

**Fertile *Goepertella* from the Jurassic of Patagonia: mosaic evolution in the
Dipteridaceae-Matoniaceae lineage**

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- **Background and Aims:**

Goepfertella has been postulated as a monophyletic group, whose precise position within the Gleichenoid families Dipteriaceae and Matoniaceae, remains poorly understood. Previously described *Goepfertella* specimens are based on frond fragments and its fertile morphology is represented by a few, poorly preserved specimens. We describe a new species based on the largest collection of fertile specimens known to date, and discuss the evolutionary history of the genus based on the additional reproductive characters provided by the fossils described.

- **Methods:**

Plant impressions were collected in Early Jurassic sediments of Patagonia, Argentina. The specimens were described, and silicone rubber casts were developed to examine in detail vegetative and reproductive features. The new species was compared with other *Goepfertella* species. Finally, a backbone analysis was performed in the context of a previously published combined matrix of Dipteridaceae, using the maximum parsimony criterion.

- **Key Results:**

The new species is described based on a combination of features that have not been previously reported. The vegetative morphology shows affinities with most fossil and extant Dipteriaceae, contrasting with the reproductive morphology which is more comparable with the scarce number of fossil dipteridaceous forms and it is more spread in the sister family, Matoniaceae. The backbone analysis indicates that the position of the new species vary among different positions among Dipteridaceae and Matoniaceae. Additional analyses, discriminating the signal of reproductive and vegetative character, are provided to discuss the base of this uncertainty.

- **Conclusions:**

We consider *Goepertella* as a member of the family Dipteridaceae since we interpret most shared features with Matoniaceae as plesiomorphic conditions for the family. In contrast, most shared features with Dipteridaceae represent apomorphies for the group. Thus, *Goepertella* would represent an early diverging genus in Dipteridaceae, considering the venation characters as the most important in order to define the family.

Keywords: Jurassic, Patagonia, Gondwana, Gleicheniales, *Goepertella unicyclia*, evolution, reproductive traits.

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Zeiller (1903) on specimens identified as *Woodwardites microlobus* from the Late Triassic (Rhaetian). Altogether, ca. 20 species of *Goepfertella* have been described from across the globe and spanning the Late Triassic to Jurassic (e.g., Zhou *et al.*, 2016). In the Southern Hemisphere, *Goepfertella* is only known from a few occurrences in the Late Triassic (Herbst, 1993, 2000; Morel *et al.*, 1999), with most of the diversity collected in Jurassic sediments of South America (see Herbst, 2000), Antarctica (Rees and Cleal, 2004) and New Zealand (Rees, 1993).

From a phylogenetic point of view, the precise *Goepfertella* position within the Dipteriaceae and the Matoniaceae remains poorly understood. Because all described *Goepfertella* specimens are based on frond fragments, and therefore the complete architecture of the frond is only hypothesized (Rees, 1993), on phylogenetic study developed by Choo and Escapa (2018) the genus it was only reconstructed as a monophyletic clade in the base of Dipteridaceae when it was scored according to the aforementioned hypothetical architecture. In the same way to the frond architecture knowledge, the fertile morphology of the genus is represented for a few, poorly preserved specimens, which fail to show details in soral and sporangial morphology, distribution and development.

In the present work, we describe a new species for the genus *Goepfertella*, based on numerous sterile and fertile specimens from the Early Jurassic Cerro Bayo locality (Patagonia, Argentina. Escapa *et al.*, 2008). Exquisitely preserved reproductive features reveal close similarities of *Goepfertella* with Dipteridaceae, but also with the sister family Matoniaceae. We provide an analysis of the phylogenetic circumscription of the genus based on the additional characters provided by the fossils described here, including the implications of the findings regarding the organization of the sori and sporangia. Furthermore, we discussed the basis of the instability of *Goepfertella* in the light of the new information presented here.

MATERIALS AND METHODS

Geologic setting and paleobotanical context

The Cerro Bayo locality is situated near Gastre in the northwest part of Chubut Province, Argentina (see Escapa *et al.*, 2014). Plant horizons at this locality belong to an unnamed unit of fluvially reworked, volcanoclastic deposits, which are overlain by volcanic and volcanoclastic deposits of the Lonco Trapial Formation. Radiometric studies have restricted the age of the site to the Early Jurassic (most likely Pliensbachian) (Cuneo *et al.*, 2013; Escapa *et al.*, 2014; Figari *et al.*, 2015). From a chronostratigraphic perspective, Cerro Bayo is considered to be an approximately lateral equivalent of Las Leoneras formation, which crops out around 80 km southeast of Cerro Bayo (Nakayama, 1973). The early sauropodomorph *Leoneosaurus taquetrensis* is the single fossil so far reported from Las Leoneras (Pol *et al.*, 2011), but plants mega or microfossils are so far unknown for the unit.

