in Spain (Pyrenees) (Valenzuela-Ríos, 2001; Martínez-Pérez and Valenzuela-Ríos, 2005), in Central Asia (Zinzilban) (Yolkin *et al*., 1989, 1994, 2008; Izokh *et al.*, 2011), Urals (Russia) (Mashkova and Snigireva, 1980), and North America: Nevada (Murphy and Matti, 1983) and Alaska (Lane and Ormiston, 1979; Savage *et al.,* 1985).

Polygnathus pannonicus Mashkova and Apekina, 1980
(Figs. 9i-j).

1978 *Polygnathus* sp. n. 1 Apekina and Mashkova: plate 73, figures 11-13, 20.
*1980 *Polygnathus pannonicus* Mashkova and Apekina: figures 2, c-d.

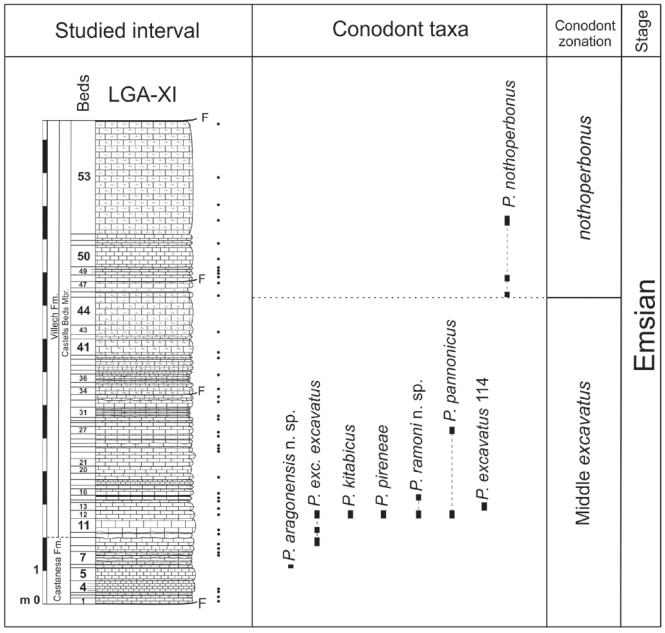


Fig. 5-. Stratigraphic column of the LGA-XI section showing the location of the levels sampled for conodonts (black dots) and ranges of selected conodont taxa. *Polygnathus nothoperbonus* is just figured to show the upper boundary of the Middle *excavatus* Zone. The age of the bottom of the section is given by lithological correlation with the top of the LGA-X section.

v1994 *Polygnathus dehiscens* Philip and Jackson – Valenzuela-Ríos: plate 8, figure 4.

v1994 *Polygnathus pannonicus* Mashkova and Apekina – Yolkin *et al*.: plate 1, figures 12-15.

2011 *Polygnathus pannonicus* Mashkova and Apekina – Izokh *et al*.: plate III, figures 5-20 (with synomymy list).

Material

Eight Pa elements from the following sections and beds: Isb-1/10M(1), Isb-1/13F(1), Bal-6/14(1), Bal-6/49(1), LGA-X/16C(1), LGA-X/42(1), LGA-XI/12(1) and LGA-XI/27a(1). Referred material: MGUV-20.990 to MGUV-20.997.

Remarks

P. pannonicus is characterized by a lanceolate and almost flatten platform. Upper surface bears short ribs that are arranged perpendicular to the platform margins; some of these ribs are formed by single aligned nodules (Fig. 9i1, j2). It is also characteristic the presence of two oblique ribs in the platform anterior margins, just in the junction with the free blade (Fig. 9i1, j2). Weakly developed adcarinal troughs, slightly deeper in the anterior region. Deep, wide and clearly asymmetric basal cavity; being more developed the outer expansion. Our specimens are very similar to the material figured by Yolkin *et al*. (1994: pl. 1, figs, 12-15) and to the holotype figured by Mashkova and Apekina (1980: figs. 2, c-d) showing all the specimens the diagnostic oblique ribs in the most anterior area of the platform margins.

