

Original Article

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Palaeopteridium andrenelii sp. nov., a new noeggerathialean species from the Middle Pennsylvanian of Portugal with new insights on the Noeggerathiales

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Abstract

Noeggerathiales were until recently a group of plants with uncertain systematic position that existed in the Carboniferous and Permian times. Recent discoveries classify them as heterosporous progymnosperms. Despite the discovery of additional specimens, the group still remains highly artificial because their reproductive organs are rarely preserved in organic connection. Within the Carboniferous of Iberian Massif, the noeggerathialeans are poorly represented. Here, we describe *Palaeopteridium andrenelii* sp. nov. from the uppermost Carboniferous of Portugal. This is the second representative of Noeggerathiales reported in the Portuguese Carboniferous after Carlos Teixeira have described the noeggerathialean *Rhacopteris gomesiana* in the 1940s from Douro Carboniferous Basin (Stephanian C/lower Gzhelian, Upper Pennsylvanian). *Palaeopteridium andrenelii* was found in upper Asturian (upper Moscovian, Middle Pennsylvanian) strata from the classical Westphalian outcrops of Ervedosa, located in the region of Alto da Serra (Fânzeres), Gondomar, in northwestern Portugal. Two reproductive structures are associated with the frond of the new fossil species. Although not organically linked, both structures could belong to parent plant (frond) and represent possible detached macrosporangia. This reinforces the *Palaeopteridium* as a noeggerathialean and the first reproductive structures found for this genus.

1. Introduction

The Noeggerathiales is a puzzling extinct group of late Palaeozoic plants known by fossils of foliage associated/disassociated with strobilli, isolated strobilous or isolated foliage (e.g. Wang *et al.* 2004, 2009; Pfefferkorn & Wang, 2016). Due to a lack of anatomically preserved specimens, these plants until recently had an uncertain systematic position, being historically considered as related to ferns, cycads, sphenopsids or to progymnosperms (e.g. Leary, 1980; Wang *et al.* 2004; Taylor *et al.* 2009). Recently, the finding and description of whole specimens found within a Permian ash-tuff with articulated foliage, (pseudo-like)strobili and stem with anatomical preservation, allowed the elucidation of the Noeggerathiales as members of the progymnosperms clade, a sister group to the seed plants (Wang *et al.* 2021; Yang *et al.* 2023).

Palaeobiogeographically, the Noeggerathiales are restricted to two floral realms, the Cathaysian floral realm (i.e. China) where these plant fossils are relatively abundant and in the Euramerican floral realm where these are considered rare (Pfefferkorn & Wang, 2016). As pointed by some authors (Leary & Pfefferkorn, 1977; Pfefferkorn & Wang, 2016) despite extensive exploration and description of several palaeofloras, noeggerathialean fossils are seldom found in Euramerica Palaeozoic floras. This bias is most probably due to their palaeoecological preferences to extra-basinal ecosystems or specific edaphic/nutrient conditions (but see Pfefferkorn & Wang, 2016). Despite its rarity, within Iberian Peninsula, at least ten noeggerathialean taxa were recognized mainly in Carboniferous basins from Spain: *Palaeopteridium reussii* (Ettingshausen) Kinston, *Palaeopteridium michiganense* (Arnold) Álvarez-Vázquez, cf. *Sauropteris guthoerlii* Hirmer, *Rhacopteris bipinnata* Němejc, *Rhacopteris elegans* (Ettingshausen) Kidston, *Rhacopteris* cf. *robusta* Kidston, cf. *Rhacopteris paniculifera* Stur, *Rhacopteris inaequilatera* Göppert, cf. *Rhacopteris dichotoma* Kidston; in Portugal, only one record is known, *Rhacopteris gomesiana* Teixeira (Teixeira, 1943; Wagner, 1983; Wagner & Álvarez-Vázquez, 2010; Correia *et al.* 2018). However, this number can be reduced to four, as the fossil taxa *Rhacopteris* is possibly not a noeggerathialean (see Pfefferkorn & Wang, 2016).

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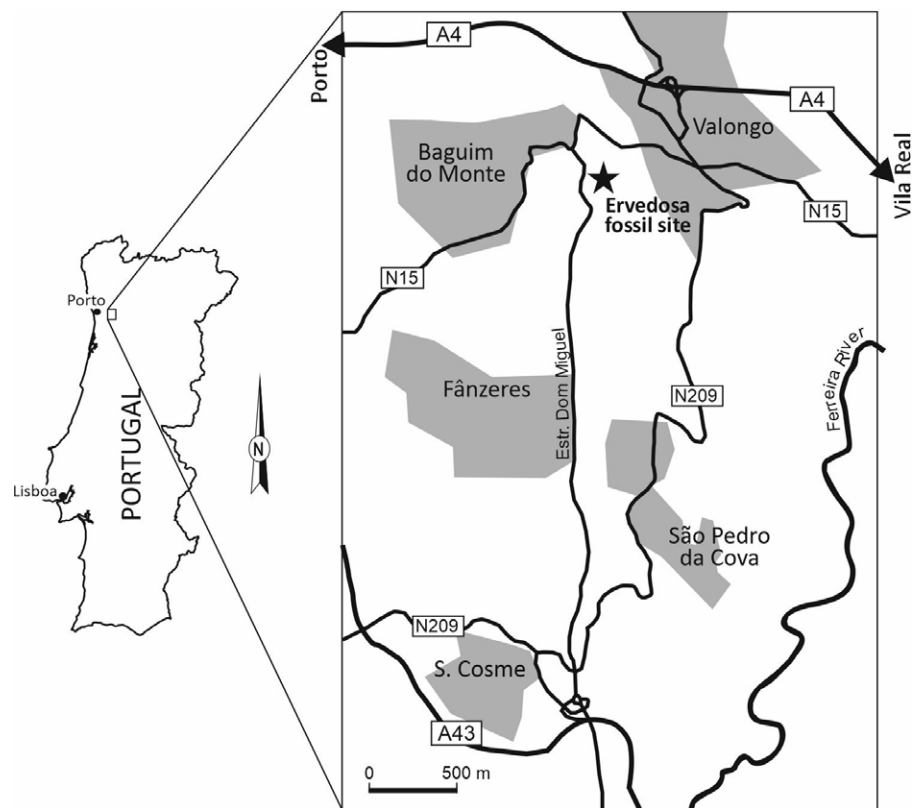


Figure 1. Locality map of the Ervedosa's (Estrada Dom Miguel) fossil site. Modified from Correia *et al.* (2020, Fig. 1).

In recent years, efforts were made to identify old and new fossiliferous outcrops and to collect and describe the palaeobiodiversity of the Portuguese Carboniferous basins. These resulted in the description of several new fossil plant taxa, many endemics to the Portuguese territory (see Correia *et al.* 2014a; Correia *et al.* 2016; Pšenička *et al.* 2017; Correia *et al.* 2018; Correia *et al.* 2019; Correia *et al.* 2020; Correia *et al.* 2021a; Correia *et al.* 2021b; Barbosa *et al.* 2022; Correia *et al.* 2023a; Correia *et al.* 2023b). Despite this effort, since the 1940s, no new noeggerathialean fossils from Portugal were described.

In this paper, we describe and illustrate a new noeggerathialean species of the fossil-genus *Palaeopteridium* and dissociated reproductive structures possibly related to macrosporangia for the uppermost Carboniferous of Portugal and discuss its implications for the palaeoecology and palaeodiversity of Noeggerathiales.