Specimens were collected at three nearby quarries (GPS coordinates are available upon request to the authors) in the general Cerro Bayo locality (Fig. 1). Plant impressions occur in fine-grained, partially silicified sediments as part of a taphocoenosis including largely dominated by conifers and ferns. The most conspicuous elements in this flora include species within Equisetaceae (Elgorriaga *et al.*, 2015), Osmundaceae (*Todites cacereii* and *Osmundopsis rafaelii*; Escapa & Cuneo 2012), Marattiaceae (Escapa *et al.*, 2014), Dipteridaceae (*Clathropteris meniscoides*; Choo *et al.* 2016) and Cupressaceae (*Austrohamia minuta*; Escapa *et al.* 2008, Bodnar and Escapa, 2016). Putative an dicksoniace vegetative fronds and seed fern leaves (e.g. Caytoniales; Elgorriaga *et al.*, 2019) complete the floral spectrum.

using the topology obtained in that combined study, as a backbone. *Goeppertella unycyclica* was scored in the context of the morphological matrix, which includes a total of 51 characters, of which 31 correspond to vegetative structures and 20 to reproductive structures (Appendix 1). All characters correspond to those used by Choo and Escapa (2018), except the N°23 that was added for the present analysis in order to analyze the evolution of the type of venation through the evolution of the order. Some character states were rescored from the original matrix based on reinterpretations and new available data.

The optimal and suboptimal positions of *Goeppertella* were determined by manually editing the backbone in TNT (Goloboff and Catalano, 2016) to move the genera to different positions, and recording the score of the tree (affinity analysis). Likewise, the maximum parsimony analysis was repeated for the vegetative and reproductive traits separately, to discuss the origin of the uncertainty in the evolutionary position of the genus. All the analyses were conducted using TNT.

RESULTS

Systematics

Class. Polypodiopsida Cronquist, Takht. & W.Zimm.

Order. Gleicheniales Schimp.

Family. Dipteridaceae Seward & Dale

Genus. *Goeppertella* Oishi & Yamasita, 1936

Type species. *Goeppertella microloba* (Schenk) Oishi & Yamasita, 1936

***Goeppertella unycyclica* Escapa & Yañez sp. nov.** (Figs. 3-8)

Regarding the reproductive characters, *G. unicyclica* is characterized by having circular to slightly elongated sori, arranged on both sides of the middle vein and borne inside the areoles, with each sori comprising a cycle of seven or eight leptosporangia. The sporangia are arranged in a uniseriate row around a well-defined, slightly concave area of insertion. They have capsules with an oblique dehiscence annulus in which cells with thickened walls are distinguished. Oishi and Yamasita (1936) established the genus *Goeppertella* after specimens previously described under the name *Woodwardites microlobus* (e.g., Schenk, 1867; Schimper, 1869; Zeiller, 1903). Despite its multiple occurrences around the north of Europe and southeast of Asia (see Arrondo and Petriella, 1982), the descriptions of reproductive organs of this species are scarce and poorly illustrated. Based on specimens from the Triassic of Germany, Schimper (1869) defined the sori as “oblong and biseriate” but the three drawings that illustrate the description are general views of the frond and the pinna, and do not explicitly show reproductive details. Based on a collection from the Triassic on Indochina, Zeiller (1903) mentioned that the sporangia cover the entire surface of the pinnule, and both fertile and sterile pinnules are morphologically similar. Although the illustrations are not conclusive, Zeiller described the sporangia as clustering in groups of 5-8, which if compared with the specimens described here, supports the idea that these groups also have unicyclic sori. A deeper review of this, and other collections of *Goeppertella microlobus*, are crucial in order to amend the genus to include details of sori organization and distribution.

Comparisons

As explained below, the *Goeppertella* specimens described here were assigned to a new species in the genus based on a combination of vegetative and reproductive features that have not been previously reported. It is important to consider, however, that the great majority of the known species have been described on the basis of poorly preserved, highly fragmentary,

and/or sterile specimens. In addition, most vegetative morphologic features show a high degree of variation among Dipteridaceae in general, and in *Goeppertella* in particular (Arrondo and Petriella, 1982; Herbst, 1992). In this context, it seems possible that further re-descriptions of previously known species may show more similarities to our specimens listed here, and therefore modifying the taxonomic decisions taken in this work.

The following section provides a comparison of the main vegetative and reproductive features described for *Goeppertella unicyclica* in reference to other described *Goeppertella* species. More extensive and detailed comparisons are included in Supporting Information 3, Table 2.

Vegetative morphology. In their review of the genus, Arrondo and Petriella (1982) focused on the significance of the subsidiary elements (interpinnular leaf appendages) for the taxonomy of the group, recognizing two main types according to whether the origin of their venation was axillary or intercalary. *Goeppertella unicyclica* shows the latter condition (see Fig. 3), where the venation arises directly from the rachis of the primary segment in structures also referred to as rachial pinnulae. The rachial pinnulae observed in the species described here resembles the rachial pinnulae described for *G. microloba* (Schenk, 1867; Zeiller, 1903; Cazaubon, 1947), *G. macroloba* (Herbst, 1964), *G. neuqueniana* (Herbst, 1966), *G. stipanicicii* (Herbst, 1992), *G. woodii* (Rees, 1993) and *G. taverai* (Herbst, 2000). Among these, a greater similarity was observed with *G. macroloba*: both species have rachial pinnules of similar dimensions and also share other additional features such as pinnules being lanced to triangular-falcate, with acute apices and entire margins.

A second feature of potential taxonomic relevance, is the presence of a continuous laminar wing that is more or less parallel to the rachis and connects the pinnae to the rachial pinnula (i.e., rachial lamina) (Arrondo and Petriella, 1982; Rees 1993). This character is

described *G. woodii* as having sori composed of ten sporangia, these details cannot be made out based on the images provided of the fertile fronds (Rees op. cit., plate 2, fig. 1, 3-4).