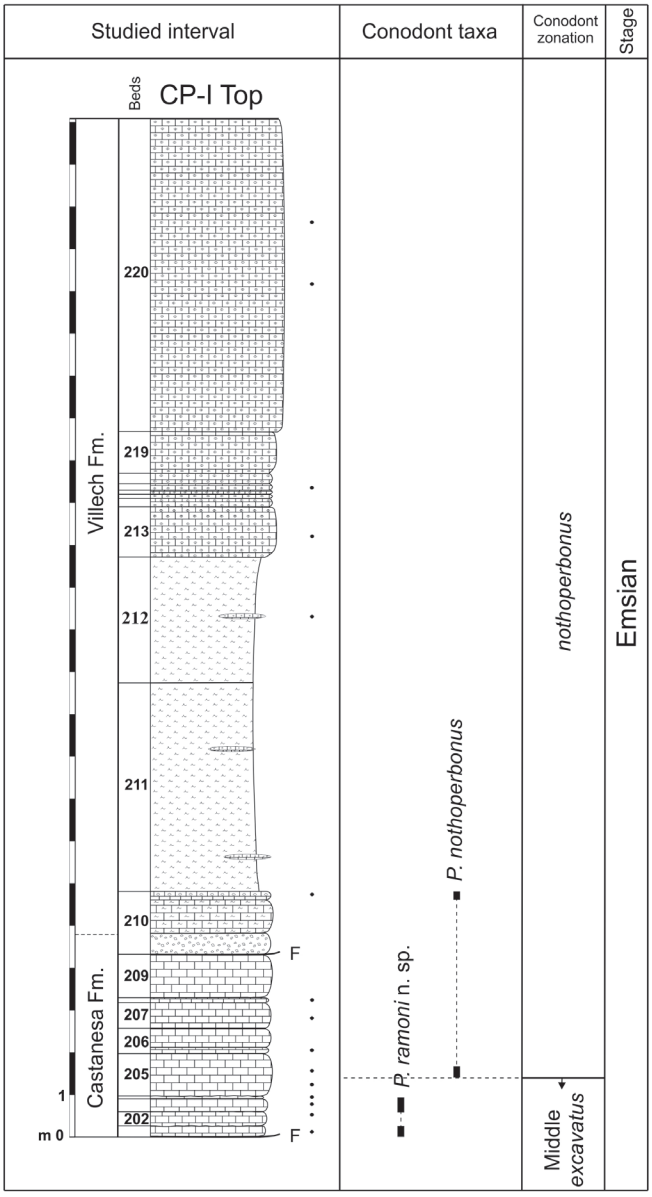


Fig. 6-. Stratigraphic column of the CP-I top section showing the location of the levels sampled for conodonts (black dots) and ranges of selected conodont taxa. *Polygnathus nothoperbonus* is just figured to show the upper boundary of the Middle *excavatus* Zone.

Stratigraphical and geographical distribution

P. pannonicus in Central Asia ranges from the *kitabicus* Zone to the Middle *excavatus* Subzone (Yolkin *et al*., 2008), but in the Spanish Central Pyrenees, the upper range reaches the *nothoperbonus* Zone. *P. pannonicus* has only been identified in Central Asia (Apekina and Mashkova, 1978; Mashkova and Apekina, 1980; Yolkin *et al*., 1994, 2008; Izokh *et al*., 2011) and Spain (Valenzuela-Ríos, 1994).

Polygnathus pireneae Boersma, 1973
(Figs. 9a-b)

*1973 *Polygnathus pireneae* Boersma: 287-288, plate 2, figures 1-12.

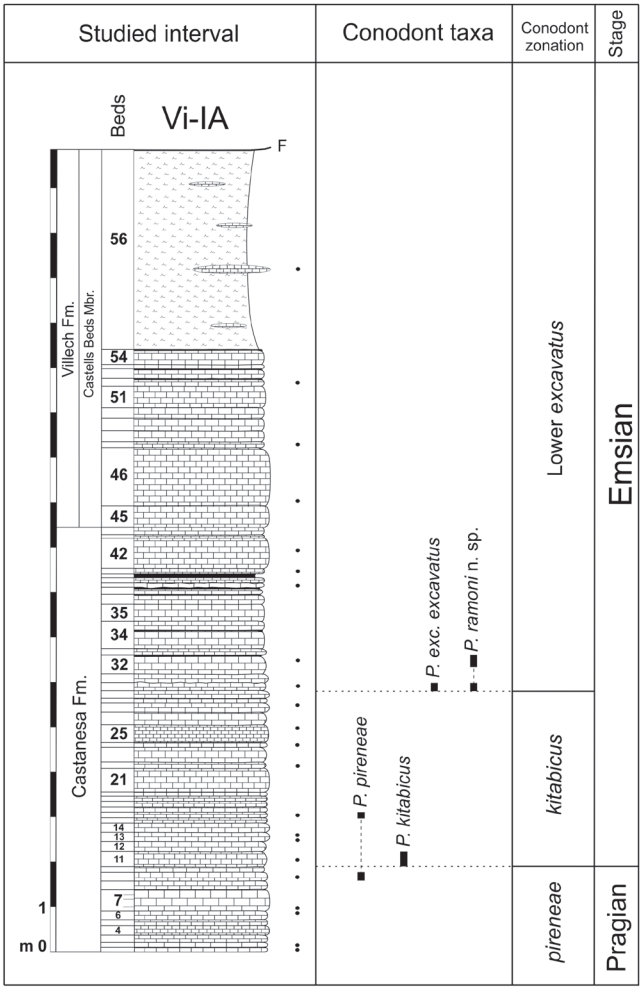


Fig. 7-. Stratigraphic column of the Vi-IA section showing the location of the levels sampled for conodonts (black dots) and ranges of selected conodont taxa.

v1994 *Polygnathus pireneae* Boersma – Valenzuela-Ríos: plate 9, figures 27, 30 (with synonymy list).
v2005 *Polygnathus pireneae* Boersma – Martínez-Pérez and Valenzuela-Ríos: plate 1, figures 1-4 (with synonymy list).
2011 *Polygnathus pireneae* Boersma – Izokh *et al*.: plate I, figures 1-6 (with synonymy list).