2. Material and methods

2.a. Fossil locality and material

The fossil material of the new noeggerathialean species was collected in an excavation during fieldwork in 2006, in upper Westphalian D (upper Asturian/upper Moscovian, Middle Pennsylvanian) outcrops of Tanjarro locality, found along the roadside of Dom Miguel (known as 'Estrada Dom Miguel'), located around Seixo (Fânzeres) region, in Gondomar, northwestern Portugal (Fig. 1). This locality of late Westphalian D plants has been described as an integral part of the Ervedosa flora (Teixeira, 1944). The outcrops of 'Estrada Dom Miguel' fossil site represent a narrow geological-stratigraphic strip that contains a diverse and well-preserved fossil macroflora. This narrow strip occurs on the geographical alignment of the classical Westphalian outcrops of

Ervedosa, which also include the localities of Montalto and Tanjarro.

The palaeobotanical material (Plates I–II) consists of a single specimen (holotype) which is also represented by a counterpart (isotype). Both plant fossil samples are preserved as adpressions (compressions and impressions; Shute & Cleal, 1986) in laminated grey shales.

2.b. Sample preparation and repository

The fossils of the new species were prepared either manually, using small chisels, hammers and stiff needles, or mechanically with a compressed air and an electrically powered vibro-tool. The specimens were later drawn using a camera lucida setup attached to a stereomicroscope to elucidate the morphology and help with the taxonomic description in Systematics part. Both part and counterpart are stored in the palaeontological collections of the Geological Museum Fernando Real of the University of Trás-os-Montes e Alto Douro (MGUTAD; Vila Real, Portugal).

3. Geological, palaeobotanical and biostratigraphic background

The Ervedosa flora occurs in upper Westphalian D (upper Asturian/upper Moscovian, Middle Pennsylvanian) strata in a separate thrust slice, into two thin strips which surroundings to the NE lower Gzhelian (Upper Pennsylvanian) rocks of Douro Carboniferous Basin (e.g. Teixeira, 1944; Wagner & Lemos de Sousa, 1982a; Wagner, 1983; Wagner & Álvarez-Vázquez, 2010). In the geological-structural and sedimentological context, Ervedosa has a genesis not very different from the Douro Carboniferous Basin (Pinto de Jesus, 2001, 2003).

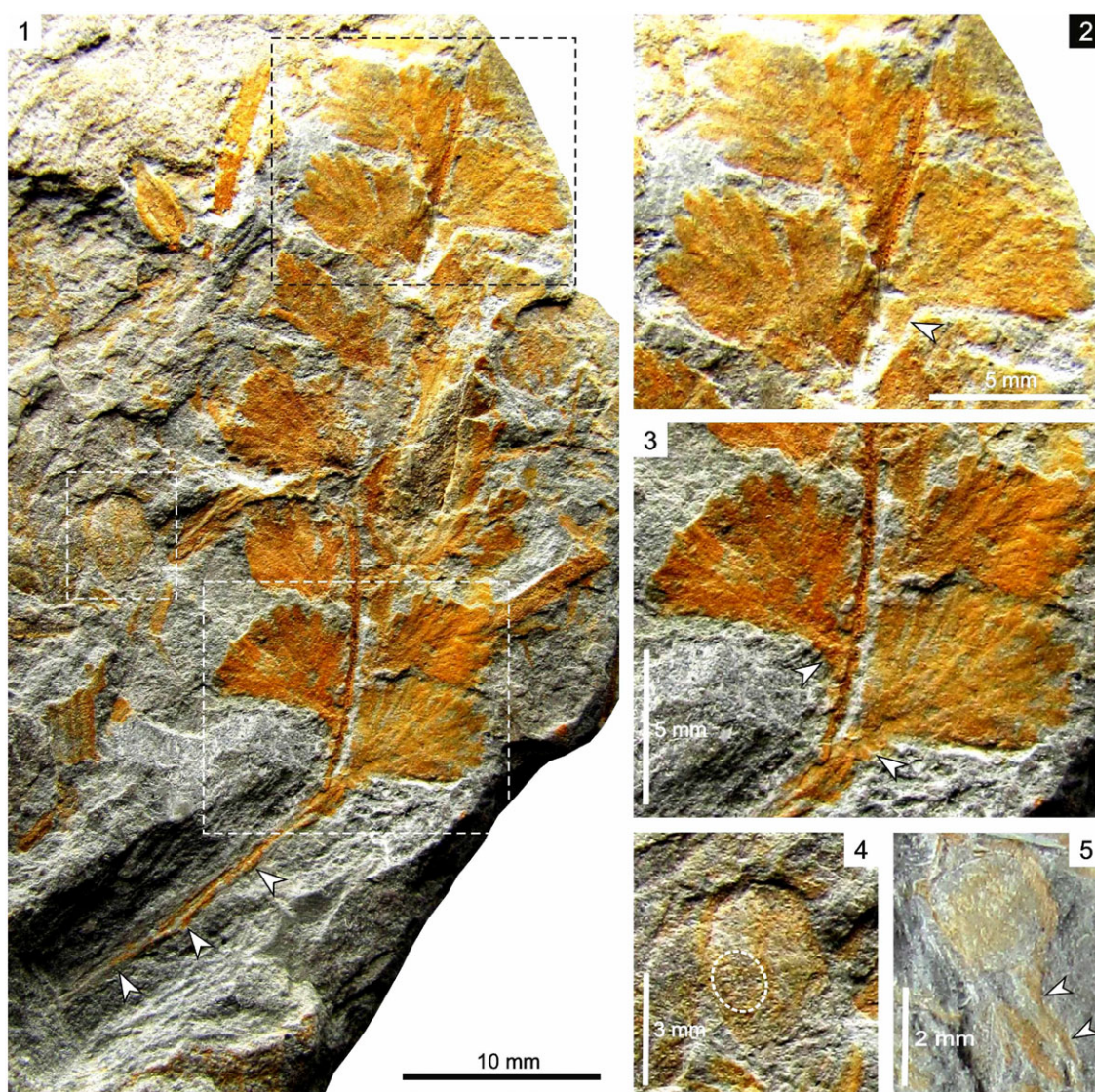


Plate I. Holotype MGUTAD-1121 of *Palaeopteridium andrenelii* sp. nov. from the Ervedosa's outcrops (upper Westphalian D/upper Asturian, Middle Pennsylvanian) of the road Dom Miguel, Seixo (Fânzeres) region, Gondomar, northwestern Portugal. 1 – General view of the holotype (white arrows indicate a very developed petiole-like, a possible penultimate rachis). 2–3 – Enlargement of rectangular boxes in Figure 1, showing details of foliage (white arrows indicate the petiolate attachment of the pinnules on an ultimate rachis). 4 – Enlargement of rectangular box in Figure 1, displaying a putative 'noeggerathialean' macrosporangium with a probable micropyle (highlighted in dashed white circle). 5 – Putative 'noeggerathialean' macrosporangium, exhibiting a multicelled gametophyte extending from ruptured spore wall (white arrows) (holotype counterpart; see Plate II, 2B).

The first studies on the Ervedosa (Westphalian D) flora date back to the 1940s and 1950s, with works by Teixeira (1941, 1942a, 1942b, 1942c, 1943, 1944, 1945, 1951, 1954) that make reference to a set of plant fossils harvested by this author in the localities of Ervedosa, Tanjarro and Montalto (Wagner & Lemos de Sousa, 1983). The original materials are stored in the collections of the Geological Surveys of Portugal in Lisbon and at the Museu de História Natural e da Ciência da Universidade do Porto (MHNCUP; Portugal). The lists initially published by Teixeira (1943, 1944, 1945, 1954) for the Ervedosa flora were commented by Wagner (1959, p. 405), and afterwards, revised by Wagner (1983, p. 156) and Wagner & Lemos de Sousa (1983, p. 132).