The best-preserved record that exists of the reproductive structures of the genus, up to the present work, is that of the sporangia found in fragments of *G. taverai* from the Lower Triassic of Chile (Las Breas Formation) (Herbst, 2000). This species is described as having circular sporangia 2-1.6 mm in diameter located along the middle veins of pinnules.

Likewise, it shows impressions of the cells of the annulus with an uncertain position but, apparently, forming a continuous structure (Plate 4, Fig. 23, op cit.). The diameter of the sporangia described for *G. taverai* are of a scale that is more similar to the sori observed in this work (about 0.9-1.1 mm) than for sporangia (about 0.2 mm). Likewise, the sporangia found in our specimens present interrupted annuli, with cells 0.03-0.05 mm wide. These striking differences may be due to a misinterpretation of the reproductive structures of *G. taverai* due to poor preservation, and it appears likely that what were described as sporangia for *G. taverai* actually represent sori. However, this is difficult to corroborate without accessing the original material because the photograph published in the aforementioned article is not to scale.

The arrangement of the sori on the lamina and the characters of sporangia within the sori could provide indirect evidence of their development (Schölch, 2000). The specimens in which a smaller number of sori was observed, the sori were found associated with the basal half of the pinnules, while in those fragments where a higher density of sori was observed, they covered more than half of the pinnula. A similar distribution was described for *G. woodii* (Rees, 1993) and would coincide with acroscopic maturation of these sets of sporangia. Likewise, the author observed that sori group together giving an appearance of elongated sori. Similarly, we observed specimens with two types of sori arrangement, isolated or superimposed, which could correspond to different stages of maturation of the

the author does not refer in his description to the presence of a receptacular area. Other *Sewardalea* species were also described from fertile impressions, but they were either described with the typical “crowded” arrangement in the sori (e.g., *Sewardalea exile* and *S. spiralis* in Nathorst, 1906) or was not detailed (Zeiler, 1903; Sierotin, 1962; Potonié, 1967; Van Konijnenburg-van Cittert *et al.*, 2020). It is interesting to note that *Sewardalea*, together with *Thaumatopteris*, have been recovered as a basal grade in the evolution of Dipteridaceae (Choo and Escapa, 2018), which can explain the presence of these plesiomorphic conditions. A detailed review of these forms, together with *Goepfertella*, will be crucial in order to understand the sequence of morphological transformation that occurred in the early evolution of this lineage.

G. unicyclica shows sori with a regular number of seven–eight sporangia forming a single ring disposed around a central insertion zone, further resembling the soral morphology of Matoniaceae. In Matoniaceae, the sporangia are closely arranged in one (occasionally two or four) concentric rows around a central area named receptacle or placenta (Skog & Litwin 1995; Klavins *et al.*, 2004), which is vascularized by multiple veins and is often delineated by a well-defined outline (Ash, 1972; Kato & Iwatsuki, 1985; Passalia *et al.*, 2018). Likewise, it has been suggested that the receptacle is probably homologous to the indusia, described for some extinct genera within Matoniaceae (e.g., Skog and Litwin, 1995; Klavins *et al.*, 2004). The fossil record shows many examples of matoniaceous species that have similar reproductive morphology to *Goepfertella*, including *Phlebopteris* (Weber, 2008; Barbacka *et al.*, 2018; Van Konijnenburg-van Cittert *et al.*, 2020), *Konijnenburgia* (Kvaček & Dašková, 2010), *Matonia* (Barbacka *et al.*, 2016), *Matonidium* (Zeba-Bano & Bose, 1981), and *Aninopteris* (Giuviulescu and Popa, 1998). Despite the similarities in sori morphology between *G. unicyclica* and Matoniaceae, the density and distribution of sori in the Patagonian species show a typical dipteridaceous arrangement. Sori in completely developed fronds in

Dipteridaceae are usually distributed across the entire surface of the lamina, while in Matoniaceae the sori are usually organized in rows on both sides of the midveins. One of the few exceptions is the recent new genus of Dipteridaceae, *Patagoniapteris*, for which a single row of sori on each side of the primary veins was described (Gnaedinger and Zavattieri, 2021).

The mosaic of vegetative and reproductive characters, evidenced in the context of this manuscript, also has implications from the phylogenetic point of view. Choo and Escapa (2018) developed a phylogenetic study where *Goepfertella* was scored following two schemes: (i) based exclusively on the observed reproductive and vegetative characters and, (ii) based on the frond architecture hypothesis originally proposed by Rees (1993). In the first case, the *Goepfertella* species were not recovered as monophyletic and form part of a large basal polytomy in the family, which includes the species belonging to several other fossil genera as terminals (e.g., *Thaumatopteris*, *Sewardalea*, *Dyctiophyllum*). Following the second scheme, *Goepfertella* is recovered as a monophyletic group, but it is also located in a similar basal polytomy. However, by removing *Goepfertella* from the analysis, a basal grade in the phylogeny of the family is recovered, which includes *Thaumatopteris* as the result of the first divergence, and *Sewardalea* as the second divergence (Fig 2, Choo and Escapa, 2018). It is interesting to note that regardless of whether architectural characters are considered or not, *Goepfertella* seems to introduce conflict in the analysis, and following our interpretation this is due to a clear conflict of characters. This is supported by the backbone analysis carried out in this study, in which *Goepfertella* occupies alternative positions as stem and crown of Dipteridaceae, and as stem of Matoniaceae (Fig. 9). However, when analyzing the affinity based exclusively on reproductive characters, and exclusively on vegetative characters, the results show differences that evidenced the origin of the character conflict. While considering just vegetative features *Goepfertella* shows affinity with

Dipteridaceae, mainly due to the characteristics of its reticulate venation; the reproductive characters analyzed in isolation show affinity with the base of Matoniaceae (Fig. 9). In this sense, the vegetative-reproductive mosaic shown by *Goepertella*, and illustrated in this work, provides further understanding of the origin of the previously postulated phylogenetic uncertainty.