Material

29 Pa elements from the following sections and beds: Isb-1/5(1), Isb-1/8(2), Isb-1/9(4), Isb-1/10M(11), Isb-1/11(1), Isb-1/12a(2), Bal-6/1b(2), Bal-6/34(1), LGA-X/2(2), LGA-XI/12(1), Vi-IA/9(1) and Vi-IA/16(1). Referred material: MGUV-5.280 to MGUV-5.283 and MGUV-20.998 to MGUV-21.022.

Remarks

Elements of *P. pireneae* have a characteristic narrow and flat platform, with the central carina reaching the posterior end of the element. Upper surface typically ornamented by rounded denticles separated from the carina by the adcarinal space, which in some specimens seems to develop an incipient depression, but never forms well developed adcarinal troughs (Fig. 9c1). Completely open and excavated basal cavity, with asymmetrical lateral expansions that in many specimens overpasses the platform margins (Fig. 9c1, d1).

P. pireneae differs from Pa elements of the similar species *P. aragonensis* n. sp., by the presence of a smaller basal cavity and the characteristic platform inflexion. Pa elements of the closer taxa *P. kitabicus*, *P. rosae* and *P. excavatus* have smaller basal cavities, more developed adcarinal troughs and an ornamentation based on ribs instead of nodes. *P. pireneae* differs from *P. sokolovi*, by exhibiting clear adcarinal troughs with nodes, and the characteristic inflexion of the platform in its posterior half.

Stratigraphical and geographical distribution

P. pireneae is the index taxa for the *pireneae* Zone. Its stratigraphical range extends from the Pragian (Valenzuela-Ríos, 1997; Slavik *et al*., 2007) to the Middle *excavatus* Subzone (lower Emsian). It has a worldwide geographical distribution.

Polygnathus ramoni n. sp.
(Fig. 8i-l)

?1975 *Polygnathus dehiscens* Philip and Jackson – Klapper and Johnson: plate 1, figures 3-4.
?2002 *Eocostapolygnathus excavatus* (Carls and Gandl) beta morphotype – Bardashev *et al*.: text-figure 14.10.

