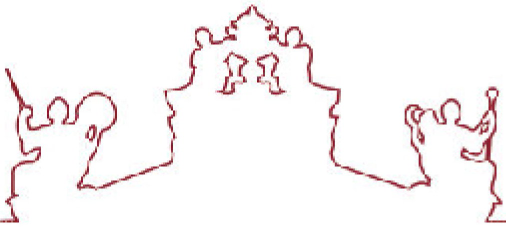

Universidade de Évora - Escola de Ciências e Tecnologia Universidade Nova de Lisboa - Faculdade de Ciências e Tecnologias

Mestrado em Paleontologia

Dissertação

Floristic Endemism of the Douro Carboniferous Basin with Description of New Species

Catarina Teixeira Barbosa

Orientador(es) | Pedro Alexandre Pereira Correia
João Muchagata Madeira Duarte

Évora 2022

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A dissertação foi objeto de apreciação e discussão pública pelo seguinte júri nomeado pelo Diretor da Escola de Ciências e Tecnologia:

Presidente	Carlos Alexandre Ribeiro (Universidade de Évora)
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Évora 2022

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Resumo

A Bacia Carbonífera do Douro (BCD) é uma bacia intramontanhosa formada durante o ciclo varisco, parte do Sulco Carbonífero Dúrico-Beirão (SCDB).

São apresentadas nesta dissertação três novas espécies endémicas da bacia carbonífera do Douro: *Lesleya ceriacoi* sp. nov., *Phyllotheca douroensis* sp. nov., e *Sphenopteris teixeirae* sp. nov. Implicações ecológicas e ambientais destas descobertas são também discutidas.

Lesleya ceriacoi sp. nov. é uma gimnospérmica primitiva (Gzheliano Inferior, Pennsylvánico Superior; NO de Portugal) do Maciço Ibérico da Cadeia Orogénica Varisca redescoberta nas coleções históricas do Herbário do Porto. *L. ceriacoi* sp. nov. tem folhas longas, relativamente estreitas, laceradas e com um ápex serrilhado, características que a distingue das outras 11 espécies do género. Estas são adaptações às condições xéricas de um intervalo de transição de um clima húmido para seco após o fim da glaciação paleozoica no Gzheliano (ca. 304–299 Ma). Estas características xeromórficas são evidências de adaptações a alterações ambientais e climáticas em bacias intramontanhosas em Pangeia Central, como a DCB, e uma indicação que o género era mais diverso do que previamente pensado.

Phyllotheca douroensis sp. nov. é uma pteridófita (Equisetales) do Estefaniano C. Este novo táxon tem afinidades próximas com *Phyllotheca etheridgei* Arber, de Nova Gales do Sul, Austrália (Pérmico, Gondwana). É possível que *P. douroensis* sp. nov. seja produto de evolução convergente entre flora Euramericana e Gondwanica.

Observações preliminares sobre uma nova associação florística na BCD, que inclui uma nova espécie, são também exploradas.

Adicionalmente e como complemento ao trabalho, é discutida a metodologia e as vantagens de moldes de fósseis em latex, em compressões paleobotânicas.

Palavras-chave: Bacia intramontanhosa do Douro, Pennsylvánico, coleções históricas, paleoecologia, evolução convergente, espécies endémicas

Abstract

The Douro Carboniferous Basin (DCB) is an intramontane basin formed during the Variscan Orogen, that is part of the Douro-Beiras Carboniferous Trough (DBCT), a pull-apart basin with a strike slip component.

Here, three new species, endemic to the DCB, are presented: *Lesleya ceriacoi* sp. nov., *Phyllotheca douroensis* sp. nov., and *Sphenopteris teixeirae* sp. nov. The ecological and environmental significance of these findings are also discussed.

Lesleya ceriacoi sp. nov. is a primitive gymnosperm from the DCB (lower Gzhelian, Upper Pennsylvanian; NW Portugal) of the Variscan Iberian Massif rediscovered in the historical collections of the Porto Herbarium. *L. ceriacoi* has long, relatively narrow, broadly dissected (lacerated) leaves with a serrate apex which distinguishes it from the 11 known species of the genus. These are specialized adaptations to drier (xerophytic) conditions during an interval of wet to dry climate transition after the end of the late Paleozoic Gondwana Ice Age in the Gzhelian (ca. 304–299 Ma). These xeromorphic traits are evidence of evolutionary adaptations to environmental and climatic change in intramontane basins like the DCB within central tropical Pangea, and an indication that the genus was more diverse than previously understood.

Phyllotheca douroensis sp. nov. is a new equisetalean from the Early Stephanian C. This new taxon has close affinities with the late Permian Gondwanan *Phyllotheca etheridgei* Arber from New South Wales, Australia. *P. douroensis* sp. nov. is possibly a product of convergent evolution between Euramerican and Gondwanan flora.

Preliminary remarks on a new floral assemblage, which includes a new species, for the DCB are also made.

Additionally, the methodology and advantages of latex moulds in palaeobotanical compressions.

Keywords: intramontane Douro Basin, Pennsylvanian, historical collections, palaeoecology, convergent evolution, endemic species

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Abbreviations

BC – Badajoz-Córdoba shear zone

DCB – Douro Carboniferous Basin

DBCT – Douro-Beiras Carboniferous Trough

MHNC-UP – *Museu de História Natural e Ciência da Universidade do Porto*

TSU – Tectono-sedimentary Units

USA – United States of America

PTFA – Porto-Tomar-Ferreira do Alentejo shear zone.

Introduction

Academic research on the Douro Carboniferous Basin (DCB) started in second half of the 19th century with works by Bernardino A. Gomes (1806–1877), Daniel Sharpe (1806–1865), Carlos Ribeiro (1813–1882) and Charles Bunbury (1809–1886) (Cleal, 2018; Gomes, 1865; Ribeiro, 1858; Ribeiro & Sharpe, 1853; Sharpe, 1849). These early researchers focused mainly on the geology and stratigraphy of the areas neighbouring the city of Oporto, with special attention to economic aspects related to coal deposits in the region, namely the localities of São Pedro da Cova and Pejão (Gomes, 1865; Ribeiro, 1858; Sharpe, 1849).

One of these works in particular — Sharpe (1849) — proves to be quite important for the work present here, since it contains some of the first comments on the plant fossils of the DCB. In it, Sharpe (Fellow of the Geological Society), describes the geology of the DCB; in it, he relays some of the first comments by Charles Bunbury (Fellow of the Royal Society and great friend of Charles Lyell, author of the Principles of Geology) on the palaeobotanical evidence therein (Secord, 2004). While quite brief and with no descriptions or illustrations included, Bunbury makes remarks on the fossils' poor state of preservation but is able to identify three species of ferns: *"Pecopteris Cyathea*", "*Pecopteris muricata*" and "*Neuropteris tenuifolia*".

The main scope of the work presented herein is the study of fossil plants endemic to the DCB, which includes the description of a new species and preliminary descriptions of two others, in addition to a new floral assemblage in the DCB. Additionally, a discussion on the palaeoecology of the region in the light of these new finds is provided. The use of latex moulds as both a preparation method and a tool for taxonomical analysis is also discussed.

The results of this thesis have been compiled from four manuscripts: one published, two in press and one in preparation.

This thesis has 6 parts:

- This introduction — where the objectives of this work are presented alongside a small historical contextualization.
- State of the Art — previous works on the geology (stratigraphy and geomorphology) and palaeontology (palaeobotany, zoology, and environment) of the DCB.
- Materials and Methods — description of the materials and methods used for this study, which includes description of the outcrops and samples studied, and techniques used. An in-depth discussion of latex moulding in Palaeobotany is also presented, adapted from Barbosa & Muchagata (in press), see Annex 4.
- Results — includes the description of 3 new species and a new assemblage.
- Discussion — implications for the palaeoclimate, palaeoecology and palaeoenvironment of the finds discussed previously. This includes data from Barbosa *et al.* (in press) and Correia *et al.* (2022), see Annex 3 and Annex 5, respectively.

- Conclusion — final remarks on the topic, including future work.

State of the Art

Geology

Earth's history is rich in transformation — this is evident in the geological layers and fossil remains all around our planet. Earth's history and evolution have been dominated by the rise and fall of supercontinents, the most renowned of which is Pangea. Animal and plant evolution has seen the rise and fall of species, and geological evidence shows that continents have changed over time as well.

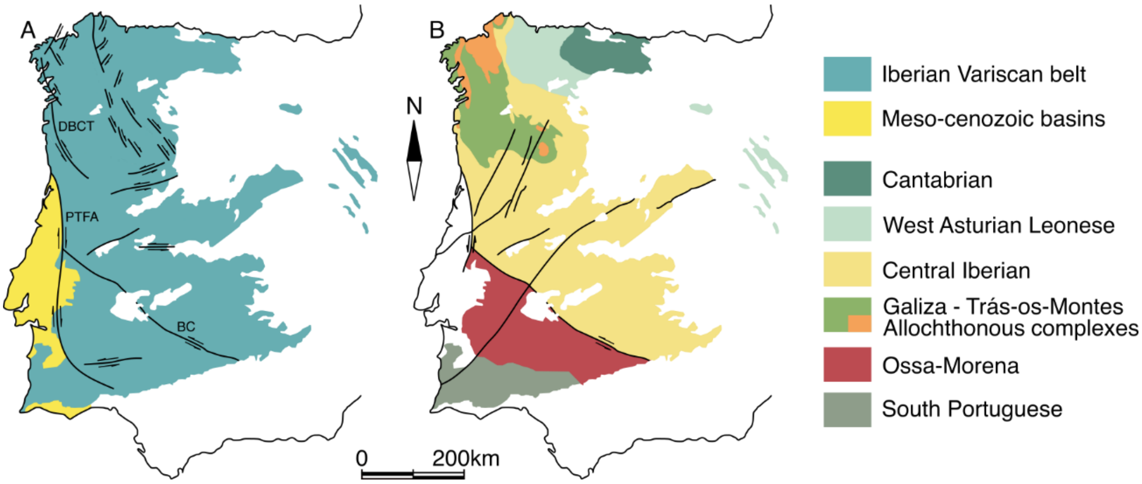

Figure 1 — A: Regional geological setting of the DBCT, within the Variscan Chain. Adapted from Pinto de Jesus (2001). B: Carboniferous Zones of Portugal according to Wagner (1983) and Lemos de Sousa and Wagner (1983a), zonation of the Hesperian massif adapted from Pérez-Estaún *et al.* (2004).

The amalgamation and subsequent drifting of supercontinents, such as Pangea, has had an incredible influence on countless aspects of our planet's history. Roughly 430 Mya, in the Silurian, Laurentia collided with Baltica and Avalonia forming Laurussia/Euramerica (Torsvik *et al.*, 2012). The collision of Gondwana and Laurussia (340Mya, Carboniferous) not only led to the formation of Pangea, but also gave rise to the Appalachian and Variscan chains (Correia & Murphy, 2020; Gutiérrez-Alonso *et al.*, 2008; Murphy & Nance, 2008). Later, Kazakhstania, Siberia/Angara, and other terranes collided with Baltica to form Laurasia (Torsvik *et al.*, 2012).

Located in the Central Iberian Zone of the Variscan Chain, the Douro-Beiras Carboniferous Trough (DBCT) (see Figure 1) is a pull-apart basin with a strike slip component (Pinto De Jesus, 2001, 2003; Pinto De Jesus & Lemos de Sousa, 2003). The DBCT is approximately 85km long, running NW-SE from São Pedro Fins (North-eastern Oporto) to Janarde (Eastern Arouca) (Correia, 2016). Within it, there are many well-documented Carboniferous deposits, from the Middle Bashkirian-Moscovian to early Gzhelian, including the Douro Carboniferous Basin (DCB) (see Figure 1 and Figure 2), an intramontane basin formed during the Variscan Orogen (Wagner, 2003; Cleal, 2008; Wagner & Álvarez-Vázquez, 2010a; Bashforth *et al.*, 2011; Correia *et al.*, 2016).

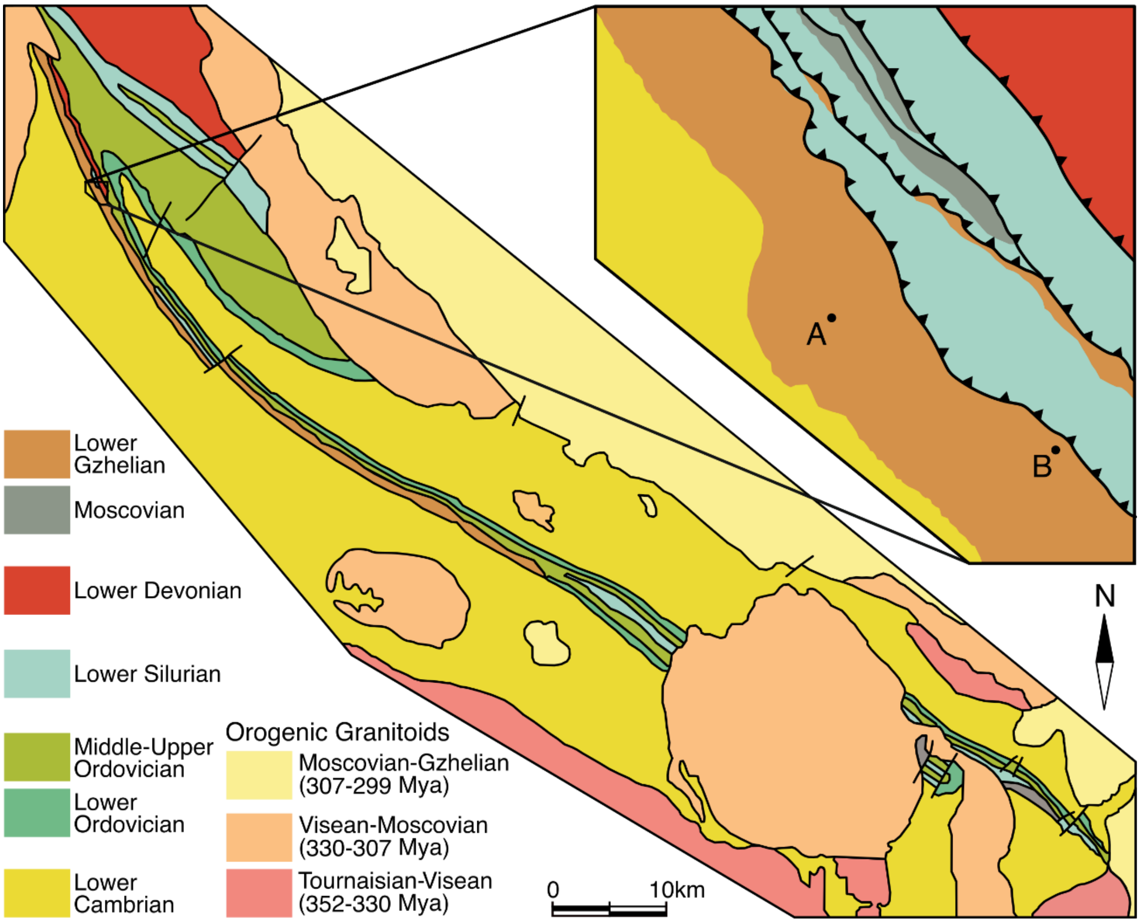

Figure 2 — Geological map of the geology of the DCB. Adapted from Pinto de Jesus (2001) and Correia (2016). A: location of outcrop of *Phyllotheca douroensis* sp. nov. (41°09'44.65"N, 08°30'25.73"W), see Figure 8. B: location of outcrop of new floral assemblage (41°09'35.8"N, 8°30'05.2"W), see Figure 9.

The DCB is located in North-western Portugal (Lemos de Sousa & Wagner, 1983a; Pinto De Jesus, 2001, 2003), with its lower levels lying unconformably on Early Cambrian strata, while the upper levels are cut by a reverse fault that caused the Silurian-Devonian formations of the Valongo Anticline to rise above the Basin (Correia *et al.*, 2016; Domingos *et al.*, 1983; Lemos de Sousa, 1984; Pinto De Jesus, 2001, 2003; Wagner *et al.*, 1984). The strata are oriented NW-SE, with inclinations of 45-90° (Correia, 2016).

The DCB consists of eight tectono-sedimentary units (TSU): A1, B1, C1, and D1, and their respective lateral facies variations (A2, B2, C2, D2) (Figure 3) (Pinto De Jesus, 2001, 2003; Lemos de Sousa, Marques, *et al.*, 2010; Lemos de Sousa, Rodrigues, *et al.*, 2010; Correia, 2016). These units mostly alternate between phytogenic siliciclastic deposits and fluvial deposits (Correia, 2016). TSUs A1/2 and C1/2 consist of fluvial/alluvial deposits, with units A1/2 being mainly composed of breccia and units C1/2 consisting of interbedded conglomerates, sandstones and siltstones. TSUs B1/2 and D1/2 are characterized by alternating beds of coal with shale and sandstone (in the case of B1/2) or siltstone, mudstone and conglomerate (in the case of D1/2).

