Famennian conodont assemblage in the Compte section (Upper Devonian, Central Pyrenees) and its comparison with Eurasian sequences

Asociación de conodontos del Fameniense en la sección Compte (Devónico Superior, Pirineos Centrales) y su comparación con sucesiones euroasiáticas

Héctor BARRERA-LAHOZ, José Ignacio VALENZUELA-RÍOS & Jau-Chyn LIAO

Abstract: A detailed study of the fossil assemblages of Famennian conodonts has been carried out in the Compte section in the Central Pyrenees. The studied section comprises the upper part of the Comabella Formation, the La Mena Fm and the lower part of the Barousse Fm. Fifty samples have been collected from a 11.73 m thick Famennian stratigraphic succession. Forty-seven lower–middle Famennian conodont taxa have been identified, belonging to four genera: *Palmatolepis*, *Polygnathus*, *Icriodus* and *Mehlina*. The identified conodont assemblages change through the studied section: in the lower part, *Palmatolepis* and *Icriodus* taxa are more frequent and in the overlying strata, *Palmatolepis* and *Polygnathus* taxa are dominant. Several conodont taxa have been recorded for the first time in Central Pyrenees zone. The conodont sequence analysis suggests a lower to middle Famennian age (from the *termi neo* to mg. *marginifera* Zones) in the Compte section (Beds 98–120). On the other hand, a comparison of the Pyrenean conodont assemblages with those from other relevant regions has been carried out. The conodont associations from Compte shows certain similarities with those from western and eastern Europe; however, sequences from central and eastern Asian exhibit some differences.

INTRODUCTION

The complex and varied lithological development of Devonian rocks in the Pyrenees was interpreted as belonging to different “facies-areas” (Mey, 1967a; 1967b). The southernmost one (the “southern facies-area”), was further subdivided into four “sub-facies-areas”. One of them, the Compte sub-facies-area, contains one of the richest Devonian conodont sequences in the world (Ziegler, 1959; Boersma, 1973a, 1973b; Valenzuela-Ríos, 1990, 1994a, 1994b, 2002; Valenzuela-Ríos & García-López, 1998; Valenzuela-Ríos & Murphy, 1997; Valenzuela-Ríos & Liao, 2012, 2024; Murphy & Valenzuela-Ríos, 1999; Sanz-López, 1995, 2002a, 2002b; Liao & Valenzuela-Ríos, 2008, 2013; Gouwy et al., 2013, 2016, 2017; Martínez-Pérez et al., 2011; Martínez-Pérez & Valenzuela-Ríos, 2012, 2014; Silvério et al., 2021). These works have demonstrated an almost complete conodont record for all Devonian stages, which has been compiled from numerous, disperse outcrops of limited stratigraphic distribution. There is, however, a site, a few meters north of el Comte, where the stratigraphic record seems to be more complete although tectonics made the Lower

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Devonian overthrust Middle and Upper Devonian rocks, as Schmidt (1931) have already depicted. Valenzuela-Ríos et al. (2017a) summarize the set of outcrops grouped in the Compte sections at Compte. Mainly, there are two large sequences: 1) the Lower Devonian one, comprising the Lochkovian, Pragian and lower Emsian; this section is labelled CP-I section and 2) the Middle, Upper Devonian and lower Carboniferous? sequence, consisting of Eifelian, Givetian, Frasnian, Famennian and, probably, lower Carboniferous rocks (compare Boersma, 1973b); this succession is named CP section. Liao and Valenzuela-Ríos (2017) presented the state-of-the-art of the CP section, which clearly shows the intervals that must be investigated in detail (mostly from middle Frasnian to the base of the Carboniferous). Subsequently, Silvério et al. (2021) partially filled this gap of information, documenting conodonts around the Frasnian–Famennian transition. Thus, a thorough examination of Famennian strata is still pending. Famennian strata in the CP section comprise three successive formations that from bottom up are Comabella Fm, La Mena Fm and Barousse Fm. Valenzuela-Ríos and Liao (2006a, 2006b) denoted that the contact between the Comabella and La Mena fms is diachronic in the Compte Subfacies-area and, consequently, a comprehensive study of the conodont record of La Mena Fm in different sections of this subfacies-area, has to be implemented in the future. Accordingly, our main aim in this report is the identification, detailed description and characterization of the conodont record of La Mena Fm in the CP section. In addition, we bracket the local age of La Mena Fm and compare the conodont record with those records of other relevant areas as western and eastern Europe, central Asia and China.

**GEOGRAPHIC AND GEOLOGIC SETTING**

The Compte section is located in the Central Pyrenees zone, NE Spain (Fig. 1A), between La Pobla de Segur and Sort localities (Lérida, Spain), at the right bank of the Noguera Pallaresa river about 2km north of Gerri de la Sal (Fig. 1B–1C). The Pyrenees is an E-W mountain range as result of Alpine Orogeny, which main structure has a double vergence. Prevariscan rocks belong to the Axial Zone comprising the basement of the Pyrenees (Barnolas & Pujalte, 2004) (Fig. 1A). Due to the complex stratigraphy, the Devonian and Carboniferous

![Figure 1. Geographical and geological background of the Compte section. A, Schematic geologic map of the Pyrenees (modified from Barnolas & Pujalte, 2004); B, geological map and Southern subfacies-area distribution in southern central Pyrenees zone (modified from Valenzuela-Ríos et al., 2015); C, geological map of the Compte section (blue star) (modified from Institut Cartogràfic I Geològic de Catalunya, 2023).](image-url)
of the Central Pyrenees have been subdivided into facies-area (Mey, 1967a, 1967b; Harteveld, 1970). The main four facies-area are North Pyrenean, Northern, Central, Western and Southern (summarized in Zwart, 1979). The latter has been further subdivided in four subfacies-area: Sierra Negra, Baliera, Renanué and Compte (Mey, 1967a; Zwart, 1979; Valenzuela-Ríos & Liao, 2006); the materials analysed herein belong to the latter (Fig. 1B). The Compte subfacies comprises strata from Lower Devonian to lower Carboniferous, and it is mainly composed of limestones, shales, marls and nodular limestones in the Upper Devonian–Carboniferous part (Boersma, 1973a; Sanz-López, 1995). The palaeoenvironments during the Upper Devonian of this area consisted of pelagic marine outer platform ramp and hemipelagic condensed carbonate ramp (Liao & Valenzuela-Ríos, 2017). The CP section exhibits the Comabella, La Mena and Barousse fms (Fig. 1C), that approximately correspond to the members A, B, C of Compte Formation respectively (Boersma, 1973a; Sanz-López, 1995). The Comabella Fm (Givetian to Famennian in this area) consists of well-bedded, massive and brecciated limestones of grey, dark grey, pink and green colours (Fig. 2A). The La Mena Fm (Famennian in this area) consists in red (pseudo)nodular “griotte” limestones (Fig. 2B), red and violet bedded limestones and marly limestones that to the top, veer to red and grey nodular limestones. The Barousse Fm (Famennian to Tournaisian) consists of pink and grey nodular limestones in the lower part (Fig. 2C) that shift to light grey nodular limestones in the upper part. Generally, the thickness of the layers varies from centimetric and decametric and some of them are even metric. There are several scarce millimetric to centimetric layers of shales, among them (Fig. 3).
MATERIALS AND METHODS

The studied stratigraphic succession is 11.73 m thick and comprises three formations (Fig. 3): the uppermost 4.53 m of the Comabella Fm (Beds 98 to 105), 5.75 m of the La Mena Fm (beds 106 to 116) and the lowermost 1.45 m of the Barousse Fm (beds 117 to 120). 50 samples have been taken between Beds 98–120, with weights between 0.4 to 3 kg, usually 0.5–0.6 kg (Tab. 1–3). Each bed has been sampled, and sometimes, several consecutive samples were taken within particular beds (Fig. 3). The samples have been processed using formic and acetic acid (~7–8%) in 5–10 L solutions. The residue obtained was separated through decantation and dried in a drying stove at a temperature about 60ºC. Afterwards, the residue was picked out using a Leica WILD M3B microscope.

The selected specimens were photographed by the Scanning Electron Microscope (model Hitachi S4800) at the University of Valencia.

SYSTEMATIC PALEONTOLOGY

Class CONODONTA Pander, 1856
Suborder OZARKODININA Dzik, 1976
Family SPATHOGNATHODONTIDAE Hass, 1959

Genus Palmatolepis Ulrich & Bassler, 1926


Table 1. Stratigraphical distribution of the samples and conodont specimens from Beds 98–104 identified in CP section in addition of the sample names, formations and sample weight. *Pa.*, *Palmatolepis*; *Ic.*, *Icriodus*; *P.*, *Polygnathus*. The sample code consists in: *i.e.*, CP/98a, means that the sample was taken in Bed 98 in the first interval of the bed.

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<td>Sample weight (kg)</td>
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<td>Palmatolepis tenuipunctata</td>
<td>0.41 0.65 0.73 0.455 0.53 0.75 0.4 1.275 0.56 0.75 0.59 0.455 0.58 0.47 0.595 0.585</td>
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<td>Pa. cf. tenuipunctata</td>
<td>1 2 17 12 5 7 2 9 8 2 2 3 2 4 7</td>
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<tr>
<td>Pa. cf. quadrantinodosalobata</td>
<td>3 1 2 2 1 1 1 1 2 3</td>
</tr>
<tr>
<td>Pa. quadrantinodosalobata</td>
<td>5 10 5 2 1 4 1 3 2 2 8</td>
</tr>
<tr>
<td>Pa. minuta minuta</td>
<td>4 2 2 1 4 1 4 5 2 2 1 3 4</td>
</tr>
<tr>
<td>Pa. crepida</td>
<td>4 4 4 6 4 19 8 2 3 5 3 3 32</td>
</tr>
<tr>
<td>Pa. termini</td>
<td>1 5 8 9 4 9 1 10</td>
</tr>
<tr>
<td>Pa. glabra prima</td>
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<td>Pa. glabra cf. prima</td>
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<td>Pa. subperlobata</td>
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<td>Pa. cf. subperlobata</td>
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<tr>
<td>Pa. lobicornis</td>
<td>1</td>
</tr>
<tr>
<td>Pa. cf. lobicornis</td>
<td>2</td>
</tr>
<tr>
<td>Pa. minuta wolskae</td>
<td>1</td>
</tr>
<tr>
<td>Pa. minuta loba</td>
<td>1</td>
</tr>
<tr>
<td>Palmatolepis sp. indet.</td>
<td>13 8 72 26 11 29 13 32 3 26 20 13 12 12 21 57</td>
</tr>
<tr>
<td>Icriodus alternatus alternatus</td>
<td>1 4 1 1 14 2 1 3 1 11 2 2</td>
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<tr>
<td>Ic. cf. (alternatus) alternatus</td>
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</tr>
<tr>
<td>Ic. alternatus mawsonae</td>
<td>1 1 3 4 5 2 2</td>
</tr>
<tr>
<td>Icriodus sp. indet.</td>
<td>2 3 1 2 1 1 5 5 2 10 5 2 1</td>
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<tr>
<td>Polygnathus brevilinearus</td>
<td>1</td>
</tr>
<tr>
<td>P. procerus</td>
<td>4 2</td>
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<tr>
<td>P. semicostatus</td>
<td>1</td>
</tr>
<tr>
<td>P. glaber glaber</td>
<td>2</td>
</tr>
<tr>
<td>Polygnathus sp. indet.</td>
<td>1 4 12 2 2 1 1 2 4 1 5 2 2</td>
</tr>
</tbody>
</table>

Figure 4I–4J

1955a *Palmatolepis crepida* n. sp.; Sannemann, p.134, pl. 6, fig. 21.
1993 *Palmatolepis crepida*; Ji & Ziegler, p. 59, pl. 22, figs. 1–7, text-fig. 13, fig. 4.
1995 *Palmatolepis crepida*; Rodríguez-Cañero, p. 9, pl. IV, figs. 6–8.
1995 *Palmatolepis crepida*; Sanz-López, p. 538, pl. 40, figs. 11–12.
2011 *Palmatolepis crepida*; Hartenfels, p. 243, pl. 41, fig. 3.
2015 *Palmatolepis crepida*; Mossoni, p. 89, pl. 1, fig. 8.
2021 *Palmatolepis crepida*; Silvério et al., p. 212, fig. 4K.


Description. Platform with oval outline or drop-shape form, generally wide. The lobe is absent or poorly developed with rounded or semicircular form, directed laterally and aligned with the azygous node or slightly anterior. Arched anterior carina, composed of numerous coarse, fused denticles; it joins the anterior end of the inner margin. Azygous node pronounced. Short posterior carina with few and tiny, poorly developed, denticles, which does not reach the posterior end. The outer anterior margin starts posteriorly than the inner margin. The outer slightly elevated developing a
parapet-like, more marked anteriorly. Posterior platform slightly or strongly elevated. Platform ornamented by random fine or coarse nodes.

**Discussion.** *Palmatolepis crepida* is characterized by oval to drop-shape form, small lobe and nodes ornamentation. It is similar to *Pa. perlobata perlobata* by node ornamentation but differs in the minor development of the lobe and less elevation of the outer platform. *Pa. crepida* differs from *Pa. tenuipunctata* by the less developed lobe and wider platform.

**Age and geographical range.** From Famennian *crepida* to *rhomboidea* Zones (Spalletta et al., 2017). *Pa. crepida* has cosmopolitan distribution.

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**Table 2.** Stratigraphical distribution of the samples and conodont specimens from Beds 104–112 identified in CP section in addition of the sample names, formations and sample weight. *Pa.*, *Palmatolepis*; *Ic.*, *Icriodus*; *P.*, *Polygnathus*; *Me.*, *Mehlina*. The sample code consists in: *i.e.*, CP/111a-1, means that the sample was taken in Bed 111 in the first interval of the bed and, additionally, in the lower part.

