Revision of the Devonian acritarch genus *Pyloferites* Quadros 1999 based on palynomorph assemblages from Brazil

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**ABSTRACT**

A large population of the acritarch genus *Pyloferites* Quadros 1999 was recovered from the Devonian strata of the Paraná Basin, Alto Garças Sub-basin (Brazil), at the Jaciara section. Based on a literature review and the examination of new material, including morphometric analyses, *Pyloferites* shows wide morphological variability, and, therefore, is herein emended. Additionally, a species emendation and a new species are instituted: *Pyloferites escobaides* (Cramer 1964) Daners et al. 2017 emend. nov., and *Pyloferites paranaensis* sp. nov. The stratigraphical distribution of *P. escobaides* is extended from the middle–late Pragian to the Famennian, while *P. paranaensis* is restricted to the Pragian to early Emsian, or possibly middle Emsian, of the Paraná Basin. The presence of *Pyloferites* in Brazil, Bolivia, Uruguay, and Spain supports a Gondwanan and Perigondwanan palaeobiogeographical distribution.

1. Introduction

Organic-walled microfossils termed acritarchs are considered an informal and probably polyphyletic group of unknown biological affinities (i.e. incertae sedis) (Servais et al. 2004 and references therein). They are present throughout the geological column, although they are more widespread in the Lower–Middle Palaeozoic. Acritarchs are a valuable tool mainly for dating and the correlation of strata, but also for contributing to palaeoenvironmental and palaeobiogeographical interpretations. As an example of their usefulness as palaeobiogeographical markers, genera such as *Bimerga, Winvaloeusia, Cordobesia*, and *Schizocystia* are exclusively reported from Devonian Gondwanan and Perigondwanan strata (e.g. Deunff 1977, 1980; Steemans et al. 2008; García Muro et al. 2017 and references therein; Rubinstein et al. 2018).

The acritarch genus *Pyloferites* was described by Quadros (1999) from the Famennian of the Amazon Basin of Brazil. A central body more or less pentagonal in outline, with processes well differentiated from the vesicle arising from each angle, and a pylome as excystment aperture, are its diagnostic features (Quadros 1999). Previously, Cramer (1964) had erected *Baltisphaeridium escobaides*, from the Pragian–Emsian of the La Vid Shale Member, in the León province of Spain. He described this species as a polygonal vesicle formed by the broad bases of the processes, and the frequent presence of an ellipsoidal opening. Eisenack et al. (1973) transferred *Baltisphaeridium escobaides* to the genus *Multiplicisphaeridium*, noting the presence of a pylome. Later, Daners et al. (2017) reassigned *Multiplicisphaeridium escobaides* to the genus *Pyloferites* due to the presence of the pylome. However, they retained *Pyloferites pentagonalis*, described by Quadros (1999), as a separate species. Daners et al. (2017) recorded *P. escobaides* in Pragian–Emsian strata of the Paraná Basin in Uruguay.

The specimens from the Brazilian part of the Paraná Basin studied herein display a variety of morphologies that enable their inclusion in the genus *Pyloferites*. The aim of this contribution is to comprehensively analyse the morphological variability of the specimens herein assigned to the genus *Pyloferites*, and using statistical methods, to determine whether it corresponds to intraspecific variability within *Pyloferites escobaides* emend. nov. or indicates more than one species. Accordingly, the genus *Pyloferites* is emended, and the species already assigned to the genus are discussed, and synonymised. The stratigraphical range and geographical distribution of the genus are also reviewed in order to understand its biostratigraphical and palaeobiogeographical potential.

2. Materials and methods

The studied samples come from the Devonian Chapada Goup, unit 2, equivalent to the Ponta Grossa Formation, of the Alto Garças Sub-basin, Paraná Basin (García Muro et al. 2020). A total of 27 samples were collected from an outcrop situated 5 km to the west of Jaciara town (15°58’37.6”S, 55°00’31.9”W), Mato Grosso, Brazil (Figures 1 and 2). They were processed at the University of Liège, EDDy (Evolution and Diversity Dynamics) Lab/Palynology laboratory, Belgium, using standard hydrochloric and hydrofluoric acid (HCl–HF–HCl).
maceration techniques (Traverse 2007). The residues were oxidised with a Schulze solution [nitric acid (HNO₃) + potassium chlorate (KClO₃)] and then screened on a 12 μm sieve.