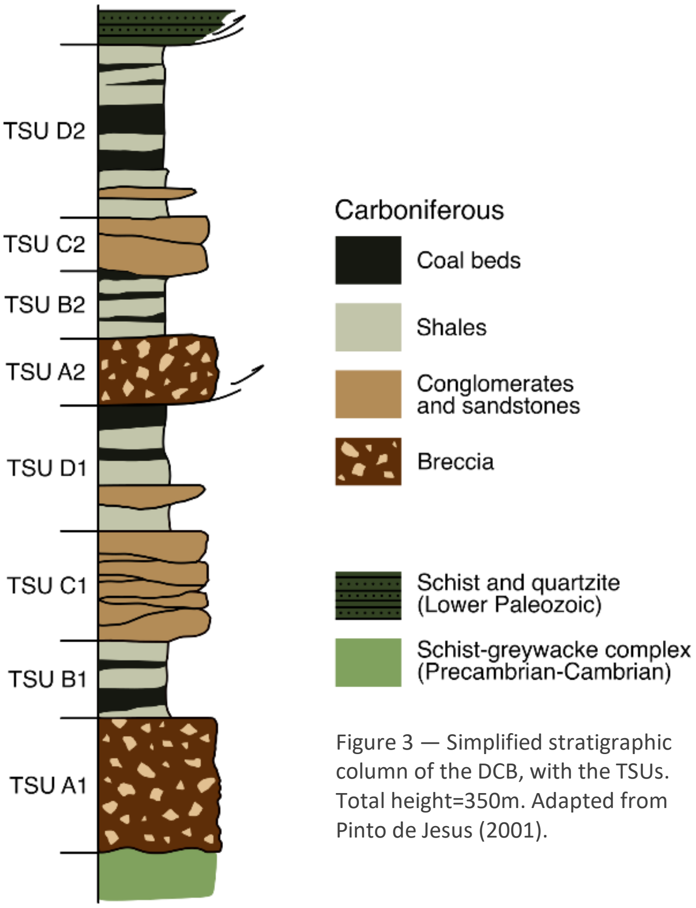

Figure 3 — Simplified stratigraphic column of the DCB, with the TSUs. Total height=350m. Adapted from Pinto de Jesus (2001).

While the Basin has been thoroughly studied since the 19th century, the first biostratigraphic studies did not come until Teixeira (1944), which were then expanded upon by other authors (Teixeira, 1944, 1954; Wagner, 1966; Corsin & Lemos de Sousa, 1972; Teixeira & Pais, 1976; Lemos de Sousa, 1977, 1978). These studies put the age of the DCB at the upper Kasimovian to lower Gzhelian (around 303 Mya). Additional studies in the fields of Palynology (Fernandes *et al.*, 1997) and palaeozoology (Eagar, 1983), have helped narrow down the age of the DCB deposits the early Gzhelian (Lemos de Sousa, Marques, *et al.*, 2010; Lemos de Sousa & Wagner, 1983b; Pinto De Jesus, 2001).

Flora

As mentioned before, the study of the Carboniferous strata of the Douro Basin began for practical reasons (coal mining), with palaeobotanical research as an afterthought. However, in the 19th century, more focus was given to the fossilized floristic elements present in the DCB, with works by Wilhelm Ludwig von Eschwege (1777–1855), Bernardino A. Gomes, Carlos Ribeiro, and Wenceslau de Lima (1858–1919). These earlier studies were then reviewed by Carríngton da Costa (Carríngton da Costa, 1931, 1938), Teixeira (i.e. Teixeira, 1944), and more recently by Pinto de Jesus (2001, 2003). Additionally, the works by Robert Wagner (1927–2018) and Manuel Lemos de Sousa (1937–present), such as Lemos de Sousa & Wagner(1983a, 1983b), Wagner (1983) and Wagner & Lemos de Sousa (1983), are a solid foundation on which the current knowledge and understanding of the topic are built upon. These works, part of a volume on the Carboniferous of Portugal by the *Serviços Geológicos de Portugal*, contain both a synthesis of previous knowledge and a review of the flora, in addition to data on stratigraphy, palaeoenvironment and structural geology. In recent years, there has been a renewed interest in the DCB from researchers like palaeobotanist Pedro Correia, whose work as a taxonomist has revealed new insights on its palaeodiversity, palaeoenvironments and palaeoclimate of this intramontane basin (see Correia, 2016; Correia & Murphy, 2020).

A current review of the DCB flora, including the three new species described here, provides 125 species from 57 genera:

Lycopodiophyta

Lycopsida

Cyperites sp. (= *Lepidophyllum*)
Lepidodendron aculeatum Sternberg
Lepidophylloides sp.
Lepidostrobophyllum cf. *hastatum* (Lesquereux) Chaloner
Sigillaria brardii Brongniart
Sigillariostrobus serreatus Teixeira

Polypodiophyta

Sphenopsida:

Sphenophyllales:

Lilpopia raciborskii (Lilpop) Connor & Schaarschimdt (= *Sphenophyllum* cf. *thonii* var. *minor* Sterzel)
Sphenophyllostachys sp.
Sphenophyllum alatifolium Renault
Sphenophyllum angustifolium Germar
Sphenophyllum costae Sterzel
Sphenophyllum longifolium (Germar) Geinitz
Sphenophyllum oblongifolium (Germar & Kaulfuss) Unger

Equisetales:

Annularia carinata von Gubier
Annularia cf. *radiata* Brongniart
Annularia noronhai Correia, Šimůnek, Cleal et Sá
Annularia paisii Correia, Bashforth, Šimůnek, Cleal, Sá et Labandeira
Annularia sphenophylloides (Zenker) von Gutbier
Annularia spicata von Gutbier
Annularia stellata (von Schlotheim) Wood
Asterophyllites equisetiformis (von Schlotheim) Brongniart
Asterophyllites longifolius (Sternberg) Brongniart
Asterophyllites sp.
Calamites carinatus Sternberg
Calamites cistii Brongniart
Calamites insignis Sauver
Calamites schuetzeiformis forma *waldenburgensis* Kidston
Calamites suckowii Brongniart

Calamostachys calathifera Sterzel

Calamostachys grandis (Zeiller) Jongmans

Calamostachys tuberculata Sternberg

Equisetites zeaformis Andrae

Iberisetum wegeneri Correia, Šimůnek et Sá

Macrostachya carinata (Germar) Zeiller

Stellotheca robusta (Feistmantel) Surange Prakash

Gymnospermophyta

Cycadopsida

Medullosales

?Cyclopteridaceae

Douropteris alvarezii Correia, Šimůnek, Cleal et Sá

Pteridospermopsida/Cycadopsida

Lesleya ceriacoi sp. nov. Correia, Barbosa, Šimůnek, Muchagata et Sá

Lesleya iberiensis Correia, Sá, Murphy, Šimůnek et Flores

Monilophyta

Pteridopsida (Polypodiopsida):

Coenopteridales:

Alloiopteris pecopteroides Gothan

Alloiopteris sp.

Alloiopteris (Sphenopteris?) teixeirae Correia, thesis

Desmopteris cf. *longifolia* Presl

Desmopteris sp.

Nemejcopteris feminaeformis (von Schlotheim) Barthel

Marattiales:

Acitheca murphyi Correia, Šimůnek, Sá et Flores

Acitheca polymorpha (Brongniart) Wagner

Germera mendescorreae (Teixeira) Brousmiche

Lobapteris corsini Wagner

Lobapteris cf. *lamuriana* Heer

Lobapteris cf. *miltoni* (Artis) Wagner

Lobapteris viannae (Teixeira) Wagner

Pecopteris arborescens von Schlotheim

Pecopteris candolleana Brongniart

Pecopteris cf. *ameromii* Stockmans & Willière

Pecopteris cf. *hemitelioides* Brongniart

Pecopteris cf. *melendezii* Wagner

Pecopteris cf. *opulenta* Corsin

Pecopteris cf. *paleacea* Zeiller

Pecopteris cyathea (von Schlotheim) Brongniart

Pecopteris daubreei Zeiller

Pecopteris densifolia Göppert

Pecopteris gruneri Zeiller

Pecopteris limae Teixeira

Pecopteris monyi Zeiller

Pecopteris puertollanensis Wagner

Pecopteris sp.

Pecopteris unita Brongniart

Filicales:

Oligocarpia gutbieri Göppert

Oligocarpia leptophylla (Bunbury) Grauvogel-Stamm & Doubinger

Oligocarpia sp.

Order uncertain:

Gondomaria discreta (Weiss) Wagner & Lemos de Sousa

Spiropteris sp.

Stellatheca sp.

Tracheophyta

Spermatopsida:

Order uncertain

aff. *Taeniopteris multinervis* Weiss

Progymnospermopsida:

Noeggerathiales:

Rhacopteris gomesiana (Heer) Teixeira

Pteridospermopsida:

Lagenostomales:

Heterangium sp.

Trigonocarpales (Medullosales):

Alethopteris zeilleri Ragot

Callipteridium (*Eucallipteridium*) *gigas* (von Gutbier) Weiss

Callipteridium (*Eucallipteridium*) *zeilleri* Wagner

Callipteridium jongmansi Bertrand

Cyclopteris sp.

Lescuropteris genuina (Grand'Eury) Remy

Linopteris neuropteroides (von Gutbier) Potonié

Neuropteris cordata Brongniart

Neuropteris crenulata Brongniart

Neuropteris gallica Zeiller

Neuropteris ovata var. *pseudovata* Gothan & Sze

Neuropteris sp.

Neuropteris zeilleri Lima

Odontopteris brardi Brongniart

Odontopteris schlotheimii Brongniart

Reticulopteris germari (Giebel) Gothan

Callistophytales:

Dicksoniites pluekenetii (von Schlotheim) Sterzel

Eusphenopteris cf. *sauveri* Crepin

Eusphenopteris rotundiloba (Němejc) Van Amerom

Pseudomariopteris cf. *busqueti* (Zeiller) Danzé-Corsin

Pseudomariopteris cordato-ovata (Weiss) Gillespie, Clendening et Pfefferkorn

Pseudomariopteris ribeyroni (Zeiller) Danzé-Corsin

(= *Pseudomariopteris corsini* (Teixeira) Wagner)

Telangiospsis sp.

Telangium sp.

Order uncertain

aff. *Rhodeopteridium subpetiolatum* Potonié

Pinophyta

Cordaitopsida (Spermatopsida):

Cordaitales (Cordaitanthales):

Botryoconus (*Cordaianthus*?) *femina* Grand'Eury

Cordaites foliolatus Grand'Eury

Cordaites sp.

Litostrobus (*Cordaianthus*?) *iowensis* Mamay

Coniferopsida (Pinopsida):

Voltziales:

Culmitzschia (*Lebachia*) *parvifolia* Florin

Ernestiodendron filiciforme (von Schlotheim pars) Florin

aff. *Culmitzschia* (*Lebachia*) *frondosa* var. *zeilleri* Florin

Ginkgophyta

Ginkgoopsida:

Order uncertain:

Dicranophyllum gallicum Grand'Eury

Dicranophyllum lusitanicum (Heer) Lima

Incertae sedis (Pteridophylla = Pteridospermopsida or Pteridopsida):

Aphlebia sp.
Ilfedia gregoriensis Pšenička, Correia, Šimůnek, Murphy et Flores
Ilfedia (Taeniopteris) jejunata Remy

(Pteridospermopsida/Cycadopsida)

Sphenopteris tenuis Schenk
Sphenopteris cf. *chaerophylloides* Brongniart
Sphenopteris cf. *cremeriana* Potonié
Sphenopteris cf. *germanica* Weiss
Sphenopteris cf. *lenis* Zeiller
Sphenopteris fayolli Zeiller
Sphenopteris matheti Zeiller
Sphenopteris sp.
Taeniopteris bertrandiana Teixeira
Taeniopteris jejunata Grand'Eury

Fauna

Research on the fauna of the DCB has been conducted since the late 1930s and saw a resurgence in the 2010s. The first studies, primarily carried out by Carlos Teixeira and Daniel Laurentiaux (Laurentiaux & Teixeira, 1948, 1950, 1958b, 1958a; Teixeira, 1939b, 1941, 1946), reported the first insects of the DCB: 11 Dictyopterans, three Palaeodictyopterans, and one Caloneurodean. Nearly 50 years later, Loureiro *et al.* (2010) report the first Caloneurodean for the DCB. Another Palaeodictyopteran and notably the first arachnid of the Basin, are reported in Correia, Murphy, *et al.* (2013) and Correia, Nel, *et al.* (2013), respectively. Recently, Correia *et al.* (2019) reappraised the genus *Eneriblatta.* Additional studies report the presence of five non-marine/limnic bivalves (Eagar, 1983; Fonseca, 1959; Teixeira, 1944; Teixeira & Fonseca, 1953) and an euryptid (Arthropoda: Chelicerata) (Correia, Nel, *et al.*, 2013).

A current review of the DCB palaeofauna provides 27 different species from 15 genera, with the majority belonging to the class Insecta (Arthropoda: Hexapoda).

Mollusca

Bivalvia
    Pterioida
        Anthraconaia cf. *lusitanica* Teixeira 1944
        Anthraconaia? *altissima* Eagar 1983
        Anthraconaia? *prolifera* Waterlot

Arthropoda

Branchiopoda

Spinicaudata

- Euestheridae
  - *Estheria (Euestheria) cebennensis* Grand'Eury, *nomen praeoccupatum*
  - *Estheria carneiroi* Teixeira, *nomen praeoccupatum*

Chelicerata

Arachnida

- Trigonotarbida
  - *Aphantomartus pustulatus* Scudder
- Eurypterida
  - cf. *Adelophthalmus* sp.

Hexapoda

Insecta

- Palaeodictyoptera
  - ?Dictyoneuridae
    - *Stenodictya lusitanica* Correia, Nel, Sá, Domingos, Carneiro et Flores
  - Eugereonidae
    - *Valdeania medeirosi* Teixeira
  - Lithomanteidae
    - *Lusiella fariai* Laurentiaux & Teixeira
  - Spilapteridae
    - *Homaloneura ribeiroi* Teixeira
- Caloneurodea
  - *Lusitaneura covensis* Loureiro, Correia et Nel
- Dictyoptera
  - *Lusitanomylacris pruvosti* Teixeira
  - *Stephanomylacris duriensis* Teixeira
  - *Stephanomylacris zbyszewskii* Teixeira
  - Phyloblattidae
    - *Eneriblatta* sp.
    - *Eneriblatta elegantissima* Teixeira
    - *Eneriblatta insignis* Teixeira
    - *Eneriblatta lusitanica* Teixeira
    - *Eneriblatta valonguesis* Teixeira

Phyloblatta carringtoni Teixeira (=?*Phyloblatta brongniarti* Handlirsch)
Phyloblatta fonsecai Teixeira
Phyloblatta portuensis Teixeira
Phyloblatta rosasi Teixeira

Palaeoenvironment

A general rise in sea level due to the waning of the late Palaeozoic Ice Age in southern Gondwana led to significant climatic and environmental changes in the central tropical regions of Pangea, including drops in humidity within central Pangea in the Gzhelian to early Permian (303,7–272,95Mya) (Cecil, 2013; Correia & Murphy, 2020; DiMichele *et al.*, 2010; Fielding *et al.*, 2008; Isbell *et al.*, 2003; Wagner, 2003; Wagner & Lyons, 1997). These greenhouse conditions resulted in significant widespread aridification that occurred in the interior of the Pangean supercontinent during its final amalgamation. As a result, parts of the tropical regions of western and central Pangea became drier and less humid during that time interval (Bashforth *et al.*, 2021; Cecil, 2013; Correia & Murphy, 2020; Wagner, 2003; Wagner & Lyons, 1997).

During the Gzhelian (303,7–298,9 Mya), the intramontane Douro Basin was characterized by a transition from subhumid to a dry tropical climate (Correia *et al.*, 2016, 2018; Correia & Murphy, 2020). A subhumid climate (Am or As/Aw according to the Köppen Climate Classification (Köppen, 2011)) is characterised by rainfall exceeding potential evapotranspiration for five months or more (ter Kuile, 1987) and a dry season no longer than 3 months (Verheye, 2009). These climates are usually characterized by open forest and savannah vegetation (Verheye, 2009). According to Holdridge (1967) and Sanchez-Azofeifa *et al.* (2013), a tropical dry climate has several months of little to no precipitation, resulting in two well-defined seasons — wet and dry (Sanchez-Azofeifa *et al.*, 2013). The dry season, which lasts from 3 to 7 months, sees an 85-100% percentage of deciduousness (seasonal leaf shedding) controlled mostly by soil moisture (Janzen, 1983 in Sanchez-Azofeifa *et al.*, 2013).

The presence of euryptids, lacustrine bivalves and terrestrial faunal elements, as well as sedimentological evidence, points towards the interface of a freshwater fluviolacustrine environment (Correia, Nel, *et al.*, 2013; Eagar, 1983; Pinto De Jesus, 2003).

Material and Methods

Fossil localities and fossil sampling

The new fossil specimens studied were collected in new lower Gzhelian (Upper Pennsylvanian) outcrops. The field work on these localities was carried out in 2004 and 2010. The fossil sites are 2 outcrops, with a total of 18 specimens, 8 of which are type specimens (3 holotypes and 5 paratypes).

Methodology and sample preparation

Some of the new fossil specimens described in this work were carefully prepared mechanically using chisels and hammers. Additionally, latex moulds were made for the holotype and paratypes of *Lesleya ceriacoi* sp. nov. (MHNCUP/PAB-29). Due its importance, latex moulding is discussed in more detail next.