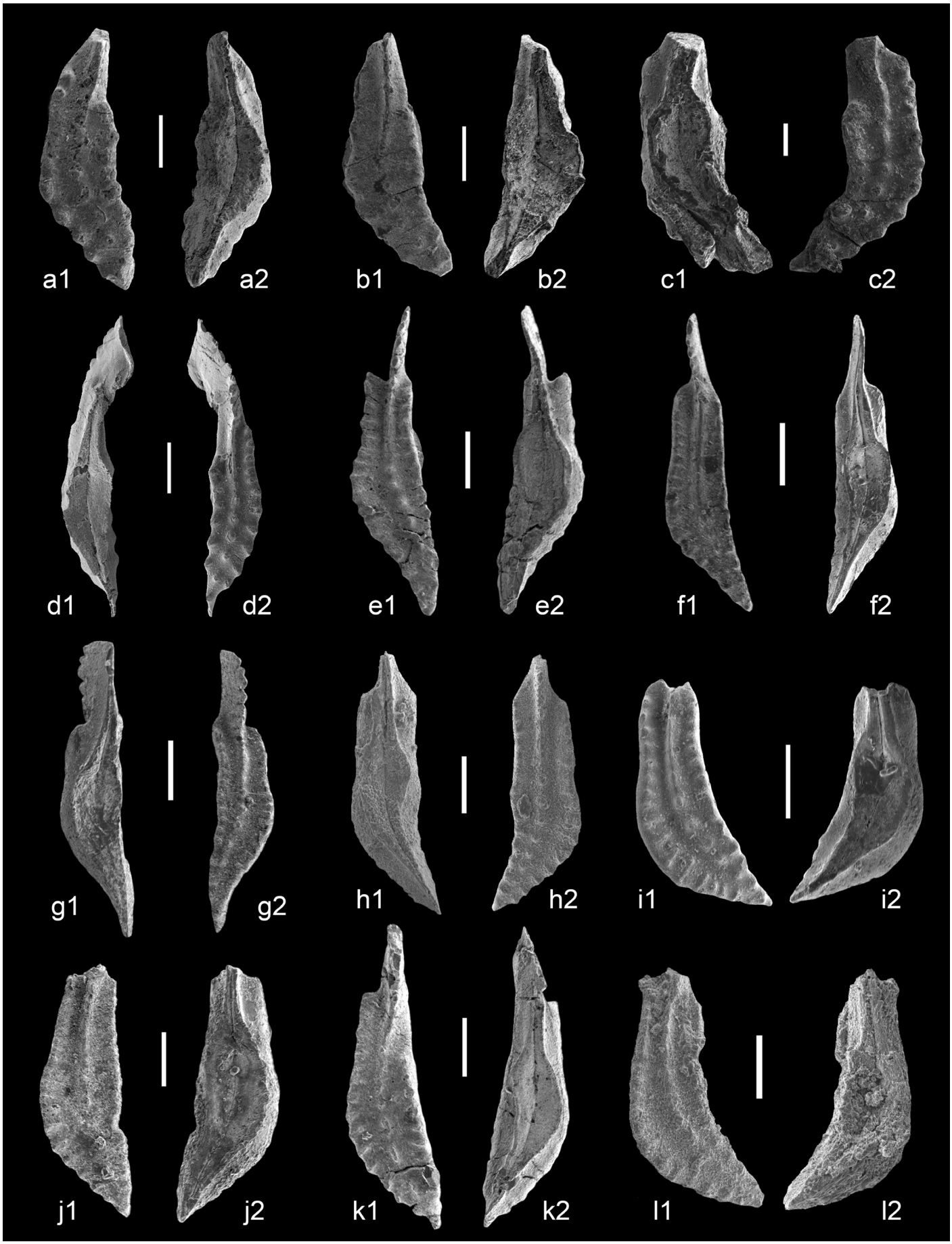
Derivatio nominis

In honor of Ramón Francisco Martínez Vidal for his continuous support and faith in our work on this "exotic" topic.

Material

Holotype: MGUV-21.033. Element illustrated in figure 8l.

Fig. 8.- (Next page) Lower Emsian conodonts from the Spanish Central Pyrenees. a) *Polygnathus aragonensis* n. sp.; holotype, a1) upper view, a2) lower view; Isábena 1 section Bed 10M; MGUV-20.854. b) *Polygnathus aragonensis* n. sp.; paratype, b1) upper view, b2) lower view; LGA XI section Bed 6, MGUV-20.856. c) *Polygnathus aragonensis* n. sp.; paratype, c1) lower view, c2) upper view; Baliera 6 section Bed 60d; MGUV-20.849. d) *Polygnathus aragonensis* n. sp.; paratype, d1) lower view, d2) upper view; Isábena 1 section Bed 10M; MGUV-20.853. e) *Polygnathus carlsi* n. sp.; holotype, e1) upper view, e2) lower view; Isábena 1 section Bed 10M; MGUV-20.868. f) *Polygnathus carlsi* n. sp.; paratype, f1) upper view, f2) lower view; LGA X section Bed 36; MGUV-20.871. g) *Polygnathus carlsi* n. sp.; paratype, g1) lower view, g2) upper view; LGA X section Bed 36; MGUV-20.872. h) *Polygnathus carlsi* n. sp.; paratype, h1) lower view, h2) upper view; Baliera 6 section Bed 16, MGUV-20.869. i) *Polygnathus ramoni* n. sp.; paratype, i1) upper view, i2) lower view; LGA X section Bed 36; MGUV-21.024. j) *Polygnathus ramoni* n. sp.; paratype, j1) upper view, j2) lower view; Isábena 1 section Bed 10M; MGUV-21.025. k) *Polygnathus ramoni* n. sp.; paratype , k1) upper view, k2) lower view; Isábena 1 section Bed 10M; MGUV-21.027. l) *Polygnathus ramoni* n. sp.; holotype, l1) upper view, l2) lower view; Baliera 6 section Bed 26, MGUV-21.033. All scale bars represent 200 µm.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Paratypes: MGUV-21.024, MGUV-21.025 and MGUV-21.027. Elements figured in figure. 8i-k.

56 Pa elements from the following sections and beds: Isb-1/10J(1), Isb-1/10M(20), Isb-1/12a(1), Isb-1/13F(4), Bal-6/7(1), Bal-6/8(1), Bal-6/9(1), Bal-6/11b(1), Bal-6/14(1), Bal-6/15(1), Bal-6/23(2), Bal-6/26(2), Bal-6/48(1), Bal-6/49(1), Bal-6/63 (1), CP-I Top/2008-207(1), CP-I Top/2008-208(3), LGA-X/16C(1), LGA-X/36(4), LGA-X/43(1), LGA-XI/12(3), LGA-XI/15(1), Vi-IA/30(2) and Vi-IA/32(1). Referred material: MGUV-21.023 to MGUV-21.078.

Type locality

Baliera 6 section, in the Baliera Valley (Huesca, Aragonian Pyrenees).

Type horizon

Bed 26, described in the Llaviero Member of the Basibé Fm. from the Basibé Sufacies-area (Southern-facies area, Aragonian Pyrenees).

Diagnosis

Pa element with the following combination of characters: long platform, slightly narrower in the anterior third with clear development of the outer platform in its posterior half, producing a sub-rounded outer margin, while the inner margin is almost straight or gently bent inwards in the posterior region. Deep and completely open basal cavity.

Description

Pa element upper side: short free blade, representing approximately less than 1/4 of the total length of the element; anterior carina with 8-9 denticles laterally compressed; straight main body, slightly lanceolate, markedly narrower in the anterior third (Fig. 8i1, j1, k1); outer platform further developed in the posterior half producing a sub-rounded outer margin contour; in contrast, the inner margin in this region of the platform is almost straight or bent gently inward; both margins are innerly curved at the posterior end of the element developing a sharp tongue; platform margins meet free blade at the same position with an angle of 90º or slightly higher (Fig. 8k1), although in some specimens the inner margin meets more posteriorly. The posterior carina bears 6-7 individualized hemispherical central denticles, approaching to the platform inner margin in the posterior half, and contacting with the inner edge in some specimens (Fig. 8i1); upper surface ornamented by ridges that are arranged perpendicular to the platform margin, being more numerous in the outer margin; inner margin often bears small rounded nodules; well-developed adcarinal troughs, outer slightly wider; both extend to the posterior third of the element.