The stratigraphic age of the Ervedosa flora was first discussed by Laveine *et al.* (1977), making reference to the early-late Westphalian D (Asturian) age with the comparison between the *Callipteridium* (*Praecallipteridium*) *jongmansii* (Bertrand) Wagner and *Callipteridium* (*Praecallipteridium*) *armasii*

(Zeiller) Wagner biozones from the Santa Susana Basin (upper Westphalian D) of the Portuguese Carboniferous and Asturian Central Massif in northwestern Spain, respectively (e.g. Wagner, 1966, 1983; Wagner & Lemos de Sousa, 1983; Correia *et al.* 2019). Wagner (1971) recorded *Callipteridium jongmansii* under name of *Callipteridium armasii* (see also Laveine *et al.* 1977; Wagner, 1983; Wagner & Lemos de Sousa, 1983). This author later described both species as a single group, grouped into a '*Callipteridium jongmansii-armasii*' complex, which appears in ages from late Westphalian to mid-to-late Cantabrian (Wagner, 1984, see chart 3). More recently, Wagner and Álvarez-Vázquez (2010) described *Callipteridium jongmansii* as only species which appears in the upper Asturian (upper Westphalian D) of Santa Susana Basin and Ervedosa (Portugal) and in the lower Asturian (lower Westphalian D) and lower? Cantabrian of Spain.

Also, in the Laveine (1977)'s work, there is the reference to the *Dicksoniites plueckenetii* Sterzel as equivalent to the late

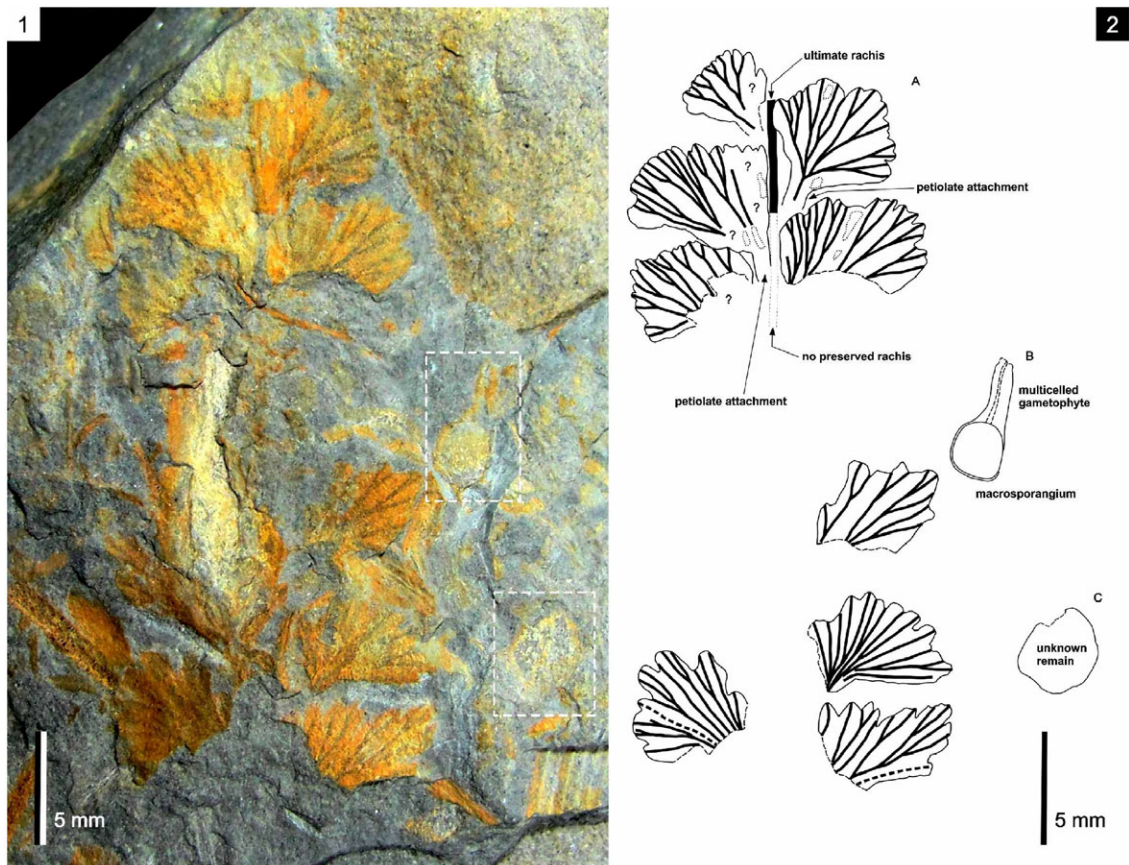


Plate II. Counterpart (isotype MGUTAD-1122) of the holotype specimen of *Palaeopteridium andrenelii* sp. nov. 1 – Highlight of partially preserved foliage and venation of the frond, displaying highlighting an associated ‘noeggerathialean’ macrosporangium-like and an oval-shaped structure of undetermined (highlighted in rectangular boxes). 2 – Interpretive line drawing of the frond foliage and venation (A), macrosporangia showing a multicelled gametophyte extending from ruptured spore wall (B), and unknown plant fragment (C) (enlargement of rectangular boxes in Figure 1).

Westphalian D age, and in correspondence with the South Wales horizon (Cleal, 1978). However, *D. plueckenetii* has been recorded in the Carboniferous of Iberian Peninsula (Iberia) in ages from Westphalian D to Stephanian C (early Gzhelian) (e.g. Wagner, 1983, 1984; see also Correia *et al.* 2018, Table 1). Other macrofloral elements present, *Alethopteris corsinii* Buisine is a species that occurs in the Westphalian C and Westphalian D horizons/units of the northeastern France (Buisine, 1961), and the species *Linopteris obliqua* (Bunbury) Zeiller and cf. *Lobopteris vestita* (Lesquerex) Wagner, two biozones which are correspond to the lower and upper units of the Asturian substage of Western European regional scale (equivalent to the middle Westphalian D and upper Westphalian D units, according to Heckel & Clayton, 2006), respectively (e.g. Wagner & Lemos de Sousa, 1983; Wagner, 1984; Correia *et al.* 2018, Figure 10). *Asterotheca* cf. *nyranensis* Němejc reported in the Ervedosa flora is another Asturian (Westphalian D) floral record, which is associated with the *obliqua* and *vestita* Zones (macrofloral zones) in the floral massifs of Spain and Czech Republic (e.g. Pšenička *et al.* 2005; Wagner & Álvarez-Vázquez, 2010, pp. 270, 273). In Portugal, this species has been reported in upper Westphalian D (upper Asturian) strata of the Santa Susana Basin (e.g. Wagner, 1983; Wagner & Lemos de Sousa, 1983).