Latex Moulds in Palaeontology and Palaeobotany

A thorough discussion of moulding (history and methodology) can be found in Barbosa & Muchagata (in press), from which this section was adapted. Latex was initially used in Palaeontology in the first half of the 20th century. Since its debut in 1938 (von Fuehrer, 1938), this replication method has been used in a wide range of fields, changing very little over the years (Green, 2001).

Moulds made for research require a high level of detail, whereas replicas made for teaching, whether in a classroom or as an exhibit, can be less detailed but must be more durable/resilient to external factors (M. B. Goodwin & Chaney, 1994; Vieira *et al.*, 2022). Here we use “mould” to mean a copy of the internal or external relief of the specimen, while a cast or replica are copies of the fossil itself. Another distinction to be made is between moulds (negatives) created with the goal of casting a positive reproduction of a fossil and moulds that are the finished product. The latter is the topic of this paper because it is the most relevant to the study of palaeobotanical compressions/impressions.

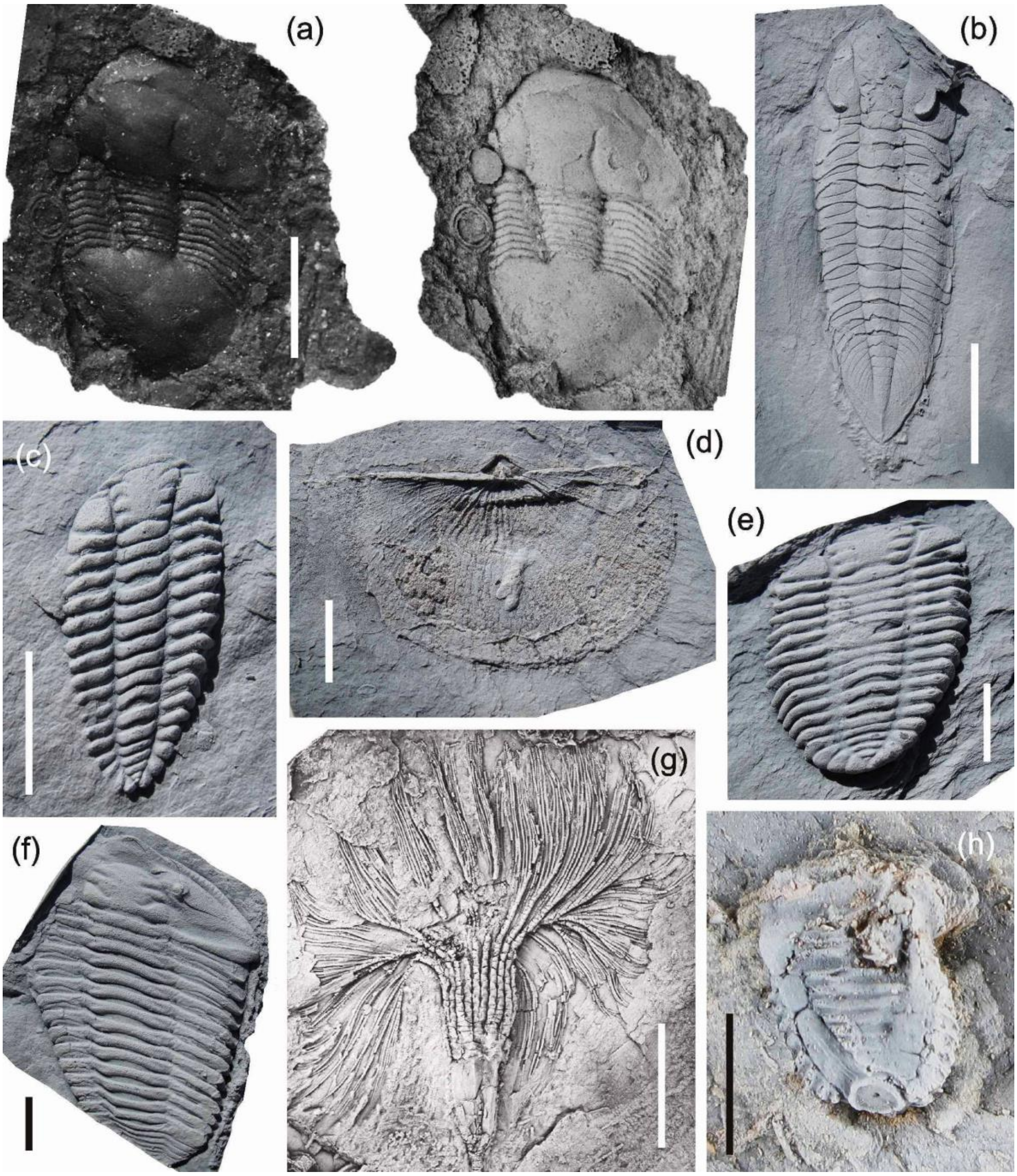

Figure 4 — Examples of latex casts of trilobite, crinoid and brachiopod fossils from the Ordovician and Devonian of Portugal and Czech Republic. (a) trilobite *Cekovia salteri*, before (left) and after (right) whitening (Zahořany Formation, middle Berounian (Upper Ordovician), Czech Republic, figured in Pereira (2017, figs 8-D)); (b) trilobite *Zeliszkella* cf. *toledana* (Middle Ordovician of Gondomar, NW Portugal); (c) and (e) trilobite *Placoparia* cf. *tournemini* (middle Ordovician of Gondomar); (d) Orthid brachiopod (Middle Ordovician of Gondomar); (f) trilobite *Neseuretus* cf. *tristani* (Middle Ordovician of Gondomar); (g) crinoid *Delgadocrinus oportovinum* (Middle Ordovician of the Valongo area, NW Portugal, figured by Domingos *et al.*, 2020); (h) crinoid *Tiaracrinus quadrifrons* (Early–Middle Devonian of S. Pedro da Cova in the Valongo Anticline, NW Portugal). Scale bars: 5 mm (h); 10 mm (a, c–f); 20 mm (b, g). Figure by Pedro Correia, originally from Barbosa & Muchagata (in press).

Even though latex rubber is typically used in research to make casts/moulds of smaller invertebrate fossils, such as trilobites, brachiopods, crinoids, insects, and so on (Ausich *et al.*, 2007; Pereira, 2017; Correia *et al.*, 2019; R. Domingos *et al.*, 2020; Angiolini *et al.*, 2003) (see Figure 4 and Figure 5c-f), it can also be used to make casts/moulds of vertebrates (Garner, 1953; Leite *et al.*, 2007; Swanson & Carlson, 2002) or even plants (Boersma, 1985; Correia *et al.*, 2016; Taylor *et al.*, 2009) (Figure 5a and b).

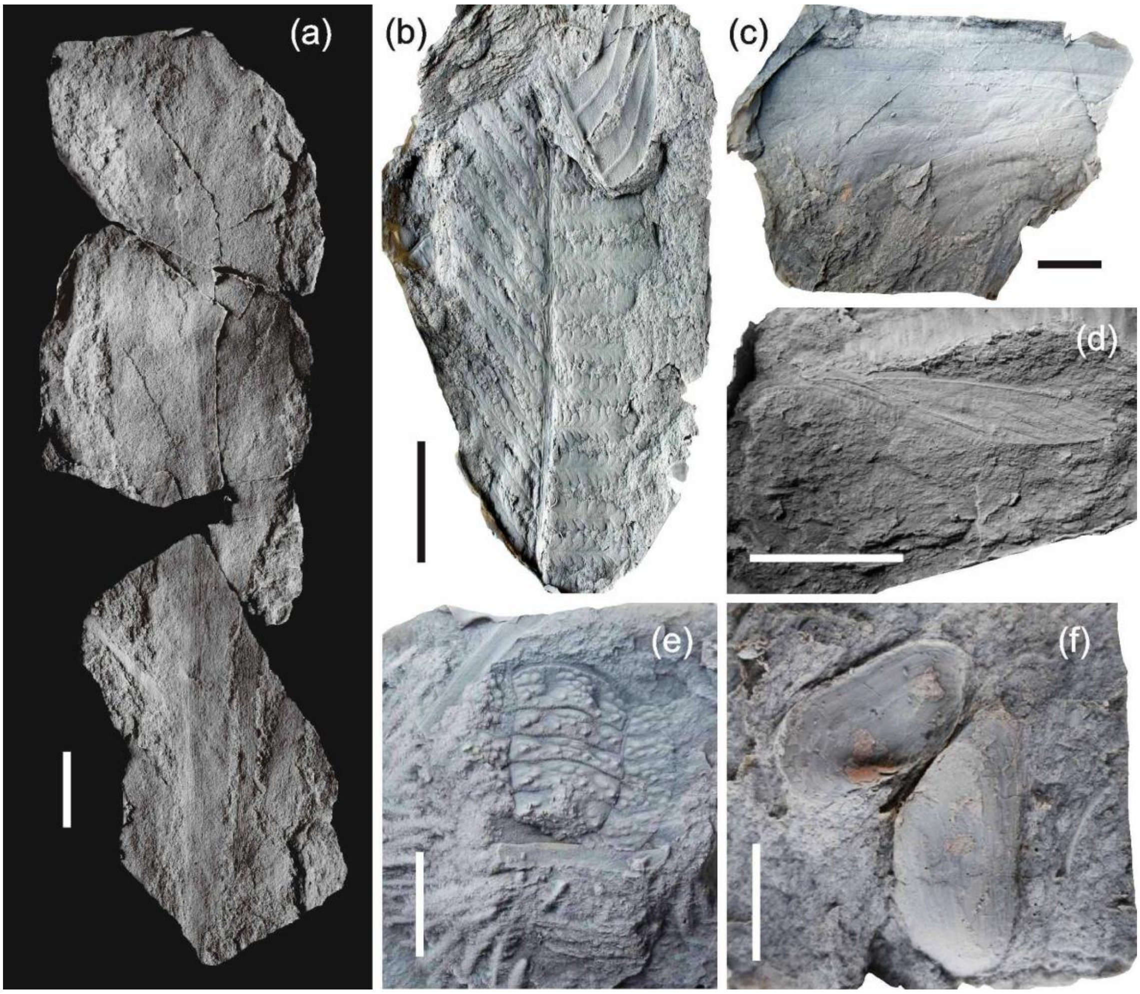

Figure 5 — Examples of latex casts of plant, arthropod and bivalve fossils from S. Pedro da Cova, Douro Carboniferous Basin (lower Gzhelian, Upper Pennsylvanian; NW Portugal). (a) *Lesleya iberiensis* (cycad-like gymnosperm); (b) *Sphenopteris* sp. (pteridosperm); (c) *Stenodyctia lusitanica* (insect); (d) *Lusitaneura covensis* (insect); (e) *Aphantomartus pustulatus* (spider-like arthropod); (f) *Anthraconaia*-like limnic bivalves. Scale bars: 5 mm (e); 10 mm (c, d, and f); 20 mm (a, b). Figure by Pedro Correia, adapted from Barbosa & Muchagata (in press).

According to Green (2001), there are several disadvantages to using latex, such as the mould's inevitable shrinkage with time that might lead to distortion (Monge & Mann, 2005). According to Heaton (1980), the composition of the latex influences the mould's "shelf life". High-ammonia latex causes moulds to lose their elasticity and become brittle, and finer features will deteriorate over time; higher-quality latex is far more durable and can last up to 15 years without degrading (Heaton, 1980). Ideally, the mould should be photographed (or 3D modelled using photogrammetric techniques) immediately. The photographic or 3D material prevents future unnecessary interventions on the fossil, which could, overtime, damage the specimen.

Additionally, latex moulding does not emit toxic fumes and can be readily cleaned off the instruments used to do the coating, since latex simply peels off after drying (Green, 2001). Finally, latex is also less expensive than silicone, has higher tensile strength, and has a longer shelf life when stored in an airtight container (Stanley, 1975).

Latex in Palaeobotany

Even though latex moulds have been used in Palaeontology for over 80 years, they continue to provide valuable information to scholars worldwide to this day. Next, two different applications of this material in the field of Palaeobotany are explored.

The first, and most common application of the technique — already prevalent in other disciplines — is to emphasize anatomical features of specimens, via moulds and/or replicas. Although latex moulds have been used in Palaeobotany before — such as Boersma (1985) — and especially in the study of cuticles, Correia *et al.* (2016) were the first to employ them in Portuguese Palaeobotany (Figure 5a) . The whitened latex mould provided additional contrast, helping to emphasize anatomical details. As such, the use of latex moulding to analyse plant impressions can be useful for reproducing the original morphology of an external mould and/or for studying internal "hidden" structures.

The second is a process of preparation dubbed latex peeling (Barbosa & Muchagata, in press). During the preparation of MHNCUP/PAB-29 (which contains the type specimens of *Lesleya ceriacoi* sp. nov.), the intention was to use latex moulding to produce images for taxonomic studies. When the moulds were peeled from the fossil, they removed a large amount of oxides and matrix particles. As a result, the moulds were no longer useable (Figure 6c), but the fossil was remarkably clean (compare Figure 6a and b), with no evident harm to the specimen itself.

The usage of latex is not recommended in every single case as the moulding might compromise the fossil and future cuticular analysis (Stankiewicz *et al.*, 1998; Zodrow *et al.*, 2000); however, since this study focuses primarily on the general morphology of the leaf, the latex casts highlight characters that would otherwise be very hard to perceive , such as venation and leaf margins (Correia *et al.*, 2016).

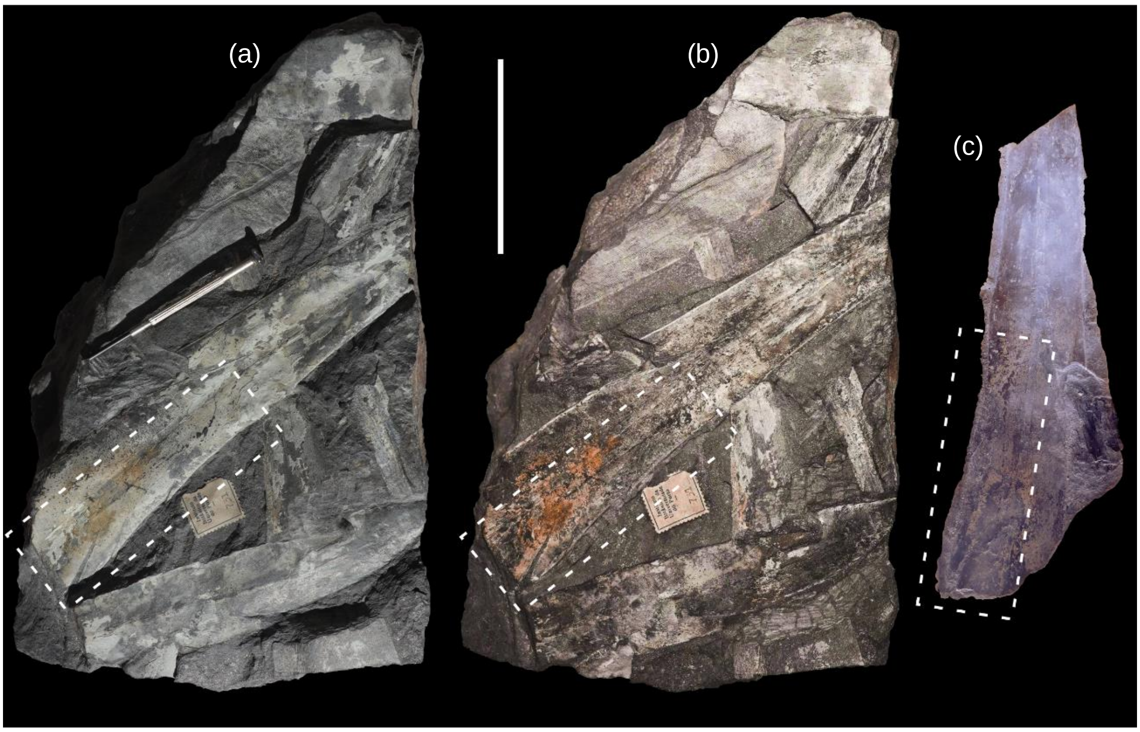

Figure 6 — Stages of preparation of specimen MHNCUP/PAB-29. (a) Fossil before preparation (superior view). (b) Fossil after mechanical preparation and latex peel (superior view). (c) Latex mould of the holotype. Note the light grey material that was transferred to the mould (white rectangle). Scale bar is 10cm.

Creating Latex Moulds

There are numerous factors to consider while deciding whether to cast a mould of a specimen. The first is whether it can be done without causing irreversible damage to the specimen, which would obviously be counterproductive. Time limitations should also be considered, as the moulding process cannot be hastened without resulting in a poor final product, wasting both time and resources. Making moulds is time-consuming and costly, so it is always worth considering whether the information gained from the process is relevant. The methodology presented here will focus on latex moulds made for the purpose of taxonomic studies, in other words, the moulds must be very detailed and well photographed but do not have to be particularly long-lasting.

It should be taken into consideration that, when the fossil is delicate or the matrix it is in is not consolidated there are several consolidating techniques (such as using diluted resins) have to be made before attempting a latex cast, since they penetrate the fossil and matrix pores creating a surface coating and protecting the fossil (Goodwin & Chaney, 1994).

The first step is to make sure the fossil is clean (Figure 7a); depending on the type of matrix the specimen is in and the level of preservation, this can be done in a variety of methods. To clean the fossil, an initial cast – a latex peel – can be made, as previously indicated. However, we should stress that specimen cleaning can be accomplished simply by washing the specimen, or by using mechanical or chemical techniques, before considering latex as a viable option.