Pa element lateral side: straight main body or slightly bent aborally in its posterior region.

Pa element lower side: deep and fully expanded basal cavity, occupying most of the element; almost symmetrical lateral expansions, restricted to the limits of the platform, placing the tip of the basal cavity in the anterior half. Basal cavity extends into the anterior and posterior region of the element as narrow, open furrows; anterior parallel sided and posterior subtriangular.

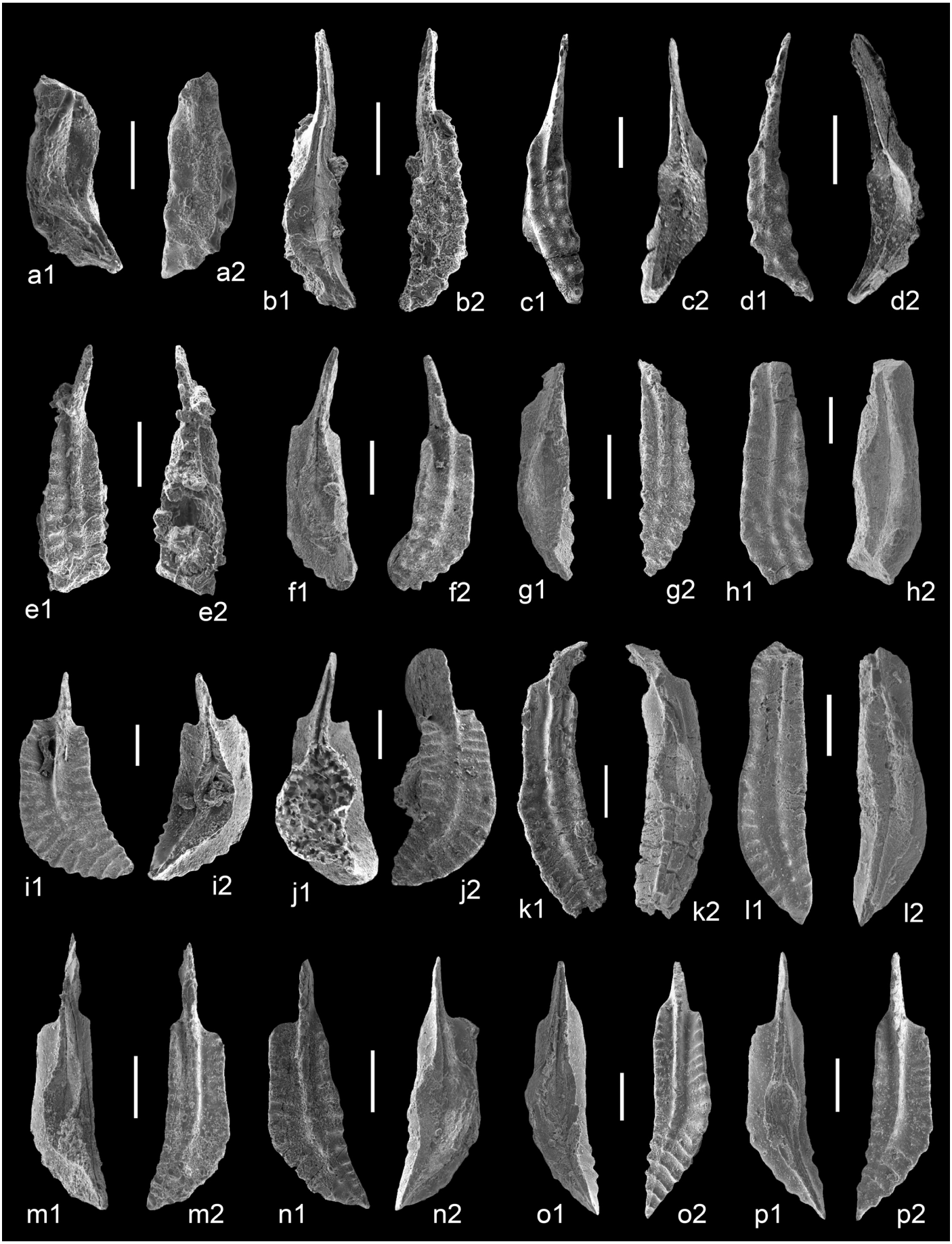
Discussion

The large and fully expanded basal cavity, well-developed adcarinal troughs and the ornamentation based on short ribes or nodes places *P. ramoni* n. sp. within the stock of primitive polygnathids. Most of these features are also present in *P. exc. excavatus*, *P. excavatus* 114, *P. kitabicus* and *P. carlsi* n. sp. However, the general platform outline with a further development of the outer platform in the posterior half separates *P. ramoni* n. sp. for this set of taxa. Pa elements of *P. kitabicus* have less-developed adcarinal troughs and a minor development of the platform ornamentation. Pa elements of *P. exc. excavatus* and *P. excavatus* 114 show more excavated external trough and a wider platform in the anterior region. *P. carlsi* n. sp. shows a "sinuous" outer margin, opposed to a more rounded outer contour of *P. ramoni* n. sp.