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<th>La Mena</th>
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</tr>
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<td>CP/104b</td>
<td>CP/105a</td>
<td>CP/106a</td>
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<tr>
<td>0.645</td>
<td>1.255</td>
<td>0.735</td>
</tr>
<tr>
<td>0.52</td>
<td>0.61</td>
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<tr>
<td>0.49</td>
<td>0.57</td>
<td>0.57</td>
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<tr>
<td>0.52</td>
<td>0.485</td>
<td>0.566</td>
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<td>0.59</td>
<td>0.025</td>
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<tr>
<td>0.715</td>
<td>1.13</td>
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</tr>
<tr>
<td>0.95</td>
<td>0.56</td>
<td>0.69</td>
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<tr>
<td>0.465</td>
<td>0.72</td>
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</tr>
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<td><strong>Pa. minuta minuta</strong></td>
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<td>1</td>
</tr>
<tr>
<td><strong>Pa. glabra prima</strong></td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td><strong>Pa. glabra cf. prima</strong></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Pa. minuta wolskae</strong></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Pa. perlobata perlobata</strong></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Pa. glabra pectinata</strong></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Pa. perlobata schindewolffi</strong></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Pa. perlobata cf. perlobata</strong></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Pa. rhomboidea</strong></td>
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<td>1</td>
</tr>
<tr>
<td><strong>Pa. cf. klapteri</strong></td>
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<td>1</td>
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<td><strong>Pa. glabra acuta</strong></td>
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</tr>
<tr>
<td><strong>Pa. glabra leptica</strong></td>
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<td>1</td>
</tr>
<tr>
<td><strong>Pa. gracilis gracilis</strong></td>
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</tr>
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<td><strong>Pa. perlobata helmsi</strong></td>
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<td>1</td>
</tr>
<tr>
<td><strong>Pa. glabra glabra</strong></td>
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<td>1</td>
</tr>
<tr>
<td><strong>Pa. quadrandinodosa inflexa</strong></td>
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<tr>
<td><strong>Palmatolepis sp. indet.</strong></td>
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</tr>
<tr>
<td><strong>P. alternatus alternatus</strong></td>
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<tr>
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<td><strong>Ic. tumulosus</strong></td>
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<td><strong>Icriodus sp. indet.</strong></td>
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<tr>
<td><strong>P. semicostatus</strong></td>
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</tr>
<tr>
<td><strong>P. padovani</strong></td>
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<td>1</td>
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<tr>
<td><strong>P. nodo. nodocostatus</strong></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>P. nodo. cf. nodocostatus</strong></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>P. nodo. ovatus</strong></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>P. communis communis</strong></td>
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<td>1</td>
</tr>
<tr>
<td><strong>P. glaber glaber</strong></td>
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</tr>
<tr>
<td><strong>P. bouckaerti</strong></td>
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</tr>
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<td><strong>P. glaber eoglaber</strong></td>
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</tr>
<tr>
<td><strong>P. subnormals</strong></td>
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</tr>
<tr>
<td><strong>P. tripylliatus</strong></td>
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<td><strong>P. lauriformis</strong></td>
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<tr>
<td><strong>Palmatolepis glabra acuta</strong></td>
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</table>

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**Figure 7A–7B**

1993 *Palmatolepis glabra acuta*; Ji & Ziegler, pl. 16, fig. 11, text-fig. 17, fig. 5.

2001 *Palmatolepis acuta*; Johnston & Chatterton; p. 24, pl. 7, figs. 1–2.

2015 *Palmatolepis glabra acuta*; Mossoni, p.89–90, pl. 5, fig. 2.

2017 *Palmatolepis glabra acuta*; Lüddecke et al., fig. 4f.

2017 *Palmatolepis glabra acuta*; Owatanova et al., p. 1075, pl. 47, figs. 5–6, pl. 50, figs., 1–6, 8.

**Materials.** Eight specimens from samples CP/111b (1), CP/111c (1), CP/112a (2), CP/112b (3) and CP/117 (1).

**Description.** Narrow platform with sigmoidal outline. It has a pronounced subtriangular parapet, which is oblique to the carina; and the projection of its margin forms an acute angle with the azygous node and the carina. Generally, the parapet is smooth. The outer margin is straight and forms a 90 degree with the anterior outer margin. Inner margin runs from anterior to posterior ends with an outline parallel to the carina. Sigmoidal carina with the posterior part straight or

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1963 *Palmatolepis serrata acuta* n. sp.; Helms, p. 468, pl. 3, figs. 1–4, 6.

1990 *Palmatolepis glabra acuta*; Perri & Spalletta, p. 60, pl. 1, figs. 4a–4b.
Table 3. Stratigraphical distribution of the samples and conodont specimens from Beds 113–120 identified in CP section in addition of the sample names, formations and sample weight. Pa., Palmatolepis; P., Polygnathus; Me., Mehlina. The sample code consists in: i.e., CP/113b, means that the sample was taken in Bed 113 in the second interval of the bed.

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<td>CP/113b</td>
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<td>P. lauriformis</td>
<td>4</td>
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<td>P. lauriformis cf.</td>
<td>2</td>
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<td>P. glaber medius</td>
<td>3</td>
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<td>P. longiusculus</td>
<td>1</td>
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<tr>
<td>Polygnathus sp. indet.</td>
<td>6</td>
<td>4</td>
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<tr>
<td>Me. strigosa</td>
<td>2</td>
<td>1</td>
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sightly curved reaching the posterior end. The posterior margin is pointed and upwards bent. The platform surface is smooth or shagreen.

**Discussion.** This species is similar to the rest of the P. glabra-stock in the outline and the development of its parapet. It differs from Pa. glabra pectinata by the orientation of the parapet, which is oblique to the carina while it is parallel in Pa. glabra pectinata. It differs from Pa. glabra distorta by the absent of the characteristic bulge in the inner platform of the latter species. Finally, the rounded outline of the outer (inner) margin separates Pa. glabra prima from Pa. glabra acuta.

**Age and geographical distribution.** From Famennian gl. pectinata to mg. utahensis Zones (Spalletta et al., 2017). Pa. gl. acuta is recorded in Italy, Germany, Russia, China and Canada.

**Palmatolepis glabra glabra** Ulrich & Bassler, 1926

Figure 7H

1926 *Palmatolepis glabra* n. sp.; Ulrich & Bassler, p. 51, pl. 9, fig. 20.
1993 *Palmatolepis glabra glabra*; Ji & Ziegler, p. 60–61, pl. 17, figs. 13–15, text-fig. 17, fig. 4.

2003 *Palmatolepis glabra glabra*; Corradini, p. 79, pl. 4, figs. 1–2.
2015 *Palmatolepis glabra glabra*; Mossoni, p. 90–91, pl. 1, fig. 15.
2017 *Palmatolepis glabra glabra*; Ovnatanova et al., p. 1075, pl. 47, fig. 4.

**Material.** One specimen from the sample CP/112c.

**Description.** Sigmoidal and slender platform. The outer anterior margin joints perpendicular the anterior margin, developing an elevated parapet with the anterior margin merging oblique with the carina and developing a short crest. The inner margin outline is parallel to the carina. Pointed posterior platform; its posterior end bends upwards. Sigmoidal carina reaching both ends. Smooth platform surface.

**Discussion.** Pa. glabra glabra is similar to Pa. glabra pectinata and Pa. glabra prima. From the former separates by a less pronounced, short and wide parapet. The platform of Pa. glabra prima is generally wider and the outer margin is straight or change direction at the azygous node, but its outline does not follow the trace of the carina.

**Age and geographical distribution.** From Famennian rhomboidea Zone to mg. marginifera Zone. (Spalletta, 2017). Pa. gl. glabra is recorded in Germany, Italy, Spain, Russia and China.
**Palmatolepis glabra lepta** Ziegler & Huddle, 1969

Figure 7C–7G

1969 *Palmatolepis glabra lepta* n. sp.; Ziegler & Huddle, p. 380–381.

1973 *Palmatolepis glabra lepta* early form; Sandberg & Ziegler: p. 101–102, pl. 2, fig. 16.

1973 *Palmatolepis glabra lepta* late (typical) form; Sandberg & Ziegler: p. 101–102, pl. 2, fig. 3.

1993 *Palmatolepis glabra lepta*; Ji & Ziegler, p. 61, pl. 19, figs. 11–15, text-fig. 17, fig. 3.

1995 *Palmatolepis glabra lepta*; Rodríguez-Cañero, p. 12, pl. V, figs. 5–7.

2011 *Palmatolepis glabra lepta* early morphotype; Hartenfels, p. 246, pl. 42, figs. 1–2.

2011 *Palmatolepis glabra lepta* late morphotype; Hartenfels, p. 245–246, pl. 42, figs. 3–6.

2015 *Palmatolepis glabra lepta*; Mossoni, p. 91–92, pl. 4, fig. 16.

2017 *Palmatolepis glabra lepta*; Ovnatanova, p. 1075–1076, pl. 53, fig. 10.

2017 *Palmatolepis glabra lepta*; Lüddecke et al., fig. 4i.

2023 *Palmatolepis glabra lepta* early morphotype; Huang et al., fig. 4D

**Material.** 94 specimens from samples CP/111c (1), CP/112a (1), CP/112b (3), CP/112e (1), CP/112f (1), CP/112g (1), CP/113b (3), CP/113c (1), CP/114b (38), CP/115 (8), CP/116 (1), CP/117 (4), CP/118a (9), CP/118b (13), CP/119 (6) and CP/120 (3). Early morphotype is recorded between samples CP/111c and CP/114b and late morphotype is recorded between samples CP/114b and CP/120.

**Description.** Slender and narrow platform with a rough sigmoidal outline. The parapet has (sub) triangular to rounded outline, turned upwards and sometimes reduced to a bulge. Subtriangular posterior platform moderately to strongly bend upwards. Azygous node. Located in the posterior third of the platform, posterior to the end of the parapet. The carina is slightly to strongly sigmoidal. Nodes on the roughly arched anterior carina are high; posterior nodes are small and much lower, reaching the pointed posterior end. Smooth platform surface.

**Discussion.** Sandberg and Ziegler (1973) and Hartenfels (2011) described two different morphotypes. The early form (Fig. 7C–7D) is distinguished by a narrow and slightly slender and sigmoidal platform and an elevated parapet with ridge-like form and subtriangular outline. The late (typical) form (Fig. 7E–7G) has mostly slender and narrow platform and the characteristic triangular parapet. *Pa. glabra* differs from others subspecies of *Pa. glabra* by the extremely narrow platform and the (sub)triangular parapet.

**Age and geographical distribution.** From Famennian gl. prima to granulosus Zones (Spalletta et al., 2017). According to Ziegler and Sandberg (1973) and Hartenfels (2011) the late form extends from the base of the mg. marginifera Zone to the granulosus Zone. The early form extends from the gl. prima Zone to the top of the gr. gracilis Zone (Ziegler & Sandberg, 1973; Hartenfels, 2011), but in South China extends to mg. marginifera Zone (Huang et al., 2023). *Pa. gl. lepta* is recorded in Germany, Italy, Belgium, Spain, Russia, Poland, Canada, USA, China.

**Palmatolepis glabra pectinata** Ziegler, 1962a

Figure 6A–6C

1962a *Palmatolepis glabra pectinata* n. ssp; Ziegler, p. 398–399, pl. 2, figs. 3–5.

1973 *Palmatolepis glabra pectinata* morphotype 1; Sandberg & Ziegler, p. 104, pl. 2, figs. 4, 12–15, pl. 5, fig. 14.

1993 *Palmatolepis glabra pectinata*; Ji & Ziegler, p. 61, pl. 16, figs. 5–10, pl. 17, figs. 1–12, figs. 1–12; text-fig. 17, figs. 7–8.

1995 *Palmatolepis glabra pectinata*; Rodríguez-Cañero, p. 12, pl. V, figs. 1–2.


2015 *Palmatolepis glabra pectinata*; Mossoni, p. 92, pl. 1, fig. 19, pl. 4, fig. 1.

2017 *Palmatolepis glabra pectinata*; Ovnatanova et al., p. 1076, pl. 50, figs. 7, 9.

2017 *Palmatolepis glabra pectinata*; Lüddecke et al., fig. 4j.

**Material.** 88 specimens from samples CP/104c (2), CP/105a (1), CP/105b (6), CP/105c (2), CP/106 (5), CP/107 (3), CP/108 (3), CP/110 (2), CP/111a-1 (2), CP/111a-2 (1), CP/111b (6), CP/111c (4), CP/112a (3), CP/112b (5), CP/112c (2), CP/112d (1), CP/112e (5), CP/112f (1), CP/112g (3), CP/113b (1), CP/114a (7), CP/115 (2), CP/117 (17), CP/118a (1), CP/118b (1) and CP/120 (2).

**Description.** Narrow and slightly sigmoidal platform with straight inner margin. Well-developed high parapet, parallel to the carina ending anteriorly to the azygous node. Inner and anterior margin meets at an obtuse angle. Outer margin straight, curving in the posterior third. Pointed posterior end upwards bent. Subtle sigmoidal carina with arched anterior part and mostly straight posterior of the azygous node. Smooth or finely shagreen platform.

**Discussion.** *Palmatolepis glabra pectinata* and *Pa. gl. acuta* have similar parapet, but in the former is parallel to the carina. *Pa. gl. pectinata* differs from *Pa. gl. distorta* by the absence of a bulge in the anterior inner platform.

**Age and geographical distribution.** From Famennian *gl. pectinata* Zone to the mg. utahensis Zone (Spalletta et al., 2017). *Pa. gl. pectinata* has cosmopolitan distribution.

**Palmatolepis glabra prima** Ziegler & Huddle, 1969

Figure 4K–4N

1962a *Palmatolepis glabra glabra*; Ziegler, p. 397, pl. 1, fig. 11–12.
1962b *Palmatolepis glabra glabra*; Ziegler, p. 58, pl. 4, figs. 14–15.


1973 *Palmatolepis glabra prima* morphotype 1; Sandberg & Ziegler, p. 103, pl. 2, figs. 2, 8–10.

1973 *Palmatolepis glabra prima*; Sandberg & Ziegler, pl. 2, figs. 1, 7.

1993 *Palmatolepis glabra prima*; Ji & Ziegler, p. 61, pl. 16, figs. 14–17, text-fig. 17, figs. 2, 9, 17.

1993 *Palmatolepis glabra prima* morphotype 1; Ji & Ziegler, p. 62, pl. 16, figs. 12–13, text-fig. 19, fig. 7.

1995 *Palmatolepis glabra prima*; Rodríguez-Cañero, p. 12, pl. IV, figs. 14–16.


1999 *Palmatolepis glabra unca*; Schülke, p. 37–38, pl. 4, figs. 1–3.

2003 *Palmatolepis glabra prima*; Corradini, p. 79, pl. 4, figs. 3–6.

2011 *Palmatolepis glabra prima* morphotype 3 (typical); Hartenfels, p. 247–248, pl. 43, figs. 1–3.

2011 *Palmatolepis glabra prima* morphotype 1; Hartenfels, p. 248, pl. 42, figs. 7–11.

2015 *Palmatolepis glabra prima*; Mossoni, p. 92–93, pl. 1, fig. 16.

2017 *Palmatolepis glabra prima*; Ovнатanova et al., p. 1079, pl. 50, fig. 10.

2017 *Palmatolepis glabra prima*; Lüddecke et al., fig. 4k.

2019 *Palmatolepis glabra prima*; Zhang, p. 245, pl. 29, figs. 9–12.

2019 *Palmatolepis glabra prima* morphotype 1; Zhang, p. 245–246, pl. 29, figs. 1–8.

2020 *Palmatolepis glabra prima* morphotype 1; Suttner et al., figs. 6.11a–11b.

2020 *Palmatolepis glabra prima* morphotype 3; Suttner et al., figs. 6.16a–16b.

**Material.** 192 specimens from samples CP/98c (25), CP/99a (15), CP/99b (4), CP/99c (20), CP/99d-1 (7), CP/99d-2 (18), CP/100 (3), CP/101a (10), CP/101b (2), CP/102b (3), CP/103 (5), CP/104a (8), CP/104b (34), CP/104c (4), CP/105b (1), CP/106 (3), CP/107 (2), CP/108 (3), CP/109a (1), CP/111a-2 (1), CP/111b (3), CP/111c (1), CP/112a (1), CP/112b (3), CP/112g (2), CP/113a (1), CP/113b (2), CP/114a (3), CP/114b (3) and CP/117 (4). The morphotype 1 is recorded between samples CP/98c and CP/104c and the morphotype 3 is recorded among samples CP/104b and CP/117.