Ervedosa flora is also characterized by the presence of some native or endemic species, such as *Linopteris florini* Teixeira and *Neuropteris* (*Mixoneura*) *ervedosensis* Teixeira described by Teixeira (1941, 1944, 1942a; 1942c; see also Wagner & Lemos

de Sousa, 1982a; Wagner & Lemos de Sousa, 1982b; Wagner, 1983). *L. florini* is a long ranging form, which is generally mid-Westphalian (Westphalian B) and early Stephanian (late Cantabrian/early Barruelian), and has been found in Portugal, Spain and Germany (Wagner & Lemos de Sousa, 1982a; Wagner & Lemos de Sousa, 1982b; Wagner, 1983). *N. ervedosensis* has been later redescribed by Teixeira (1944) as a probable form of *Neuropteris ovata* Hoffmann, *Neuropteris ovata* Hoffmann forma *ervedosensis* Teixeira. It is noted that according to Wagner and Lemos de Sousa (1983), *Neuropteris ovata* forma *ervedosensis* is a species in its own rights and probably unrelated to *Neuropteris ovata*. Other floral elements such as *Lobopteris micromiltonii* (P. Bertrand) Wagner and *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute & Zoderow compose the Ervedosa flora, which tend to suggest mid-Westphalian D (Asturian) to late Cantabrian (early Stephanian) ages attributed to the floral massifs of Iberian Peninsula (e.g. Wagner & Lemos de Sousa, 1983; Wagner, 1984; Wagner & Álvarez-Vázquez, 2010, see comments in p. 276). These latter species suggest a higher age than that previously established, for a Cantabrian age, but the set of species above-mentioned places flora of Ervedosa with age most likely to the late Westphalian D.

4. Systematic description

The taxonomic classification system is according to Taylor *et al.* (2009) and Novikoff and Barabasz-Krasny (2015).

Table 1. Summary of the main characteristics of foliage for comparison between *Palaeopteridium andrenelii* sp. nov. and other similar noeggerathialean fossil taxa

Noeggerathialean fossil taxa	<i>Palaeopteridium andrenelii</i> sp. nov.	<i>Palaeopteridium reussii</i> (Ettingshausen) Kidston, 1923	<i>Rhacopteris lindseaeformis</i> Bunbury sp.	<i>Rhacopteris inaequilatera</i> (Göppert) Stur, 1875
Pinnule shape	Fan-shaped (flabelliform or semiflabelliform)	Semiflabelliform to flabelliform (fan-shaped)	Semiflabelliform to flabelliform	Semiflabelliform to flabelliform
Distal margin form (pinnule apex)	Crenate/lobed distal margins	Dentate-serrate distal margins/circular-shaped apex	Distal margins cleft into segments	Finely crenulate distal margins/truncate-shaped apices
Number teeth/lobes on margin distal	12–14 teeth/lobes	10–20 teeth	No data	No data
Venation pattern (vein dichotomy)	Veinlets of equal strength, divided in three to four times	Thin veinlets, divided in two to five times	Veinlets of equal strength, divided in two or three times	Veins dichotomizing two or three times
Pinnule attachment	Petiolate attachment	Strong and short ‘petiolate’ attachment, sometimes absent	Strong and short ‘petiolate’ attachment, sometimes absent?	Strong and short ‘petiolate’ attachment, sometimes absent?
Pinnule symmetry	Relatively symmetrical	Symmetrical	Asymmetrical	Asymmetrical

Division: †Progymnospermophyta Bold *et al.*

Class: †Noeggerathiopsida Kryštofovich

Order: †Noeggerathiales Němejc emend. Wang *et al.* (2021)

Fossil-family: Discinitaceae Zhifeng & Thomas

Fossil-genus: *Palaeopteridium* Kidston (1923)

Type species: *Palaeopteridium reussii* (Ettingshausen) Kidston (1923) from Westphalian Series of the Carboniferous Rocks of Great Britain.

Basionym: *Asplenites reussii* Ettingshausen (1852), ‘Steinkohlenflora von Stradonitz in Böhmen’, Abhandl. K.K. geol. Reichsanst., Band I, Abth. 3, No. 4, p. 16, pl. I, Figures 8, 9 (Kidston, 1923, p. 201)

***Palaeopteridium andrenelii* sp. nov.**
(Plates I, 1–3; Plate II, 1)

Etymology. The specific name ‘*andrenelii*’ honours André Nel from Muséum National d’Histoire Naturelle (Paris), a world expert in palaeoentomology and honourable colleague who has been cooperating with us on the systematic study of new insect fossils recently described in the Douro and Buçaco Basins (Loureiro *et al.* 2010; Correia *et al.* 2014b; Correia *et al.* 2021c; Correia & Nel, 2023; Correia *et al.* 2023c).

Holotype. Specimen MGUTAD-1121 (Plate I, 1–3) is composed of a counterpart – isotype MGUTAD-1122 (Plate II, 1).

Type locality. Outcrops located in the northeast banks of road Dom Miguel, Seixo (Fânzeres) region, Gondomar, northwestern Portugal (Fig. 1).

Type horizon and age. Horizon composed of laminated and compact grey shales; late Westphalian D (late Asturian/late Moscovian, Middle Pennsylvanian).

Diagnosis. Bipinnate frond with subopposite or alternate pinnules, relatively symmetrical and spaced, sometimes touching or slightly overlapping, obliquely attached to an ultimate rachis by a very narrow base (1.5–2.0 mm long and 0.8–1.0 mm wide) – petiolate attachment. Ultimate rachis very thin, straight or slightly flexuous, detached from a possible penultimate rachis. Fan-shaped (flabelliform or semiflabelliform type) pinnules, of 7–8 mm long and a maximum fan width of about 5–6 mm, with entire lateral and crenate/lobed distal margins. Distal margins bearing irregular and asymmetrical 12–14 crenate-shaped teeth/lobes of about 0.3–1.0 mm long. Venation pattern of open dichotomous showing a

single vein entering each pinnule, giving rise to a series of radiating veinlets of equal strength which in their course to the margin divide three or four times. There are 14–20 veins on distal margin of pinnule.

Description of the holotype. The frond is at least up to 37 mm long, with subopposite or alternate pinnules, relatively symmetrical and spaced, sometimes touching or slightly overlapping (Plate I, 3), and obliquely attached on an ultimate (last order) rachis by a very narrow base (1.5–2.0 mm long and 0.8–1.0 wide) – petiolate attachment (Plate I, 2, 3, white arrows; Plate II, 2A). The ultimate rachis is very thin, of 0.2–0.5 mm wide, which is detached from a possible penultimate rachis (petiole-like) up to 15 mm long and 1.0–1.5 mm wide (Plate I, 1, white arrows). The petiole displays a prominent central vein. The pinnules are 7–8 mm long and 5–6 mm wide and fan-shaped (flabelliform or semiflabelliform type), having entire lateral and crenate/lobed distal margins. The crenate/lobed margins have 12–14 crenate-shaped teeth/lobes, relatively irregular and asymmetrical, of about 0.3–1.0 mm long. The venation is dichotomous displaying veinlets of equal strength, well visible, and which in their course to the margin are divided in three to four times (Plate II, 1, 2). The veins are very few in number – there are 14–20 veins on distal margin of pinnule.

Remarks. Some upper pinnules of the frond appear to display slightly cleft or slotted distal margins (see Plate I, 2), but it is likely this is damage on the pinnule lamina due to the taphonomy (see holotype counterpart and restoration of foliage in Plate II, 1, 2A).