Stratigraphical and geographical distribution

P. ramoni n. sp. ranges from the Lower *excavatus* Subzone to the *nothoperbonus* Zone (Emsian). Its geographi-

Fig. 9.- (Next page) Pragian-Lower Emsian conodonts from the Spanish Central Pyrenees. a) *Polygnathus pireneae* Boersma, 1973; a1) lower view, a2) upper view; Isábena 1 section Bed 10M; MGUV-20.999. b) *Polygnathus pireneae* Boersma, 1973; b1) lower view, b2) upper view; Isábena 1 section Bed 8; MGUV-5.280 (originally figured in Martínez-Pérez and Valenzuela-Ríos, 2005: pl. 1, fig. 3). c) *Polygnathus pireneae* Boersma 1973; c1) upper view, c2) lower view; LGA X section Bed 2; MGUV-21.004. d) *Polygnathus pireneae* Boersma 1973; d1) upper view, d2) lower view; LGA X section Bed 2; MGUV-21.005. e) *Polygnathus kitabicus* Yolkin *et al*., 1994; e1) upper view, e2) lower view, Isábena 1 section Bed 8; MGUV-5.284 (originally figured in Martínez-Pérez and Valenzuela-Ríos, 2005: pl. 1, fig. 5). f) *Polygnathus kitabicus* Yolkin *et al*., 1994; f1) lower view, f2) upper view; Baliera 6 section Bed 8; MGUV-20.924. g) *Polygnathus kitabicus* Yolkin *et al*., 1994; g1) lower view, g2) upper view; Baliera 6 section Bed 14; MGUV-20.925. h) *Polygnathus sokolovi* Yolkin *et al.*, 1994; h1) upper view, h2) lower view; Isábena 1 section Bed 10J; MGUV-21.086. i) *Polygnathus pannonicus* Mashkova and Apekina, 1980; i1) upper view, i2) lower view; Baliera 6 section Bed 49; MGUV-20.991. j) *Polygnathus pannonicus* Mashkova and Apekina, 1980; j1) lower view, j2) upper view; LGA X section Bed 16C; MGUV-20.990. k) *Polygnathus rosae* Martínez-Pérez *et al*., 2010; k1) upper view, k2) lower view; Baliera 6 section Bed 12; MGUV-21.082 (originally figured in Martínez-Pérez *et al*., 2010: pl. 1, figs. 4a-c). l) *Polygnathus rosae* Martínez-Pérez *et al*., 2010; l1) upper view, l2) lower view; Isábena 1 section Bed 10M; MGUV-21.079 (refigured in Martínez-Pérez *et al*., 2010: pl. 1, figs. 1a-c, holotype). m) *Polygnathus exc. excavatus* Carls and Gandl, 1969; m1) lower view; m2) upper view; Baliera 6 section Bed 49; MGUV-20.889 (originally figured in Martínez-Pérez *et al.* 2011: fig. 6, a1-a2). n) *Polygnathus exc. excavatus* Carls and Gandl, 1969; n1) upper view, n2) lower view; Isábena 1 section Bed 10M; MGUV-20.883. o) *Polygnathus excavatus* 114 Carls *et al*., 2008; o1) lower view, o2) upper view; Baliera 6 section Bed 50; MGUV-20.906. p) *Polygnathus excavatus* 114 Carls *et al*., 2008; p1) lower view, p2) upper view; Baliera 6 section Bed 49; MGUV-20.905. All scale bars represent 200 µm.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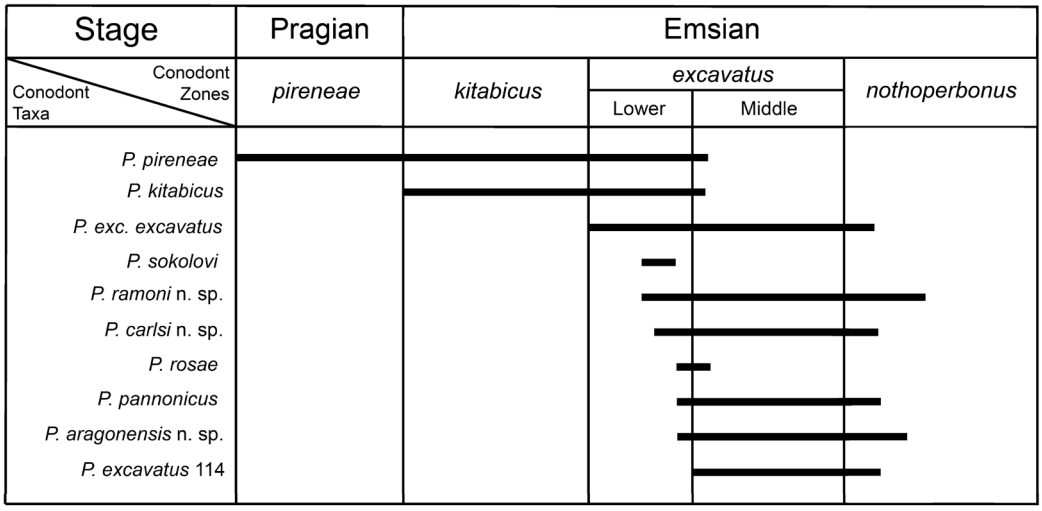

Fig. 10.- Distribution chart of Pyrenean *Polygnathus* species around the Pragian/Emsian boundary.

cal distribution seems to be restricted to the Spanish Central Pyrenees.