Specimens of the genus *Pyloferites* were measured, and light photomicrographs were taken under Nomarski differential interference contrast illumination with an Olympus BX51 microscope and an Infinity 1 digital camera. Specimen locations are referred to in the text and plate captions using England Finder coordinates, which are given in parentheses. The palynological slides are housed in the EDDy Lab/Palynology repository. Sample numbers are detailed in Figure 1.

The following morphological variables were considered for bivariate and multivariate statistical analyses: length, width, and number of processes, type of ramification (digitated, second order, third order), vesicle major and minor diameter, wall ornamentation (psilate, scabrate, striae), pylome diameter, and the presence or lack of a thickened rim surrounding the pylome. Principal component analysis (PCA) was applied to the dataset of morphological variables measured from 181 specimens, recorded throughout the section, to display relationships among specimens. Additionally, a linear regression analysis, using InfoStat © 2018 (Di Rienzo et al. 2018), was performed to identify any relationships among the morphological variables. Histograms, including kernel density plots, were performed for the width and length of the processes, using the software PAST (Harper 1999; Hammer et al. 2009). These morphological variables are the ones that best support a separation into two species.

### 3. Results

Taking into account all measured features, the PCA biplot does not contribute to a separation into two species. The first two principal component axes represent 24.9% and 18.5%, respectively, of the variance (Figure 3). However, a new PCA was conducted considering only the width and length of the processes, and the analysis showed that these two parameters were the most appropriate characteristics with which to separate the specimens into two species. The

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Figure 1. Geographical map of the Jaciara section. Modified from Grahn et al. (2010a) and García Muro et al. (2020).

Figure 2. Sedimentological section with locations of the studied samples and stratigraphical distribution of *Pyloferites escoboides* emend. nov. and *Pyloferites paranaensis* sp. nov. in the section. Modified from García Muro et al. (2020).
first two principal component axes represent 61.3% and 38.7%, respectively, of the variance (Figure 4). Additionally, the histogram of process width shows a bimodal pattern that allows us to differentiate the Pyloferites escobaides emend. nov. population with thinner processes from the P. paranaensis sp. nov. population with broader processes (Figure 5, 1). The histogram of process length, however, shows more variability. A bimodal distribution can be observed and enables a separation between specimens with processes longer than 5 μm (P. escobaides emend. nov.) and those with processes shorter than 5 μm (P. paranaensis sp. nov.) (Figure 5, 2). The species are described in detail below.

The regression analysis of the various morphological characteristics does not reveal a clear relationship, since the linear correlation analyses are not statistically significant (p > 0.05). As an example, the presence of a thickened rim around the pylome is not generally related to either the size of the vesicle or its ornamentation. Nevertheless, there is an expected linear correlation between the diameter of the vesicle and the diameter of the pylome (p < 0.0001). Interestingly, the most remarkable relationship is a weak positive linear regression between the width of the processes and the presence of a thickened rim around the pylome (p < 0.0001) (Figures 6 and 7). The data supporting the findings of this study are available within the article and the Supplementary material.

4. Systematic palaeontology

Group ACRITARCHA Evitt 1963

Genus Pyloferites Quadros 1999 emend.

Type species. Pyloferites pentagonalis Quadros 1999, by original designation.

Original diagnosis (Quadros 1999, 19). Vesicle approximately pentagonal in outline, psilate or slightly micropunctate; pylome in the proximal face, occupying from the central part up to 2/3 of the central body. The processes, perfectly differentiated from the central body, extend radially from the pentagon angles, and freely communicate with the vesicle cavity. In addition to these processes, other processes may also occur, irregularly distributed on the distal and proximal faces, giving a total of eight to 10 processes. They are branched up to second or third order. (Translated from the original diagnosis in Portuguese.)