**Description.** Sandberg and Ziegler (1973) described three morphotypes of *Pa. glabra prima*, in the Compte section the morphotypes 1 and 3 have been identified. The morphotype 1 (Fig. 4K–4L) is characterized by a wide and elongated platform with slightly subrhombic outline. The outer platform might have a lobe-like margin but not a developed lobe. The inner platform is elevated with a feeble rounded parapet in the anterior part; pointed posterior end, downwards turned. Sigmoidal carina with nodes reaching both ends. Smooth platform surface. The morphotype 3 (Fig. 4M–4N) is characterized by a slender and slightly sigmoidal platform with a straight outer margin. Rounded and elevated but not pronounced parapet that ends anteriorly to the azygous node in the inner platform. Pointed posterior end upwards turned.

**Discussion.** According to Sandberg and Ziegler (1973) there are three morphotypes. The first morphotype (M1) is characterized by a wider platform and it is related to *Pa. klapperi*. It is similar to *Pa. tenuipunctata* but can be distinguished by the absence of a lobe and greater width. Also, it differs from *Pa. klapperi* by the absence of a ramp in the outer platform. The third morphotype (M3, more typical) is narrower and can be separated from other subspecies of *Pa. glabra* by the rounded and slightly elevated parapet in the inner platform.

**Age and geographical distribution.** From Famennian the *gl. prima* Zone to mg. utahensis Zone (Spalletta et al., 2017). *Pa. gl. prima* has cosmopolitan distribution.

*Palmatolepis gracilis gracilis* Branson & Mehl, 1934

Figure 711–712.

1934 *Palmatolepis gracilis n. sp.;* Branson & Mehl, p. 238, pl. 18, fig. 8.

1993 *Palmatolepis gracilis gracilis*; Ji & Ziegler, p. 63, pl. 6, figs. 4–7, text-fig. 14, fig. 2.

1995 *Palmatolepis gracilis gracilis*; Rodríguez-Cañero p. 12, pl. V, figs. 11–13.

2011 *Palmatolepis gracilis gracilis*; Hartenfels, p. 249–250, pl. 44, figs. 1–3.

2015 *Palmatolepis gracilis gracilis*; Mossoni, p. 94, pl. 2, figs. 15–16.

2017 *Palmatolepis gracilis gracilis*; Ovнатanova et al., p. 1079–1080, pl. 48, fig. 8, pl. 53, figs. 7–8.

2017 *Palmatolepis gracilis gracilis*; Lüddecke et al., fig. 4i.

**Material.** Two specimens from samples CP/112a (1) and CP/112c (1).

**Description.** Small, narrow and slender platform with slightly asymmetrical fusiform outline. It has a reduced lobe and raised margin rim. Straight, oblique anterior carina that curves strongly near the azygous node;
straight to slightly arched posterior carina reaching the posterior end. Pointed posterior margin. Long free blade, as large as the platform length or longer. The keel is constricted or twisted at the middle of the platform. Smooth or finely shagreen platform surface.

**Discussion.** *Pa. gracilis gracilis* is similar to *Pa. minuta minuta* in the platform outline and size of juvenile specimens of *Pa. minuta minuta*, they can be distinguished by the twisted keel and the length of the free blade, additionally, the basal cavity of *Pa. min. minuta* is more reduced than *Pa. gr. gracilis*.

**Age and geographical distribution.** From Famennian *gr. gracilis* to *ultimus* Zones (Spalletta et al., 2017). *Pa. gr. gracilis* has cosmopolitan distribution.

*Palmatolepis cf. klapperi* Sandberg & Ziegler, 1973

1973 *Palmatolepis klapperi* n. sp.; Sandberg & Ziegler, p. 104, pl. 2, figs. 6, 17–28, pl. 5, fig. 12.
1993 *Palmatolepis klapperi*; Ji & Ziegler, p. 67, pl. 18, figs. 1–8, text-fig. 17, fig. 18.
2011 *Palmatolepis klapperi*; Hartenfels, p. 258, pl. 43, figs. 8–11.
2019 *Palmatolepis klapperi*; Zhang, p. 229, pl. 31, figs. 9–12.

**Material.** One specimen from sample CP/107.

**Description.** Biconvex, oval platform with oval outline that turns downwards at the posterior end. Arched inner platform without developing a lobe. Slightly elevated outer platform that develops an elongated bulge-like called ramp. The outer margin meets the carina at an obtuse angle. Strongly arched anterior carina; short posterior carina with few, minute denticles that does not reach the posterior end. Elongated, narrow and pointed posterior margin. The free blade is absent and the platform surface is shagreening.

**Discussion.** *Pa. klapperi* separates from *Pa. glabra prima* morphotypes 1 and 2 by the characteristic curvature of the inner platform, the ramp in the outer platform and the intersection of the anterior outer margin with the free blade. The specimen from Compte section (Fig. 6E) has a not well-preserved ramp and the characteristic curvature is slighter pronounced.

**Age and geographical distribution.** From Famennian *gl. prima* to *mg marginifera* Zones (Spalletta et al., 2017). *Pa. klapperi* is recorded in Germany, Morocco, Belarus, China, Iran and USA.

*Palmatolepis lobicornis* Schülke, 1995

1995 *Palmatolepis lobicornis* n. sp.; Schülke, p. 40–41, pl. 4, figs. 1–17.
1999 *Palmatolepis lobicornis*; Schülke, p. 40–41, pl. 2, fig. 10.
2004 *Palmatolepis lobicornis*; Klappler et al., p. 379, fig. 7.30.

2013 *Palmatolepis lobicornis*; Strelchenko & Kruchek, pl. 1, fig. 29.
2016 *Palmatolepis lobicornis*; Huang & Gong, figs. 6.2, 6.11.
2019 *Palmatolepis lobicornis*; Zhang, p. 242, pl. 20, figs. 5–16.
2021 *Palmatolepis lobicornis*; Silvério et al., p. 213, fig. 4L.

**Material.** Five specimens from samples CP/99c (2), CP/99d-2 (1), CP/102b (1) and CP/104b (1).

**Description.** Platform relative wide and with subtriangular outline. Convex anterior inner margin; convex outer platform that starts posteriorly than the inner. Well-developed lobe, with rounded outline and projected laterally, with a small bulge in the anterior side. The platform develops weak sinuses around the lobe. Arched anterior carina; straight posterior carina that reaches close to the posterior end. Posterior platform turned upwards. Posterior end slightly pointed or rounded and turned downwards. Short free blade. Smooth platform surface; which have small nodes in the outer platform.

**Discussion.** *Pa. lobicornis* is similar to *Pa. subperlobata* in the platform outline and the smooth surface. Nevertheless, it differs by the presence of a small bulge in the lobe, rounded posterior end and more developed sinuses. Besides, the outer platform of *Pa. superlobata* exhibits two files of nodes.

**Age and geographical distribution.** From Famennian *min. minuta* to *rhomboidea* Zones (Spalletta et al., 2017). *Pa. lobicornis* is recorded in Germany, France, Spain, Belarus, Turkey, China, Canada and USA.

*Palmatolepis marginifera marginifera* Helms, 1959

19959 *Palmatolepis quadratinodosa marginifera*; Helms, p. 649, pl. 5, figs. 22–23.
1993 *Palmatolepis marginifera marginifera*; Ji & Ziegler, p. 64, pl.13, figs. 7–10, pl.14, figs.1–6, text-fig.17, fig.14.
1995 *Palmatolepis marginifera marginifera*; Sanz-López, p. 523–524, pl. 41, figs. 6–7, 11.
2003 *Palmatolepis marginifera marginifera*; Corradini, p. 80, pl. 5, figs. 1–3.
2011 *Palmatolepis marginifera marginifera*; Hartenfels, p. 260–261, pl. 41, figs. 6–8.
2013 *Palmatolepis marginifera marginifera*; Mossoni et al., p. 24, fig. 6.18.
2015 *Palmatolepis marginifera marginifera*; Mossoni, p. 96, pl. 2, fig. 18, pl. 3, fig. 2.
2017 *Palmatolepis marginifera marginifera*; Ovatanova et al., p. 1091–1092, pl. 47, figs. 1–2, 9, pl. 51, figs. 6–7, 9–10.
2017 *Palmatolepis marginifera marginifera*; Lüddecke et al., figs. 4m–4n.
2019 *Palmatolepis marginifera marginifera*; Zhang, p. 234, pl. 27, figs. 9–12.
Material. 16 specimens from samples CP/114a (1), CP/114b (1), CP/115 (3), CP/117 (6), CP/119 (3) and CP/120 (2).

Description. Elongated (Fig. 8G) or wide (Fig. 8F) platform with oval outline. Straight inner margin, or slightly concave in the anterior and convex in the posterior. The outer platform has a well-developed parapet, which is smooth with a crest (Fig. 8G) or denticulate with coarse nodes parallel to the carina (Fig. 8F); the parapet ends near the azygous node (Fig. 8F) or extend beyond it (Fig. 8G). Arched anterior carina; straight posterior carina reaching the posterior end. The posterior margin is pointed to subtriangular and is turned upwards. No free blade and smooth surface.

Discussion. *Pa. mg. marginifera* is similar to some taxa from the quadrantinodosa-stock, e.g. *Pa. quadrantinodosa* quadrantinodosa and *Pa. quad. inflexa* and also, *Pa. stoppeli*, but it differs from all of them by the well-developed parapet in the outer platform. Also, it separates from *Pa. mg. utahensis* by the absence of nodes in the inner platform. It differs from *Pa. mg. duplicata* by having one parapet. Ji and Ziegler (1993) described *Pa. mg. sinensis* using as diagnostic character the extension of the parapet, which reaches the posterior end of the platform. However, Corradini (2003) did not accept this taxon and assumed that this character is part of the specific variability.

Age and geographical distribution. From Famennian *mg. marginifera* to *rg. trachytera* Zones (Spalletta et al., 2017). *Pa. mg. marginifera* has cosmopolitan distribution.

**Palmatolepis minuta loba** Helms, 1963

Figure 5C

1963 *Palmatolepis minuta loba* n. ssp.; Helms, p. 470, pl. 2, figs. 13–14, pl. 3 fig. 12.
1993 *Palmatolepis minuta loba* Ji & Ziegler, p. 64–65, pl. 10, figs. 1–16, text-fig.13, figs.11–12.
1995 *Palmatolepis minuta loba*; Rodríguez-Cañero, p. 16, pl. III, fig. 17.
2003 *Palmatolepis minuta loba*; Corradini, p. 80, pl. 6, fig. 9.
2011 *Palmatolepis minuta loba*; Hartenfels, p. 262, pl. 46, figs. 7–8.
2013 *Palmatolepis minuta loba*; Mossoni et al., p. 24, fig. 5.11.
2015 *Palmatolepis minuta loba*; Mossoni, p. 98, pl. 1, fig. 11.
2019 *Palmatolepis minuta loba*; Zhang, p. 252–253, pl. 32, figs. 5–8.

Material. One specimen from sample CP/99d-2.

Description. Small platform with lanceolate outline and developed lobe. Roughly convex anterior inner margin with straight margins anterior and posterior to the lobe; small sinuses are present. Elongated, rounded subtriangular lobe, laterally oriented, anterior to the well-developed azygous node. Straight anterior carina, slightly arched. Thin posterior carina that does not reach the posterior end. Posterior end pointed and turned upwards bent. Free blade about 1/3 to 1/5 of the platform length. Smooth platform surface.

Discussion. *Pa. minuta loba* is similar to *Pa. min. minuta*, but differs by the well-developed lobe. It separates from *Pa. min. wolskae*, by the presence of the posterior carina.

Age and geographical distribution. From Famennian *crepida* to *rhomboidea* Zones (Spalletta et al., 2017). *Pa. min. loba* is recorded in Italy, Germany, Spain, Turkey, Poland, Russia, Iran and China.

**Palmatolepis minuta minuta** Branson & Mehli, 1934

Figure 4G–4H

1934 *Palmatolepis minuta*; Branson & Mehli, p. 236, pl. 18, figs.1, 6–7.
1962b *Palmatolepis minuta minuta*; Ziegler, pl. 3, figs. 1–10.
1993 *Palmatolepis minuta minuta*; Ji & Ziegler, p. 65, pl. 7, figs. 1–19; pl. 9, figs. 8–18, text-fig. 13, figs. 9, 15–16.
2011 *Palmatolepis minuta minuta*; Hartenfels, p. 261–262, pl. 46, figs. 1–6.
2013 *Palmatolepis minuta minuta*; Mossoni et al., p. 24, fig. 6.17.
2015 *Palmatolepis minuta minuta*; Mossoni, p. 97–98, pl. 2, fig. 7.
2017 *Palmatolepis minuta minuta*; Ovatanova et al., p. 1092, 1095, pl. 46, figs. 3, 8, pl. 47, fig. 10, pl. 48, figs. 12, 14, pl. 52, fig. 1.
2017 *Palmatolepis minuta minuta*; Lüddecke et al., figs. 4o–4r.


Description. Flat platform with biconvex, lanceolate outline, with a small lobe, which in some specimens is absent. Convex anterior and inner margins; outer posterior margin is slightly concave. Rounded small lobe, at the same level than the azygous node. Straight to slightly arched anterior carina; denticulate posterior carina; with discrete denticles or fused in a thin crest, that almost reaches the posterior end. Pointed and slightly turning upwards posterior margin. The carinas are arranged in a sigmoid pathway. Short free blade, about 1/4 or 1/5 of the platform length. Arched or straight keel. Platform surface smooth or finely shagreen.

Discussion. This taxon is similar to other *minuta* taxa; the difference with *Pa. min. loba* is explained there. It separates from *Pa. min. wolskae* by the presence of the posterior carina. Juvenile specimens can be confused with small platforms of *Pa. gr. gracilis* but besides the differences explained there, they can also be discriminated by wider platform of *Pa. min. minuta*.
Age and geographical distribution. From Famennian *min. minuta* to *granulosus* Zones (Spalletta et al., 2017). *Pa. min. minuta* has cosmopolitan distribution.

*Palmatolepis minuta wolskae* Szulczewski, 1971

![Figure 5D](image)

1971 *Palmatolepis minuta wolskae* n. ssp.; Szulczewski, p. 36, pl. 15, figs. 2, 12–14.
1993 *Palmatolepis minuta wolskae*; Ji & Ziegler, p. 85 pl. 11, figs. 1–11, text-fig. 13, figs. 7–8.
1995 *Palmatolepis minuta wolskae*; Rodríguez-Cañero, p. 16, pl. III, fig. 18.
2003 *Palmatolepis minuta wolskae*; Corradini, p. 80, pl. 6, figs. 7–8.
2015 *Palmatolepis minuta wolskae*; Mossoni, p. 99–100, pl. 5, fig. 4.
2019 *Palmatolepis loba wolskae*; Zhang, p. 253, pl. 32, figs. 9–12.

**Material.** Four specimens from samples CP/98b (1), CP/99d-2 (1), CP/105a (1) and CP/105b (1).

**Description.** Flat platform with lanceolate to subtriangular outline. Concave or straight inner anterior margin. Poor developed lobe; some specimens develop a posterior sinus. Slightly arched anterior carina; well-developed azygous node and absent posterior carina. Pointed posterior end turned upwards. Smooth platform surface.