5. Discussion

5.a. Comparisons

In comparison with other noeggerathialean species, *Palaeopteridium andrenelii* sp. nov. (Plates I, 1–3; Plate II, 1) bears a close resemblance to *Palaeopteridium reussii* (Ettingshausen) Kidston, 1923. This species occurs in the Duckmantian and Bolsavian (Westphalian B, C) of Bohemia (Czech Republic), lower Asturian of Spain and Westphalian Series of South Staffordshire Coalfield (Britain) and Namurian (Serpukhovian–Bashkirian) from West-Central of Illinois (USA) (Kidston, 1923; Leary & Pfefferkorn, 1977; Wagner & Álvarez-Vázquez, 2010). *P. reussii* bears semiflabelliform to flabelliform (fan-shaped) pinnules with dentate distal margins in which,

showing 10–20 dentate-teeth and having 10 to 20 veins which are divided up to three times (e.g. Kidston, 1923, pp. 201, 202, pl. LV; Leary & Pfefferkorn, 1977, p. 16–19, Figure 7A–C, pl. 4, Figures 1–5; Wagner & Álvarez-Vázquez, 2010, p. 274, pl. XVII, Figures 5, 6). The major difference between *P. reussii* and *P. andrenelii* sp. nov. is in the form of the distal margins of the pinnules. The distal pinnule margins of *P. reussii* are notably dentate to serrate (e.g. Kidston, 1923, pl. LV, Figure 2a; Leary & Pfefferkorn, 1977, Figure 7A–C; Leary & Trask, 1985, pl. 4, Figure 1), while those of *P. andrenelii* sp. nov. are relatively crenate or lobed (Plate II, 2). Other differences occur in the lower and upper parts of the pinnules. The pinnules of *P. reussii* have an apex shape more circular, while pinnules of *P. andrenelii* sp. nov. show irregular distal margins. On the other hand, the pinnules of the Portuguese species shows a more petiolate attachment (Plate II, 1, 2) when compared to the pinnule attachment of *P. reussii* pinnules which is stronger and shorter or less developed and, sometimes, it is highlighted by the absence of a petiole (e.g. Kidston, 1923, pl. LV; Leary & Pfefferkorn, 1977, Figure 7A–C; pl. 4, Figures 1–5; Wagner & Álvarez-Vázquez, 2010, pl. XVII, Figures 5, 6; see summary of the main characteristics of foliage for comparison in Table 1).

P. andrenelii sp. nov. shares with *Rhacopteris lindseaeformis* Bunbury sp. (= *Rhacopteris [Anisopteris] paniculifera* Stur, 1875) the semiflabelliform-flabelliform pinnule shape with crenulate distal margin, but it differs from the latter in the symmetry of pinnules. The pinnules of *R. lindseaeformis* are notably asymmetrical, having one of lateral margins more developed and distal margins cleft into segments (Kidston, 1923, pp. 204, 205, text-Figure 9, pl. XLIX, Figures 1–4, pl. LI, Figure 2; Boureau & Doubinger, 1975, pp. 624, 627, Figures 530, 534; Taylor *et al.* 2009, pp. 555, 562, Figure 14.79). In addition, *P. andrenelii* sp. nov. differs from *R. lindseaeformis* in the venation pattern. *R. lindseaeformis* pinnules show radiating veinlets of equal strength which, in their course to the pinnule margin, are divided two or three times. In contrast, the pinnules of *P. andrenelii* sp. nov. display veinlets of equal strength, well visible, and which in their course to the margin are divided in three to four times (Plate II, 1, 2; see Table 1). *R. lindseaeformis* is described from the Carboniferous Limestone Series and is there restricted to the Lower Limestone Group but is widely distributed in the Oil-Shale Group of the Carciferous Series (Mississippian) of Britain (Kidston, 1923, p. 207; Taylor *et al.* 2009, pp. 555, 562).

P. andrenelii sp. nov. also is comparable to the *Rhacopteris inaequilatera* (Göppert) Stur, 1875 (= *Anisopteris inaequilatera* Göppert) which has semiflabelliform to flabelliform (fan-shaped) pinnules with finely crenulate distal margins. Nevertheless, *P. andrenelii* sp. nov. differs from *R. inaequilatera* in the apex shape of pinnules. *R. inaequilatera* pinnules show notably truncate-shaped apices (Kidston, 1923, p. 208, pl. XLIX, Figures 5, 6, pl. LI, Figure 3; see also Boureau & Doubinger, 1975, p. 621, Figure 528). There is also some dissimilarity in the venation pattern between two species. In *R. inaequilatera*, the veins dichotomize two or three times when they reach the pinnule margin (detailed description in Kidston, 1923, p. 208), while those of *P. andrenelii* sp. nov. are divided in three to four times (Plate II, 1, 2; see Table 1). *R. inaequilatera* occurs in lower Carboniferous/Mississippian (Calciferous Sandstone Series – Oil-Shale Group) of Britain (Kidston, 1923; Boureau & Doubinger, 1975).

5.b. Generic placement

The new fossil species described herein (Plates I, 1–3; Plate II, 1) shares macro-morphological features with *Palaeopteridium* Kidston, 1923 and *Rhacopteris* Schimper, 1869. *Rhacopteris*,

similarly as *Palaeopteridium* belongs to the noeggerathialeans. Both fossil-genera are typical floristic elements of the Euramerican floral realm and bear very similar morphological traits in the pinnule general shape, bearing semiflabelliform to flabelliform (fan-shaped) pinnules, of which are compared favourably with the new Portuguese species. However, *Palaeopteridium* and *Rhacopteris* differ in the apical margin of pinnules. *Rhacopteris* has usually more divided pinnules (i.e. strongly slotted leaflets) than *Palaeopteridium* (e.g. Kidston, 1923; Boureau & Doubinger, 1975) [some species with non-slotted leaflets, such as ‘*Rhacopteris circularis*’ Walton, 1926 (see Boureau & Doubinger, 1975, p. 622), have been classified as belonging to the genus *Rhacopteris*; however, this taxonomic misunderstanding needs to be revised and the species should be transferred to the genus *Palaeopteridium*]. *Palaeopteridium* has usually only teeth in distal pinnule margin (e.g. Leary & Pfefferkorn, 1977; Pfefferkorn & Wang, 2016, Figure 4). The pinnules of the new Portuguese species are not slotted, having dentate or lobed distal margins (Plate I, 2, 3; Plate II, 2A).

Palaeopteridium andrenelii sp. nov. also shares some basic features (fan-shaped pinnules) with the fossil-genera *Anisopteris* (Oberste-Brink) Hirmer, 1940 (see Boureau & Doubinger, 1975, p. 621) and *Nothorhacopteris* Archangelsky, 1983 (see Taylor *et al.* 2009, pp. 651, 677). *Anisopteris* belongs to quite different group [all the ‘*Anisopteris*’ species described in literature are different by stratigraphy and by systematic classification and the legitimacy of genus as valid name is questionable (various species classified to the genus *Anisopteris* were previously attributed to the genus *Rhacopteris*; see Kidston, 1923, pp. 203–9; Boureau & Doubinger, 1975, pp. 623–7)]. The South American Carboniferous–early Permian *Nothorhacopteris* is of a different floristic province, and it belongs to different taxonomic group (Taylor *et al.* 2009, p. 677).

Therefore, on the basis of these generic diagnostic morphological features and the phytogeographical differences, the new Portuguese species fits well into the fossil-genus *Palaeopteridium*.