Emended diagnosis. Vesicle of variable shape – triangular, square, polygonal, or rounded – with three to 23 processes. Process hollow, freely communicating with the vesicle cavity, broad-based and terminally digitated or branched up to third order. In some cases, the junctions of the process bases define the vesicle shape; processes can be arranged around the pylome or irregularly on the vesicle. Occasionally, processes are short (up to 10% of the vesicle diameter), simple, with rounded tips or digitated from or beginning very close to their bases. Vesicle wall 1–1.5 μm thick, psilate, slightly microspinose, and/or finely striate. Excystment by a rounded to elliptical, frequently deformed pylome that encompasses 75–95% of the vesicle diameter. Around the pylome, a thickened rim 1–2 μm thick may be present.

Pyloferites escobaides (Cramer 1964) Daners et al. 2017 emend. nov.

Plates 1–3

Basionym. Baltisphaeridium escobaides Cramer 1964: 294, pl. 11, fig. 16.

Synonymy.

1973 Multiplicisphaeridium escobaides (Cramer 1964), Eisenack, Cramer & Diez: 623.
1997 Evitia escobaides (Cramer 1964) Sarjeant & Vavrdová: 9 (not illustrated).
1999 Pyloferites pentagonalis Quadros: 19, pl. 2, figs 12–14 (type species).
2001 Pyloferites pentagonalis Quadros 1999, Le Hérissé: 122 (not illustrated).
2007 Multiplicisphaeridium escobaides Cramer 1964, Mendlowicz Mauller et al.: 10, fig. 6, 3.
2011 ?Multiplicisphaeridium escobaides (Cramer 1964), Eisenack et al. 1973, Racheboeuf et al. 2012 (not illustrated).
2011 Pyloferites pentagonalis Quadros 1999, Wicander et al.: 80–81, pl. 1, fig. 16.
2015 Gorgonisphaeridium sp., Gutiérrez et al.: 133, fig. 5, E.
2017 *Pyloferites escobaides* (Cramer 1964) Daners et al.: 127, fig. 3, 10.

2018 *Evittia? escobaides* (Cramer 1964) Sarjeant & Vavrdová 1997, Trindade & Carvalho: 78 (not illustrated).

2021 *Pyloferites pentagonale* Quadros 1999, Lakin et al.: 7, fig. 10, t.

2021 *Pyloferites escobaides* (Cramer 1964) Daners et al. 2017, Myszynski et al.: 8, fig. 3, F.

**Original diagnosis** (Cramer 1964, 294). ‘Central body and basal part of the processes hollow, moderately thin walled and transparent. The walls are psilate at ×1200 magnification. The processes have very broad bases giving the central body a roughly polygonal form. The processes may be bifurcated several times at the top; the final parts of the processes are solid. A round to ellipsoidal opening is often present. Number of processes in optical section 5 to 10 (7)’.

**Emended diagnosis.** Vesicle polygonal to rounded, bearing three to 20 broad-based processes, hollow, freely communicating with the vesicle cavity, distally digitated or irregularly branched up to third order. In some cases, the confluence of the process bases defines the vesicle shape. Processes are disposed around the pylome or irregularly distributed on the vesicle. Sometimes, the branches arise close to the base. Vesicle wall 1–1.5 µm thick, slightly microspinose and/or scabrate, frequently finely striate. Excystment by a circular to elliptical, frequently deformed pylome that encompasses 75–95% of the vesicle diameter. Around the pylome, there may be a rim 1–2 µm thick.

**Dimensions.** Diameter of the vesicle 10 (22) 29 µm; process length 1–12.5 µm, process basal width 1–7 µm; diameter of the pylome 9 (15) 25 µm (75 specimens measured).