**Discussion.** Main difference with other *minuta* taxa lies on the absent of posterior carina.

Age and geographical distribution. From Famennian *termini* to *rhomboidea* Zones (Spalletta et al., 2017). *Pa. min. wolskae* is recorded in Italy, Spain, Poland, France and China

*Palmatolepis perlobata helmsi* Ziegler, 1962b

![Figure 7J](image)

1962b *Palmatolepis helmsi* n. sp.; Ziegler, p. 184, pl. 8, figs. 16–17.
1979 *Palmatolepis perlobata helmsi*; Sandberg & Ziegler, p. 179, pl. 1, figs. 20–21.
1993 *Palmatolepis perlobata helmsi*; Ji & Ziegler, p. 66, pl. 18, figs. 7–10, text-fig. 15, fig. 9.
1995 *Palmatolepis perlobata helmsi*; Sanz-López, p. 521, pl. 42, fig. 2.
2011 *Palmatolepis perlobata helmsi*; Hartenfels, p. 479, pl. 47, figs. 4–5.

**Material.** Eight specimens from samples CP/112a (1), CP/112c (1), CP/117 (3) and CP/119 (3).

**Description.** Subtriangular platform with the widest zone in the anterior half. Subtriangular, barely developed to almost absent lobe. Convex outer margin, slightly elevated with straight anterior and posterior parts meeting at an acute angle. Strongly arched anterior; straight to slightly arched posterior carina that does not reach the posterior end; the carinas pathway draws a subtle sigmoidal layout. The posterior margin is turned upwards. Free blade absent. Platform surface smooth or shagreen.

**Discussion.** *Pa. perlobata helmsi* differs from other members of the *perlobata* group by the less developed lobe. *Pa. per. perlobata* also has a weak-developed lobe, but this taxon has a platform ornamented by nodes. Besides the posterior carina of *Pa. per. perlobata* reaches the posterior end.

Age and geographical distribution. From Famennian *rhomboidea* to *ac. aculeatus* (Spalletta et al., 2017). *Pa. per. helmsi* is recorded in Germany, Belgium, Spain, Italy, Poland, Russia, Morocco, China and Australia.

*Palmatolepis perlobata perlobata* Ulrich & Bassler, 1926

![Figure 6D](image)

1926 *Palmatolepis perlobata perlobata* n. sp.; Ulrich & Bassler, p. 49–50, pl. 7, figs. 19, 21–22.
1995 *Palmatolepis perlobata perlobata*; Rodríguez-Cañero, p. 16, pl. IV, figs. 1–2.
1995 *Palmatolepis perlobata perlobata*; Sanz-López, p. 520, pl. 41, fig. 13.
2003 *Palmatolepis perlobata perlobata*; Corradini, p. 81, pl. 7, fig. 10.
2011 *Palmatolepis perlobata perlobata*; Hartenfels, p. 263, pl. 47, fig. 6.
2013 *Palmatolepis perlobata perlobata*; Strelchenko & Kruchek, pl. 1, fig. 6.
2017 *Palmatolepis perlobata perlobata*; Ovnatanova et al., p. 1099, pl. 48, fig. 10.

Material. One specimen from sample CP/104c.

Description. Wide platform with slightly sigmoidal outline. Convex and elevated outer platform. Weakly developed lobe with rounded subtriangular outline. Sinuses are present. Sigmoidal arched anterior carina; straight to slightly curved posterior carina that reaches the posterior end; the carinas pathway draws a sigmoidal layout. Subtriangular and markedly turned upwards margin. Free blade absent. The platform surface is covered by nodes.

Discussion. This taxon is similar to Pa. per. schindewolfi in the platform outline, but the posterior carina of the latter doesn’t reach the posterior margin and has a feeble ornamented platform.

Age and geographical distribution. From Famennian min. minuta Zone to the upper part of gl. pectinata Zone. (Spalletta et al., 2017). Pa. per. perlobata is recorded in Germany, Italy, Russia, Spain, Morocco, Iran, China and USA.

Palmatolepis perlobata schindewolfi Müller, 1956

1956 Palmatolepis schindewolfi n. sp.; Müller, p. 27, pl. 8, figs. 22–31, pl. 9, fig. 33.
1979 Palmatolepis perlobata schindewolfi; Sandberg & Ziegler, p. 180, pl. 1, figs. 22–24, pl. 2, fig. 13.
1993 Palmatolepis perlobata schindewolfi; Ji & Ziegler, p. 67, pl. 18, figs. 9–15, text-fig.15, fig. 3.
1995 Palmatolepis perlobata schindewolfi; Rodríguez-Cañero, p. 18, pl. IV, figs. 4–5.
1995 Palmatolepis perlobata schindewolfi; Sanz-López, p. 521–522, pl. 41, figs. 14–17, pl. 42, fig. 1, pl. 54, fig. 6.
2003 Palmatolepis perlobata schindewolfi; Corradini, p. 82, pl. 7, figs. 1–5.
2011 Palmatolepis perlobata schindewolfi; Hartenfels, p. 268–269, pl. 47, figs. 1–3.
2015 Palmatolepis perlobata schindewolfi; Mossoni, p. 102–103, pl. 2, fig. 20, pl. 5, fig. 1a–1b.
2017 Palmatolepis perlobata schindewolfi; Lüddecke et al., fig. 5d.
2017 Palmatolepis perlobata schindewolfi; Ovnatanova et al., p. 1100, pl. 52, figs. 3–5.

Material. One specimen from sample CP/117.

Description. Relatively wide platform with strongly arched outer margin. Platform markedly constricted close to azygous node. High outer margin, almost developing a parapet and ornamented by straight ribs, some of which are aligned fused nodes. Triangular, pointed lobe located approximately in the half-length of the platform and clearly anteriorly to the azygous node, which settles clearly in the posterior third. Strongly arched anterior carina; straight posterior carina that almost reaches the posterior end. The carinas pathway draws a sigmoidal layout. Posterior margin pointed and strongly turned upwards. Absent free blade. Inner and outer margins ornamented with irregular nodes and ribs.

Discussion. The differences between Pa. per. sigmoidea and Pa. per. schindewolfi are discussed there. Besides, the former has a strong platform constriction in the posterior third.
Age and geographical distribution. From near to the base of the Famennian mg. marginifera Zone to gr. manca Zone (Spalletta et al., 2017). *Pa. per. sigmoidea* is recorded in Germany, Spain, Russia, China and USA.

_Palmatolepis quadrantinodosa inflexa_ Müller, 1956

1956 _Palmatolepis quadrantinodosa inflexa_ n. ssp.; Müller, p. 67, pl. 10, figs. 5, 8, 11.


1974 _Palmatolepis inflexa_; Dreesen & Dusar, p. 54, pl. 6, fig. 11.


1993 _Palmatolepis quadrantinodosa inflexa_; Ji & Ziegler p. 68, pl. 15, figs. 4–12, text-fig.17, fig. 10.

2003 _Palmatolepis quadrantinodosa inflexa_; Corradini, p. 82, pl. 5, fig. 13.

2017 _Palmatolepis quadrantinodosa inflexa_; Lüddecke et al., fig. 5f.

2017 _Palmatolepis inflexa_; Ovнатanova et al., p. 1083, pl. 47, fig. 3, pl. 48, fig. 11, pl. 51, figs. 4–5.

2019 _Palmatolepis inflexa inflexa_; Zhang, p. 233, pl. 26, figs. 13–16.

Material. Six specimens from samples CP/112g (2), CP/113a (1), CP/113c (1), CP/114a (1) and CP/120 (1).

Description. Narrow platform with suboval outline. Outer platform elevated forming a smooth bulge or parapet-like. Straight anterior inner margin, slightly concave that changes to slightly arched and convex posteriorly. Curved anterior carina; subtriangular posterior carina composed of few and small denticles or a thin crest that does not reach the posterior margin, which is subtriangular and slightly turned up. Absent free blade. Platform surface shagreen.

Discussion. _Pa. quadrantinodosa inflexa_ has high morphological variability. Sandberg and Ziegler (1973) describe three morphotypes and Sandberg and Ziegler (1973) and Dreesen (1977) report intermediate forms between this taxon and _Pa. quad. inflexoidea_. The platform outline is similar with the _quadrantinodosa_-stock and _Pa. marg. marginifera_. It differs with _Pa. quad. inflexoidea_ by the wider platform, the more anterior position of the azygous node and the presence of a posterior carina. It differs with _Pa. mg. marginifera_ by the absence of a true parapet. It differs from _Pa. stoppei_ by a marked narrower platform.

Age and geographical distribution. From the Famennian gr. gracilis Zone to the lower part of the mg. utahensis Zone (Spalletta et al., 2017). _Pa. quad. inflexa_ has a broad geographical distribution.

_Palmatolepis quadrantinodosa inflexoidea_ Ziegler, 1962b

1962b _Palmatolepis quadrantinodosa inflexoidea_ n. ssp.; Ziegler, p. 176, pl. 5, figs. 14–18.
carina meeting in an acute angle. Curved anterior carina; short posterior carina, composed of two to three nodules, that does not reach the posterior end. Broad subtriangular posterior margin moderately turned up.

**Discussion.** The distinctive character of *Pa. quad. quadratinodosa* is the presence of nodes in the outer platform. Sandberg and Ziegler (1973) described two morphotypes based in the orientation of the nodes: the first by rows and the second irregularly.

**Age and geographical distribution.** This taxon is exclusively recorded in the Famennian mg. *marginifera Zone* (Spalletta et al., 2017). *Pa. quad. quadratinodosa* is recorded in Belgium, Poland, China, Canada and USA.

*Palmatolepis quadratinodosalobata* Sannemann, 1955b

**Figure 4E–4F**

1955b *Palmatolepis quadratinodosalobata* n. sp.; Sannemann, p. 328, pl. 24, fig. 6.
1973 *Palmatolepis quadratinodosalobata* morphotype 1; Sandberg & Ziegler, p. 105–106, pl. 4, fgs. 27–32.
1993 *Palmatolepis quadratinodosalobata*; Ji & Ziegler, p. 69, pl. 23, fgs. 5–7, fig. 12, fgs. 3, 7–8.
1995 *Palmatolepis quadratinodosalobata*; Rodríguez-Cañero, p. 18, 20, pl. III, fgs. 10–11.
2003 *Palmatolepis quadratinodosalobata*; Corradini, p. 83, pl. 5, fgs. 7–9.
2013 *Palmatolepis quadratinodosalobata*; Mossoni et al., p. 25–27, fig. 5.14.
2015 *Palmatolepis quadratinodosalobata*; Mossoni, p. 103, pl. 1, fig. 14.
2017b *Palmatolepis quadratinodosalobata*; Valenzuela-Ríos et al., fig. 4.7.
2017 *Palmatolepis quadratinodosalobata*; Ovatanova et al., p. 1104, 1107, pl. 45, fgs. 3, 5.
2019 *Palmatolepis quadratinodosalobata* morphotype 1; Zhang, p. 217, pl. 21, fgs. 5–8.

**Material.** 43 specimens form samples CP/98b (5), CP/98c (10), CP/99a (5), CP/99b (2), CP/99c (1), CP/99d–2 (4), CP/100 (1), CP/101b (3), CP/102b (2), CP/103 (2) and CP/104b (8).

**Description.** Subtriangular platform with well-developed lobe, approximately aligned with the azygous node. Roughly biconvex margins. Convex posterior inner margin and convex anterior inner margin, appears anterior to the outer margin. The lobe is well developed and elongated and positioned at the same level of the azygous node. Subtriangular to semicircular lobe outline directed laterally or slightly anteriorly; some specimens develop a thin ridge obliquely connecting the azygous node with the tip of the lobe (Fig. 4F). Slightly arched to straight anterior carina; straight posterior carina that almost reaches the posterior end. Posterior platform pointed and turned up. Free blade short. Outer platform ornamented by coarse discrete or fused nodes forming ridges perpendicular to the anterior carina; this ornamentation is restricted to the part anterior to the azygous node.

**Discussion.** *Pa. quadratinodosalobata* is similar to *Pa. subperlobata* and *Pa. lobicornis* in the platform outline and well-developed lobe, however it differs from both by the coarse node ornamentation in the outer platform. Sandberg and Ziegler (1973) described the morphotype 1 based in the presence of nodes in the inner platform, which differs from *Pa. poolei* by the size of the lobe. Later, Ji and Ziegler (1993) described another two morphotypes. The morphotype 2 is most typical, characterized by a wider platform, well developed lobe and nodes in the outer platform. The morphotype 3, is characterized by a narrower platform, slightly arched to straight carina, pointed lobe and nodes in the outer platform. On the other hand, *Pa. quadratinodosalobata* differs with *Pa. sandbergi*, which has nodes along entire outer platform.

**Age and geographical distribution.** From Famennian *crepida to rhomboidea Zones* (Spalletta et al., 2017). The morphotype 1 appears from gl. *pectinata to rhomboidea Zones* (Sandberg & Ziegler, 1973). *Pa. quadratinodosalobata* has cosmopolitan distribution.

*Palmatolepis regularis* Cooper 1931

**Figure 4O–4P**

1931 *Palmatolepis regularis* n. sp.; Cooper, p. 242, pl. 28, fig. 36.
1993 *Palmatolepis cf. regularis*; Ji & Ziegler, p. 20, fgs. 1–2, text-fig. 16 fgs. 7, 9.
1995 *Palmatolepis cf. regularis*; Rodríguez-Cañero, p. 20, pl. IV, fgs. 11–12.
2004 *Palmatolepis regularis*; Klapper et al., p. 381, fgs. 7.28, 7.31.
2011 *Palmatolepis regularis*; Hartenfels, p. 270–271, pl. 41, fig. 5.
2015 *Palmatolepis regularis*; Mossoni, p. 104, pl. 1, fig. 12.
2019 *Palmatolepis regularis*; Zhang, p. 239, pl. 18, fgs. 5–8.

**Material.** Two specimens from sample CP/99a.

**Description.** Sigmoidal platform with parallelogram outline without lobe. Anterior inner margin meets the carina anteriorly than the outer margin. Outer platform slightly elevated and bent. Strongly arched anterior carina; posterior carina, composed of several aligned nodules, straight or slightly oblique, almost reaching the posterior end, which is pointed and upwards turned.
The carinas pathway draws a sigmoidal layout. Short free blade. Smooth platform surface.

**Discussion.** Cooper (1931) described the holotype from a specimen imbedded in a shale matrix. Later, Ziegler (1962b) pointed that the described holotype belongs to the lower view and questioned its description. The next descriptions (see synonymy), based on platform outline similarities, have the cf. attribution. Klapper *et al.* (2004) provided upper views of the paratypes and a coincident description and platform outline with the holotype and finally, rejected the cf. attribution. Ji and Ziegler (1993) described two morphotypes of *Pa. regularis*, based on the platform width. The first morphotype has a narrower platform, however, the description is still questionable because of the similarity of this platform with *Pa. arta*. On the other hand, the anterior margins of *Pa. arta* appear at the same level, instead the inner anterior margin of *Pa. regularis* starts anteriorly to the outer margin. *Pa. regularis* differs with *Pa. subperlobata*, *P. linguiloba* and *Pa. ibicornis* by the absence of lobe.