The next step is to prepare the latex mixture (Figure 7b). The liquid rubber is transferred into a container and mixed with a few drops of Chinese ink, which is used to colour the translucent rubber to improve contrast (Green, 2001). Raw latex is slightly translucent and white/yellowish in colour, which makes it difficult to photograph: the transparency obscures intricacies and surface topography of the mould, and the colour reflects too much light, reducing contrast and obscuring details (Heaton, 1980). According to Heaton (1980), colours like red, orange, or grey generate the best contrast, yet grey is not advised because the perfect shade is difficult to mix. Green (2001), on the other hand, recommends merely using “either a drop of Indian ink or graphite powder,” which is the most frequent method nowadays. The ideal tone, according to Parsley *et al.* (2018), is dark and even.

Following the preparation of the mixture, it is applied in a thin layer to the surface of the fossil, making sure that no air bubbles form, as these would compromise the quality of the final mould. It is common practice to humidify the surface of the specimen with soapy water for optimum surface contact, which prevents the formation of air bubbles (Baird, 1955). In this case, the latex was applied using a standard glass rod (Figure 7c). A pressurized air hose is an alternative means of spreading (Heaton, 1980). The specimen is then dried in a dehydrator or oven at a temperature of 70-80°C (Figure 7d). It is possible for the mould to dry naturally, but this will take longer.

Repeat the process of spreading a layer of latex and curing it (in an oven or at room temperature) until the mould is adequately thick (Figure 7e). The layers that follow the first can be poured with less care because they just offer support and volume and have no bearing on the mould's surface details.

As demonstrated by Saleh *et al.* (2020), the proper removal of the latex cast is critical. The authors identify a specimen in which the incorrect/incomplete removal of the latex after numerous moulds resulted in mould remnants mimicking morphological structures, which were mistakenly identified as soft tissue. This case emphasizes the need of knowing a specimen's history as well as the dangers of subjecting a fossil to too many interventions.

It is essential to keep track of a specimen's history inside an institution, not just for scholars who might be interested in researching it, but also for the specimen's preservation (Saleh *et al.*, 2020). Attaching a full record of the preparation processes and research methods employed on a fossil should allow researchers to get a better picture of the fossil and avoid unnecessary harm.

It is conventional to glue – using latex or diluted resins like Paraloid B-72 – the mould to a piece of cardboard once it has been removed to give it additional structural stability and make it easier to handle (Figure 7f).

The next step is to whiten the mould, which increases contrast and highlights details, making the specimen easier to photograph (Parsley *et al.*, 2018). There are several approaches to this, here two are discussed. Virtual whitening is also an option, and it has a lot of potential for larger specimens (Hammer & Spocova, 2013; Parsley *et al.*, 2018).

The most frequent approach to whiten fossils is using a dry application of ammonium chloride (NH_4Cl) (Parsley *et al.*, 2018). There are a number different setups (Branson & Mehl, 1933; Cooper, 1935; Feldmann, 1989; Green, 2001; Sakamoto, 1970; Teichert, 1948), but they all follow the same basic principle: ammonium chloride is heated inside a glass tube over a flame, and the vapour is blown into the fossil (using a squeeze bulb, compressed air, or even breath). This process, according to Parsley *et al.* (2018), creates a finer grained coating that is more stable in humid circumstances for longer periods of time than the wet method. Ammonium chloride whitening is quite safe and controllable, allowing for more consistent outcomes (Parsley *et al.*, 2018).

Another option is to burn a strip of magnesium ribbon and position the mould above it, facing the rising smoke (Figure 7g). This should be done with caution since the magnesium oxide burns extremely hot and can completely coat the mould, rendering it unusable. Fortunately, the magnesium oxide is easy to clean from the mould, allowing for other attempts. This approach was formally introduced in 1947, however it is likely that it has been in use for much longer (Parsley *et al.*, 2018; Rasetti, 1947). The highly reflective nature of magnesium oxide and the challenge in achieving an even coat are clear disadvantages of this approach, even if it can be used successfully (see Correia *et al.*, 2016).

The final step, and the technique's ultimate goal, is photography. The primary light should come from the upper left corner, and the secondary light should come from the bottom right corner to act as a bounce light, according to traditional specimen lighting practices (Figure 7h).

After the images are taken, rinse the ammonium chloride or magnesium oxide off the mould with clear running water to prevent it from being damaged or corroded.

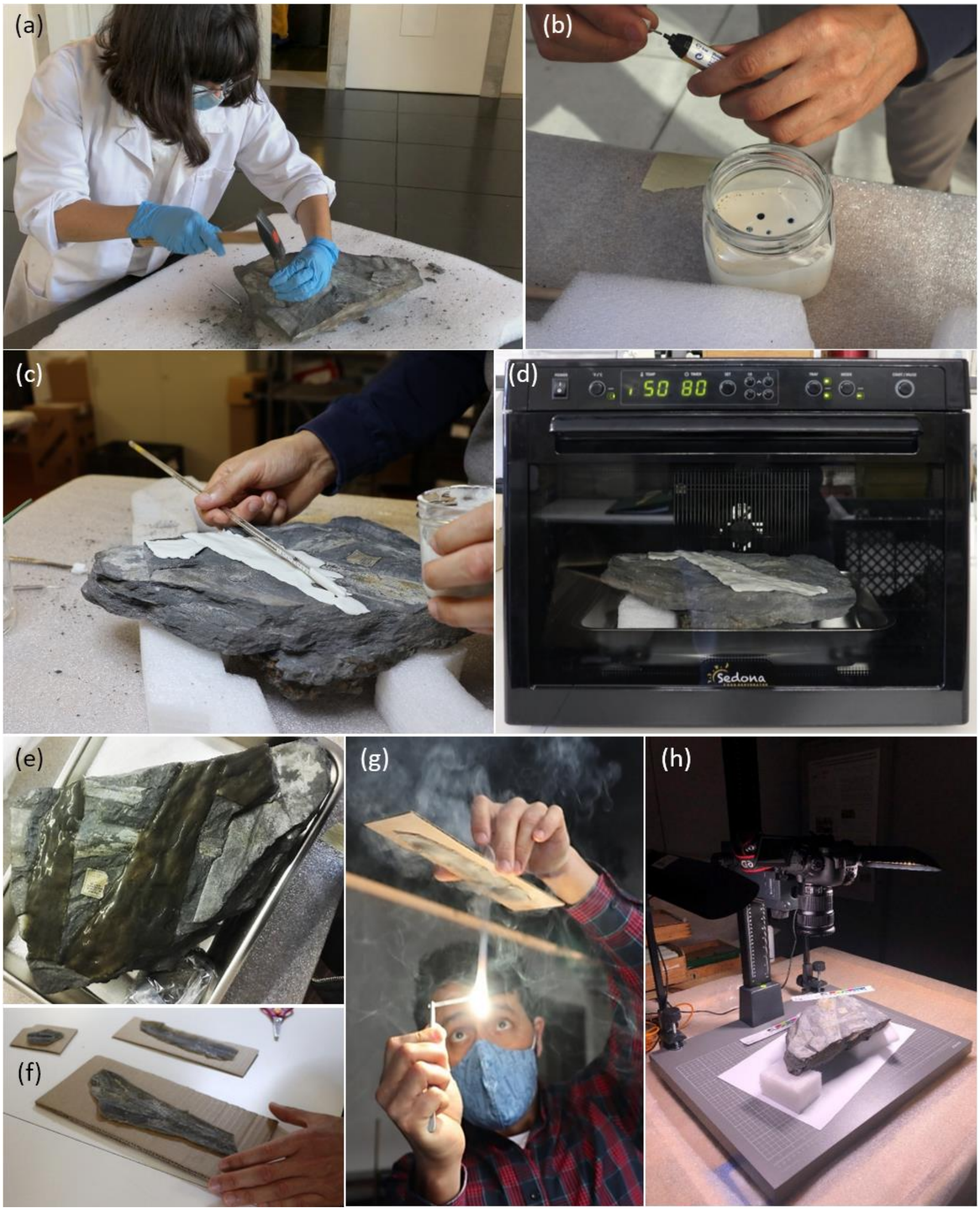

Figure 7 — Steps of the latex moulding process, photographs by João Muchagata. (a) Make sure the fossil is clean, fossil being prepared; (b) mix latex with a dye; (c) apply thin layer of latex on the fossil, careful not to create air bubbles; (d) allow to cure either at room temperature or in an oven; (e) Apply the next layers and allow to cool, carefully peel the mould from the fossil, starting from the edges and progressing inward; (f) glue the mould to a piece of cardboard; (g) latex mould being whitened (Pedro Correia); (h) photographing the mould: example of copy stand setup from the PO Herbarium, at the MHNC-UP. Adapted from Barbosa & Muchagata (in press).

Plates and Illustrations

Photographs were taken with the copy stand of the PO Herbarium (Figure 7h), which includes a Canon EOS 6D Mark II camera with an EF 24-105mm f/3.5-5.6 IS STM lens, a Kaiser RS10 Camera stand with RTP camera arm and RB 5020 ds2 LED lighting unit. Additional photography was made with a Canon EOS 6D camera, Macro 100mm 1:2.8L IS lens, and Canon Macro Twin Lite MT-24EX lighting unit. Image processing and plate editing were done using Adobe Photoshop and CorelDraw.

In order to observe finer details, photographs were taken at the *Museu de História Natural e Ciência da Universidade do Porto* (MHNC-UP) with a Zeiss Axiocam 305 colour camera mounted on a Zeiss SteREO Discovery.V20 motorized microscope with a SYCOP 3 control panel. A SCHOTT VisiLED Controller MC 1000 was used to control the lighting and image processing was done using the Zeiss Zen 2.6 Lite Microscope software.

Furthermore, illustrations of specimens MHNCUP/PAB-466, MHNCUP/PAB-467, and MHNCUP/PAB-346 (previously MHNCUP/PAB-130919) — respectively *Sphenopteris teixeirae* sp. nov., *Linopteris* cf. *neuropteroides*, *Phyllotheca douroensis* sp. nov. — were drawn to support taxonomic description. These were based on existing photographs and on-hand observation of the specimens, and made using traditional as well as digital means (namely, a Wacom Intuos M CTL-6100WL tablet and PaintTool SAI version 1.1.0 and Inkscape 1.1). The subjectivity of illustration allows the artist/researcher to highlight, emphasise, add, or alter, while still accurately representing the subject (Dalby & Dalby, 1980; Jastrzebski, 1985).

Preservation and taphonomy of the studied fossil samples

The specimens are preserved in compressed shales. The fragmented specimens are found in parautochthonous deposits, meaning they were transported for a relatively short distance before deposition, in association with fluvio-lacustrine sandstone deposits. The effects of compressive tectonics (linked to the Variscan orogen) are not prevalent.

Depository

The specimens and respective latex moulds described here are housed at the *Museu de História Natural e Ciência da Universidade do Porto* (MHNC-UP).

Lesleya ceriacoi sp. nov.

Approximately 100 years ago, a fossil was collected and deposited at the PO Herbarium, where it sat unidentified, for nearly a century. The fossil is supposed to have been collected by Carlos Teixeira (1910–1982), one of the founders of the *Sociedade Geológica de Portugal*. Teixeira is considered one of the main figures in geosciences in 20th century Portugal. He also had an interest in of Botany and Palaeontology, and played an active role in enriching the collections of the current Museu de História Natural e da Ciência da Universidade do Porto. On a fateful afternoon, by chance, the fossil was rediscovered, which led to the description of a new species of ancient plant. The fossil specimen is described here and, in Correia *et al.* (2022).

The specimen (Figure 6) contains five fragments of a single leaf of *Lesleya ceriacoi* sp. nov.: one holotype (Plate 1) and four paratypes (Plate 2 and Plate 3), in association with *Cordaites* leaves and pecopterid remains. The sample measures 201mm wide and 365mm long. The largest and best-preserved fragment (MHNCUP/PAB-29a) (Plate 1) was chosen as the holotype, as it displays the greatest number of diagnostic characters. Specimen MHNCUP/PAB-29 exhibits adpressions (compressions/impressions; *sensu* Shute & Cleal, 1996) preserved in laminated and compact (compressed) grey shales, rich in quartz clasts.

Phyllotheca douroensis sp. nov.

The fossil, collected in an excavation by Artur Sá, Pedro Correia, and Rúben Domingos in 2010 (41°09’44.65”N, 08°30’25.73”W), in the Douro Basin, consists of a single specimen (Plate 6 and Plate 7) preserved as an adpression (compression/impression; *sensu* Shute & Cleal, 1996) in a laminated shale bed. The specimen, MHNCUP/PAB-346 (holotype), is a leaf whorl with a large foliar sheath attached to a broad axis. The sample is 52 mm long and 42 mm wide, while the fossil itself measures 15–17mm wide and 35mm long.

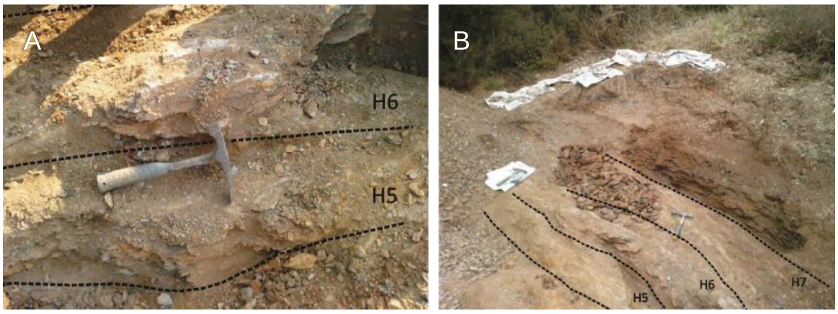

Figure 8 — Lower Gzhelian outcrop (41°09’44.65”N, 08°30’25.73”W), see Figure 2.
A: H5 and H6 horizons; new *Phyllotheca* species was found on horizon 6.
B: Different horizons of the outcrop. Pictures taken during fieldwork in 2010.

The fossil site (Figure 8) preserves various fossiliferous levels containing remains of diverse fauna and flora. The new *Phyllotheca* species was found in the H6 horizon, in association with a diverse flora: ferns (*Acitheca* Schimper, *Asterotheca* Presl ex Corda, *Cyathocarpus* Weiss, *Lobatopteris* Wagner, *Oligocarpia* Göppert, *Spiropteris* Schimper, *Stellatheca* Danzé), pteridosperms (*Callipteridium* (Weiss) Zeiller, *Cyclopteris* Brongniart, *Dicksoniites* Sterzel, *Douropteris* Correia *et al.*, *Eusphenopteris* Gothan ex Simson-Scharold non Kidston, *Neuropteris* (Brongniart) von Sternberg, *Pseudomariopteris* Danzé-Corsin, *Sphenopteris* (Brongniart) von Sternberg, *Telangium* Benson), and calamitaleans (*Annularia* von Sternberg, *Asterophyllites* Brongniart, *Calamites* Suckow, *Calamostachys* Schimper, *Sphenophyllum* Brongniart) (Correia *et al.*, 2019).

This assemblage is accompanied by faunal elements, such as the arachnids, eurypterids, insects (Dictyoptera and Palaeodictyoptera), limnic bivalves, and myriapods mentioned in a previous section.

Floral assemblage

The specimens were collected on an excavation in São Pedro da Cova (outcrop: 41°09'35.8"N, 8°30'05.2"W) by Pedro Correia, in 2004 (Figure 9). The fossils were preserved as adpressions (compression/impression; sensu Shute & Cleal, 1996), in laminated and compact grey shales. This assemblage is represented here by the fossil specimens in Plates 8-18. All the specimens are stored in the Palaeobotany collection of the *Museu de História Natural e Ciência da Universidade do Porto*.

Figure 9 — New floral assemblage outcrop (41°09'35.8"N, 8°30'05.2"W), see Figure 2. Picture taken during fieldwork in 2004.

This new assemblage includes:

Pteridospermopsids

- *Linopteris neuropteroides* — Plate 8A–D, Plate 9, Plate 10, Plate 15CFG
- *Rhodeopteridium* sp. — Plate 15C-E
- *Eusphenopteris nummularia* — Plate 8F–H, Plate 11, Plate 12, Plate 15F
- *Gondomaria* cf. *discreta* — Plate 8IJ, Plate 15F

Cycadopsids

- *Cyclopteris* sp. — Plate 15A

Sphenopsids/Equisetopdsids

- *Sphenophyllum* cf. *costae* —Plate 13, Plate 16
- *Sphenophyllum* cf. *majus* — Plate 14

Cordaitopsids

- *Cordaites* sp. — Plate 13A, B, E

Gymonspermopsids (Pteridopsida?)

- *Sphenopteris teixeirae* sp. nov. — Plate 17, Plate 18

Insertae sedis

- Root fragments — Plate 8E

Lithology and fossil record

The Carboniferous strata in the São Pedro da Cova region are steeply dipping and tectonically compressed, with coal beds interbedded with fluvial deposits and laminated grey shales rich in fossil plants. The shales preserve a diverse megaflora, predominantly made up of Cordaitopsida, Lycopsida, Pteridopsida, Pteridospermopsida and Sphenopsida, in association with faunal elements such as arthropods and bivalves; the sandstone strata vary in thickness and are relatively oxidised. The sandstone and shale levels correspond to units B1/2-D1/2. At the base, there are breccia deposits that correspond to TSU A1.