**Occurrence.** Upper Pragian–possibly middle Emsian of the Chapada Goup unit 2, Paraná Basin, Brazil.

**Distribution.** Pragian–Emsian of the Cantabrian Mountains, Spain (Cramer 1964); late Famennian of the Amazon Basin, Brazil (Quadros 1999; Le Hérisse 2001); Pragian–Emsian of the Paraná Basin, Brazil (Mendlowicz Mauller et al. 2007); probably Lochkovian–Pragian of Bolivia (doubtful assignment of Racheboeuf et al. 2012); late Famennian of Bolivia (Wicander et al. 2011; Lakin et al. 2021); as reworked from Devonian sediments in the Permian of the Paraná Basin, Uruguay (Gutiérrez et al. 2015); Pragian–Emsian of the Paraná Basin, Uruguay (Daners et al. 2017); Pragian–Emsian and Givetian of the Parnaiba Basin, Brazil (Trindade and Carvalho 2018); late Emsian–late Eifelian, Paraná Basin, Brazil (Myszynski et al. 2021). Steemans et al. (2021) recorded *Pyloferites* sp. from the middle to early late Frasnian of the Parnaiba Basin (Brazil). However, due to the lack of a specific assignment or illustration, it cannot be assigned with certainty to a *Pyloferites* species. The occurrence of *P. escobaides emend. nov.* from the Lower to Upper Devonian would extend the stratigraphical range of the species over almost the entire the Devonian Period. The presence of *Pyloferites escobaides* in Bolivia, Brazil, and Uruguay suggests a palaeogeographical distribution restricted to western Gondwana, as well as Gondwanan influence in Spain.

**Discussion.** *Pyloferites pentagonalis* was described by Quadros (1999) for the Upper Devonian of Brazil, and *Multiplicisphaeridium escobaides* was described by Cramer (1964) for the Lower Devonian of Spain. Although these
Plate 1. *Pyloferites escobaides* emend. nov. 1, 23-61698 (F42/4); 2, 23-61854 (K46/1); 3, 23-61854 (K45/1); 4, 1-61654 (P49); 5, 1-61654 (Q44/3); 6, 2-61655 (F28/2); 7, 2-61655 (H37/3); 8, 3-61658 (G23/2); 9, 3-61658 (K29); 10, 3-61658 (U48/4); 11, 3-61658 (V32/2), showing the vesicle wall finely striate; 12, 5-61836 (G45), showing a detached operculum lying partially inside the vesicle; 13, 4-61660 (G46/4); 14, 4-61660 (C45); 15, 5-61662 (H44/2); 16, 5-61662 (S41-2), showing the thickened rim around the pylome; 17, 6-61664 (V39/1); 18, 6-61664 (T48/2); 19, 8-61668 (M44/4); 20, 8-61668 (M40), showing one process branched from the base. The slide numbers and the England Finder coordinates are indicated for all specimens. Scale bar = 20 μm.
authors illustrated quite different morphological entities, the specimens of the Jaciara section studied herein evidence wide intraspecific variability, including forms displayed by both these authors and a complete gradation between them. This justifies the integration of them all into a single species, with the specimens illustrated by Quadros and Cramer as possible extreme representatives of a single taxon. Furthermore, the different morphologies were recorded in almost all the samples of the Jaciara section, thus suggesting that the variability of the species is stratigraphically