**Age and geographical distribution.** From Famennian min. minuta Zone to lower half of rhomboidea Zone (Spalletta *et al.*, 2017). *Pa. regularis* is recorded in Spain, Italy, Germany, Belarus, Poland, Turkey, Uzbekistan, Mongolia, China, Canada and USA.

*Palmatolepis rhomboidea* Sannemann, 1955b

Figure 6F–6G

1955b *Palmatolepis rhomboidea* n. sp.; Sannemann, p. 329, pl. 24, fig. 14.

1993 *Palmatolepis rhomboidea*; Ji & Ziegler, p. 70, pl. 21, figs. 1–5, text-fig. 13, fig. 18.

1995 *Palmatolepis rhomboidea*; Sanz-López, p. 526, pl. 41, fig. 4, pl. 46, fig. 1.

1999 *Palmatolepis rhomboidea*; García-López *et al.*, pl. l, fig. 8.

2003 *Palmatolepis rhomboidea*; Corradini, p. 83, pl. 3, figs. 19–21.

2004 *Palmatolepis rhomboidea*; Klapper *et al.*, fig. 7.14.

2011 *Palmatolepis rhomboidea*; Narkiewicz & Bultynck, pl. XI, fig. 12.

2013 *Palmatolepis rhomboidea*; Mossoni *et al.*, p. 27–28, fig. 5.9.

2013 *Palmatolepis rhomboidea*; Savage, figs. 12.27–12.29.

2015 *Palmatolepis rhomboidea*; Mossoni, p. 104–105, pl. 1, fig. 9.

2019 *Palmatolepis rhomboidea rhomboidea*; Zhang, p. 230, pl. 26, figs. 1–4.

2020 *Palmatolepis rhomboidea*; Suttner *et al.*, fig. 6.13a–6.13b.

2020 *Palmatolepis rhomboidea*; Izokh *et al.*, fig. 3r–3s.

**Material.** 10 specimens from samples CP/113c (1), CP/114a (4), CP/117 (2), CP/118b (2) and CP/119 (1).

**Description.** Broad platform with suboval outline. The margin of the outer platform has an elevated ramp-like. Curved anterior carina; very short or absent posterior carina. The posterior margin is slightly pointed and can be somewhat turned up. Shagreen platform surface.

**Discussion.** The differences between *Pa. stoppeli* and *Pa. quad. inflexa* have been discussed above. Besides, the wider platform, *Pa. stoppeli* develops a ramp-like elevation on the outer margin. On the other hand, it differs from *Pa. mg. marginifera* by the lack of a true parapet in the outer platform.

**Age and geographical distribution.** From Famennian upper part of gr. gracilis Zone to the lower half of mg. marginifera Zone (Spalletta *et al.*, 2017). *Pa. stoppeli* is recorded in Belgium, Italy, Spain, Germany, Poland, Russia, China, USA and Canada.

*Palmatolepis subperlobata* Branson & Mehl, 1934

Figure 5A

1934 *Palmatolepis subperlobata*; Branson & Mehl, p. 235, pl. 18, figs. 11, 21.
1993 *Palmatolepis subperlobata*; Ji & Ziegler, p. 72, pl. 20, figs. 3–9, pl. 21, figs. 11–12, text-fig. 16, figs. 5–6, 8.
1997 *Palmatolepis subperlobata*; Over, p. 170, 172, figs. 10.2–10.3, 10.6–10.7, 10.9.
1999 *Palmatolepis subperlobata*; Schülke, p. 50–51, pl. 7, figs. 15–25.
2003 *Palmatolepis subperlobata*; Corradini, p. 84, pl. 3, figs. 1–4.
2004 *Palmatolepis subperlobata*; Klapper et al., p. 380, figs. 7.35–7.36.
2007 *Palmatolepis subperlobata*; Klapper, pl. 2, figs. 1, 9.
2008 *Palmatolepis subperlobata*; Sánchez de Posada et al., pl. 2, fig. 4.
2015 *Palmatolepis subperlobata*; Mossoni, p. 108–109, pl. 1, fig. 7.
2016 *Palmatolepis subperlobata*; Huang & Gong, figs. 5.3–5.4.
2019 *Palmatolepis subperlobata*; Zhang et al., fig. 6.15.
2019 *Palmatolepis subperlobata*; Zhang, p. 243, pl. 22, figs. 1–16.
2021 *Palmatolepis* cf. *subperlobata*; Silvério et al., p. 212, fig. 4M.

**Material.** Three specimens from samples CP/99a (2) and CP/99b (1).

**Description.** Platform slightly elongated, with subtriangular outline and well-developed lobe with sinuses. The inner margin meets the carina at a more anterior position than the outer and is slightly concave. The outer margin is moderately elevated and slightly convex in the anterior part and concave in the posterior one. Elongated lobe with subtriangular to rounded outline and laterally or anteriorly oriented in a position anterior to the azygous node. Arched to sigmoidal anterior carina; straight posterior carina, composed of several tiny nodules, ending close to the posterior end. Pointed to subtriangular posterior margin and slightly turned upwards. Short free blade. Platform surface shagreen or smooth that can be ornamented by fine nodes in the outer platform.

**Discussion.** *Pa. subperlobata* is similar to *Pa. triangularis* and *Pa. ultima* in the platform outline and the well-developed lobe, but it differs by having a less coarse, or lacking, platform ornamentation. Also, it shows some similarities with the *perlobata*-stock, but it separates from this group by a less elongated platform, less elevated outer platform and by the lobe outline. Finally, it can also be similar to *Pa. tenuipunctata*, but it can be discriminated by a less elongated platform and more developed lobe.

**Age and geographical distribution.** From Famennian *subperlobata* to *mg. marginifera* Zones (Spalletta et al., 2017). *Pa. subperlobata* has cosmopolitan distribution.

*Palmatolepis tenuipunctata* Sannemann, 1955a

**Figure 4C–4D**

1955a *Palmatolepis tenuipunctata* n. sp.; Sannemann, p. 136, pl. 6, fig. 22.
1993 *Palmatolepis tenuipunctata*; Ji & Ziegler, p. 72, pl. 19, figs. 1–6, text-fig. 16, fig. 2.
1995 *Palmatolepis tenuipunctata*; Rodríguez-Cañero, p. 21, pl. IV, figs. 9–10.
1999 *Palmatolepis tenuipunctata*; García-López et al., pl. I, fig. 4.
2001 *Palmatolepis tenuipunctata*; Johnston & Chatterton; p. 27, pl. 10, figs. 6–9, 11, 13–14.
2003 *Palmatolepis tenuipunctata*; Corradini, p. 84, pl. 3, figs. 11–13.
2011 *Palmatolepis tenuipunctata*; Hartenfels, p. 276–277, pl. 41, fig. 2.
2013 *Palmatolepis tenuipunctata*; Strelchenko & Kruchek, pl. 1, fig. 7.
2015 *Palmatolepis tenuipunctata*; Mossoni, p. 109, pl. 1, fig. 13.
2017b *Palmatolepis tenuipunctata*; Valenzuela-Rios et al., fig. 4.6.
2019 *Palmatolepis tenuipunctata*; Zhang, p. 246–247, pl. 23, figs. 9–12.
2020 *Palmatolepis tenuipunctata*; Bahrami et al., fig. 9.41.

**Material.** 83 specimens from samples CP/98a (1), CP/98b (2), CP/98c (17), CP/99a (12), CP/99b (5), CP/99c (7), CP/99d-1 (2), CP/99d-2 (9), CP/101a (8), CP/101b (2), CP/102a (2), CP/102b (3), CP/103 (2), CP/104a (4) and CP/104b (7).

**Description.** Elongated platform with slightly sigmoidal outline and a small lobe. The anterior inner margin is moderately convex or straight and meets the carina in a convex pathway (Fig. 4D). Outer margin meets the carina posteriorly to the inner margin, convex and elevated in the anterior half. Small lobe with rounded outline, laterally or posteriorly oriented and located anteriorly to the azygous node. Anterior carina moderate curved; straight to slightly curved posterior carina that almost reaches the posterior end. The carinas pathway...
draws a sigmoidal layout. Subtriangular, pointed and turned upwards posterior margin. Smooth platform surface.

**Discussion.** In the Compte section, specimens from *Pa. tenuipunctata* are similar to those of *Pa. gl. prima* M1 in the platform outline. Nevertheless, they can be separated by the presence of a true lobe and the narrower platform of the former. The differences with *Pa. per. schindewolfii* have been described above.

**Age and geographical distribution.** From Famennian min. *minuta* to *gl. pectinata* Zones (Spalletta et al., 2017). *Pa. tenuipunctata* has cosmopolitan distribution.

*Palmatolepis termini* Sannemann, 1955a

Figure 4A–4B

1955a *Palmatolepis termini* n. sp.; Sannemann, p. 149, pl. 1, figs. 1–3.
1993 *Palmatolepis termini*; Ji & Ziegler, p. 72, pl. 12, figs. 6–10, text-fig.13, fig. 5.
1995 *Palmatolepis termini*; Rodríguez-Cañero, p. 21, pl. IV, figs. 9–10.
1999 *Palmatolepis termini*; García-López et al., pl. I, fig. 6.
2003 *Palmatolepis termini*; Corradini, p. 84, pl. 3, figs. 9–10.
2006 *Klapperilepis termini*; Dzik, p. 122, figs. 86M–86V, 133.
2013 *Palmatolepis termini*; Strelchenko & Kruchek, pl. I, fig. 25.
2019 *Palmatolepis termini*; Zhang et al., fig. 6.21.

**Material.** 47 specimens from samples CP/98a (1), CP/98b (5), CP/98c (8), CP/99a (9), CP/99b (4), CP/99C (9), CP/99d-1 (1), CP/99d-2 (10).

**Description.** Elongated platform with lanceolate outline and without lobe. From the azygous node, one (Fig. 4B) or two (Fig. 4A) rows of nodes appear and extends along the anterior platform to the anterior margins. Inner margin meets the carina anteriorly. Straight anterior carina that strongly curved next to the azygous node; poorly developed or absent posterior carina that does not reach the posterior end. Pointed posterior margin. Flat or strongly turned upwards posterior platform. Smooth platform surface.

**Discussion.** The lanceolate platform outline is similar to *Pa. min. minuta* in but the presence of a row(s) of nodes in the anterior platform clearly distinguished both taxa.

**Age and geographical distribution.** From Famennian *min.* to *gl. prima* Zones (Spalletta et al., 2017). *Pa. tenuipunctata* has cosmopolitan distribution.

**Genus Polygnathus** Hinde, 1879

**Type species.** *Polygnathus dubius* Hinde, 1879, Givetian–Frasnian, Europe, North America, Asia, North Africa.

*Polygnathus bouckaerti* Dreesen & Dusar, 1974

Figure 7N–7O

1974 *Polygnathus bouckaerti* n. sp.; Dreesen & Dusar, p. 11–12, pl. 1, figs. 1–7, pl. 2, figs. 1–12.

1993 *Polygnathus bouckaerti*; Matyja, pl. 30, fig. 9, pl. 31, fig. 1.
1995 *Polygnathus bouckaerti*; Matyja & Narkiewicz, pl. IV, fig. 5.

**Material.** Two uncomplete specimens from samples CP/110 (1) and CP/111a-1 (1).

**Description.** Free blade is not preserved. Asymmetric and arched platform with oval outline; arched short carina, composed of 8 to 12 denticles that ends in the second third of the platform just before the subtriangular tongue with transverse ridges. Deep and narrow arcedinal throughs running parallel to the carina; lateral transversal short ridges or nodes are present in the anterior two thirds of the platform margins.

**Discussion.** Besides very different platform outline, *P. bouckaerti* can be distinguished from the *nodocostatus*-stock by the development of a tongue, which limits the extension of the carina to the anterior two thirds of the platform. It also differs from *Polylophodontata* taxa by the absence of the characteristic patterns of the platform ornamentation.

**Age and geographical distribution.** From Famennian *rhomboidea* to *mg. marginifera* Zones (Dreesen & Dusar, 1974). *P. bouckaerti* is recorded in Belgium, Spain and Poland.

*Polygnathus brevilaminus* Branson & Meh, 1934

Figure 5J

1934 *Polygnathus brevilaminus* n. sp.; p. 146, pl. 21, figs. 3–6.
1993 "Polygnathus brevilaminus"; Ji & Ziegler, p. 75, pl. 35, figs. 1–3.
1997 *Polygnathus brevilaminus*; Çapkın, p. 176, pl. 4, fig. 8.
1999 *Polygnathus brevilaminus*; García-López et al., pl. II, figs. 2–3.
2003 *Polygnathus? brevilaminus*; Corradini, p. 87, pl. 8, figs. 1–2.
2006 *Ctenopolygnathus brevilaminus*; Dzik, p. 84–85, figs. 55–56, 129.
2011 *Ctenopolygnathus brevilaminus*; Hartenfels, p. 236–237, pl. 61, fig. 5.
2013 *Polygnathus brevilaminus*; Bahrami et al., fig. 8FF–8GG, 8PP–8QQ.
2018 *Polygnathus brevilaminus*; Bahrami et al., fig. 6.36–6.37.
2019 *Polygnathus brevilaminus*; Zhang, p. 283, pl. 41, figs. 12–14.
2023 *Polygnathus brevilaminus*; Yuan & Sun, fig. 10C–10E.

**Material.** One specimen from sample CP/99a.

**Description.** Short and narrow rectangular platform with parallel margins; it does not reach the end of the element. Long and high free blade with denticles of different size and high, meets the straight carina obliquely. Carina extends beyond the platform at the
posterior end. Deep adcarinal grooves; platform lateral margins ornamented by fine nodes. Inner anterior platform margin joints at an obtuse angle the free blade and in an anterior position with respect to the outer margin; the latter joins perpendicularly the free blade.

**Discussion.** This taxon is distinguished by the short and narrow platform, which doesn’t reach the end of the element and by its ornamentation, as well. The genus status of *P. brevilaminus* has been questioned and even some authors consider that a new genus should be erected (Ji & Ziegler, 1993; Corradini, 2003). Müller and Müller (1957) established the new genus *Ctenopolygnathus*, to accommodate this taxon (Dzik, 2002, 2006; Harfenfels, 2011).

**Age and geographical distribution.** From Frasnian *linguiformis* (FZ13b) Zone to Famennian *granulosus* Zone (Spalletta et al., 2017). *P. brevilaminus* has a broad geographical distribution.

**Polynagathus communis communis** Branson & Mehl, 1934

Figure 6H1–6H2

1934 *Polynagathus communis* n. sp.; Branson & Mehl, p. 293, pl. 24, figs. 1–4.
1993 *Polynagathus communis* Communis; Ji & Ziegler, p. 76, pl. 35, figs. 4–6, text-fig. 21, figs. 2, 5.
1999 *Polynagathus communis communis*; García-López et al., pl. II, fig. 5.
2000 *Polynagathus communis communis*; Çağkınoğlu & Gedik, pl. 5, figs. 25–26.
2006 *Neopolygnathus communis*; Dzik, p. 102, figs. 70A–70S, 130.
2011 *Neopolygnathus communis*; Harfenfels, p. 241–242, pl. 61, figs. 1–4.
2013 *Polynagathus communis communis*; Bahrami et al., fig. 8H–8K, 8P.
2013 *Polynagathus communis communis*; Savage, figs. 11.23–11.25, 13.17–13.18.
2015 *Polynagathus communis communis*; Mossoni, p. 121, pl. 4, fig. 11.
2016 *Neopolygnathus communis communis*; Weiner & Kalvoda, fig. 5k.
2017 *Neopolygnathus communis communis*; Lüdecke et al., fig. 4e.
2019 *Polynagathus communis communis*; Zhang, p. 273, pl. 43, figs. 9–10, pl. 52, figs. 17–18.
2020 *Polynagathus communis communis*; Bahrami et al., fig. 8.19, 8.22.