To summarize, *Goepertella* has phylogenetic instability and takes different positions near to the base of the family Dipteridaceae (Choo and Escapa, 2018) due to the combination of derived vegetative and plesiomorphic reproductive characters. This position is also evidenced in the characteristics of its venation which, despite being anastomosed, shows a degree of anastomosis that is notably simpler than in other representatives of the family (Oishi and Huzioka, 1941; Cazaubón, 1947; Arrondo and Petriella, 1982; Herbst, 1993; Rees 1993). This allows us to hypothesize that, if the morphological organization shown by *Goepertella* is a early diverging form in the evolution of the Dipteridaceae, there would have been two changes during the evolution of the family: one in the distribution of the sori, from an ordered distribution to a disordered one, and one in the anastomosed venation, from forms with lower to higher degrees of areolation. In her study about morphological traits of the family, Choo (2017) discussed the relationship between sporangia distribution, venation and lamina dissection, and concluded that the presence of such characters would be correlated. According to the author, dissected fronds typically have small pinnae, which do not require a complex irrigation system (they were found to be strongly correlated with free veins). Following this same line of thought, the increase in the complexity of its veining as a consequence of the fusion of the lamina, would have allowed a change in the distribution of the sporangia towards more disordered and dispersed configurations.

Further progress in testing this hypothesis will require new studies expanding the character sampling, also including continuous characters as part of the analysis, since many

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DATA AVAILABILITY

The data set generated during the current study are available from <http://morphobank.org/permalink/?P4530>

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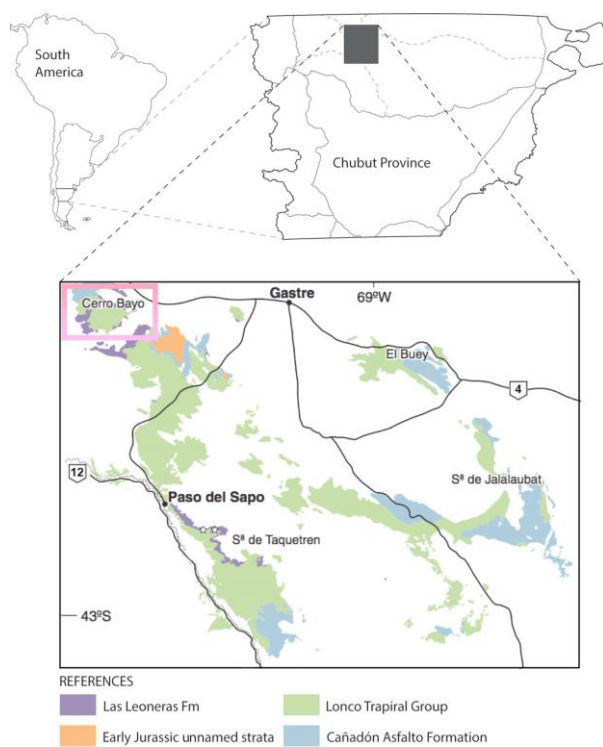
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Fig. 6. (A) Fragments of fertile pinnae. The area included in the dotted margin box corresponds to image D. MPEF-Pb 3573. (B) fragments of pinnae showing two fertile pinnulae. Sori are distributed on the basal portion of the pinnula (dotted margin box) suggesting apparent acroscopic maturation within the pinnula. MPEF-Pb 6939. (C) fragments of two fertile pinnulae showing round sori, alone or partially overlapping. Pinna rachis is covered by trichome bases (arrowheads). MPEF-Pb 6573. (D) detail of image A showing two fertile pinnulae, bearing partially overlapping sori. MPEF-Pb 3573. Scale bars = (A) 1 cm, (B, D) 5 mm, (C) 2 mm. Abbreviations: PR, pinna rachis.

Fig. 7. (A-E) Detail of fertile pinnula. (A) Circular to slightly elongated sori, partially overlapping, borne inside of areolae. MPEF-Pb 11117. (B-C) sori are arranged on both sides of the midvein and composed by seven-eight sporangia (numbers). MPEF-Pb 6939. (D) sporangia borne around an insertion area (arrowheads). MPEF-Pb 11117 (E) sporangia are leptosporangium type with oblique dehiscence ring. MPEF-Pb 6927. Scale bars = (A-C) 2 mm, (D) 1 mm, (E) 0.1. Abbreviations: PLV, pinnule lateral vein; PMV, pinnule midvein; PR, pinna rachis; SR, sporangial ring.