Plate 3. *Pyliferites escobaides* emend. nov. 1, 16-61684 (M48/4); 2, 17-61686 (E39/1); 3, 17-61686 (L47/4); 4, 18-61688 (T27); 5, 18-61688 (P41/3); 6, 18-61688 (P40/3); 7, 19-61690 (G42-1); 8, 19-61690 (J31/1), showing the junction of the process bases defining the vesicle shape; 9, 20-61692 (N46/2); 10, 20-61692 (H25/3); 11, 21-61694 (J49); 12, 21-61694 (T41/4); 13, 25-61702 (R47); 14, 25-61702 (U35); 15, 25-61702 (J50/1); 16, 26-61704 (N50/3); 17, 26-61704 (J37/1); 18, 27-61706 (E41) 19, 27-61706 (G46); 20, 27-61706 (S35/4). The slide numbers and the England Finder coordinates are indicated for all specimens. Scale bar = 20 µm.
Plate 4. *Pyloferites paranaensis* sp. nov. 1, 24-61700 (V38); 2, 2-61655 (H39/1); 3, 2-61655 (E45/3), showing processes digitate from the bases; 4, 2-61655 (M46); 5, 2-61655 (X31); 6, 3-61658 (V27/4); 7, 4-61660 (E46/1); 8, 4-61660 (H46/2); 9, 5-61662 (D46/3); 10, 5-61662 (H47); 11, 5-61662 (L44/2); 12, 6-61664 (M47/4); 13, 8-61668 (H44); 14, 8-61668 (Y30/1); 15, 9-61670 (G45/3); 16, 9-61670 (K36/3); 17, 10-61671 (F41/2); 18, 10-61841 (Q30/3); 19, 11-61674 (J39); 20, 11-61674 (V33). The slide numbers and the England Finder coordinates are indicated for all specimens. Scale bar = 20 μm.
Plate 5. Pyloferites paranaensis sp. nov. 1, 12-61676 (W40); 2, 12-61843 (T30/2); 3, 13-61678 (F30/2); 4, 13-61678 (M27/1); 5, 13-61844 (X37); 6, 14-61680 (J26/1); 7, 14-61680 (H34/4); 8, 14-61680 (L45/3); 9, 14-61680 (Q38); 10, 15-61682 (G43/3); 11, 15-61682 (L29/4); 12, 15-61682 (E40/1); 13, 16-61684 (E46/3), showing the scabrate ornamentation of the wall; 14, 16-61684 (H47/4); 15, 16-61684 (T32); 16, 16-61684 (V35); 17, 17-61686 (U41/1), paratype; 18, 17-61686 (Q33); 19, 18-61688 (H42); 20, 18-61688 (L25/2). The slide numbers and the England Finder coordinates are indicated for all specimens. Scale bar = 20 μm.
Plate 6. *Pyloferites paranaensis* sp. nov. 1, 18-61688 (R26/2); 2, 18-61688 (T47/3); 3, 19-61690 (D46); 4, 20-61692 (G33); 5, 20-61692 (P43); 6, 20-61692 (S29/4); 7, 21-61694 (J42/3), paratype; 8, 21-61694 (I25); 9, 21-61694 (T41/2); 10, 25-61702 (M29); 11, 25-61702 (S26/2); 12, 25-61702 (U34/3), showing scattered microspines and striate wall; 13, 26-61704 (F39); 14, 26-61704 (J27/1); 15, 26-61704 (P24/4); 16, 26-61857 (K37); 17, 26-61704 (V48/4); 18, 27-61706 (H40/1), showing processes digitate from the bases; 19, 27-61706 (Q39/2), holotype; 20, 27-61706 (P34/4). The slide numbers and the England Finder coordinates are indicated for all specimens. Scale bar = 20 \( \mu m \).
independent. Wicander et al. (2011, 79) also observed the similarity of the two taxa, informally considering them synonyms: *Pyloferites pentagonalis (= Multiplicisphaeridium escobaides Cramer 1964)*.