**Material.** Four specimens from samples CP/106 (1), CP/107 (1), CP/109a (1) and CP/114a (1).

**Description.** Narrow and slightly arched, almost straight and symmetrical platform with lanceolate to ovate outline. Deep and narrow adcarinal grooves, high platform margins are elevated bearing nodes which are limited to the margins. Long, straight free blade, about half of element length, with 8 high denticles. The carina bents at its midlength, separating a denticulated anterior segment from a thin crest with few, if any, poorly developed and isolated denticles; it reaches the posterior end. Pointed posterior margin. Bulb-like basal cavity located in the anterior part of the platform; it follows posteriorly in a sulcate keel and anteriorly continues in an open and deep groove that narrows progressively to became appressed at the anterior end.

**Discussion.** The platform outline of *P. com. communis* can superficially resemble the *P. glaber*-stock; however, the platform of the latter is clearly bowed, wider, with sallow, or absent, adcarinal grooves and without ornamentation on the lateral margins. Basal cavity is very narrow, restricted to a pit, that continues to both ends in narrow, appressed sulci that close to both ends.

**Age and geographical distribution.** From Famennian *crepida* Zone to Tourmaisian *anchoralis* Zone (Spalletta et al., 2017). *P. com. communis* has a broad geographical distribution.

**Polynagathus glaber eoglaber** Ji & Ziegler, 1993

Figure 5K

1993 *Polynagathus eoglaber* n. sp.; Ji & Ziegler, p. 78, pl. 36, figs. 10–15, text-fig. 21, fig. 10.
2003 *Polynagathus glaber eoglaber*; Corradini, p. 82, pl. 8, fig. 2.
2015 *Polynagathus glaber eoglaber*; Mossoni, p. 124, pl. 5, fig. 14.

**Material.** Two specimens from samples CP/111a-2 (1) and CP/111b (1).

**Description.** Small and symmetrical platform with lanceolate outline and bowed margins. Straight carina that extends beyond the posterior part of the platform, forming a posterior free blade. Deep and narrow (restricted to an area adjacent to the carina) adcarian grooves. Smooth platform surface.

**Discussion.** The free blade of the figurated specimen is broken (Fig. 5K), but the bowed, wide platform with restricted adcarinal grooves and smooth platform surface and posterior carina are distinctive characters in the *glaber*-stock.

**Age and geographical distribution.** From Famennian *min. minuta* to *gr. gracilis* Zones (Spalletta et al., 2017). *P. gb. eoglaber* is recorded in France, Italy and China.

**Polynagathus glaber glaber** Ulrich & Bassler, 1926

Figure 8M–8N

1926 *Polynagathus glaber* n. sp.; Ulrich & Bassler, p. 46, pl. 7, fig. 13.
1993 *Polynagathus glaber glaber*; Ji & Ziegler, p. 79, pl. 36, figs. 1–6, text-fig. 21, fig. 11.
2003 *Polynagathus glaber glaber*; Corradini, p. 87–88, pl. 8, figs. 3–5.
2011 *Polynagathus glaber glaber*; Harfenfels, p. 284, pl. 51 figs. 1–3.
2015 *Polygnathus glaber glaber*; Mossoni, p. 125, pl. 2, fig. 13.
2017 *Polygnathus glaber glaber*; Lüddecke et al., fig. 5i.
2017 *Polygnathus glaber glaber*; Ovnanova et al., pl. 49, figs. 5, 7.
2019 *Polygnathus glaber glaber*; Zhang, p. 274, pl. 43, figs. 1–4.
2020 *Polygnathus glaber glaber*; Bahrami et al., fig. 8. 24.

**Material.** 35 specimens from samples CP/99c (2), CP/110 (2), CP/111a-1 (2), CP/111a-2 (1), CP/111b (1), CP/111c (2), CP/112a (5), CP/112b (4), CP/112e (2), CP/112g (2), CP/114b (1), CP/115 (1), CP/117 (6), CP/118a (1), CP/118b (1) and CP/119 (2).

**Description.** Bowed platform almost symmetrical with ovate to lanceolate outline. Moderately deep adcarinal grooves running through the platform close to the carina. Straight carina or slightly arched with fused denticles. Short free blade. Inner anterior margin joins the free blade in a more anterior position than the outer margin. Platform surface smooth or shagreen. Basal cavity located in the anterior third and reduced to a pit, which continues in narrow appressed sulci that taper to both ends.

**Discussion.** *P. gb. glaber* is similar to *P. gb. medius* in the platform outline, but it differs by deeper adcarinal grooves and because the platform anterior margins of *P. gl. medius* join the free blade at the same point conferring the platform a more symmetrical aspect. On the other hand, it differs from *P. gb. bilobatus* by the lack of a lobe in *P. gb. glaber*. The carina of *P. gb. eoglaber* extends beyond the platform posteriorly with the differences with *P. com. communis* are described above.

**Age and geographical distribution.** From Famennian *mg. marginifera* to *mg. utahensis* Zones (Spalletta et al., 2017). *P. gb. medius* is recorded in Germany, Spain, Italy, Turkey, Uzbekistan and China.

*Polygnathus lauriformis* Dreesen & Dusar, 1974

**Figure 8I–8K**

1974 *Polygnathus lauriformis* n. sp.; Dreesen & Dusar, p. 16, pl. 1, figs. 8–11, pl. 3, figs. 1–12.
1990 *Polygnathus lauriformis*; Perri & Spalletta, p. 65, pl. 5, figs. 6a–6b.
1993 *Polygnathus lauriformis*; Matyja, pl. 29, fig. 4.
1995 *Polygnathus lauriformis*; Sanz López, p. 500, pl. 47, figs. 7–10.
1998 *Polygnathus lauriformis*; Perri & Spalletta, pl. 1.3.1, fig. 11a–11b.
1999 *Polygnathus lauriformis*; García-López et al., pl. II, fig. 8.
2006 *Polygnathus lauriformis*; Woroncowa-Marcinowska, fig. 15.
2006 *Polygnathus lauriformis*; Dzik, p. 81, figs. 51N, 51O, 52A–52L.

**Material.** 41 specimens from samples CP/112c (1), CP/112f (2), CP/112g (5), CP/113a (4), CP/113c (4), CP/114a (12), CP/114b (5), CP/115 (3), CP/117 (1), CP/118b (3) and CP/119 (1).

**Description.** Moderately narrow and almost symmetrical platform with lanceolate outline. High and short free blade with 5–6 high denticles. Straight or slightly curved carina. Adcarinal grooves restricted to the anterior half. The margins might develop ridges in the anterior half (Fig. 8P). Anterior margins join the long free blade at the same point. Straight to slightly arched carina formed by moderately isolated denticles. High free blade bearing denticles, which are higher than those of the carina, and decreasing in high from the anterior end to the platform. Pointed posterior platform end. Except for the marginal nodes, the platform is smooth. Fine keel and reduced to a pit basal cavity.

**Discussion.** The differences with *P. gb. glaber* are discussed there.

**Age and geographical distribution.** From Famennian *mg. marginifera* to *mg. utahensis* Zones (Spalletta et al., 2017). *P. gb. medius* is recorded in Germany, Spain, Italy, Turkey, Uzbekistan and China.

*Polygnathus lauriformis* Dreesen & Dusar, 1974

**Figure 8I–8K**

1974 *Polygnathus lauriformis* n. sp.; Dreesen & Dusar, p. 16, pl. 1, figs. 8–11, pl. 3, figs. 1–12.
1990 *Polygnathus lauriformis*; Perri & Spalletta, p. 65, pl. 5, figs. 6a–6b.
1993 *Polygnathus lauriformis*; Matyja, pl. 29, fig. 4.
1995 *Polygnathus lauriformis*; Sanz López, p. 500, pl. 47, figs. 7–10.
1998 *Polygnathus lauriformis*; Perri & Spalletta, pl. 1.3.1, fig. 11a–11b.
1999 *Polygnathus lauriformis*; García-López et al., pl. II, fig. 8.
2006 *Polygnathus lauriformis*; Woroncowa-Marcinowska, fig. 15.
2006 *Polygnathus lauriformis*; Dzik, p. 81, figs. 51N, 51O, 52A–52L.

**Material.** 41 specimens from samples CP/112c (1), CP/112f (2), CP/112g (5), CP/113a (4), CP/113c (4), CP/114a (12), CP/114b (5), CP/115 (3), CP/117 (1), CP/118b (3) and CP/119 (1).

**Description.** Moderately narrow and almost symmetrical platform with lanceolate outline. High and short free blade with 5–6 high denticles. Straight or slightly curved carina. Adcarinal grooves restricted to the anterior half. The margins might develop ridges in the anterior half (Fig. 8P). Anterior margins join the long free blade at the same point. Straight to slightly arched carina formed by moderately isolated denticles. High free blade bearing denticles, which are higher than those of the carina, and decreasing in high from the anterior end to the platform. Pointed posterior platform end. Except for the marginal nodes, the platform is smooth. Fine keel and reduced to a pit basal cavity.

**Discussion.** The differences with *P. gb. glaber* are discussed there.

**Age and geographical distribution.** From Famennian *mg. marginifera* to *mg. utahensis* Zones (Spalletta et al., 2017). *P. gb. medius* is recorded in Germany, Spain, Italy, Turkey, Uzbekistan and China.
Polygnathus longiusculus Çapkinoğlu, 1997

Figure 8Q

1999 Polygnathus longiusculus; Sanz-Lópe et al., pl. 2, fig. 16.
2015 Polygnathus longiusculus?; Mohamed, fig. 20a.

Material. One specimen from sample CP/118b.

Description. Narrow, elongated and symmetrical platform with ovate outline. Long, straight free blade, about half of the element, which continues in the straight carina depicting a straight medium line-like. Carina composed of nine denticles, which are closer (even fused) anteriorly and discrete posteriorly. Platform margins ornamented by nodes and ridges. Shallow and narrow adcarinal grooves. Pointed posterior margin.

Discussion. Platform outline and marginal nodes are similar to *P. fallax*, but the disposition of denticles on the carina distinguished both taxa.

Age and geographical distribution. *P. longiusculus* is exclusively recorded in the Famennian *mg. marginifera* Zone (Çapkinoğlu, 1997). *P. longiusculus* is recorded in Spain and Turkey.

Polygnathus nodocostatus nodocostatus Branson & Mehl, 1934

Figure 6I–6K

1934 Polygnathus nodocostatus; Branson & Mehl, p. 246, pl. 20, figs. 9–13, pl. 21, fig. 15.
1993 Polygnathus nodocostatus; Ji & Ziegler, pl. 34, figs. 13–15, text-fig. 20, fig. 1.
1995 Polygnathus nodocostatus nodocostatus; Lüddecke et al., p. 505, pl. 47, figs. 1–2.
1997 Polygnathus nodocostatus nodocostatus; Corradini, p. 89, pl. 9, figs. 1–2.
2003 Polygnathus nodocostatus nodocostatus; Hartenfels, p. 289, pl. 53, figs. 5–7.
2013 Polygnathus nodocostatus nodocostatus; Strelchenko & Kruchek, pl. I, fig. 43.
2015 Polygnathus nodocostatus nodocostatus; Mossoni, p. 128, pl. 2, figs. 3, 14.
2017 Polygnathus nodocostatus nodocostatus; Lüddecke et al., fig. 5l.
2019 Polygnathus nodocostatus; Zhang, p. 278–279, pl. 42, figs. 1–5.
2020 Polygnathus nodocostatus nodocostatus; Suttner et al., fig. 6.20a–6.20b.
2021 Polygnathus nodocostatus nodocostatus; Sattari et al., fig. 6.23.

Material. 15 specimens from samples CP/105a (1), CP/105b (1), CP/107 (1), CP/109a (2), CP/111c (1), CP/112a (1), CP/112b (1), CP/112c (3), CP/112d (1), CP/112e (1), CP/114b (1) and CP/116 (1).

Description. Slightly asymmetrical platform with diverse outlines, mainly ovate to rhombic. Platform width ranges from broad (more frequent) to narrow (Fig. 6I). Short free blade with few, high denticles. Straight to arched carina that does not reach de posterior end. The inner margin is straight or moderately convex, while the outer margin is convex. The platform is ornamented by rows of nodes, subparallel to the carina; nodes in broad-platform specimens are aligned in “V” forming ridges join the carina in an acute angle. Deep and short adcarinal grooves are restricted to the anterior part of the platform. The keel is fine and on the anterior third, a reduced basal cavity appears in the anterior third; it continues in thin keels.

Discussion. *P. nod. nodocostatus* is similar to others *nodocostatus*-stock taxa. *P. nod. ovatus* has a comparable platform outline, but the latter has a symmetrical platform with a marked constriction in the posterior third and an irregular arrangement of the nodes. *P. nodoundatus* shows a concave margin in the anterior outer platform, a strongly asymmetrical platform and irregular arrangement of the nodes. The absence of a collar separates *P. nod. nodocostatus* from *P. perplexus*. The platform of *P. granulosus* has a heart-like outline (broader in the anterior side and narrower in the posterior side), straight margins, irregular arrangement of nodes and absence of V-like ridges in the anterior side. *P. margaritatus* is similar to the narrow forms of *P. nod. nodocostatus*, but the distinctive collar and nearly fused rows of nodes parallel to the carina in the former, separates both taxa. The strongly asymmetrical and nearly sigmoidal outline of the platform distinguished *P. pennatuloideus* inform *P. nod. nodocostatus*. The carina of *P. diversus* is clearly offset.

Age and geographical distribution. From Famennian crepida to gr. expansa Zones (Spalletta et al., 2017). *P. nod. nodocostatus* has a broad geographical distribution.

Polygnathus nodocostatus ovatus Helms, 1961

Figure 6L–6M

1995 Polygnathus nodocostatus ovatus; Sanz-Lópe et al., p. 505.
1997 Polygnathus nodocostatus ovatus; Çapkinoğlu, p. 181, pl. 5, fig. 11.
2013 Polygnathus nodocostatus ovatus; Rytina et al., pl. 2, fig. 9.
2017 Polygnathus nodocostatus ovatus; Rytina et al., fig. 5m.
2023 Polygnathus nodocostatus ovatus; Huang et al., fig. 11B.

Material. Eight specimens from samples CP/105a (4), CP/105b (1), CP/109a (1), CP/112C (1) and CP/114b (1).

Description. Platform varies from broad to narrow, nearly symmetrical with ovate to lanceolate outline.
Short free blade with fused denticles. Platform shows a constriction in the posterior part (broad forms) or in the anterior part (narrow forms). Slightly curved carina that ends before the posterior end. Platform ornamented by nodes, some of them fused in ridges, irregularly arranged or aligned in faint lines perpendicular or oblique to the carina (broad forms); the narrow forms have less nodes and most of them run parallel to the margins. Reduced basal cavity continues in thin keels.