5.c. Reproductive structures associated with *Palaeopteridium*-type fronds and its parental relationship

Leary (1980) described a specimen of *Lacoea* Read (1946), a spore- or pollen-bearing organ (sporophyll type) with affinities to early gymnosperms (progymnosperms), from the Lower Pennsylvanian deposits of Rock Island County, Illinois (USA). The Leary’s specimen is found closely associated with *Archaeopteris*-like foliage known as *Palaeopteridium*, which has previously been suggested as the foliage of the *Lacoea*-bearing parent plant (Leary, 1980). *Lacoea* has been compared with *Discinities*, one of the several fossil-genera of fructifications described by Leary (1973) (see also Leary & Pfefferkorn, 1977, p. 16). *Discinities* was established by K. Feistmantel (1879) and revised by Bek and Šimůnek (2005). Feistmantel (1879) believed that *Discinities* showed affinity to sphenopsids (see also Wang *et al.* 2004, p. 243). Němejč (1937, 1941) added several fossil species to the genus and found that these strobili appear together with fronds of *Palaeopteridium* and *Rhacopteris*. Several other authors (Němejč, 1937, 1950; Hirmer, 1940; Zimmermann, 1959; Leary & Pfefferkorn, 1977; Remy & Remy, 1977; Meyen, 1987; Gao & Thomas, 1994; Wang & Shen, 2000) referred *Discinities* to noeggerathialean plants (Wang *et al.* 2004). Leary & Pfefferkorn (1977) included a tentative suggestion of a possible evolutionary sequence from an *Archaeopteris*-like form through forms similar to Noeggerathiales and *Lacoea* to *Discinities* (Leary, 1980). Wang (2000) described *Discinities sinensis* as the first noeggerathialean strobilus that has been found as a

petrification from the Permian of Shizuishan, Ningxia (China), yielding information on the structure of the *Discinites* spores. Bek (2001) and Bek and Šimůnek (2005) provided a new knowledge about the morphology and phylogeny of *Discinites* spores based on adpression materials (Wang *et al.* 2004). In both cases, the reproductive structures were found not to be biologically connected to frond, which is why it is not possible to conclude which of the examples represents a clear affinity. Perhaps even more interesting, both *Lacoea* and *Discinites* produce *Calamospora*-type spores (see Leary, 1980; Wang *et al.* 2004, Table 2). This last fact means that these reproductive structures may actually have belonged to the same noeggerathialean parent plant.

In the new noeggerathialean fossil described here, two very small reproductive structures are in close association with the frond fragment (Plate I, 4, 5; Plate II, 1, 2). They have lengths of about 4 to 5 mm and a width of about 2–3 mm. These structures most likely correspond to macrosporangia. One of the ‘macrosporangia’ shows a multicelled gametophyte extending from ruptured spore wall (Plate I, 5, white arrows; Plate II, 2B). Although not organically linked, both structures could belong to parent plant (noeggerathialean frond) described above. However, better preserved and articulated specimens are necessary to confirm the identity of these structures.

6. Biostratigraphic and palaeoecological considerations

A diverse macroflora was found together with *Palaeopteridium andreinii* sp. nov., which is composed of several groups of plants, consisting in a different rate of marattialean ferns (e.g. *Asterotheca*, *Acithea*, *Cyathocarpus*, *Lobatopteris*), sphenopsids (e.g. *Sphenophyllum*, *Annularia*, *Calamites*, *Asterophyllites*, *Calamostachys*), pteridosperms (e.g. *Linopteris*, *Callipteridium*, *Neuropteris*, *Odontopteris*, *Macroneuropteris*, *Sphenopteris*), cordaitopsids (*Cordaites*), and ginkgoopsids (*Dicranophyllum*). The presence of species stratigraphically important such as *Sphenophyllum* cf. *majus* Bronn (cf. *Sphenophyllum emarginatum* (Brongniart) Koenig, *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute & Zoderow, *Neuropteris* cf. *flexuosa* Sternberg (cf. *Neuropteris machadicostai* Teixeira), and *Callipteridium jongmansii* (Bertrand) Wagner confirms the late Westphalian D/Cantabrian age previously established to the Ervedosa flora.

From a palaeoecological point of view, the dominance of taxa of pteridopsids (ferns), sphenopsids, and pteridosperms indicate that the resident floras were essentially composed by mesophytes to hygrophytes, of which grown in clastic wetlands during intervals of moist subhumid climate. This scenario is also based on the absence or rarity of ‘walchian’ conifers and other derived taxa (primarily gymnosperms) typical of dry subhumid and semiarid climate regimes (see in Bashforth *et al.* 2021, Table 1, the segregation of habitats, floral types, and main plant groups that existed in tropical Euramerican Pangaea during the Pennsylvanian, according to seasonality of precipitation and climate).

7. Conclusions

This study describes a new noeggerathialean species, *Palaeopteridium andreinii* sp. nov., based on adpression (compressions-impressions) fossils from the classical Westphalian outcrops of Ervedosa (Gondomar), in northwestern Portugal. This new endemic species is the first record of the fossil-genus *Palaeopteridium* in the Portuguese Carboniferous. Putative

reproductive structures, possibly isolated macrosporangia, found in close association with the frond fragment, might also represent the first record of these structures for this genus.

Palaeopteridium andreinii sp. nov. has palaeoecological affinities with the noeggerathialean genus *Rhacopteris*, with which shared the same clastic wetland environments in Ervedosa, in western Iberia, during intervals of moist subhumid climate in the late Moscovian (Middle Pennsylvanian).

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References

- Archangelsky S (1983) *Nothorhacopteris*, a new generic name for some Carboniferous monopinnate fronds of Gondwanaland (= *Rhacopteris ovata* Auct. and *Pseudorhacopteris* Rigby, 1973). *Review of Palaeobotany and Palynology* 38, 157–72.
- Barbosa C, Correia P, Muchagata J, Domingos R and Sá AA (2022) *Phyllothea douroensis* sp. nov., a new equisetalean fossil-species from the Douro Carboniferous Basin (Upper Pennsylvanian; NW Portugal): palaeobiogeographical, systematic and evolutionary implications. *Biosis: Biological Systems* 3, e001.
- Bashforth AR, Dimichele WA, Eble CF, Falcon-Lang HJ, Looy CV and Lucas SG (2021) The environmental implications of upper Paleozoic plant-fossil assemblages with mixtures of wetland and drought-tolerant taxa in tropical Pangea. *Geobios* 68, 1–45.
- Bek J (2001) *Discinites* spores: An example of unusual variation. First Meeting of the CIMP Spores and Pollen Subcommittee, National University of Ireland, Cork, 2–7 September, 2001, p. 11.
- Bek J and Šimůnek Z (2005) Revision of the cone genus *Discinites* from the Bohemian Carboniferous continental basins of Bohemia. *Palaeontology* 48, 1377–97.
- Boureau Éd and Doubinger J (1975) *Traité de paléobotanique IV (2): Pteridophylla (première partie)*. Paris: Masson et Cie Editeurs, 768 pp.
- Buisine M (1961) *Études géologiques pour l'Atlas de topographie souterraine publiées par le Service Géologique des HBNPC*. I. Flore fossile. 4.° Fasc. — Contribution à l'étude de la flore du terrain houiller. Les Aléthoptéridées du Nord de la France. 2 Vol. Houllères du Bassin du Nord et du Pas-de-Calais. Lille.
- Cleal CJ (1978) Floral biostratigraphy of the upper Silean Pennant Measures of South Wales. *Geological Journal* 13, 165–94.
- Correia P, Barbosa C, Šimůnek Z, Muchagata J and Sá AA (2023a) A new species of *Lesleya* (Spermatopsida) from the Carboniferous of Iberia and its palaeoecological and evolutionary significance. *Historical Biology* 35, 185–96.
- Correia P, Bashforth AR, Šimůnek Z, Cleal CJ, Sá AA and Labandeira CC (2020) The history of herbivory on sphenophytes: a new calamitalean with an insect gall from the Upper Pennsylvanian of Portugal and a review of arthropod herbivory on an ancient lineage. *International Journal of Plant Sciences* 181, 387–418.
- Correia P and Nel A (2023) Increasing the palaeoentomological diversity in Portugal: a new and rare record of Oedischiidae (Orthoptera) from the Pennsylvanian of Douro Basin. *Historical Biology* 35, 838–42.