**Pyloferites paranaensis** sp. nov.

Plates 4–6

**Synonymy.**

2013 *Multiplicisphaeridium escobaides* Cramer 1964, Grahn et al.: 39, pl. 1, fig. 14.

2015 *Papulogabata lobata* Hashemi & Playford 1998, Gutiérrez et al.: 133, pl. 5, figs A–B.

2015 *Papulogabata* cf. *P. annulata* Playford 1981, Gutiérrez et al.: 133, pl. 5, fig. C.

**Derivation of name.** Refers to the Paraná Basin, where the samples were collected.

**Holotype.** Plate 5, figure 19, slide 27-61706 (Q39/2).

**Paratypes.** Plate 5, figure 7, slide 21-61694 (U42/3); Plate 4, figure 17, slide 17-61686 (U41/1).

**Diagnosis.** Vesicle polygonal to rounded. The base of the processes is markedly broad, with no clear differentiation from the central body. Processes can be arranged around the pylome or irregularly distributed on the vesicle. Processes hollow, freely communicating with the vesicle cavity, frequently digitate. Vesicle wall psilate, slightly microspinose and/or ornamented with fine striation. Excystment by a large pylome. A thickened rim may be present around the pylome.

**Description.** Vesicle triangular, polygonal, or rounded, with three to 23 processes (frequently around seven). The confluence of process bases may define the vesicle shape. Processes hollow, freely communicating with the vesicle cavity, broadly based, often wider than long, distally branched up to second order or digitate. Short processes (up to 10% of the vesicle diameter) are digitated from or very close to their bases, or rarely simple, with rounded tips. Processes can be arranged around the pylome or irregularly distributed on the vesicle. Vesicle wall psilate, slightly microspinose and/or finely striate. Excystment by a broad rounded to elliptical pylome, sometimes surrounded by a rim 1–2 μm thick.

**Dimensions.** Diameter of the vesicle 13 (23) 31 μm; process length 1–5 μm and process width 1–8 μm; diameter of the pylome 9 (15) 26 μm (106 specimens measured).

**Comparison.** *Pyloferites escobaides* has longer processes than *P. paranaensis* that are never broader than they are high. The genus *Papulogabata* presents a discoidal thickening on the vesicle, which is opposite to the cyclopyle (Playford and Dring 1981). *Nanocyclopia* has a smaller pylome in relation to the vesicle diameter; the vesicle is always rounded, without processes.

**Location.** Upper Pragian–possibly middle Emsian of the Chapada Goup, unit 2, Paraná Basin, Brazil.

**Distribution.** *Pyloferites paranaensis* sp. nov. is only recognised in the Paraná Basin of Brazil and Uruguay, from the parastratotype section of the Ponta Grossa Formation, Tibagi–Telémaco Borba section (Grahn et al. 2013), as reworked from Devonian rocks in the Permian of the Paraná Basin, Uruguay (Gutiérrez et al. 2015).

**Discussion.** *Pyloferites paranaensis* specimens from the lower levels of the Jaciara section have fewer processes and, in general, simpler branching types (e.g. specimens illustrated in Plate 4). Specimens with more processes and those that are more digitated tend to be more frequent towards the upper part of the section (e.g. Plate 6, figures 1, 3, 7, 15). Although some specimens could be considered transitional forms between *P. escobaides* and *P. paranaensis* (e.g. Plate 1, figure 11; Plate 2, figure 18; Plate 3, figure 6), their processes are longer than those of *P. paranaensis* and are also longer than they are wide.

5. Discussion

According to the morphometric analysis carried out in this contribution, a wide intraspecific variability was recognised and all forms were grouped into two species. Taking into account all previous records, both species are present from the middle or late Pragian, and the record of *P. escobaides* emend. nov. now extends to the Famennian (Quadros 1999). The morphology of *P. escobaides* emend. nov. seems to be more variable in the Lower Devonian, while the Upper Devonian records of the species exhibit vesicles that are mostly pentagonal to square in outline (Quadros 1999; Wicander et al. 2011; Lakin et al. 2021). Towards the end of the Devonian, global palaeoenvironmental changes took place, which could have driven morphological changes in *P. escobaides*. However, the Late Devonian records are still scarce, and more research is needed before a conclusive interpretation can be reached.

The Jaciara section was deposited under shallow-platform conditions in a progressive flooding model, in which three facies associations, organised in four metre-scale coarsening-upwards cycles limited by flooding surfaces, were recognised (García-Muro et al. 2020 and references therein). *Pyloferites escobaides* emend. nov. and *P. paranaensis* sp. nov., as well as all their morphological varieties herein analysed, were recorded in all the outcrop samples except for sample 23, where no representatives of the genus were found (Figure 2). Thus, the intraspecific variability and the different species of *Pyloferites* do not seem to be ecophenotypic responses to locally varying ecological conditions. In fact, they appear to evidence high adaptability to a changing environment represented by coarsening-upward cycles limited by flooding events. Additionally, both species, with representatives of all transitional morphologies, were documented in the southern and northern parts of the Paraná Basin, with different sedimentological histories during most of the Devonian Period (e.g. Grahn et al. 2010b; Rodrigues de Vargas et al. 2020; and references therein). More detailed palynological contributions on the Brazilian and other Gondwanan basins are needed to corroborate the stratigraphical ranges of both *Pyloferites* species, and their morphological variability over time.
Even though the stratigraphical distribution of the genus *Pyloferites* apparently spans almost the entire Devonian, it is not a common taxon in acritarch assemblages. According to Cramer (1964), *Baltsphaeridium escobaides* is rarely recorded in the Pragian–Emsian of the La Vid Shale Member (Spain). Daners et al. (2017), who proposed a new combination for the species, measured only three specimens from the Pragian–Emsian of the Paraná Basin, in Uruguay, without specifying whether this low number of specimens was due to their rare occurrence. Quadros (1999), who created the monospecific genus *Pyloferites*, with *P. pentagonalis* as its type species (herein interpreted as a junior synonym of *B. escobaides* Cramer 1964), only measured four specimens recorded from the Famennian strata of the Amazon Basin. Lakin et al. (2021) mentioned the uncommon presence of ‘*P. pentagonalis*’ in the Late Famennian of Bolivia.