**Discussion.** This differences with *P. nod. nodocostatus* have been described there.

**Age and geographical distribution.** From Famennian gl. *prima* to styriacus Zones (Spalletta et al., 2017). *P. nod. ovatus* is recorded in Germany, Spain, Turkey and China.

**Polygnathus padovanii** Perri & Spalletta, 1990

*Polygnathus padovanii* n. sp.; Perri & Spalletta, p. 66, pl. 6, figs. 1–5, pl. 7, figs. 1–3.

1990 *Polygnathus padovanii* n. sp.; Perri & Spalletta, p. 66, pl. 6, figs. 1–5, pl. 7, figs. 1–3.

1993 *Polygnathus limbatus* n. sp.; Matyja, p. 38, pl. 28, figs. 1–12.

1995 *Polygnathus padovanii*; Sanz-López, p. 507, pl. 48, fig. 1.

2003 *Polygnathus padovanii*; Corradini, p. 89–90, pl. 10, fig. 1.

2011 *Polygnathus padovanii*; Hartenfels, p. 299, pl. 51, figs. 6–10.

2017 *Polygnathus padovanii*; Ovнатanova et al., p. 1132, pl. 48, fig. 9.

2017 *Polygnathus padovanii*; Lüddecke et al., fig. 5n.

2020 *Polygnathus padovanii*; Bahrami et al., figs. 8.23, 8.43, figs. 9.16, 9.18.

2021 *Polygnathus padovanii*; Sattari et al., fig. 5.28–5.29.

2022 *Polygnathus padovanii*; Bahrami et al., fig. 6.39.

**Material.** Nine specimens from samples CP/104c (1), CP/112e (2), CP/112g (2), CP/113a (2), and CP/113b (2).

**Description.** Moderately asymmetric and bowed platform with lanceolate outline. High anterior margins; the outer is straight and denticulated and the inner is bowed outwards; this differential development of the anterior part confers the platform an asymmetrical aspect, which is limited, however, to this first anterior fourth. The anterior margins join the blade at almost right angles. Straight carina that curves in the posterior half and reaches the posterior end. Platform is ornamented by thick and long transverse ridges along the platform. Wide and deep adcarinal grooves in the anterior part of the platform that change to narrow and shallow in the posterior part. Free blade about one third the length of the element, with about 6–7 denticles. The posterior end is pointed and moderately turned downwards. Reduced basal cavity continues in thin keels.

**Discussion.** The platform outline shows great variability and, in some cases, can be similar to *P. subnormalis* in Compte section; however, the latter is strongly asymmetrical, has more elevated anterior margins, deeper and broader adcarinal grooves, shorter ridges and the anterior margins do not join the free blade at the same point. Matyja (1993) described *P. limbatus* in the polish Pomerania region; this species shares diagnostic characters with *P. padovanii* like slender, arched and asymmetrical platform, elevated anterior margins with flange-like form and transversal ridges. Consequently, *P. limbatus* was considered as a junior synonym of *P. padovanii* (Corradini, 2003; Hartenfels, 2011).

**Age and geographical distribution.** According to Perri and Spalletta (1990) the range extends from Famennian *mg. utahensis* to *r. trachytiera* Zones. Including the synonym list of *P. limbatus* as *P. padovanii*, the range extends to *gl. pectinata* Zone in the Lublin-basin area and *mg. marginifera* Zone in West-Pomerania (Matyja, 1993). Corradini (2003) mentioned a longer record in the Carnic Alps from the original range. Hartenfels (2011) extends its range to *granulosus* Zone in the Thuringia region. In central Iran region, the lower range is recorded from the *rhomboidea* Zone (Sattari et al., 2021) and in the North Iran region, is recorded from *gl. pectinata* to *granulosus* Zones (Bahrami et al., 2022). *P. padovanii* has a broad geographical distribution.

**Polygnathus procerus** Sannemann, 1955b

*Polygnathus procerus* n. sp.; Sannemann, p. 150, pl. 1, fig. 11.

1955b *Polygnathus procerus* n. sp.; Sannemann, p. 150, pl. 1, fig. 11.

1993 *Polygnathus procerus*; Ji & Ziegler, p. 83–84, pl. 38, figs. 4–8, text-fig. 21, fig. 1.

1993 *Polygnathus procerus*; Matyja, pl. 24, fig. 10, pl. 26, fig. 1.

1999 *Polygnathus procerus*; Schülke, p. 63–64, pl. 13, figs. 1–11.

1999 *Polygnathus procerus*; García-López et al., pl. II, fig. 7.

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2003 *Polygnathus procerus*; Corradini, p. 90, pl. 8, fig. 14.
2007 *Polygnathus procerus*; Chohamalian, fig. 100–10P.
2008 *Polygnathus procerus*; Sánchez de Posada et al., pl. 1, figs. 18–19.
2013 *Polygnathus procerus*; Bahrami et al., fig. 800.
2016 *Polygnathus procerus*; Huang & Gong, figs. 7.4, 7.18.
2020 *Polygnathus procerus*; Suttner et al., fig. 6.21a–6.21b.
2021 *Polygnathus procerus*; Zamani et al., pl. 4, fig. 10.

**Material.** Six specimens from samples CP/99a (4) and CP/99b (2).

**Description.** Small, slender, slightly asymmetrical platform with lanceolate outline. Straight, fan-shape free blade with 9 denticles; it represents about 1/3 of the platform length. Bowed platform with posterior half strongly turned downward. Outer margin with a sinuous outline with a weak constriction in the anterior half; inner margin straight. High anterior margins and slightly concave outwards, the outer more markedly. Deep and broad adcarinal grooves in the anterior half that shallows to disappear in the posterior half. Carina denticles fused in a thin arched crest to the posterior end. Weak transverse ridges irregularly spaced and more abundant in the posterior half. Reduced basal cavity continues in thin keels.

**Discussion.** *P. procerus* resembles *P. praecursor*; however, the narrower and slenderer platform ornamented with fine transverse ridges separate both taxa.

**Age and geographical distribution.** Initially, Ji and Ziegler (1993) extend the range from Frasnian *rot. rotundiloba* (FZ2b) to *gl. prima* Zones. In the Montagne Noire, Schülke (1999) limited its range to the Famennian, from the upper part of the *triangularis* Zone to *gl. prima* Zone. In Sardinia, Corradini (2003) extended the record to the *gl. pectinata* Zone. However, in Central Iran Bahrami et al., (2013) extended its range downward from Frasnian *bogartensis* (FZ13a) Zone and Zamani et al. (2021) recorded this species from the *linguiformis* (FZ13) Zone. In South China, Huang and Gong (2016) recorded this species from the *minuta* to *gl. pectinata* Zones. *P. procerus* is recorded in France, Italy, Spain, Turkey, Iran and China.

*Polygnathus semicostatus* Branson & Mehl, 1934

**Figure 5L–5N**

1934 *Polygnathus semicostatus* n. sp.; Branson & Mehl, p 247–248, pl. 21, figs. 1–2.
1974 *Polygnathus semicostatus*; Dreessen & Orchard, p. 3, pl. 1, figs. 1–8, pl. 2, figs. 1–25.
1979 *Polygnathus semicostatus*; Sandberg & Ziegler, p. 187, pl. 5, figs. 1–5.
1993 *Polygnathus semicostatus*; Ji & Ziegler, p. 84, text-fig. 19, fig. 4.
1993 *Polygnathus semicostatus*; Sanz-López, p. 513, pl. 47, figs. 4–6, 11–12.
2003 *Polygnathus semicostatus*; Corradini, p. 90, pl. 10, fig. 6.
2009 *Polygnathus semicostatus*; Over et al., fig. 4.3–4.4.
2011 *Polygnathus semicostatus*; Hartenfels, p. 299–300, pl. 59, figs. 1–10, pl. 61, fig. 6.
2011 *Polygnathus semicostatus*; Narkiewicz & Bultynck, pl. XII, fig. 6.
2013 *Polygnathus semicostatus*; Rytina et al., pl. 2, fig. 11.
2013 *Polygnathus semicostatus*; Bahrami et al., p. 382, fig. 9L.
2020 *Polygnathus semicostatus*; Bahrami et al., fig. 8.25–8.27, 8.44.

**Material.** 28 specimens from samples CP/101b (1), CP/105a (7), CP/105b (4), CP/105d (1), CP/106 (5), CP/109b (1), CP/110 (4), CP/111a-1 (3), CP/112f (1) and CP/112g (1).

**Description.** Broad to elongated platform with tongue-shape outline. Short, straight free blade with fused denticles; it continues “in line” with the straight carina, consisting also of a crest of fused denticles that do not reach the posterior end because in the posterior third a tongue with transverse ridges develops. Straight to oblique anterior margins, slightly high, joining the free blade at the same point. Narrow and moderately shallow adcarinal grooves that end before the posterior tongue. Posterior platform turned downward. Long, transverse ridges run from the margins perpendicular to the carina up to the adcarinal grooves. Reduced basal cavity continues in thin keels.

**Discussion.** This species has a high morphological variety, Dreessen and Orchard (1974) described eight morphological trends, which were based on the increase of the number of transversal ridges in the posterior platform, the flexion of the platform, the deepening of the adcarinal grooves and the wide of the tongue. The two most frequent forms are: 1) the “central morphotype” with a tongue-shape outline platform, margins convex or straight and the wide tongue with transverse ridges; 2) the morphotype 3 of Dreessen and Orchard (1974), characterized by a narrower platform and a constriction of the posterior end at the last nodule level. *P. semicostatus* differs from *P. obliquicosostatus* because the latter has oblique transverse ridges.

**Age and geographical distribution.** From Famennian termini to *ultimus* Zones (Spalletta et al., 2017). *P. semicostatus* has a broad geographical distribution.

*Polygnathus subnormalis* Vorontsova & Kuzmin, 1984

**Figure 7P**

1984 *Polygnathus subnormalis* n. sp.; Vorontsova & Kuzmin, p. 62, pl. 1, figs. 6–10.
1990 *Polygnathus subnormalis*; Kuzmin, p. 67–68, pl. 4, figs. 7, 10.
1994 *Polygnathus subnormalis*; Metzger, p. 640, 644, fig. 19.10–19.22.
1997 *Polygnathus subnormalis*; Çapkınoğlu, p. 181, pl. 5, fig. 18.
1997 *Polygnathus subnormalis*; Mawson & Talent, p. 222, fig. 15.9–15.14.
2003 *Polygnathus subnormalis*; Corradini, p. 91, pl. 10, fig. 2.
2005a *Polygnathus subnormalis*; Çapkınoğlu, fig. 5.24.
2019 *Polygnathus subnormalis*; Zhang, p. 270, pl. 52, figs. 25–28, 37.
2020 *Polygnathus subnormalis*; Suttner et al., fig. 6.17a–6.17b.
2021 *Polygnathus subnormalis*; Zhang et al., fig. 4Y–4AB, 4AK.

**Material.** Five specimens from samples CP/112b (1), CP/112f (1), CP/113b (1) and CP/113c (2).

**Description.** Moderately slender, strongly asymmetrical platform with lanceolate outline. Short free blade, about 1/4 of platform length, with denticles fused in a thin crest that continues in the curved and bowed carina, which is represented by a thin crest that ends close before the posterior end. High anterior margins; the outer anterior is slightly constricted, bear a few denticles and joins the free blade at a markedly anterior position than the inner one. A denticulate inner anterior margin, outward bowed. Deep anterior adcarinal grooves that shallow posteriorly. Platform ornamented by fine transverse ridges. Posterior margin is moderately downward turned.

**Discussion.** The difference with *P. padovanii* has been discussed above. The platform outline of *P. buzzmakovi* is similar, but the more symmetrical and wider platform, ornamented by fine ridges and nodes and straight anterior margins enables separation between the two taxa.

**Age and geographical distribution.** From Famennian *granulosus* Zones (Kuzmin, 1990). *P. subnormalis* is recorded in Russia, Italy, Turkey, Spain, Australia, Mongolia, China and USA.

*Polygnathus triphyllatus* Helms, 1961
Figure 7Q–7R
1961 *Polygnathus triphyllatus* Helms, p. 696, pl 1, figs. 2–3, pl. 3, figs. 12, 15–17.
1994 *Polygnathus cf. triphyllatus*; Metzger, p. 644, fig. 19.7–19.9.
1997 *Polygnathus triphyllatus*; Çapkınolu, p. 181, pl. 5, figs. 16–17.
2003 *Polygnathus triphyllatus*; Corradini, p. 91, pl. 91, figs. 11–13.
2006 *Polynodosus triphyllatus*; Dzik, p. 81, 82, fig. 54A–54I.
2020 *Polygnathus triphyllatus*; Bahrami et al., fig. 9.1.
2022 *Polygnathus triphyllatus*; Bahrami et al., figs. 5.7, 7.20.

**Material.** Eight specimens from samples CP/112e (3), CP/112g (1), CP/113a (2), CP/114a (1) and CP/118a (1).

**Description.** Symmetrical, slightly curved platform with a strong constriction about the middle part conferring an inverted violin-shape outline. Concave anterior margins joining the free blade at different positions (the inner more anteriorly). Platform ornamented by parallel rows of coarse nodes. Shallow adcarinal grooves. Short free blade. Juvenile specimens (Fig. 7Q) have a small, slender, arched and constricted platform, with moderately deep adcarinal groves and ornamented by a unique row of nodes, parallel to the carina, in both sides.

**Discussion.** The most distinctive feature of *P. triphyllatus* is the middle constriction of the platform. Pa elements described as *P. cf. diversus* in Metzger (1994) may belong to juvenile specimens of *P. triphyllatus*.

**Age and geographical distribution.** From the upper half of the Famennian *gr. gracilis* Zone to the lower half of the *mg. marginifera* Zone (Spalletta et al., 2017). *P. triphyllatus* is recorded in Italy, Spain, Germany, Poland, Turkey, Iran and USA.

Order PRIONIODONTIDA Dzik, 1976
Family ICRIODONTIDAE Müller & Müller, 1957

**Genus Icriodus** Branson & Mehl, 1938

**Type species.** *Icriodus expansus* Branson & Mehl, 1938, Givetian–Frasnian, Europe, North America, North Africa.

*Icriodus alternatus alternatus* Branson & Mehl, 1934
Figure 5E–5F
1934 *Icriodus alternatus alternatus* n. sp.; Branson & Mehl, p. 225–226, pl. 13, figs. 4–6.
1984 *Icriodus alternatus alternatus*; Sandberg & Dreesen, pl. 2, figs. 5, 11.
1993 *Icriodus alternatus alternatus*; Ji & Ziegler, p. 55, pl. 5, figs. 5–8, text-fig. 6, fig. 2.
1995 *Icriodus alternatus alternatus*; Sanz-López, p. 428–429, pl. 35, fig. 12, pl. 36, fig. 4–11.
2003 *Icriodus alternatus alternatus*; Corradini, p. 92, pl. 2, figs. 9–12.
2013 *Icriodus alternatus alternatus* morphotype 1; Hartenfels, pl. 39, figs. 1–3.
2013 *Icriodus alternatus alternatus*; Bahrami et al., p. 384, 386, fig. 9F–9K.
2015 *Icriodus alternatus alternatus*; Mossoni, p. 143–144, pl. 1, fig. 5.
2017b *Icriodus alternatus alternatus*; Valenzuela-Ríos et al., fig. 4.1.
2017 *Icriodus alternatus alternatus*; Ovnatalova et al., pl. 54, figs. 6–8.
2020 *Icriodus alternatus alternatus*; Suttner et al., figs. 6.5a–6.5b.