Polygnathus rosae Martínez-Pérez *et al*., 2010
(Figs. 9k-l)

2010 *Polygnathus rosae* n. sp. Martínez-Pérez *et al*.: figures 7a–f.

Material

14 Pa elements from the following sections and beds: Bal-6/8(1), Bal-6/12(1), Isb-1/10M(10), Isb-1/12(1) and Isb-1/13F(1). Referred material: MGUV-21.079 to MGUV-21.083 and MGUV-21.301 to 21.305.

Remarks

Polygnathus rosae has a very characteristic long, narrow and straight flat platform with equally-developed weak adcarinal troughs in the anterior part of the platform; a slightly asymmetrical element with a characteristic constriction in the anterior third of the platform; a central carina reaching the posterior end of the element; platform margins ornamented by small ribs that are arranged perpendicularly to the carina, although some small and rounded denticles can be identified in the inner margin, where the ribs are more numerous; and an asymmetric basal cavity unusually long, narrow and shallow, but not inverted.

P. rosae has a number of features common on primitive polygnathids. The narrower and shallower basal cavity together with the development of weak adcarinal troughs and ornamentation separates *P. rosae* from *P. pireneae, P. rosae* has a much more elongated platform, with a characteristic constriction, than *P. kitabicus.* The greater development of the adcarinal troughs, their asymmetrical depth and the carina displacement towards the inner platform margin distinguished *P. excavatus* from *P. rosae.*

Stratigraphical and geographical distribution

The stratigraphical distribution of *Po. rosae* is restricted to a short interval around the Lower and Middle *excavatus* subzones (lower Emsian) (Martínez-Pérez *et al.*, 2010). It has been recorded exclusively in the Spanish Central Pyrenees.

Polygnathus sokolovi Yolkin *et al.*, 1994
(Fig. 9h)

1969 *Polygnathus linguiformis dehiscens* Philip and Jackson – Flood: plate 2, figure 3.
1978 *Polygnathus* sp. n. 2 Apekina and Mashkova: plate 73, figure 10.
v1989 *Polygnathus hindei* Mashkova and Apekina – Yolkin *et al.*: plate 1, figures 7-8.
*v1994 *Polygnathus sokolovi* Yolkin *et al*.: plate 1, figures 5-8.
1994 *Polygnathus dehiscens* Philip and Jackson – Valenzuela-Ríos: plate 8, figure 36.
2011 *Polygnathus sokolovi* Yolkin *et al*. – Izokh *et al*.: plate II, figures 1-6 (with synonymy list).

Material

A single broken Pa element from Isb-1/10J (MGUV-21. 086).

Remarks

P. sokolovi has a flat and narrow platform with a distinct angularity of the outer platform margin just behind its midlength in contrast to the slight curvature of the inner one. Upper platform surface ornamented by rounded nodules on its inner edge and very slightly laterally compressed nodules on the outer edge. Adcarinal troughs weakly developed, with isolated hemispheric nodules at the adcarinal space (Fig. 9h1). Deep and fully expanded basal cavity, occupying most of the lower platform surface.

P. sokolovi differs from other related taxa by the combination of the sharp platform inflexion and the presence of isolated hemispherical nodules in the adcarinal spaces.

Stratigraphical and geographical distribution

In the Zinzilban stratotype (Uzbekistan), *P. sokolovi* ranges from the upper part of the *pireneae* Zone into the lower part of the *kitabicus* Zone. However, the pyrenean record

comes from the Lower *excavatus* Subzone, extending its known range upwards. It has been recorded in Spain (Spanish Central Pyrenees), Central Asia (Zinzilban) (Apekina and Mashkova, 1978; Yolkin *et al*., 1989, 1994) and Australia (Flood, 1969).

4. Evolution and early diversification of the genus *Polygnathus*, with special attention to the Spanish Central Pyrenees

Discussion regarding the origin of the genus *Polygnathus* involved two different proposals, which has been summarized by different authors (Sweet, 1988; Mawson, 1995, 1998; Bardashev *et al*., 2002). One proposal suggests that *Polygnathus* evolved during the Pragian from *Eognathodus* (Klapper and Philip, 1972; Cooper, 1973; Klapper and Johnson, 1975). The other proposal suggests that *Polygnathus* could have evolved from the genus "*Ozarkodina*" (Lane and Ormiston, 1979; Sweet, 1988). Currently, the former proposal is the more accepted (see e.g, Mawson, 1995, 1998; Bardashev *et al*., 2002).