Fig. 8. (A-F) Silicone rubber casts of fertile fragments of primary segments and pinnae (A) Fragment of fertile pinna. MPEF-Pb 3573. (B) apparently early stages of maturation of the fertile pinna showing isolated sori. MPEF-Pb 3573. (C) apparently later stages of maturation of the fertile pinna showing partially overlapping sori. MPEF-Pb 3573. (D) Fragment of primary segment showing the insertion area of fertile pinnae and rachial pinnula. MPEF-Pb 3573. (E) a sorus (left) and two sori partially overlapping (right); leptosporangium with oblique dehiscence ring occupying $\frac{3}{4}$ parts of the sporangium circumference (arrowhead). MPEF-Pb 6939. (F) partially overlapping sorus next to pinna rachis; pinna rachis showing trichome bases (arrowhead). MPEF-Pb 3573. Scale bars = (A-D) 5 mm, (E) 0.05 mm, (F)

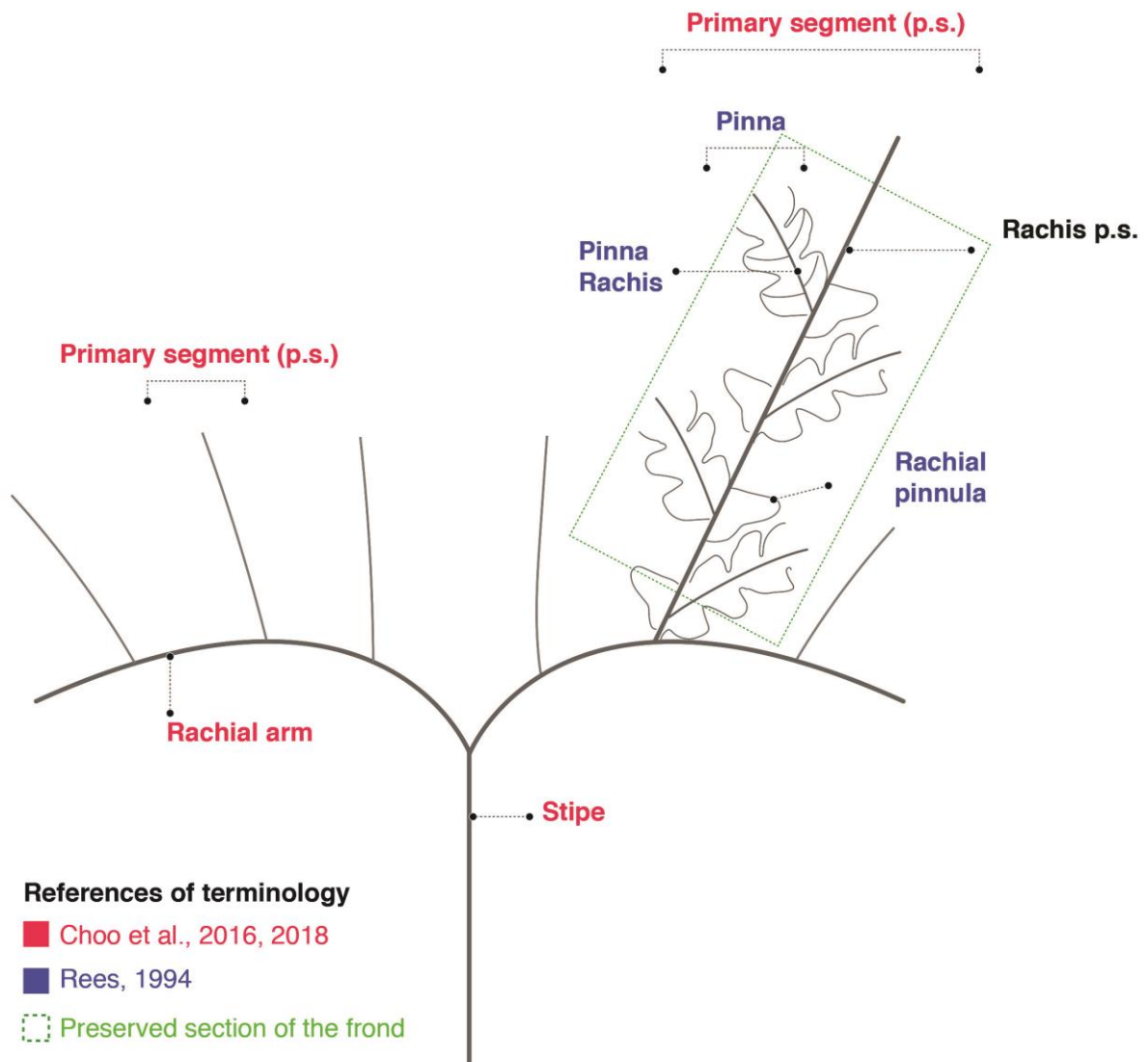
Figure 1



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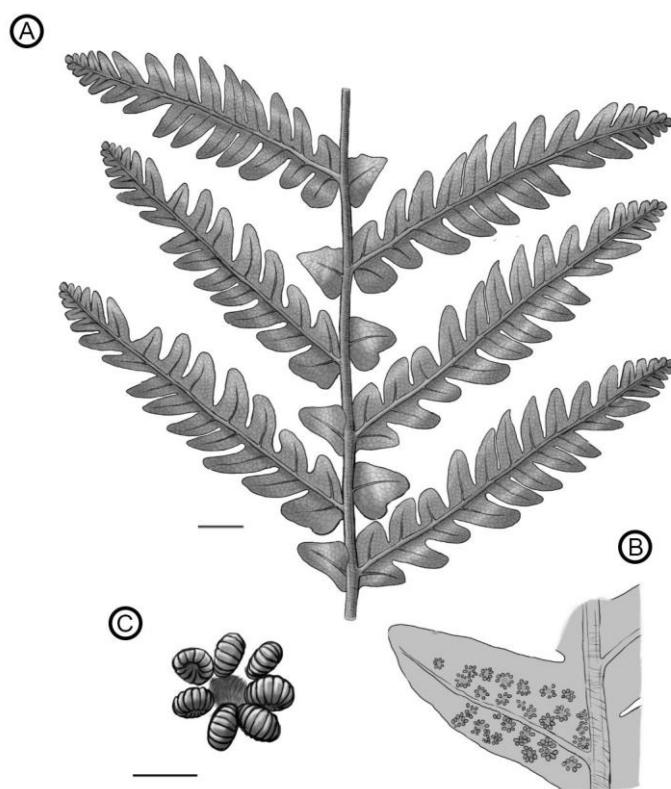
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Figure 2