The outcrops described belong to TSU B1 (see Figure 3).

Results

Lesleya ceriacoi sp. nov.

Systematic Description

Division **Tracheophyta**

Class **Spermatopsida**

Order and Family **uncertain**

Genus ***Lesleya***

Type species

Lesleya grandis Lesquereux, 1879 (syntype, ISM 8654 - Soft shaly sandstone, base of the Chester Limestone). Two remaining specimens were cited by Watt, 1974 as being at Harvard, however, no catalogue numbers were given (Lendemer, 2002). The type specimens were assigned to Lesquereux by Professor A.H. Worthen (Lendemer, 2002).

Distribution of genus

Namurian (regional stratigraphic stage of NW Europe equivalent to the Serpukhovian and Bashkirian, Carboniferous) to Asselian (Early Permian) (see Correia *et al.* (2016, 2022), De Stefani (1901), Grand'Eury (1877, 1890), Kurtze (1839), Leary & Pfefferkorn (1977), Lesquereux (1880, 1884), Remy & Remy (1975, 1978), Zeiller (1888, 1890)).

Systematic remarks and diagnostic characters used for species differentiation

The taxonomic classification of the genus *Lesleya* for order and family levels remains uncertain (DiMichele *et al.*, 2016; Taylor *et al.*, 2009). Bashforth *et al.* (2016) have placed *Lesleya* within Phasmatocycadales and Phasmatocycadaceae, in accordance with Doweld (2001) and Anderson *et al.* (2007). However, this attribution to order and family levels is obscure or unclear. In relation to the higher taxonomic levels, it seems that most authors tend to place *Lesleya* within Gymnospermophyta (Florin, 1933), with close affinities to Cycadopsida and Pteridospermopsida (Florin, 1933; Leary, 1990, 1993, 1998; Leary & Pfefferkorn, 1977; Remy & Remy, 1977, 1978; Taylor *et al.*, 2009; Wagner, 2003). All this said, because Gymnospermophyta and Pteridospermopsida are not monophyletic, they cannot be considered valid taxonomic ranks. Regarding Cycadopsida, Leary (1990) found similarities with the seed habit of modern cycads, but this systematic affinity is quite uncertain as a result of being based on one single, very incomplete, poorly preserved leaf specimen of *Lesleya* – only the species *L. cheimarosa* has seeds on petioles (Leary, 1990, fig. 1). Fructifications of other *Lesleya* species are unknown. A formal classification of the gymnosperms and pteridosperms for higher ranks is Spermatopsida (Tracheophyta), seed-producing plants *sensu lato* (Anderson *et al.*, 2007; Kenrick & Crane, 1997; Pryer *et al.*, 2004).

Due to the fragmentary nature of most *Lesleya* material (Lesquereux, 1879, 1884; Remy & Remy, 1975, 1978; Zeiller, 1890), the different species of *Lesleya* are classified using leaf characters such as the leaf shape, type of margin and the venation pattern (Correia *et al.*, 2016; Leary, 1980; Leary & Pfefferkorn, 1977; Šimůnek, 1996).

Lesleya ceriacoi **sp. nov.**

Plate 1, Plate 2, Plate 3, Plate 4

Holotype

Specimen MHNCUP/PAB-29a is stored at the MHNC-UP (Plate 1 and Plate 4A).

Paratypes

Specimens MHNCUP/PAB-29b, MHNCUP/PAB-29c, MHNCUP/PAB-29d and MHNCUP/PAB-29e (Plate 2, Plate 3 and Plate 4B–E).

Type locality

Douro Carboniferous Basin, north-western Portugal (Figure 2).

Type horizon and age

Compressed (compact) and laminated grey shales, rich in quartz clasts. The age is early Gzhelian (ca. 303 Ma) of the Late Pennsylvanian Epoch.

Etymology

The new species is named after the Head of Collections and Research of the MHNC-UP Luis Ceríaco, for his important contribution as a herpetologist to the knowledge of the biodiversity of Africa, where he has led several expeditions and discovered many new endemic species.

Diagnosis

Large lanceolate leaf with serrate margins in the apical part, broad at the middle with straight margins gradually tapering into a narrow basis. Teeth widely spaced (ca. 2 teeth/cm), asymmetrical and with irregular arrangement. Broad midvein, divided in veins in the apical part. Oblique lateral veins arise in very acute angle from midrib, curve slightly and divide twice to thrice, reaching the margin in acute angle. Vein density 10–12 veins/cm on the leaf margin.

Description

The holotype MHNCUP/PAB-29a (Plate 1 and Plate 4A) is a lower-to-middle part of a leaf with a preserved length of 218 mm and width 49 mm. The leaf margins are lacerated, having discrete lacerations in the top and lower regions of specimen (Plate 1B) and a deep laceration at the middle that almost reaches the midvein, dividing lamina into two separate segments (Plate 1A and C); the lacerations occur through the lateral veins. The margins remain relatively straight, becoming gradually narrower towards the basal part of leaf (Plate 1A). The lateral veins are relatively spaced (10–12 veins/cm on leaf margin) and divided two to three times, forking two times close the midvein with a later (third) bifurcation occurring near the margin. They are oblique, slightly curved from the midvein to the margin, forming angles of 5–14° with the midvein, and 20–23° with the margin. The midvein is broad (2.5–4.0 mm wide) with an irregular border at the base, bearing several longitudinal striations.

Paratype MHNCUP/PAB-29b (Plate 2 and Plate 4B) is an upper part of a leaf with a nearly complete acute leaf apex. The leaf has a preserved length of 165 mm and a maximum width of 37 mm. The leaf margins are serrate in the apical part and slightly to deeply lacerated at the middle and basal parts of specimen (Plate 2B). The teeth of serrate margins are 1.5–5.5 mm in length, widely spaced with two teeth per cm on the margin (an average of 2–6 leaf teeth on apex margins), asymmetrical, and irregularly arranged (Plate 2B and C). The teeth of the serrate parts of the margins are 1.5-5.5mm in length, widely spaced with two teeth per cm on the margin (and average of 2-6 teeth on the apex margins), asymmetrical, and irregularly arranged. The midvein is relatively thin (0.5–2.0 mm wide) and ends by dividing into multiple arching smaller veins in the leaf apex. Paratype MHNCUP/PAB-29c (Plate 3A and Plate 4C) is a middle-to-upper part of a leaf with a preserved length of 94 mm and a maximum width of 63 mm. Its leaf margins are deeply lacerated and midvein is relatively thin (2.0–2.2 mm). Paratype MHNCUP/PAB-29d (Plate 3B and Plate 4D) is a middle/lower part of a leaf of 59 mm in length and 41 mm in width. Its leaf margins are substantially entire and straight. The midvein is thin with a width of 1.2 mm. Paratype MHNCUP/PAB-29e (Plate 3C and Plate 4E) is an incomplete part of a leaf base of 52 mm in length and 28 mm in width. Its leaf margins are entire, relatively straight and asymmetrical. The midvein is broad (about 4.0 mm wide) and longitudinally striated. All four paratypes display oblique lateral veins, closely spaced, and slightly curved from the midvein to the margin, forming very acute angles with the midvein.

The reconstruction of a specimen of the new *Lesleya* species is in Plate 5. It is based on the different preserved leaf parts (Plate 4), which compose a nearly complete leaf. Its total length is estimated to about 60 cm.

Comparison and discussion

The five specimens described herein (Plate 4) display typical morphological features of the genus *Lesleya*. *Lesleya* foliage is described as simple, large and wide leaves, of lanceolate/sublanceolate shape, with an entire to pinnatifid (having lobes with incisions that extend less that half-way toward the midrib) margin, gradually narrowing towards the base, and having very oblique veins, curved or sinuous, equal, simple/pinnate to repeatedly dichotomous (Correia *et al.*, 2016; Leary, 1980; Leary & Pfefferkorn, 1977; Leary & Trask, 1985; Lesquereux, 1880, p. 142; Remy & Remy, 1978; Šimůnek, 1996). Please see summary of comparative species in Table 1.

In comparison with all known species of *Lesleya*, *Lesleya ceriacoi* sp. nov. bears a closer resemblance to *Lesleya grandis* Lesquereux, 1879 from the Westphalian B-C (313–308Mya, Duckmantian–Bolsovian) of the USA. *L. grandis* has wide leaves with deeply pinnatifid margins in both apical and lower leaf parts. However, leaves of *L. grandis* display a cuneate base with arched margins and obtuse apex (Lesquereux, 1879, pl. XXV, figs. 1–3), whereas *L. ceriacoi* sp. nov. shows an acute/subacute and serrate apex and straight margins that gradually taper into a narrow base. Furthermore, leaves of *L. ceriacoi* sp. nov. are significantly larger and show more inclined lateral veins with a lower vein density, and a midvein divided in veins in the apex.

L. ceriacoi sp. nov. also bears some similarities to *L. weilerbachensis* Remy & Remy, 1975 from the Westphalian C-D (311–305Mya, Bolsovian-Asturian) of Germany (e.g., Remy & Remy, 1975, 1978; Correia & al., 2016). *L. weilerbachensis* has wide leaves with serrate margins and bears very inclined lateral veins and a midvein divided in veins at the apex. However, *L. weilerbachensis* shows straight lateral veins, an obtuse apex and cuneate base and its serrate margins have symmetrical teeth with a regular arrangement. In contrast, *L. ceriacoi* sp. nov. shows slightly curved lateral veins, an acute/subacute apex and straight margins that gradually narrow towards the base. In addition, leaves of *L. ceriacoi* sp. nov. are substantially larger, have deeply lacerated margins and an irregular tooth arrangement with few, asymmetrical, widely spaced teeth (an average of 2–6 leaf teeth on apex margins).

L. ceriacoi sp. nov. also shows a superficial similarity to *L. iberiensis* Correia & al., 2016, a Portuguese congener of same age (early Stephanian C/early Gzhelian) found in the Douro Basin (Correia *et al.*, 2016). Both species display very inclined and slightly curved lateral veins with a similar vein density and a broad midvein. However, the leaf margins are greatly different. The margins of *L. iberiensis* are entire and arched towards base, forming a long, cuneate base. In addition, they also are distinguished by the leaf size.

L. delafondii Zeiller, 1890 from the upper Autunian (Asselian/lower Permian) of France (Correia *et al.*, 2016) has wide and serrate leaves with a venation pattern similar to that of *L. ceriacoi* sp. nov. However, *L. ceriacoi* sp. nov. differs from *L. delafondii* in the tooth size and arrangement. Serrate margins of *L. delafondii* have substantially smaller, more numerous teeth, with a regular arrangement on leaf margin (Florin, 1933, p. 4). Furthermore, lacerated margins do not occur in *L. delafondii*. The holotype of *L. delafondii* does not have a leaf base or apex (Zeiller, 1890, fig. 2), so comparing these features is not possible.

Phyllotheca douroensis sp. nov.

Systematic Description

Division **Tracheophyta**

(or **Sphenophyta**)

Class **Equisetopsida**

Order **Equisetales** DC. ex von Berchtold and Presl, 1820

Family **Phyllothecaceae sensu lato** Brongniart, 1828

(**Phyllothecaceae sensu stricto** ≡ **Gondwanostachyaceae** Meyen, 1969)

Genus ***Phyllotheca*** (Brongniart) Townrow, 1955

1828 *Phyllotheca* Brongniart, p. 152.

1955 *Phyllotheca* Brongniart emend. Townrow, p. 39–40.

Type species

Phyllotheca australis Brongniart, 1828 emend. Townrow, 1955; rode unit uncertain, Hawkesbury River, Sydney Basin, New South Wales (Mcloughlin, 1992; Mcloughlin *et al.*, 2005).

Generic diagnosis

See Boureau (1964, pp. 392–396) and Townrow (1955, pp. 39–40)

Distribution of the genus

Cosmopolitan genus; late Carboniferous to Early Cretaceous (Boureau, 1964; Maheshwari, 1974; Mcloughlin, 1992; Scott, 1987).

Phyllotheca douroensis **sp. nov.**

Plate 6 and 7

Holotype

MHNCUP/PAB-130919 (Plate 6 and 7).

Type locality

São Pedro da Cova region, Douro Basin, north-western Portugal (Figure 8).

Stratigraphic age

Early Stephanian C (middle Gzhelian, ca. 303 Ma), Late Pennsylvanian, Carboniferous.

Type horizon

Compressed and laminated grey shales; horizon H6 (Figure 8).

Etymology

The specific epithet “*douroensis*” refers to the Douro Basin from which the fossil was collected.

Diagnosis

Leaf whorl with a single, large and well-developed foliar sheath, totally opened in disc shape, and basally attached to a broad axis; densely covered with simple to divided veins; veins mainly divided two times (rarely thrice); sheath margins irregular and entirely dentate; dentate margins having small and asymmetrical.

Description of the holotype

The holotype MHNCUP/PAB-130919 (Plate 6) consists of a nearly complete leaf whorl, partially fused into a single, large and well-developed disc shaped foliar sheath which is attached to a broad axis. The leafy axis has a width of about 5 mm and is poorly preserved. The foliar sheath is large of 4.5–7.5 mm in width and has a total length of about 22 mm. The foliar sheath is densely covered with simple to divided veins, mostly divided twice to rarely thrice. The sheath margins are irregular and entirely dentate, with small and asymmetrical teeth.

Comparison and discussion

The new *Phyllotheca* species, *Phyllotheca douroensis* sp. nov., displays a large and well-developed foliar sheath totally released from the stem to the node (or distally opened), which are diagnostic features of the fossil-genus *Phyllotheca* described by Brongniart (1828) (see also Mcloughlin, 1992).

Among all known species of *Phyllotheca*, *P. douroensis* sp. nov. is most similar to the Gondwanan *Phyllotheca etheridgei* Arber, 1905 from the late Permian of Newcastle Series, New South Wales, Australia (Boureau, 1964; Saksena, 1952, 1954). Basal leaf whorls of *P. etheridgei* show a large and well-developed disc shaped foliar sheath with dentate margins (Figure 10) and size comparable to that of *P. douroensis* sp. nov. However, they differ from the venation pattern in foliar sheaths. The veins of foliar sheath of *P. douroensis* sp. nov. are divided at least twice to thrice, while veins of foliar sheaths of *P. etheridgei* are simples, without any divisions (Figure 10). Furthermore, there are some dissimilarities in the sheath margins of both species: *P. etheridgei* shows regular dentate margins, while the dentate margins of *P. douroensis* sp. nov. are relatively irregular or asymmetrical. Nevertheless, the preservation state of the fossil material by compression might have had some taphonomic influence on apparent asymmetrical shape of the foliar sheath of *P. douroensis* sp. nov.

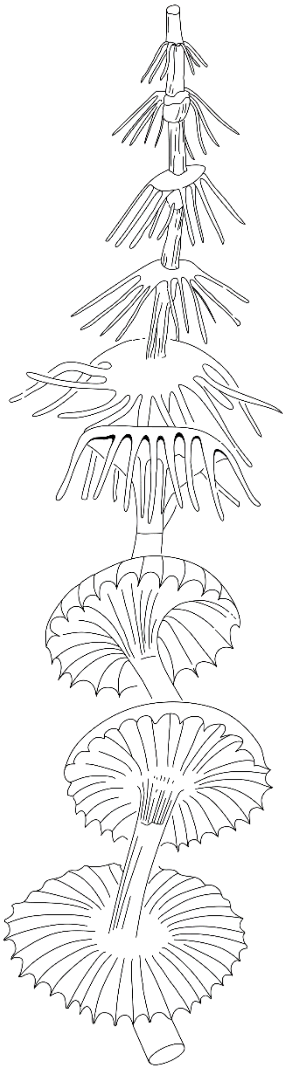

Figure 10 — *Phyllotheca (Raniganjia?) etheridgei* Arber, 1905 (Permian of Newcastle Series, New South Wales, Australia) (Gondwana) showing foliar polymorphism.

Reconstruction according to Saksena (1954; see Boureau 1964, p. 402, fig. 366).

Remarks

Only a single leaf whorl is described for the *P. douroensis* sp. nov., but based on its broad axis it is likely that it corresponds to a basal leaf whorl from a leafy axis with similar foliar polymorphism to that of *P. etheridgei* (Figure 10).

Floral assemblage

Gymnospermophyta

Class **Cycadopsida**

Order **Medullosales**

(or order **Trigonocarpales**)

Family **Cyclopteridaceae**

Genus ***Cyclopteris*** Brongniart, 1828

Cyclopteris sp.

Plate 15A

Type species: Cyclopteris orbicularis Brongniart, 1831 (see Cleal & Shute, 2003)

Description: Large orbiculate (basal) pinnule of cordate to deltoid or triangular shape, with an entire margin. Numerous veins radiate from where the foliar structure was attached to a rachis or a stem. The veins are dichotomous and the midvein is absent.

Class **Gymnospermopsida**

(or class **Pteridospermophyta?**)

Order **Lyginopteridales**

Family **uncertain**

Genus ***Sphenopteris*** Sternberg, 1825

Type species

Sphenopteris elegans (Brongniart, 1822)

Generic diagnosis

Sphenopteris is usually applied to incised, lobate pinnules with constricted bases (Knight & Wagner, 2012).