- Correia P, Nel A, Sá AA, Domingos R, Carneiro A and Flores D** (2014b) A new Palaeodictyoptera from the late carboniferous of Portugal. *Annales de la Société Entomologique de France*, (n.s.) **49**, 398–401.
- Correia P, Pereira S, Cavaleiro M, Correia M, Sá AA and Nel A** (2023c) The first poroblattinid roachoid from the uppermost Carboniferous of Portugal. *Historical Biology* **35**, 242–8.
- Correia P, Pereira S, Šimůnek Z and Cleal CJ** (2023b) *Florinanthus bussacensis* sp. nov., a new cordaitalean cone from the Upper Pennsylvanian of Portugal. *Review of Palaeobotany and Palynology* **316**, 104942.
- Correia P, Sá AA, Murphy JB, Šimůnek Z and Flores D** (2016) *Lesleya* Lesquereux from the Pennsylvanian of the Iberian Massif: part of a dryland megafloora from the Variscan orogen, northwestern Portugal. *Canadian Journal of Earth Sciences* **53**, 883–95.
- Correia P, Schubnel T and Nel A** (2021c) What is the roachoid genus *Eneriblatia* (Dictyoptera: Phylloblattidae) from the Carboniferous of Portugal. *Historical Biology* **33**, 777–82.
- Correia P, Šimůnek Z, Cleal CJ and Sá AA** (2019) *Douropteris alvarezii* gen. nov., sp. nov., a new medullosalean pteridosperm genus from the early Gzhelian (Late Pennsylvanian) of Douro Basin (NW Portugal). *Geological Journal* **54**, 1567–77.
- Correia P, Šimůnek Z, Cleal CJ, Vallois B, Domingos R and Sa AA** (2021b) On a new species of the calamitalean fossil-genus *Annularia* from the Douro Basin (lower Gzhelian; NW Portugal). *Historical Biology* **33**, 258–67.
- Correia P, Šimůnek Z, Pšenička J, Sá AA, Domingos R, Carneiro A and Flores D** (2014a) New paleobotanical data on the Portuguese Pennsylvanian (Douro Carboniferous Basin, NW Portugal). *Comunicações Geológicas* **101**, 409–14.
- Correia P, Šimůnek Z and Sá AA** (2021a) The equisetalean *Iberisetum wegeneri* gen. nov., sp. nov. from the Upper Pennsylvanian of Portugal. *Historical Biology* **33**, 3495–505.
- Correia P, Šimůnek Z, Sá AA and Flores D** (2018) A new Late Pennsylvanian floral assemblage from the Douro Basin, Portugal. *Geological Journal* **53**, 2507–31.
- Ettingshausen C von** (1852) Steinkohlenflora von Stradonitz in Böhmen. *Abhandlungen der kaiserlich-königlichen Geologischen Reichsanstalt* **I**, 1–18.
- Feistmantel K** (1879) *Eine neue Pflanzengattung aus Böhmisches Steinkohlenschichten*. Sitzungsberichte der königl. Böhmisches Gesellschaft der Wissenschaften in Prag, pp. 298–303.
- Gao Z and Thomas BA** (1994) A new species of *Discinites* from the Lower Permian of China. *Review of Palaeobotany and Palynology* **81**, 185–92.
- Heckel PH and Clayton G** (2006) The Carboniferous System. Use of the new official names for the subsystems, series, and stages. *Geologica Acta* **4**, 403–7.
- Hirmer M** (1940) Noeggerathiinae. In *Die Karbon Flora des Saargebietes, Abt. 3. Filicales and Verwood* (eds M Hirmer & P Gothan), pp. 3–44. Palaeontographica, B, Suppl. Band A.
- Kidston R** (1923) Fossil plants of the Carboniferous rocks of Great Britain. *Memoirs of the Geological Survey of Great Britain, Palaeontology II* (Part 3), 200–74, pls. XLVIII–LXVIII.
- Laveine JP** (1977) Report on the Westphalian D. In *Symposium on Carboniferous Stratigraphy (Czechoslovakia – 1973)* (eds VM Holub & RH Wagner), pp. 71–87. Prague: Geological Survey.
- Laveine JP, Coquel R and Loboziak S** (1977) Phylogénie générale des Calliptéridacées (Pteridospermopsida). *Géobios* **10**, 757–848.
- Leary RL** (1973) *Lacoea*, a Lower Pennsylvanian noeggerathalian cone from Illinois. *Review of Palaeobotany and Palynology* **15**, 43–50.
- Leary RL** (1980) *Lacoea* with sporangia and *Calamospora* spores from Rock Island, Illinois. *Review of Palaeobotany and Palynology* **29**, 23–28.
- Leary RL and Pfefferkorn HW** (1977) *An Early Pennsylvanian flora with Megalopteris and Noeggerathiales from West-Central Illinois*, Vol. Circular no. 500. Urbana: Illinois State Geological Survey, Circular 500.
- Leary RL and Trask CB** (1985) *Early Pennsylvanian Paleotopography and Depositional Environments, Rock Island County, Illinois*. Illinois: Illinois State Geological Survey, Guidebook, **18**, pp. 1–42.
- Loureiro JP, Correia P, Nel A and Pinto de Jesus A** (2010) *Lusitaneura covensis* nov. gen. & nov. sp., first Caloneurodea from the Carboniferous of Portugal (Insecta: Pterygota: Panorthoptera). *Annales de la Société Entomologique de France*, (n.s.) **46**, 242–6.
- Meyen SV** (1987) *Fundamentals of Palaeobotany*. London: Chapman and Hall, 432 pp.
- Němejc F** (1937) On *Discinites* K. Feistmantel. *Bulletin International de l'Académie des Sciences de Bohême* **2**, 1–7.
- Němejc F** (1941) Further fructifications of the type *Discinites* in addition to some remarks on the Archaeopteriden of the Middle Bohemian coal basins. *Mitt. Tschechoslowakische Akademie der Wissenschaften* **19**, 1–13.
- Němejc F** (1950) The natural systematic of plants in the light of the present palaeontological documents. *Acta Musei Nationalis Pragae* **6B**, 1–83.
- Novikoff A and Barabasz-Krasny B** (2015) System of embryophytes. In *Modern Plant Systematics* (eds A Novikoff & B Barabasz-Krasny), pp. 23–63. Lviv, Ukraine: Liga-Pres. <https://www.phytomorphology.org/personal-information/system-of-embryophytes/>
- Pfefferkorn HW and Wang J** (2016) Paleocology of Noeggerathiales, an enigmatic, extinct plant group of Carboniferous and Permian times. *Palaeogeography, Palaeoclimatology, Palaeoecology* **448**, 141–50.
- Pinto de Jesus A** (2001) *Génese e evolução da Bacia Carbonífera do Douro (Estefaniano C inferior, NW de Portugal); Um Modelo*. PhD thesis, Department of Geology, Faculty of Sciences, University of Porto. Published thesis.
- Pinto de Jesus A** (2003) *Evolução sedimentar e tectónica da Bacia Carbonífera do Douro (Estefaniano C inferior, NW de Portugal)*. *Caderno do Laboratório Xeolóxico de Laxe Coruña* **28**, 107–25.
- Pšenička J, Correia P, Šimůnek Z, Sá AA, Murphy JB and Flores D** (2017) Revision of *Ilfeldia* and establishment of *Ovulepteris* gen. nov. from the Pennsylvanian of Europe, with a discussion on their concepts. *Review of Palaeobotany and Palynology* **236**, 59–73.
- Pšenička J, Zodrow EL, Mastalerz M and Bek J** (2005) Functional groups of fossil marattiales: chemotaxonomic implications for Pennsylvanian tree ferns and pteridophylls. *International Journal of Coal Geology* **61**, 259–80.
- Read CB** (1946) A Pennsylvanian florule from the Forkston Coal in the Dutch Mountain outlier, Northeastern Pennsylvania. *Professional Paper (U.S. Geological Survey)* **210-B**, 17–27.
- Remy W and Remy R** (1977) *Die Floren des Erdaltertums*. Essen: Verlag Glückauf GmbH, 468 pp.
- Schimper WP** (1869–1874) *Traité de paléontologie végétale ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel*, Vols. 1–3 atlas. Paris: Baillière et fils. 1: 1–740, pls. 1–53, 1869. 2: 1–522, pls. 54–75, 1870; 522–968, pls. 76–90, 1872. 3: IV + 1–896, pls. 91–110, 1874.
- Shute CH and Cleal CJ** (1986) Palaeobotany in museums. *Geological Curator* **4**, 553–9.
- Stur DRJ** (1875) Beiträge zur Kenntnis der Flora der Vorwelt—Die Culm Flora, Teil 1. Die Culm Flora des mährisch-schleischen Dachschiefers. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* **8**, 1–106.
- Taylor TN, Taylor EL and Krings M** (2009) *Paleobotany. The biology and Evolution of Fossil Plants*, second edition. San Diego, CA: Academic Press, 1230 pp.
- Teixeira C** (1941) W. de Lima e a Flora fóssil do Permo-Carbónico português. Fragmentos de uma monografia inédita, coordenados. *Comunicações dos Serviços Geológicos de Portugal* **XXII**, 1–17.
- Teixeira C** (1942a) O Carbónico das margens do Douro e seus caracteres paleontológicos. *Boletim da Sociedade Portuguesa de Ciências Naturais (Lisboa)* **13**(Supl. 3), 121–33.
- Teixeira C** (1942b) Sobre a existência de duas formações carboníferas de idades diferentes nos arredores do Porto. *Boletim da Sociedade Portuguesa de Ciências Naturais (Lisboa)* **13**(Supl. 3), 517–26.
- Teixeira C** (1942c) *Notas sobre a flora westfaliana de alguns afloramentos carboníferos dos arredores do Pôrto*. Porto: Universidade do Porto.
- Teixeira C** (1943) Sur un “Rhacopteris” du Stéphanien Portugais. *Comunicações dos Serviços Geológicos de Portugal* **XXIV**, 1–5, pls. I–VI.
- Teixeira C** (1944) O Antracólítico continental português. (Estratigrafia e Tectónica). PhD thesis, Universidade do Porto. Published thesis.