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Figure 3



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Figure 4

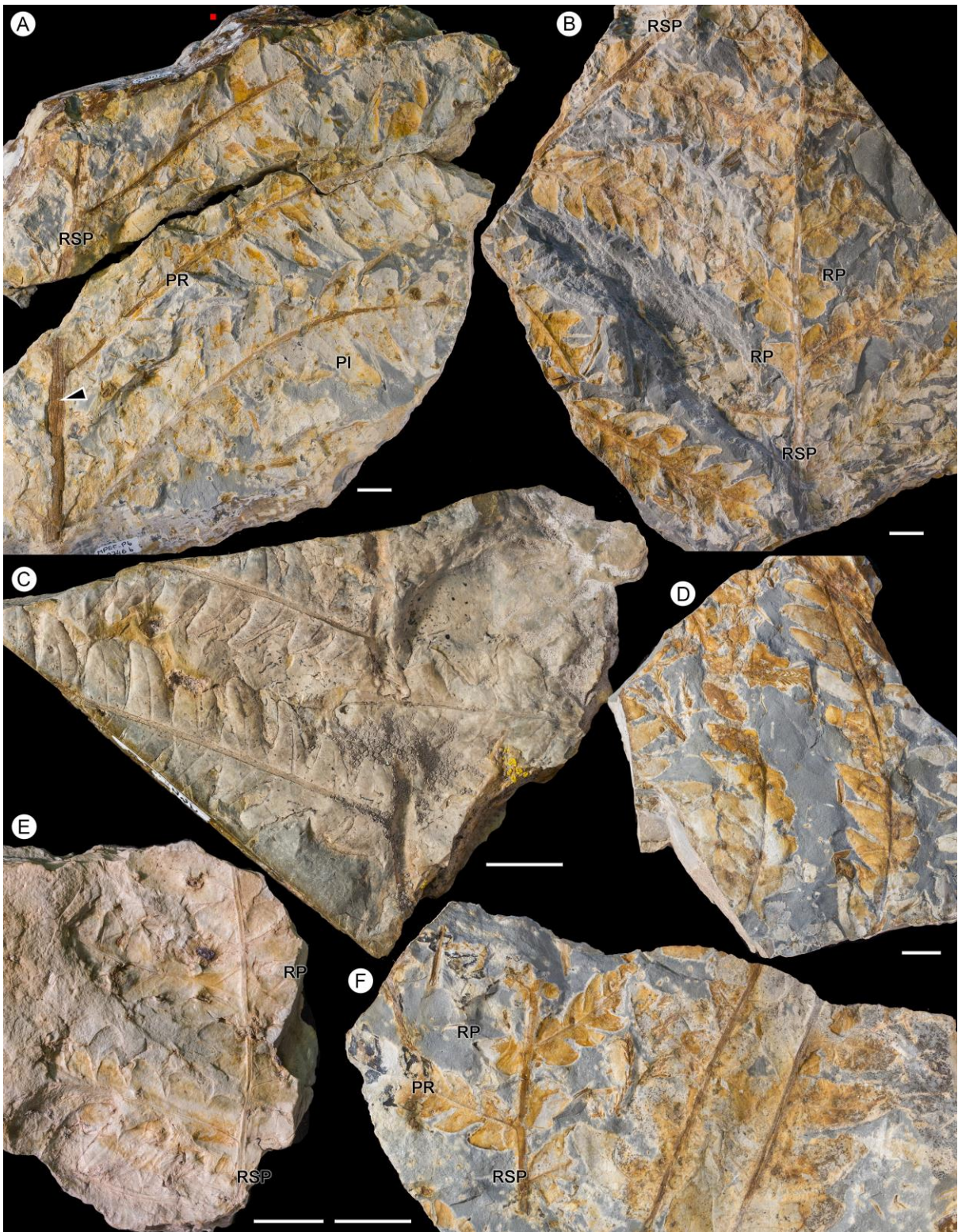


Figure 5



Figure 6

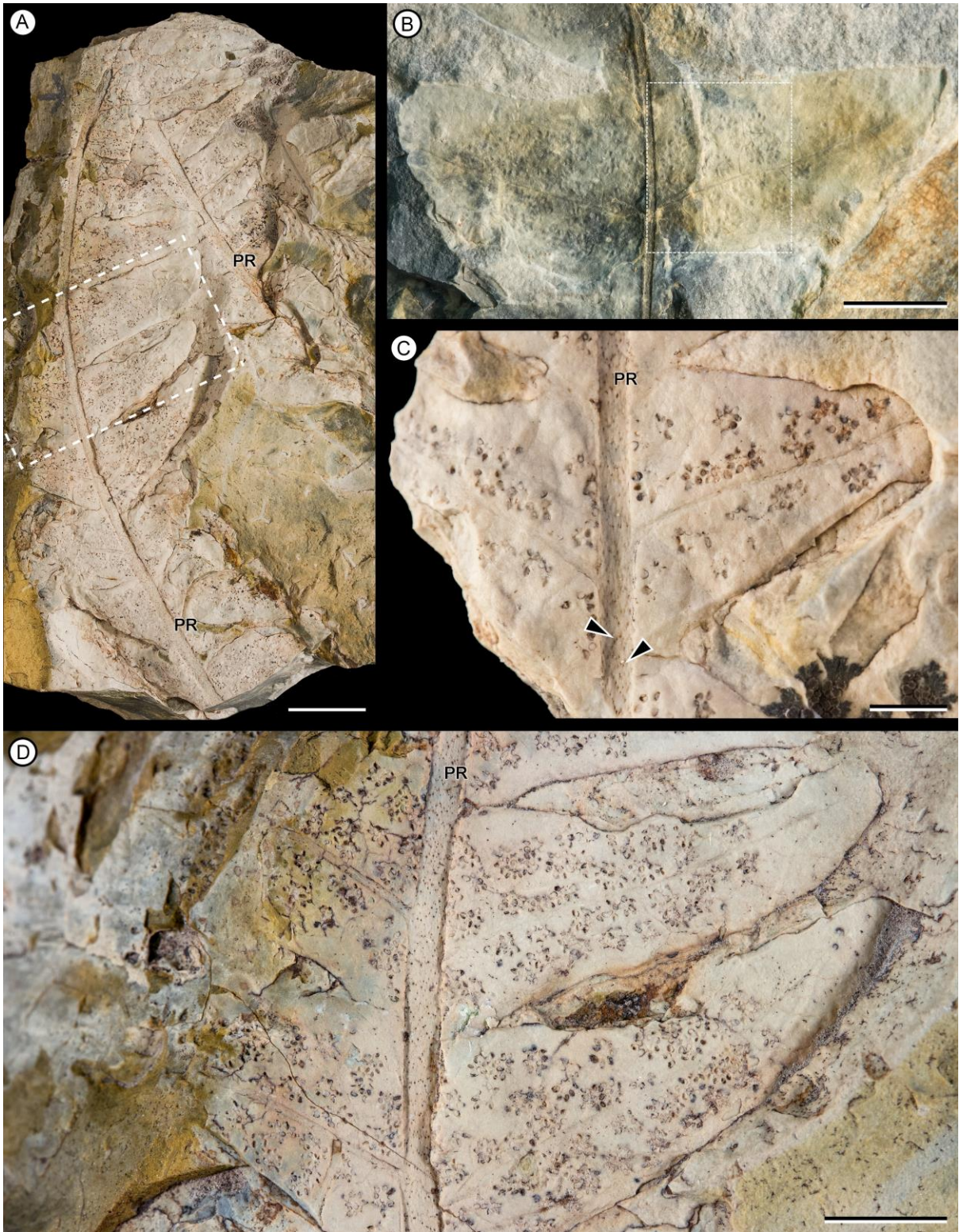