*Pyloferites escobaides* emend. nov. and *P. paranaensis* sp. nov. are particularly frequent in the late Pragian–Emsian of the Jaciara section herein studied. Large populations of both species were found, which allowed us to measure 181 of the better preserved *Pyloferites* specimens for the morphometric analysis. The overrepresentation of *Pyloferites* in the Jaciara section, compared with its presence in other localities, may be due either to particular ecological or taphonomic conditions in the studied area, or to the scarcity of detailed taxonomic investigations of Devonian organic-walled phytoplankton from other regions of Gondwana, particularly South America and Spain. Notably, this taxon has not been recorded from North Gondwana (North Africa, Saudi Arabia), where Devonian acritarch assemblages have been extensively studied (e.g. Bär and Riegel 1974; Jardine et al. 1974; Moreau Benoit 1984; Le Hérisse 2002; Bougara et al. 2017). This is also the case for other Gondwanan taxa, such as *Bimerga* and *Cordobesia*, that are restricted to South American basins (e.g. Pôthie de Baldis 1977; Wood 1995; Daners et al. 2017; García Muro et al. 2017, 2018 and references therein; Rubinstein et al. 2018).

The presence of *P. escobaides* emend. nov. in Bolivia, Brazil, and Uruguay suggests a Gondwanan distribution for this species. Its record in the Lower Devonian of Spain (Armorica) supports its connection with Gondwana. It also suggests that there were probably no significant barriers between Armorica (formerly a Perigondwanan terrane) and Gondwana at that time, possibly because the Palaeeothys Ocean that separated them had only recently begun to open up (Torsvik and Cocks 2013). Records of *P. escobaides* from the Middle and Late Devonian are restricted to Gondwana, probably because Armorica was moving away from Gondwana during this period. The highly diverse and very well-preserved organic-walled phytoplankton assemblage from Devonian sediments of the Jaciara section (unpublished data), together with spores (García Muro et al. 2020), also supports close palaeogeographical relationships with other Devonian South American basins in Brazil, Argentina, Bolivia, and Uruguay.

### 6. Conclusions

The genus *Pyloferites* is emended in the light of its abundance and high variability recognised in the Lower Devonian Jaciara section, Paraná Basin, Brazil. Statistical analyses of the morphological variables allowed us to distinguish two species: *Pyloferites escobaides* emend. nov. and *Pyloferites paranaensis* sp. nov. *Pyloferites escobaides* emend. nov. displays a South American distribution from the middle–late Pragian to the Famennian, while it is constrained to the Lower Devonian in Spain. This species exhibits a wide morphological variability in the Lower Devonian. However, it seems to evolve morphologically into a square or pentagonal shape towards the Upper Devonian. The presence of *P. escobaides* in Spain, restricted to the Lower Devonian, could be related to the separation of Armorica from Gondwana during the Middle–Late Devonian. *Pyloferites paranaensis* sp. nov. shows a more restricted stratigraphical and geographical distribution, from the late Pragian to possibly the middle Emsian in the Paraná Basin. In summary, the genus *Pyloferites* proves to be a useful biostratigraphical and palaeobiogeographical marker for the Devonian, especially for west Gondwana.

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The authors report there are no competing interests to declare.

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