Distribution of genus

Late Devonian to Late Cretaceous (see Kimura, 1987; Rajanikanth & Sukh-Dev, 1989; Speden, 1971; Wagner & Lemos de Sousa, 1982)

***Sphenopteris teixeirae* sp. nov.**

Plate 17 and Plate 18

Holotype

Specimen MHNCUP/PAB-467 designated here is stored at the MNHCUP.

Type locality

Outcrops located in the region of São Pedro da Cova, in Douro Carboniferous Basin, north-western Portugal (Figure 9).

Type horizon and age

Horizon composed of laminated and compact grey shales; early Stephanian C (early Gzhelian, Late Pennsylvanian).

Etymology

The new species is named after Carlos Teixeira (1910–1982). Teixeira was one of the founders of the *Sociedade Geológica de Portugal* and the *Centro de Estudos de Geologia da Faculdade de Ciências da Universidade de Lisboa*. During his tenure at the *Universidade do* Porto he studied Botany under Gonçalo Sampaio (1865–1937) and Geology under Carrington da Costa, two monumental figures of Portuguese science in the 20th century. He went on to participate in the overhaul of the *Serviços Geológicos de Portugal*, working alongside Georges Zbyszewski (1909–1999), Orlando Ribeiro (1911–1997), and António Quaresma Viana (1887–1949). He is considered one of the main figures of Portuguese Geosciences in 20th century Portugal, having played an active role in enriching of the collections of the current Museu de História Natural e da Ciência da Universidade do Porto.

Diagnosis

Characters for a single ultimate pinna: pinna with a relatively sinuous rachis; small pinnules of tongue-shape, marginally decurrent, bearing 7-8 lobes, showing bifid basal lobes; strong venation.

Description

Relatively sinuous rachis. Pinna Dimensions: pinna ca. 35mm long and 15–17mm wide, length/breadth ratio = 2–2.3. Pinnules alternate and laterally overlapping. Pinnules in the apical parts of pinna are, less developed, shorter, and have less lobes (ca. 6). Basal pinnules are better developed, bearing 7-8 lobes. Basal lobes are usually bifid, regardless of position of the pinnule along the pinna. A single vein enters each pinnule and forks at the apex of each lobe. Dimensions: 9–12mm long and 4–5mm wide, length/breadth ratio = 1.8–3; Pinnule insertion angle 46–52°.

Comparison

Sphenopteris teixeirae sp. nov. closely resembles *Sphenopteris sampaiana* Teixeira, 1939 as separate species from *Sphenopteris* (*Germera*) *mendescorreae* (Álvarez-Vázquez, 2019, pp. 25–27; Teixeira, 1939a,

p. 12). Pinnules of *S. sampaiana* retain the same size throughout the pinna and possess stiff, simple or bifid lobes with acute apices, but bears 12-13 bifid lobes (Wagner & Álvarez-Vázquez, 2010b, p. 27).

Gymnospermophyta/Pteridospermatophyta

Class **Pteridospermopsida**

Order **Medullosales**

(or Order **Trigonocarpales**)

Family **Potonieaceae**

Genus ***Linopteris*** Presl, 1838

Linopteris cf. *neuropteroides*

Plate 8A-D, Plate 9, Plate 10, Plate 15CFG

Type species: *L. gutbieriana* Presl ?*L. brongniartii* (Gutbier) Potonié (see Zodrow *et al.*, 2007)

Description: The described material corresponds to individual pinnules with high morphological variability (heterophylly), of several sizes, consisting in large and subfulcate to very small and weakly auriculate or cordate (intercalated) pinnules.

Comparison: The material closely resembles *Linopteris neuropteroides* (von Gutbier) Potonié group, established by (Zodrow *et al.*, 2007) (see also Sauveur, 1848, figs 89, 90; Wagner, 1964, fig. 87), mainly in the pinnule shape and the pattern of vein meshes. The material can be compared with the Portuguese species *Linopteris florini* Teixeira, however, the size of the pinnules differs quite substantially.

.

Pteridospermatophyta

Class **Pteridospermopsida**

Order **Callistophytales**

Family **uncertain**

Genus ***Eusphenopteris*** Novik 1947

Eusphenopteris nummularia

Plate 8H-F, Plate 11, Plate 15F

Type species: *Eusphenopteris obtusiloba* (Brongniart) Novik (according to Boersma & Gastaldo (1983))

Description: Material consists of fragments of ultimate pinnae and individual pinnules. The pinnules are obliquely inserted at slightly flexuous rachises. The pinnules with about 10 small, rounded to cordate/coriaceous lobes; the basal lobes are deeply incised. Nervation is not preserved.

Class **Pteridospermopsida?**

Order **uncertain**

Family **uncertain**

Genus ***Rhodeopteridium*** Zimmerman, 1959

Rhodeopteridium sp.

Plate 15C-E

Description: The preserved material consists of squatted leaves in narrow to linear segments, pointed or bluntly ended.

Comparison and discussion: The material shows some resemblance with *Sphenophyllum saxifragaefolioides* Leyh and *Rhodeopteridium stachei* (Stur) Purkyňová from the intramontane basin of Valdeinfierno (Lower Namurian/Upper Mississippian), Sierra Morena (Pšenička & Schultka, 2009; Wagner *et al.*, 1983, pp. 101, 111) e *Rhacopteris bipinnata* Němejc (Wagner & Álvarez-Vázquez, 2010b, p. 265).

Pinophyta

Class **Pinopsida**

(or class **Cordaitopsida**

Order **Cordaitales**

(or order **Cordaitanthales**)

Family **Cordaitantaceae**

Genus ***Cordaites*** Unger, 1850

Cordaites sp.

Plate 13ABE

Type species: Cordaites borassifolius (Sternberg) Unger, 1850

Description: The material consists of a single fragment of a large leaf.

Polypodiophyta

Order and Family **uncertain**

Genus ***Gondomaria*** Teixeira, 1964 emend. Wagner, 2004

Gondomaria cf. *discreta* (Weiss) Wagner & Lemos de Sousa, 1982

Plate 8IJ, Plate 12, Plate 15F

Type species: *Gondomaria alethifolia* Teixeira, 1964

Selected synonyms: *'Callipteris' discreta* Weiss, 1870 and *Rhachiphyllum schenkii* (Heyer) Kerp, 1988

Description: The described materials comprise several ultimate pinnae and terminal pinnae. The pinnules are relatively small, lobed (pinnatifid), with a rounded to subtriangular shape, having a contracted base at rachis and marginally decurrent; they have odontopterid to alethopterid-like venation.

Discussion and comparison: *Gondomaria* is a taxon with fern-like foliage/callipterid foliage that is characterized by having a mix of characters from different pteridosperm genera, such as *Odontopteris*, *Mariopteris*, *Alethopteris* and *Callipteridium*. The Portuguese materials display close resemblance with *Gondomaria discreta* (Weiss) Wagner & Lemos de Sousa, 1982 and *Gondomaria grandeuryi* (Zeiller) Wagner & Castro, 1998.

Class **Sphenopsida**

Order **Sphenophyllales**

Family **Sphenophyllaceae**

Genus ***Sphenophyllum***

Sphenophyllum cf. *costae*

Plate 13CD and Plate 16

Description: The described material is composed of a third to fourth order (tertiary-quaternary) axis distally divided and composed of five whorls with 10-12 linear-laciniate leaves (5-6mm long, 0.3-0.5 mm wide); tertiary axis bearing two prominent longitudinal ribs; tertiary axis 0.8-1.5mm wide. Three strong ribs on the primary and secondary axes.

Sphenophyllum cf. *majus*

Plate 14

Description: The preserved material consists of an articulated axis bearing relatively well-developed leaves, flaring and quite incised, which represents a diagnostic character of *Sphenophyllum majus*.

Comparison: *Sphenophyllum majus* displays foliar polymorphism (heterophilia) (Jongmans, 1911, figs 372a, 373), the Portuguese sample corresponds to a form with flaring and incised of this species (Boureau, 1964; Wagner & Lemos de Sousa, 1982).

Discussion

Lesleya ceriacoi sp. nov.

The DCB was characterized by a relatively seasonal climate during Gzhelian (Bashforth *et al.*, 2021; Correia & Murphy, 2020). A drier climate led to the appearance of several endemic species with xeromorphic characteristics and, at the same time, to the disappearance of typical wetland and coal-forming floras. The Carboniferous–early Permian genus *Lesleya* is a xeromorphic plant (or xerophyte) that has been recently documented in lower Gzhelian strata of the DCB (Correia *et al.*, 2016). *Lesleya* is an element of Euramerican floras that was adapted to seasonally dry environments of the western and central tropical Pangea (Bashforth *et al.*, 2014, 2016, 2021; Correia *et al.*, 2016; DiMichele *et al.*, 2010, 2016). This plant, a member of the larger dry-climate adapted flora, commonly known as "drought-tolerant flora", has been considered a primitive gymnosperm and possible ancestor of modern cycads (Florin, 1933; Leary, 1990; Remy & Remy, 1978; Taylor *et al.*, 2009).

The diversity and environmental conditions of the Pennsylvanian Euramerican dryland floras, which include the genus *Lesleya*, have been extensively studied (Correia *et al.*, 2016; Correia & Murphy, 2020; DiMichele *et al.*, 2010, 2016). However, their morphological and ecological adaptations to intramontane environments are poorly understood.

History of the Genus

While rare in Europe, the genus *Lesleya* is relatively common in some localities in the USA. It was erected by Lesquereux (1879, 1880) with the type species *Lesleya grandis* Lesquereux. Lesquereux (1884) described a second species, *Lesleya microphylla*, based on two specimens from Kansas. Since 1884, nine additional species have been described from the Pennsylvanian and Permian strata of England, France, Germany, and Italy. These species are based only on one or a few specimens. Zeiller (1888, 1890) described *Lesleya ensis* Zeiller, 1888 from the Stephanian of Commentry in France and *L. delafondii* Zeiller, 1890 based on a single specimen. Florin (1933) later studied the same specimen and determined that *Lesleya* was a primitive gymnosperm based on haplocheilic stomata.

Grand'Eury (1890) revised *Lesleya angusta* Grand'Eury, 1877 and described *Lesleya simplicinervis* Grand'Eury, 1890. Both species are from the Stephanian of Saint Etienne, France.

De Stefani (1901) described *Lesleya cocchii* De Stefani from Italy, although this species was later found in the Le Crusot and Puits Saint-Paul (France) localities of the Stephanian (Zeiller, 1906).

Remy & Remy (1977) transferred *Taeniopteris eckardtii* to *Lesleya* (*Lesleya eckardtii*), although its assignment to the genus remains doubtful. These authors described another two species of *Lesleya*: *L. weilerbachensis* Remy & Remy, 1975 (Westphalian) and *L. gimmii* Remy & Remy, 1978 (Stephanian) — both from Germany.

Lesleya cheimarosa Leary & Pfefferkorn, 1977 was first discovered in Brown County (Illinois, USA). Subsequently, other specimens have been found in Rock Island County (Leary, 1981). Known from the middle to late Namurian (Early Pennsylvanian), it might be the oldest *Lesleya* in the world. Remy & Remy (1978) suggest a relationship between *Lesleya* and primitive cycads (DiMichele *et al.*, 2016). Leary (1990) found ovules on basal part of a petiole of a *Lesleya* leaf and interpreted it as a similarity with modern cycads, meaning that *Lesleya* could be a possible ancestor (Taylor *et al.*, 2009, p. 669).

Šimůnek (1996) studied cuticles of Bohemian *Lesleya* and found them to match pteridosperms and cycads. Leary (1998) suggested a relationship with the Gondwanan genus *Glossopteris* Brongniart (DiMichele *et al.*, 2016; Wagner, 2003, p. 36).

Álvarez-Ramis (1997) described *Lesleya doubingeria* from the Puertollano Basin (Stephanian C) in Ciudad Real (south-central Spain), however, this has since been disputed (Wagner & Álvarez-Vázquez, 2010a). The first representative from Iberia was *L. iberiensis*, from the lower Gzhelian (Upper Pennsylvanian) of the DCB (Correia *et al.*, 2016).

Ecology and Habit of *Lesleya ceriacoi* sp. nov.

The leaf fossils of *Lesleya ceriacoi* sp. nov. are associated with fragmented leaves of the genus *Cordaites* Unger – a coniferopsid gymnosperm, and with fragments of marattialean fern foliage (Figure 6). Recent studies (Correia *et al.*, 2016; Correia and Murphy, 2020) have demonstrated that *Lesleya* and *Cordaites* preferred moisture-deficient seasonally dry environments within DCB. The occurrence of these plants together with other xerophytes (such as walchian conifers, taeniopterids, and dicranophyllalean conifers) in the fossil record of the DCB (Wagner and Lemos de Sousa, 1983; Pšenička *et al.*, 2017; Correia *et al.*, 2016, 2018), suggests that seasonally dry climatic conditions prevailed in this region during the Gzhelian (303.7-298.9 Mya), at the end of the Late Pennsylvanian (307.0-298.9 Mya). These dry seasonal conditions are consistent with a dry subhumid to semiarid climate (Bashforth *et al.*, 2021, table 1; Cecil, 2013, table 2). Similar biomes have been documented in Lower and Middle Pennsylvanian deposits of the Illinois Basin (USA) (Bashforth *et al.*, 2016, 2021; DiMichele *et al.*, 2016). Their taphocoenoses (assemblages where not all species present in the community are represented as fossils, and not all the fossil species within the assemblage lived in the community) are composed mainly of the gymnosperms *Lesleya*, *Cordaites*, and *Taeniopteris*, and walchian conifers, indicating that drought-tolerant floras colonized various tropical regions of the central Pangea throughout the Pennsylvanian (323.2-298.9 Mya). The dispersion of these plants into central tropical Pangea occurred when new dryland (seasonally dry) environments appeared (Correia & Murphy, 2020).

Interestingly, the presence of associated remains of marattialean ferns (Figure 6) suggests that these drought-tolerant floras coexisted with relict mesophytes–hygrophytes (Bashforth *et al.*, 2021, table 1), possibly from a wetland vegetation reduced to small and scattered (riparian?) refugia within a predominantly dryland setting. A mix of wetland and drought-tolerant taxa may also indicate that the resident floras lived in different soil moisture conditions and that they were transported to the same sites of deposition and preserved under a regime of seasonal precipitation. The floras of the DCB grew in siliciclastic environments adjacent to fluvial and limnic habitats within an intramontane region (Bashforth *et al.*, 2021). *L. ceriacoi* sp. nov. occurs in a siltstone interlayered with a conglomeratic sandstone deposit. Such a sedimentological record suggests that this plant lived near fluvial environments, the same environmental interface described for the habitat of *L. iberiensis*, where this species was also found with leaves of Cordaites (Correia *et al.*, 2016, fig. 7). Similar ecological conditions have been documented in Early Pennsylvanian (323.2–315Mya) macrofloral deposits from New Brunswick (Canada), where leaves of *Lesleya* and *Cordaites* are found together in seasonally dry habitats associated with marginal fluvial depositional environments (Bashforth *et al.*, 2014). This also is essentially the same flora reported by Bashforth *et al.* (2016) from the margin of the Illinois Basin (Indiana, USA), in the late Bolsovian (early/middle Moscovian — 315.2–307.0Mya), where Lesleya was found in association with *Cordaites* and marattialean fern foliage.

Adaptation strategies and the morphological traits of *Lesleya ceriacoi* sp. nov. leaves

Lesleya ceriacoi sp. nov. exhibits a very long and relatively narrow leaf that is broadly dissected (lacerated) with a serrate apex. Several factors could explain this. Leaf form is closely associated with climate (Guerin *et al.*, 2012; Schmerler *et al.*, 2012; Xu *et al.*, 2008). The leaf form tends to become narrower in during intervals of drought, as narrow leaves can reduce transpiration in drier periods (Farris, 1984; Xu *et al.*, 2008, 2009). Other aspects of leaf form, such toothed margins, evolve along an environmental gradient (Schmerler *et al.*, 2012). As the principal photosynthetic organ, leaves are sensitive to environmental changes in the process of evolution and plant adaptations (Xu *et al.*, 2008). Xeromorphic traits, like those found in taxa like *Lesleya,* are thought to be ecological adaptations to seasonally dry environments (Bashforth *et al.*, 2014, 2016, 2021; Correia & Murphy, 2020; DiMichele *et al.*, 2010, 2016). *L. ceriacoi* sp. nov. provides novel xeromorphic morphological traits for the genus in Euramerican drought-tolerant floras. The evidence of evolutionary adaptation to a changing environment in the DCB within central tropical Pangaea during the Late Pennsylvanian. This adaptation to environmental change is consistent with the appearance of *Lesleya* in the early Gzhelian (Late Pennsylvanian) of Iberia immediately after a transition from glacial to interglacial (and so humid to dry) conditions in central tropical Pangaea during the Kasimovian–Gzhelian (around 303.7 Mya) interval (Correia *et al.*, 2016; Correia & Murphy, 2020).

On the other hand, some adaptive morphological traits, such as the toothed margins, may be the result of a response to a more seasonal environment, or even biotic factors such as herbivory (Givnish & Kriebel, 2017; Schmerler *et al.*, 2012). In addition, plant-insect associations documented in the fossil record of Douro Basin suggest that resident (endemic) plant species could have developed some antagonistic traits, like leaf teeth, as a defence mechanism against attacks from herbivorous insects (Correia *et al.*, 2020). The insect-induced plant galls are known to become more prevalent on modern vegetation as climate shifts to dried conditions. Such a response in the DCB is consistent with sedimentological indicators of seasonal precipitation at the time that *L. ceriacoi* sp. nov. appeared.