Figure 7

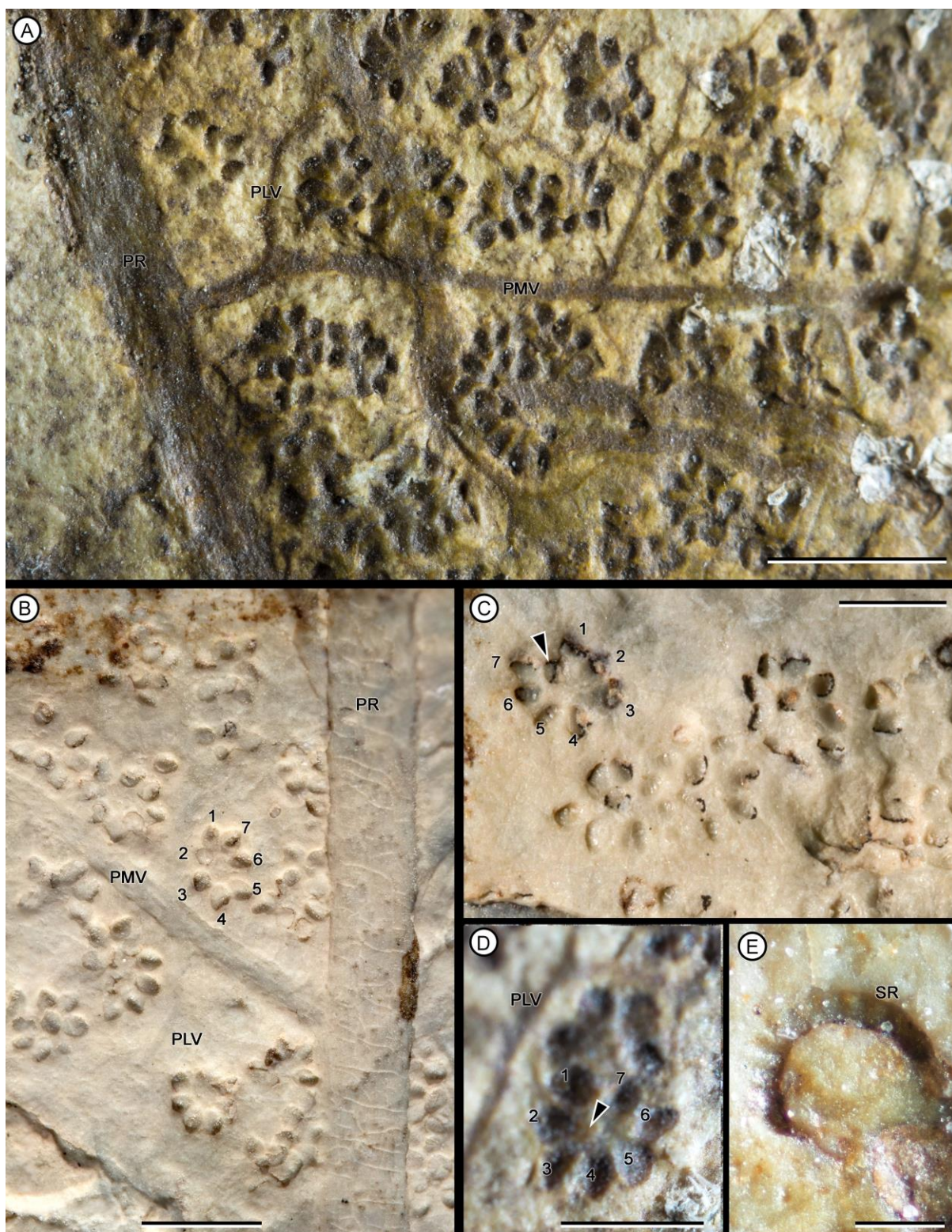


Figure 8

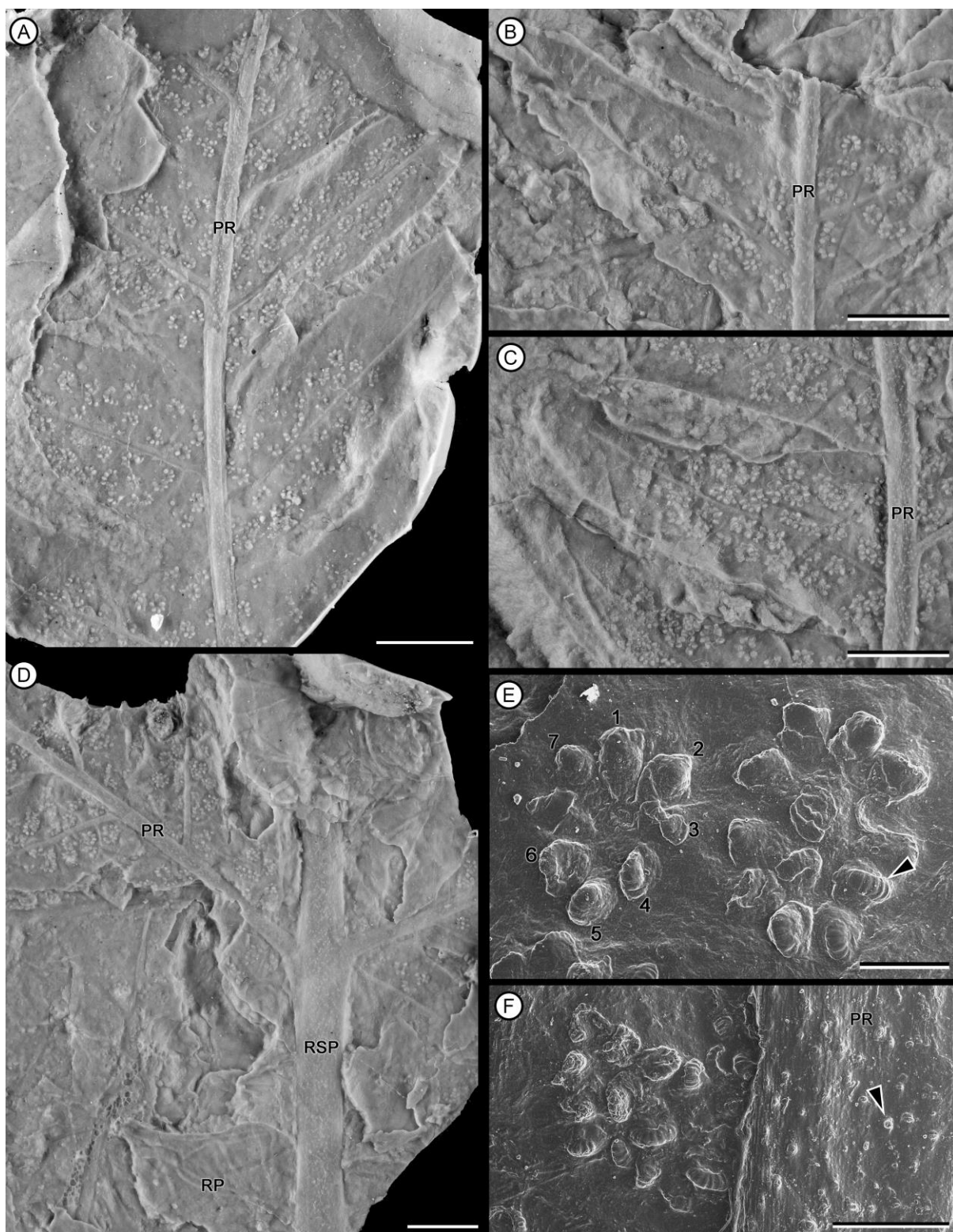


Figure 9