**Material.** 49 specimens from samples CP/98a (1), CP/98b (4), CP/98c (1), CP/99a (1), CP/99b (14), CP/99c (2), CP/99d-1 (1), CP/99d-2 (3), CP/101a (1), CP/101b (11), CP/102b (2), CP/104a (2), CP/104c (5) and CP/111a-1 (1).

**Description.** Biconvex to very slightly concave-convex, elongated and narrow platform with parallel sides composed of 6–7 transversal rows of disconnected, rounded, laterally compressed denticles with the middle row ones located anterior to the corresponding lateral ones. The middle row continues posteriorly with two cusps aligned with this row. Rounded, semicircular expansions reaching the third or fourth lateral rows. Expanded, fully excavated drop shaped basal cavity, which is wider and deeper posteriorly.

**Discussion.** This taxon is similar to *Ic. alternatus helmsi*, however, the latter differs because the cusp
is not aligned with the middle row. Sandberg and Dreesen (1984) reported two morphotypes of *Ic. alt. alternatus* according to the compression of the middle row denticles. The first morphotype is characterized by the laterally compressed and elongated middle row denticles and the second morphotype is characterized by the rounded middle row denticles.

**Age and geographical distribution.** From Frasnian *bogartensis* (FZ13a) Zone to Famennian *gl. pectinata* Zone (Bultynck, 2003). *Ic. alt. alternatus* has cosmopolitan distribution.

*Icriodus alternatus mawsonae* Yazdi, 1999

Figure 5G–5H

1991 *Icriodus alternatus* n. ssp.; Clausen et al., pl. 8, fig. 4. 1999 *Icriodus alternatus mawsonae* n. ssp.; Yazdi, p. 197, pl. 1, fig. 15, pl. 2, figs. 3–4.

1999 *Icriodus alternatus mawsonae*; Talent et al., pl. 5, fig. 9.

2000 *Icriodus alternatus mawsonae*; Yazdi et al., p. 201, fig. 4.9–4.13.

2007 *Icriodus alternatus mawsonae*; Gholamalian, p. 465, fig. 9R.

2009 *Icriodus alternatus mawsonae*; Gholamalian et al., pl. 1, fig. 5.

2020 *Icriodus alternatus mawsonae*; Becker et al., fig. 19.18.

**Material.** 18 specimens from samples CP/98a (1), CP/98c (1), CP/99a (3), CP/99b (4), CP/99d-2 (5), CP/101b (2) and CP/102b (2).

**Description.** Biconvex to moderately concave-convex, elongate platform. Lateral rows composed of 8–9 denticles that can be fused. Middle row weakly developed or absent, in the posterior half of the platform. When transversal rows consist of three denticles, the middle one is advanced anteriorly. Reduced cusp of irregular shape. Drop shaped basal cavity, wider and deeper posteriorly, shallowing and narrowing anteriorly. Basal cavity expansions reach different positions; frequently the posteriorly, shallowing and narrowing anteriorly. Basal cavity expansions reach different positions; frequently the outer one roughly extends more anteriorly than the inner.

**Discussion.** The weak or absent middle row denticles in the posterior half distinguish this taxon from *Ic. alt. alternatus*.

**Age and geographical distribution.** From Frasnian *ultima* (FZ13c) Zone to the Famennian first half of the *gl. prima* Zone (Spalletta et al., 2017). *Ic. alt. mawsonae* is recorded in Iran, Pakistan and Morocco.

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Figure 8. A, Palmatolepis quadratinodosa inflexa, sample CP/113c; B, Palmatolepis quadratinodosa inflexa, sample CP/112g; C, Palmatolepis stopelli, sample CP/113c; D, Palmatolepis quadratinodosa inflexoida, sample CP/114a; E, Palmatolepis quadratinodosa quadratinodosa, sample CP/114a; F, Palmatolepis marginifera marginifera, sample CP/114a; G, Palmatolepis marginifera marginifera, sample CP/115; H, Palmatolepis perlata sigmoidea, sample CP/117; I, Polygnathus lauriformis, upper view, CP/113a; I2, Polygnathus lauriformis, lower view, sample CP/113a; J, Polygnathus lauriformis, sample CP/113a; K, Polygnathus lauriformis, sample CP/113c; L1, Mehlina strigosa, upper view, sample CP/114a; L2, Mehlina strigosa, lateral view, sample CP/114a; M1, Polygnathus glaber glaber, upper view, sample CP/112b; M2, Polygnathus glaber glaber, lower view, sample CP/112b; N, Polygnathus glaber glaber, sample CP/112a; O1, Polygnathus glaber glaber, sample CP/112a; O2, Polygnathus glaber medius, lateral view, sample CP/119; P, Polygnathus glaber medius, sample CP/117; Q, Polygnathus longiusculus, sample CP/118b; scale bar = 100 μm.
or slightly anteriorly directed. Deep, broadly expanded asymmetrical basal cavity that narrows anteriorly.

**Discussion.** The number of denticles and the platform shape shows similarities with *lc. alt. alternatus*, however, the presence of a spur and the closer (almost touching) arrangement of denticles separates *lc. tumulus* from the former taxon. *lc. iowaensis* *iowaensis* has greater develop of the transversal ridges and the posterior carina process is turned downwards.

**Age and geographical distribution.** In the Cadí nappe the range is recorded from Famennian *gl. pectinata* to *rhomboidea* Zones (Sanz-López, 1995). *lc. cornutus* is recorded in Spain.

Suborder **OZARKODININA** Dzik, 1976
Family **SPATHOGNATHODONTIDAE** Hass, 1959

Genus **Mehlina** Youngquist, 1945

**Type species.** *Mehlina gradata = Mehlina irregularis* Youngquist, 1945, Frasnian–Famennian, Europe, North America.

*Mehlina strigosa* Branson & Mehl, 1934

Figure 8L1–8L2
1934 *Spathodus strigosus* Branson & Mehl, p. 187, pl. 17, fig. 17.
1962b *Spathognathodus strigosus*; Ziegler, p. 111, pl. 12, figs. 21–23 (cum syn.).
1984 *Mehlina strigosa*; Ziegler & Sandberg, p. 183, fig. 4.
1991 *Mehlina strigosa*; Perri & Spalletta, p. 60, pl. 3, fig. 6.
1997 *Mehlina strigosa*; Çapkınoğlu, p. 183, pl. 4, figs. 3–7.
2005a *Mehlina strigosa*; Çapkınoğlu, fig. 5.28–5.29.
2011 *Mehlina strigosa*; Bahrami et al., p. 1, figs. 31–32.
2015 *Mehlina strigosa*; Mossoni, p. 119–120, pl. 5, fig. 16.
2017 *Mehlina strigosa*; Lüddecke et al., fig. 4c–4d.
2020 *Mehlina strigosa*; Suttner et al., fig. 6.4.

**Material.** Five specimens from samples CP/112c (1), CP/112f (1), CP/114a (2) and CP/114b (1).

**Description.** Pa elements with concave-convex upper margin and stepped lower one, with the posterior part lower. The blade has 14–15 fused and aligned denticles, with different heights. Anteriorly there are two or three slightly higher, decreasing in high to the cusp, which is conspicuous. Posterior to the cusp denticles increase in high up to the one before the last two, then they diminish in high. Slightly expanded asymmetrical semicircular platform lobes located in mid position, Reduced basal cavity beneath the lobes.

**Discussion.** This taxon can be similar to *Me. gradata*, but the latter has the denticles backwards inclined.

**Age and geographical distribution.** From Famennian *termini* Zone to Tournaisian *bransoni* Zone (Spalletta et al., 2017). *Me. strigosa* has a broad geographical distribution.

**DISCUSSION**

Following Spalletta et al. (2017) the conodont assemblage in the section Compte, which is mainly composed by the *glabra*-stock, *minuta*-stock, *perlobata*-stock, *quadrantinodosa*-stock, *nodocostatus*-stock, *marginifera*-stock and *glaber*-stock, points to a lower–middle Famennian age. La Mena Fm is approximately bounded between the records of *Pa. rhomboidea* and *Pa. mg. marginifera*, revealing the presence of the *rhomboidea–mg. marginifera* conodont Zones.

The Compte section conodont assemblage is rich and diverse allowing its comparison with others assemblages worldwide. The Pyrenean Cadi Nape zone (east of Compte section) yields different Upper Devonian outcrops with conodont faunas (Sanz-López, 1995). The La Coma Oriola section comprises a lower–middle Famennian conodont sequence, similar to Compte section: both sections share the *lc. alternatus*-stock, *P. nodocostatus*-stock, *Pa. glabra*-stock, *Pa. perlobata*-stock, *Pa. quadrantinodosa*-stock and *P. glaber*-stock. However, *lc. alt. helmsi*, *Pa. protorhomboidae*, *P. webbi*, *Pa. subnormalis*, and the presence of *Icriodus* and the **paleo**...
Matyja, 2003, Pe. planus, P. brevilaminus, P. nod. nodocostatus, P. padovanii, P. procerus, P. semicostatus, P. triphylatus, Pa. quad. inflexa, Pa. quad. inflexoidea, Pa. mg. marginifera, Pa. gracilis-stock and all the species of the P. glaber-stock. The faunas of Sardinia are composed by the dominance and variety of *Palmatolepis* with several *Icriodus* taxa and a variety of *Polygnathus*, sharing similarities with Compte, however, several frequent taxa (e.g., *Ic. olivieri, P. diversus*, morphotypes of *Pa. gl. pectinata*) and other genera (*Pe. planus*) and are not recorded in the Compte section.

The Pizzul West section in the Carnic Alps (Mossoni et al., 2013) yields a similar conodont assemblage with few *fc. alt. alternatus* and *Ic. olivieri*. The groups represented are: the *glabra*-stock, except *Pa. gl. lepta*, the *minuta*-stock, the *perlobata*-stock, except *Pa. per. sigmoidea* and *Pa. per. helmsi*, the *P. glaber*-stock, excluding *P. gb. eoglaber*. Other taxa recorded are *Pa. regularis, Pa. stoppeli, Pa. subperlobata* and *Pa. tenuipunctata*.

The German Buschtiech section in the Thuringian zone (Girard et al., 2017) provides a rich conodont fauna. Recorded conodont faunas are similar to those from the Compte section, especially regarding diversity and abundance of taxa of *Palmatolepis*. However, there are several taxa which are not recorded in the Compte section: *Pa. circularis, Ic. olivieri, P. diversus, Pa. min. subgracilis, Bi. stabilis, Me. gradata* and *Po. pennatuloideus*.


Conodont faunas from Büyükkada Island area (Çapkınoglu, 1997) in Istanbul region (Northwestern Turkey) are similar to those of Compte with abundance of *Palmatolepis* and relative diversity of *Polygnathus*. The *glabra*-stock, *perlobata*-stock, *minuta*-stock, *marginifera*-stock, *quadrantinodosas*-stock and *gracilis*-stock are the most frequent palmatolepids. The record of *polygnathids is diverse consisting of *glaber*-stock, *nodocostatus*-stock, *P. semicostatus, P. subnormalis, P. diversus, P. fallax, P. longiusculus, P. brevilaminus, P. triphylattus*. Other conodonts are *Ic. cornutus, Me. strigosa* and *Me. arcuata*. Conodont faunas from Tuzla Peninsula area in Istanbul region (Çapkınoglu, 2005b) share similarities with the previous zone; in addition, *Pa. planus, Pa. inclinatus, P. ladinensis, Pa. ibiocornis, P. procerus* and *Pa. regularis* are recorded.


Conodont faunas from the Shar’yu River area in the Polar Urals region (North Russia) are characterized by the dominance of *Palmatolepis* with few *Polygnathus* taxa (Ovnatanova et al., 2017). The assemblage is composed of *Pa. subperlobata, Pa. klappeii*, almost full *glabra*-stock without *Pa. gl. pectinata, perlobata*-stock without *Pa. per. sigmoidea* and *Pa. per. helmsi*, *Pa. poolei, P. quadrantinodosalobata, Pa. rhomboidea, Pa. stoppeli, quadrantinodosas-stock, minuta-stock, Pa. mg. marginifera, P. gb. glaber, P. fallax* and *P. padovanii*.

**CONCLUSIONS**

The Compte section has yielded an ample record of Famennian conodonts consisting of 47 taxa, belonging to four genera. Several taxa have been recorded for the first time in the Spanish Central Pyrenees area: *Pa. gl. acuta, Pa. gl. lepta, Pa. quad. quadratinoidea, Pa. longiusculus, P. subnormalis, Ic. alt. mawsonae*. In the upper part of the Comabella Fm (Beds 98a to 104b) the conodont assemblage is mainly composed of *Palmatolepis crepida, Pa. tenuipunctata, Pa. glabra prima* (M1) and *Icriodus alternatus* group. In the transition to the overlying La Mena Fm (Beds 104c to 106) the conodont association changes and the most frequent taxa are components of the *Pa. glabra* group, *Pa. perlobata* group and *Polygnathus nodocostatus* group and *P. semicostatus*. Through the La Mena Fm (Beds 107 to 116), *Pa. glabra* group, *Pa. perlobata* group, *Pa. rhomboidea*, *Pa. minuta minuta* and several *Polygnathus* species are the most frequent taxa. The *Pa. quadratinoidea* group appears in the upper part of La Mena Fm (Bed 112g). The mainly assemblage in the lower part of the following Barousse Fm (Beds 117 to 120) is composed of species of the *Pa. glabra* group, *Pa. quadratinoidea* group and *Pa. glabra* group. The *Pa. glabra* group shows a strong morphological variety in the Compte section allowing the identification of several morphotypes. The *Pa. gl. prima* morphotype 1 is recorded from Bed 98c to Bed 104c and the morphotype 3 from Bed 104b to Bed 117b. The early morphotype of *Pa. gl. lepta* is recorded from Bed 111c to Bed 114b and the late morphotype from Bed 114b to Bed 120. The conodont sequence suggests a lower to middle Famennian age in the upper part of Comabella Fm to the base of Barousse Fm. Comparing with other conodont assemblages, there are some similarities with the faunas from western and eastern Europe. The faunas from Montagne Noir, Sardinia, Rhenish Massif Pomerania, and Turkey shares similar taxa, however, the Compte section is characterized in this interval by the lack of any taxa of the genera *Ancyrognathus, Alternognostus, Bispathodus, Branmehea* and *Polygnathus*. The conodont faunas from China provide numerous endemic taxa. Conodonts from shallower facies in Iran have more *Polygnathus, Icriodus* and *Polygnathus* taxa and scarce *Palmatolepis* taxa. The recorded association contributes to enlarge the, insufficient, information for the studied interval in this Perigondwanan region and augments the global database for the Famennian.

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