- Teixeira C** (1945) O Antracólítico continental português. (Estratigrafia e Tectónica). *Boletim da Sociedade Geológica de Portugal (Porto)* **5**, 1–139.
- Teixeira C** (1951) Plantas fósseis do Permo-Carbónico português. II. *Comunicações dos Serviços Geológicos de Portugal XXXII*, 1–43.
- Teixeira C** (1954) *Notas sobre Geologia de Portugal. O Sistema Permo-Carbónico*. Lisboa: Serviços Geológicos de Portugal.
- Wang J** (2000) Discovery of a petrified *Discinites* (Noeggerathiales) cone from the Permian of Shizuishan, Ningxia, China: *D. sinensis* sp. nov. *Chinese Science Bulletin* **45**, 560–6.
- Wang J, Hilton J, Pfefferkorn HW, Wang S, Zhang Y, Bek J, Pšenička J, Seyfullah LJ and Dilcher D** (2021) Ancient noeggerathialean reveals the seed plant sister group diversified alongside the primary seed plant radiation. *PNAS* **118**, e2013442118.
- Wang J, Pfefferkorn HW and Bek J** (2009) *Paratingia wudensis* sp. nov., a whole noeggerathialean plant preserved in an earliest Permian air fall tuff in Inner Mongolia, China. *American Journal of Botany* **96**, 1676–89.
- Wang J and Shen G** (2000) A new species of *Discinites* (Noeggerathiales) from the Upper Permian of Weibei Coalfield, North China. *Review of Palaeobotany and Palynology* **110**, 175–90.
- Wang J, Zhang G, Bek J and Pfefferkorn HW** (2004) A new morphological type of operculate microspore, *Discinisporea* gen. nov., from the Permian petrified Noeggerathialean strobilus *Discinites sinensis* Wang. *Review of Palaeobotany and Palynology* **128**, 229–45.
- Wagner RH** (1966) Palaeobotanical dating of Upper Carboniferous folding phases in N.W. Spain. *Memorias del Instituto Geológico y Minero de España, Tomo LXVI*, 169 pp.
- Wagner RH** (1971) The Westphalian D floras of the Olloniego and Esperanza formations in the Central Asturian Coalfield. *Trabajos de Geología (Oviedo)* **4**, 461–506.
- Wagner RH** (1983) The palaeogeographical and age relationships of the Portuguese Carboniferous floras with those of other parts of the Western Iberian Peninsula. In *The Carboniferous of Portugal* (eds MJ Lemos de Sousa & JT Oliveira), Vol. **29**, pp. 153–77. Lisboa: Memórias dos Serviços Geológicos de Portugal.
- Wagner RH** (1984) Megafloral zones of the Carboniferous. In *Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère* (eds PK Sutherland & WL Manger), Vol. **2**, pp. 109–34. Illinois.
- Wagner RH and Álvarez-Vázquez C** (2010) The Carboniferous floras of the Iberian Peninsula: a synthesis with geological connotations. *Review of Palaeobotany and Palynology* **162**, 239–324.
- Wagner RH and Lemos de Sousa MJ** (1982a) A middle Westphalian flora from the Alvarelos strip near the Serra de Bougado, Santo Tirso, North Portugal. *Comunicações dos Serviços Geológicos de Portugal* **68**, 257–66.
- Wagner RH and Lemos de Sousa MJ** (1982b) Systematics and distribution of *Linopteris florini* Teixeira and *Linopteris gangamopteroides* (De Stefani) Wagner. *Comunicações dos Serviços Geológicos de Portugal* **68**, 247–56.
- Wagner RH and Lemos de Sousa MJ** (1983) The Carboniferous megafloras of Portugal – A revision of identifications and discussion of stratigraphic ages. In *The Carboniferous of Portugal* (eds MJ Lemos de Sousa & JT Oliveira), Vol. **29**, pp. 127–52. Lisboa: Memórias dos Serviços Geológicos de Portugal.
- Yang Y, Wang SJ and Wang J** (2023) Stem anatomy confirms *Tingia unita* Is a Progymnosperm. *Biology* **12**, 494.
- Zimmermann W** (1959) *Die Phylogenie der Pflanzen*, 2nd edition. Stuttgart: Fischer, 777 pp.