The lacerations on *L. ceriacoi* sp. nov. leaves may result from several factors. They may be features of old leaves or a result of leaf senescence (the leaf became dry, and fissures started to occur along the veins after its death). Laceration may also be a taphonomic result of an active tectonic-depositional environment, as was the case in the DCB. On the other hand, these lacerations could indicate something about leaf stiffness or even thickness of the lamina. Nevertheless, the degree of blade dissection in modern plants is also correlated with climate (Royer *et al.*, 2005; Xu *et al.*, 2008). The deep lacerations taking place simultaneously on both leaf margins of *L. ceriacoi* sp. nov. (Plate 3A and Plate 4C) suggest that this species may has developed dissected leaf margins as adaptive traits to the specific climatic conditions of Douro Basin. It is also interesting to note the entire leaf margins of the Portuguese congener *L. iberiensis*, which coexisted with *L. ceriacoi* sp. nov. in the same intramontane environment of the DCB. This co-occurrence indicates that these species probably grew in ecologically distinct habitats within the Douro Basin. It could be argued that the lacerations are a variable phenotypic trait within a single species (*L. iberiensis*), however, this is unlikely considering the significant differences between the two species, especially in the apex margins (see Table 1**)**.

Importance of Museum Collections

Natural history collections remain one of the most important places for the discovery of new taxa, both living and extinct (Allmon, 2005; Funk, 2018; Green, 1998). As repositories of thousands of specimens, collected across several decades, these collections are on the cutting edge of species discovery (Green, 1998). However, due to many compounding factors (such as lack of specialists or lack of material of the same taxon), there is a significant gap between a specimen's collection in the field and its publication as a new taxon (Agnarsson & Kuntner, 2007; Fontaine *et al.*, 2012; Hopkins & Freckleton, 2002). This delay between the time the specimen of an unknown taxon was accessioned into a collection and the time it was described was called "shelf life" by Fontaine *et al.* (2012). In many cases, a specimen's shelf life can surpass several decades, until a trained taxonomist encounters the specimen and is able to identify and describe it as a new taxon (Fontaine *et al.*, 2012; Z. A. Goodwin *et al.*, 2020).

Due to a complex history — marked by the destruction of important collections such as that of the National Museum of Lisbon in 1978 and chronic disinvestment — the main natural history collections in Portugal are not comparable in size and diversity with their European and North American counterparts. Nevertheless, Portuguese collections are still unique at a global stage due to the country's position in a biodiversity hotspot (currently and historically), as well as its colonial history. In recent years, several new species have been described based on animal specimens found in Portuguese natural history collections (Ceríaco, 2015; Hallerman *et al.*, 2020; Marques *et al.*, 2019, 2020).

In herbarium collections, a quarter of new species descriptions are made more than 50 years after specimen collection (Bebber *et al.*, 2010). Fontaine *et al.* (2012) point to an average of 35 years between collection and description of new extant plants. Although these studies do not include fossil specimens, a similar situation occurs: many unstudied fossils are sitting on shelves that could hold new and important discoveries. One such example of this is the Palaeozoic crinoid *Delgadocrinus oportuvinum*, which was collected by Nery Delgado (1835-1908) near Valongo (NW Portugal) before being rediscovered and studied by Ausich *et al.* (2007) about a century later.

Phyllotheca douroensis sp. nov.

The equisetalean fossil-genus *Phyllotheca* sensu Brongniart 1828 is a cosmopolitan genus widespread across the Gondwanan and Laurasian continents during the Carboniferous and Permian (Boardman *et al.*, 2016; Boureau, 1964; Oshurkova, 1996; Prevec *et al.*, 2010; Rozefelds *et al.*, 2019; Taylor *et al.*, 2009).

The formation of the supercontinent Pangaea, which caused global-scale changes in the Earth's temperature in the late Palaeozoic, had a decisive impact in the global distribution of floras. These floras were segregated into four major phytogeographic provinces or floral realms: Angara, Euramerica, Cathaysia and Gondwana (Cocks & Torsvik, 2011; Oshurkova, 1996; Pfefferkorn & Wang, 2016; Sunderlin, 2010; Vai, 2003; Wagner, 2003). Euramerica, Gondwana, and Angara have distinct differences in their terrestrial plants, and although Euramerican and Angaran provinces shared similar palaeoecologies and biomorphs, these palaeoprovinces developed different floral assemblages and coal forming plants (Oshurkova, 1996). Euramerica was characterized by tropical to subtropical climatic conditions in low altitudes and its environments were dominated by lycopsids. In contrast, Angaran landscapes were typically dominated by *Cordaites,* which developed in a colder climate associated with higher altitudes, particularly in Siberian regions (Oshurkova, 1996; Wagner, 2003). More conclusive floral signatures are based on a large number of species and genera replaced by endemic plants in both provinces (Oshurkova, 1996; Wagner, 2003).

Distributed among several floristic realms, equisetaleans have a very broad geographic distribution (Boureau, 1964; Elgorriaga *et al.*, 2015). Due to this wide range, many equisetaleans developed in highly restricted environments with unique ecological conditions, leading to endemic species with characteristic morphologies (Boureau, 1964; Naugolnykh, 2002; Oshurkova, 1996; Verbitskaya & Radchenko, 1968; Weber, 2008).

In 1828, Brongniart described the family Phyllothecaceae based on the fossilized vegetative parts of the *Phyllotheca* genus (Brongniart, 1828; Roesler *et al.*, 2008). Phyllothecaceae *sensu lato* comprises two families: Gondwanostachyaceae *sensu stricto* and Tchernoviaceae *sensu stricto*, two biologically and phytogeographically distinct groups (Meyen, 1967). The two families have very distinct reproductive structures but have similar *Phyllotheca*–type foliage (Boardman & Iannuzzi, 2010; Cúneo & Escapa, 2006; Meyen, 1967, 1969, 1971, 1987; Roesler *et al.*, 2008; Srivastava & Agnihotri, 2010; Weber, 2008). Since both groups arose in places with similar ecological conditions (Gondwana and Angara, respectively), this homoplasy is likely due to convergent evolution (Meyen, 1967, 1987; Naugolnykh, 2002; Roesler & Iannuzzi, 2012; Taylor *et al.*, 2009, p. 368), which can mask the true phylogenetic relation of the two families (Cúneo & Escapa, 2006; Meyen, 1987).

The presence of this taxon in DCB may suggest distant migrations of typical Gondwanan and Angaran floras to the Euramerican province. Naugolnykh & Uranbileg (2018) documented a large-scale floral migration between Angaran and Gondwanan floral realms and proposed the existence of a migration gateway between Gondwana and southern Asia in the Middle Permian. This might suggest a similar explanation for the Gondwanan elements (like *Phyllotheca*) found in the Euramerican realm. However, this scenario seems unlikely due to the palaeoclimatic and palaeontological differences between the realms (Wagner, 2003), which suggests it might be a form of convergent evolution. The presence of similar characteristics in floras of different realms has been justified as convergent evolution before, largely due to the different types of fruiting bodies (Archangelsky & Arrondo, 1969; Asama, 1969; Meyen, 1969, 1971, 1987; Srivastava & Agnihotri, 2010).

Assemblage

Research regarding this new assemblage is on its beginning stages, however a few tentative remarks can be made. Since the results are so preliminary a few specimens have only been identified to the genus level. These generic IDs were largely based on background knowledge and less so on comparison with existing material or illustrations.

Conclusion

In this thesis, a new gymnosperm, *Lesleya ceriacoi* sp. nov., and a new equisetalean, *Phyllotheca douroensis* sp. nov., are presented, as well as preliminary findings of a new fossil assemblage from the DCB.

Lesleya ceriacoi sp. nov., a 303-million-year-old fossil of a previously unknown gymnosperm species from the Upper Pennsylvanian of Portugal, was rediscovered in the historical herbarium collection of the Museu de História Natural e da Ciência da Universidade do Porto (MHNC-UP). It displays a sophisticated leaf shape with novel xeromorphic morphological traits for its genus. This discovery provides valuable insights into the morphological and ecological adaptations of Euramerican drought-tolerant floras to the intramontane environments within central tropical Pangea. These adaptations occurred during a climate transition interval at the end of the Late Pennsylvanian (Gzhelian). Furthermore, the discovery of this new species indicates that the genus was much more diverse than presently understood from its spotty fossil record.

Phyllotheca douroensis sp. nov. is a new equisetalean from the Early Stephanian C. As an element of the Gondwanan flora, the presence of this genus might suggest a migration from Gondwana to Euramerica. However, this seems unlikely due to the palaeoclimatic differences between the realms. Hence, the similarities between *Phyllotheca douroensis* sp. nov. and Gondwana flora suggest it is a case of convergent evolution.

Additionally, a more thorough study of the new assemblage presented here, which has already yielded a new endemic species for the DCB, is already underway. A tentative description of *Sphenopteris teixeirae* sp. nov. is provided. The specific epithet of this new taxon was dedicated to Carlos Teixeira, one of the most important figures in Portuguese geosciences.

These three new taxa (one from a historical collection and two from relatively recent excavations during fieldwork) highlight the need to not only continue collecting specimens in the field and exploring outcrops but also the importance of museum collections. A well maintained and organized collection is an open door to a myriad of new taxa; and the steady incorporation of new material, whether through institutional excavations or through donations by researchers or amateur palaeontologists, is only going to increase the scientific value of the collection.

Finally, latex moulds and casts are discussed; they have been a staple of palaeontological studies for nearly a century, and with good reason: they continue to supply researchers with valuable insights. Latex moulds are a valuable addition to any palaebotanist's toolkit, even though, like any other method, they have downsides.

Depending on the objective, latex moulding can take many different forms. Researchers can perceive a greater number of diagnostic traits in poorly preserved fossils (ultimately the purpose of a latex mould in this context), which is critical for taxonomic descriptions, particularly in potential type specimens. Even a preliminary "latex peel" improves the clarity of a fossil specimen significantly. As such, this has the potential to lead to a slew of new discoveries and advancements in the field.

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Plates

Plate 1 — Holotype MHNCUP/PAB-29a of *Lesleya ceriacoi* sp. nov. A: Specimen of a lower-to-middle part of a leaf with straight margins towards leaf base, showing a deep laceration on the lamina (white dashed rectangular box). B: Enlargement of top part of specimen in (A), displaying margins with discrete to deep lacerations (white/black dashed rectangular boxes). C: Enlargement of lower/middle part of specimen in (A), exhibiting a deep laceration on blade (white dashed rectangular box). Scale bars: 20 mm. Adapted from Correia *et al.* (2022).

Plate 2 — Paratype MHNCUP/PAB-29b of *Lesleya ceriacoi* sp. nov.; early Gzhelian, Douro Carboniferous Basin (Portugal). A: Specimen of an upper part of a leaf with a nearly complete acute leaf apex, showing serrate and lacerate margins. B: Enlargement of top part of specimen in (A), displaying serrate margins on leaf apex (black dashed rectangular boxes) and deep/discrete lacerations on the lamina (white dashed rectangular boxes). C: Enlargement of serrate margin on leaf apex in (B), showing six leaf teeth (white arrows). D: Enlargement of serrate margin on leaf apex in (B), showing two leaf teeth (white arrows) and one discrete laceration (black dashed rectangular box). Scale bars: 20 mm (A and B); 10 mm (C and D). Adapted from Correia *et al.* (2022).

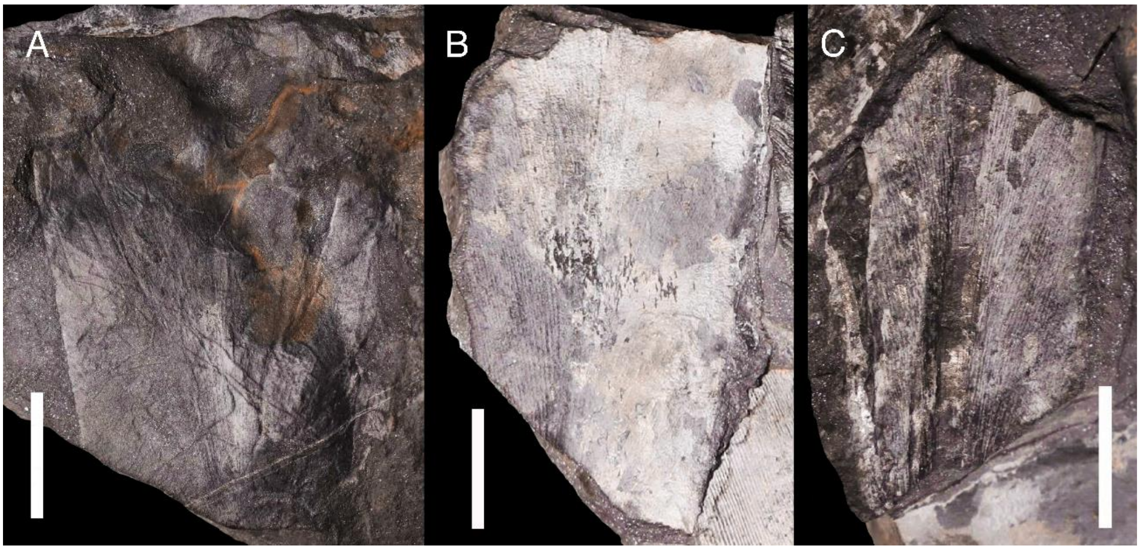

Plate 3 — Paratypes of *Lesleya ceriacoi* sp. nov.; early Gzhelian, Douro Carboniferous Basin (Portugal). A: Specimen of a middle-to-upper part of a leaf showing deeply lacerated margins (MHNCUP/PAB-29c); specimen preserved at the back side of fossil sample (Fig. 1B). B: Specimen of a middle/lower part of a leaf (MHNCUP/PAB-524 29d). C: Specimen of a lower part of a leaf (MHNCUP/PAB-29e). Scale bars = 20 mm. Adapted from Correia *et al.* (2022).

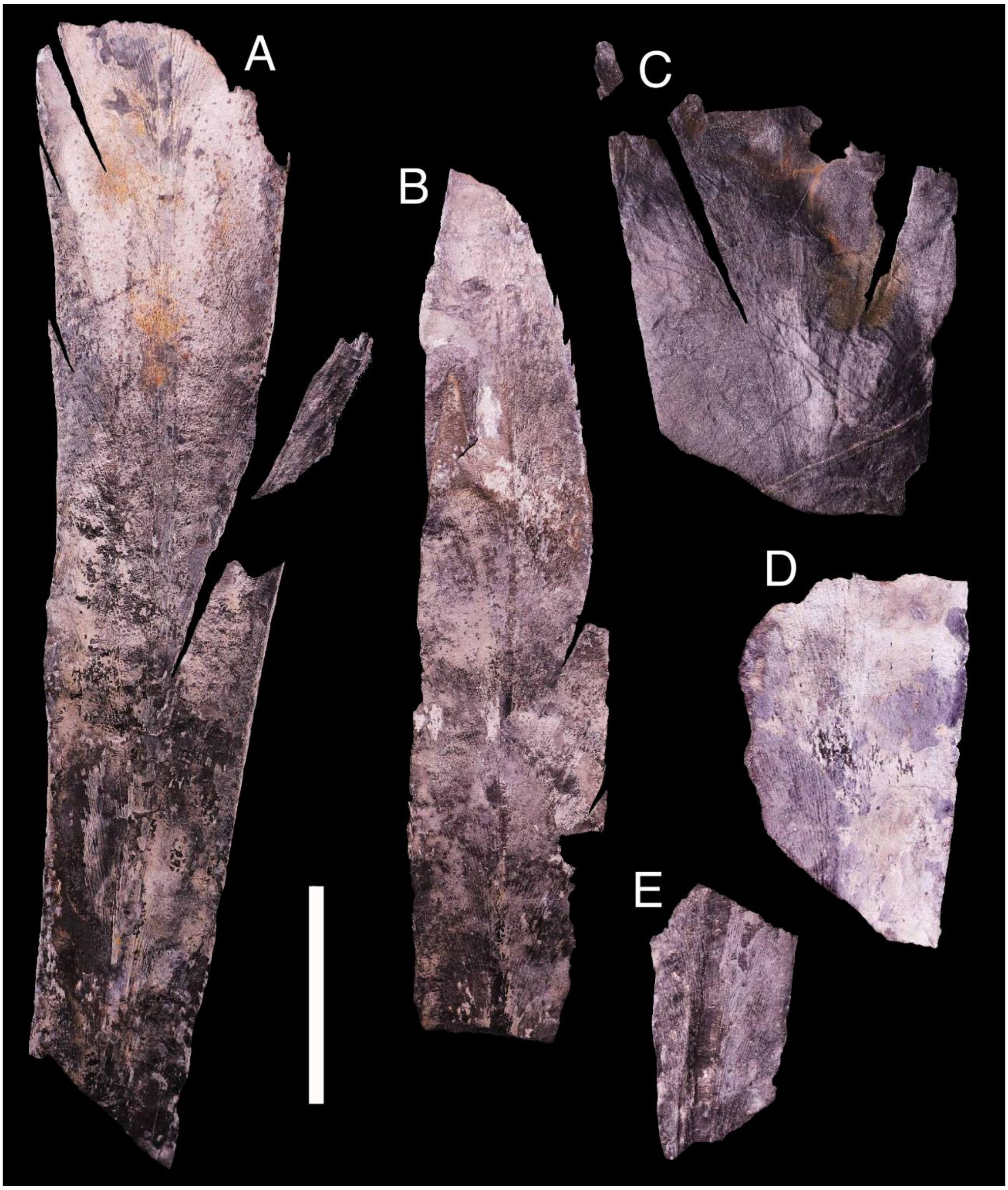

Plate 4 — Different preserved leaf parts of *Lesleya ceriacoi* sp. nov. A: holotype MHNCUP/PAB-29a. B: Paratype MHNCUP/PAB-29b. C: Paratype MHNCUP/PAB-29c. D: Paratype MHNCUP/PAB-29d. E: Paratype MHNCUP/PAB-29e. Scale bars = 50 mm. Adapted from Correia *et al.* (2022).