For decades, the earliest *Polygnathus* species described was *P. pireneae* from the Lower Devonian strata of the Spanish Central Pyrenees (Boersma, 1973). However, some authors have recently included two Pragian *Eognathodus* taxa, *E. trilinearis zeravshanicus* (Bardashev and Ziegler, 1993) and *E. trilinearis* Cooper, 1973 as primitve *Polygnathus* (*P. trilinearis* and *P. zeravshanicus* respectively) (Mawson *et al*., 1992, Mawson, 1998). These two taxa ara characterized by bear a third row of denticles, which represents the novel feature that allows distinction between polygnathids and eognathodids (with just two rows of denticles) (Mawson, 1995, 1998); besides, they show a more developed platform. In any case, all these basal *Polygnathus* species appeared during the Pragian (Valenzuela-Ríos, 1997; Slavik *et al*., 2007) and it was not until the uppermost Pragian-early Emsian where the genus underwent its great diversification, becoming in very important components of the conodont fauna. The comparison between the scarce species recorded in the Pragian with the high number of taxa described during the lower Emsian shows an extraordinary increase in their palaeodiversity, which is represented in the Spanish Central Pyrenees by the record of up to 10 species in the *excavatus* Zone. The stratigraphical distribution of these species shows a *Polygnathus* radiation during the Lower *excavatus* Zone (see Fig. 10). This radiation is documented by the strong change in the fossil record content, with the first record of seven different taxa during the Lower *excavatus* Zone (Fig. 10). This phenomenon had already been described by Yolkin *et al.* (1994, 2008) and Izokh *et al.* (2011) in the Emsian stratotype area in Zinzilban (Uzbekistan, Central Asia), however some differences stand out.

The Zinzilban record shows an early radiation of the group involving mainly the *sokolovi-tamara* branch and the *pannonicus* branch during the late *pireneae-kitabicus* zones (Yolkin *et al*., 1994, 2008; Izokh *et al*., 2011). Conversely, the Pyrenean *Polygnathus* record shows an important radiation of the genus during the Lower *excavatus* Zone, recording for the first time during this interval up to five new taxa (*P. exc. excavatus, P. ramoni* n. sp., *P. carlsi* n. sp., *P. rosa* and *P. aragonensis* n. sp.), together with the first record in the Pyrenees of *P. sokolovi* and *P. pannonicus* (Fig. 10).

This data suggest a two-pulse radiation of the genus during the Pragian/Emsian interval. However, it is important to remark that although some taxa are shared by both regions (*P. pireneae*, *P. kitabicus*, *P. exc. excavatus*, *P. excavatus* 114, *P. pannonicus* and *P. sokolovi*), other taxa involved seem to be endemic for each region and/or pulse. In the Iberian Peninsula we have identified four endemisms, *P. rosae*, *P. ramoni* n. sp., *P. carlsi* n. sp. and *P. aragonensis* n. sp. characterizing the radiation during the Lower *excavatus* Zone. Meanwhile, in Central Asia, the endemic taxa *P. hindei*, *P. tamara* and *P. pannonicoformis* (Izokh *et al*., 2011) characterized the early radiation of the group during the *kitabicus* inverval in the Zinzilban region. This two-pulse radiation of the genus is also supported by a similar pattern described in the *Icriodus* record in the Pyrenees (Martínez-Pérez, 2010a, b).

Therefore, these data suggest that this time interval represents an important evolutive and adaptative moment for the genus, where the group started to innovate, and different morphologies appeared. However, geographical and/or environmental factors made that the same group of species evolved in different ways, characterizing each geographic area with a few different endemic species.

5. Concluding remarks

A significant conodont assemblage from six Pyrenean Lower Devonian sections (LGA-X, LGA-XI, CP-I top, Vi-IA, Isb-1 and Bal-6) is recovered; but only those polygnathids species around the Pragian/Emsian boundary are discussed herein. Among these conodonts, the occurrence of *P. pireneae*, *P. kitabicus*, *P. exc. excavatus*, *P. excavatus* 114, *P. sokolovi*, *P. pannonicus* and *P. rosae* stands out. *P. pannonicus* and *P. sokolovi* are recorded outside Asia for the first time. In addition, three new *Polygnathus* species are described: *P. aragonensis* n. sp., *P. carlsi* n. sp. and *P. ramoni* n. sp. Although the biostratigraphical implications of these faunas are out of the present work, they allow us to identify the beginning of the *kitabicus* Zone, Lower *excavatus* and Middle *excavatus* subzones by the entries of their index taxa. This abundance and diversity of polygnathid species suggests that during the late Pragian-early Emsian a *Polygnathus* evolutionary radiation took place, increasing considerably the number of species of the genus. Although this phenomena was already described in Emsian stratotype area in Zinzilban (Uzbekistan, Central Asia), the study of the Spanish material has allowed us to describe accurately this radiation, identifying two different pulses in the different regions studied, one during the *kitabicus* Zone in Zinzilban and

a second one during the Lower *excavatus* Zone in the Spanish Central Pyrenees. This radiation is also corroborated by a similar evolutive pattern described for the conodont genus *Icriodus* from the Spanish Central Pyrenees.

This early polygnathid record suggests that this group was a very successful genus, becoming theirs species in important part of the conodont faunas during the late Pragian-early Emsian ecosystems and the base of the Emsian conodont-zonation.

Acknowledgments

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