Plate 5 — Suggested reconstruction of the plant architecture of *Lesleya ceriacoi* sp. nov. described as a probable primitive cycad with affinities to the arborescent pteridosperms, based on the different leaf parts. Artistic work by Vitor Silva, adapted from Correia *et al.* (2022).

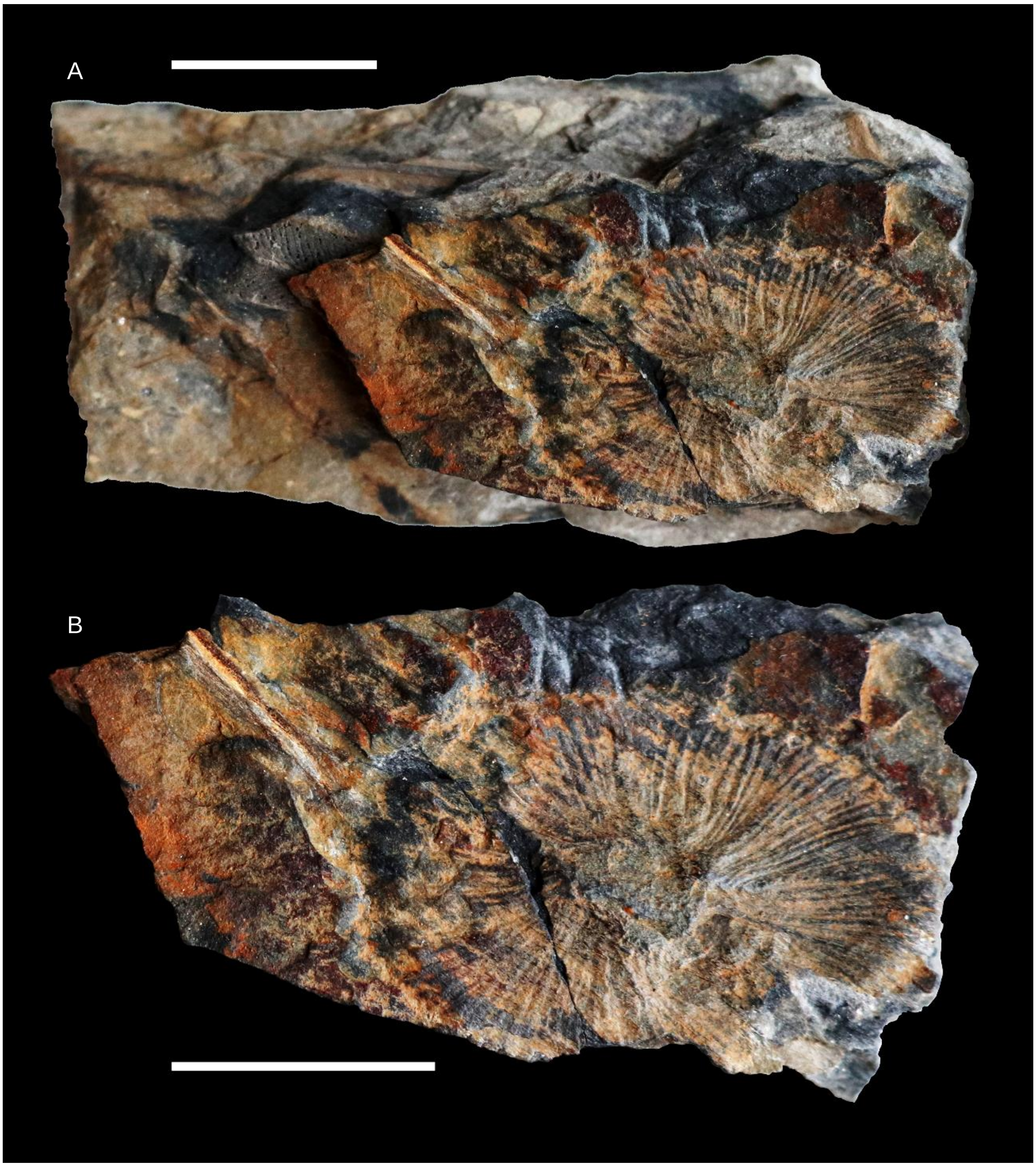

Plate 6 — *Phyllotheca douroensis* sp. nov. Scale bars: 10mm. A: Holotype specimen MHNCUP/PAB-346 (previously MHNCUP/PAB-130919) characterised by a leaf whorl, probably basal, attached to a broad axis. B: Detail of holotype.

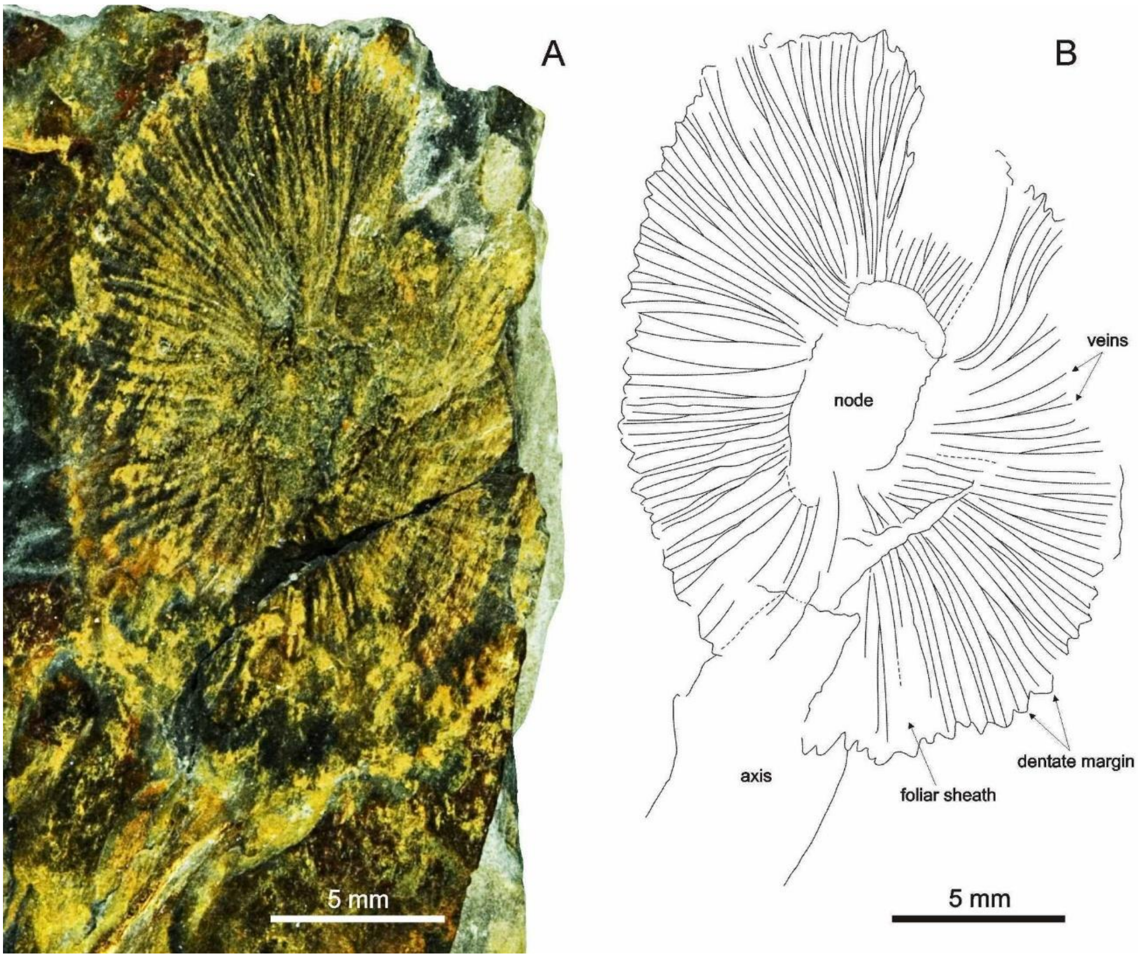

Plate 7 — A: Close up the holotype of *P. douroensis* sp. nov. B: Camera-lucida hand drawing of holotype, highlighting the large and well-developed disc shaped foliar sheath of the new species. Photography and illustration by Pedro Correia.

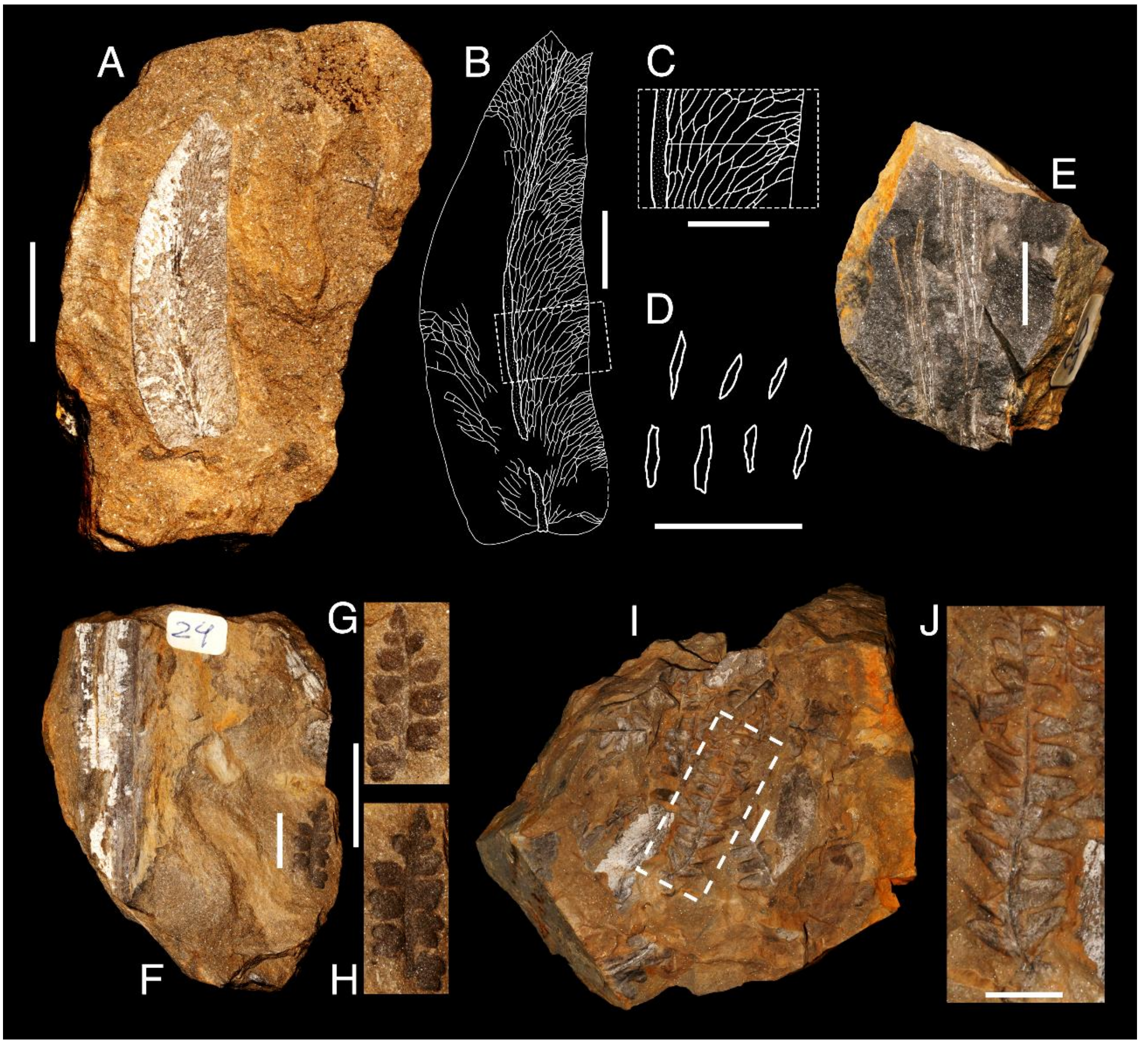

Plate 8 — New floral assemblage Pteridospermopsids, scale bars: 10mm. Stickers on the specimens are numbers attributed during field work. A: *Linopteris* cf. *neuropteroides*, MHNCUP/PAB-466. B: Illustration of (A). C: Detail from white square of (B), white transversal bar is used to count the number of cells. D: Cell shapes. E: Fossil roots, MHNCUP/PAB-462. F: *Eusphenopteris nummularia*, MHNCUP/PAB-461a. G: Detail from MHNCUP/PAB-461b, counter mould of (F). H: Detail from (F). I: *Gondomaria discreta* (white square), MHNCUP/PAB-464. J: Detail from (I).

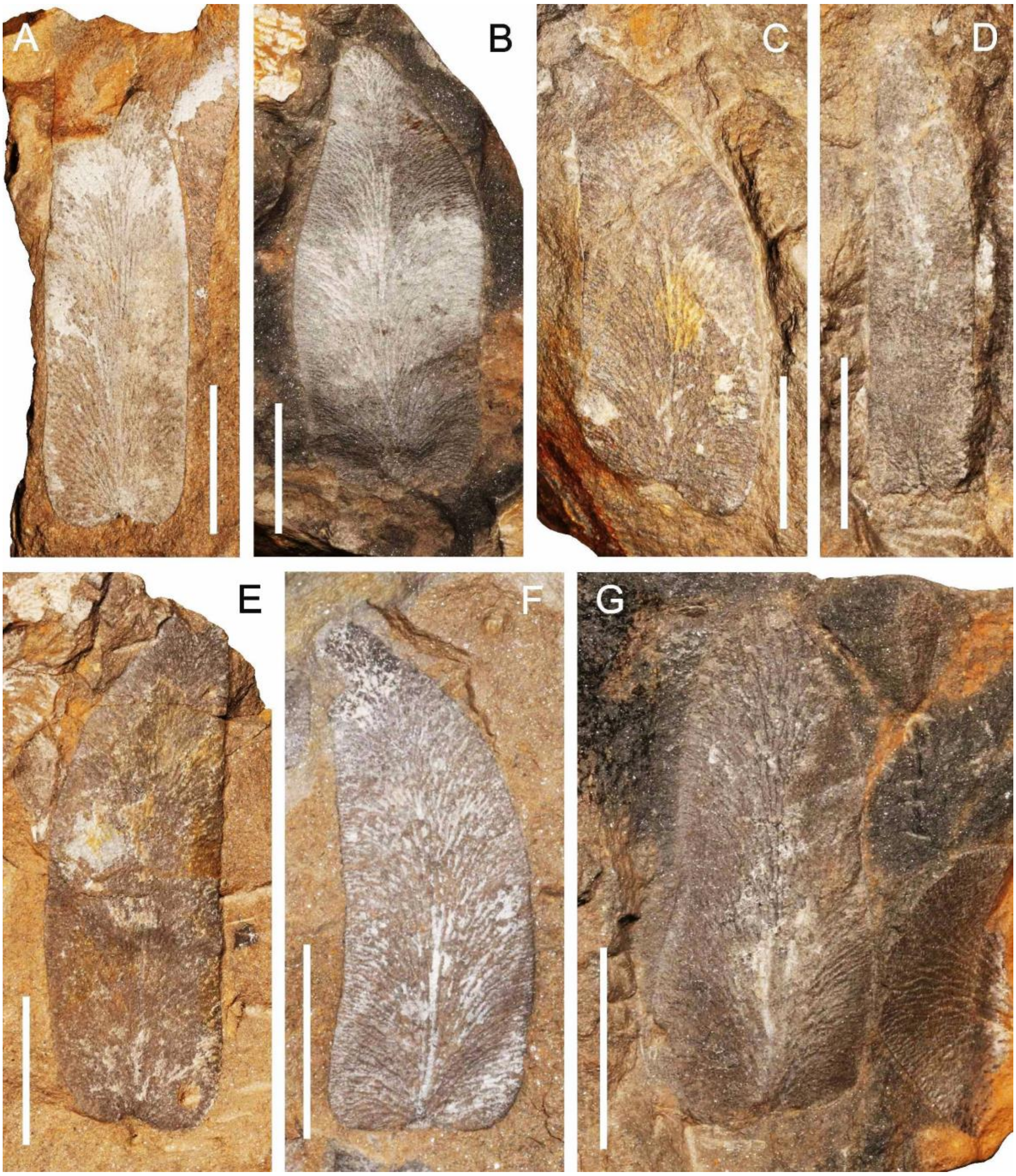

Plate 9 — Additional material of *Linopteris* cf. *neuropteroides* from the new fossil assemblage. Scale bars: 10mm. Plate by Pedro Correia.

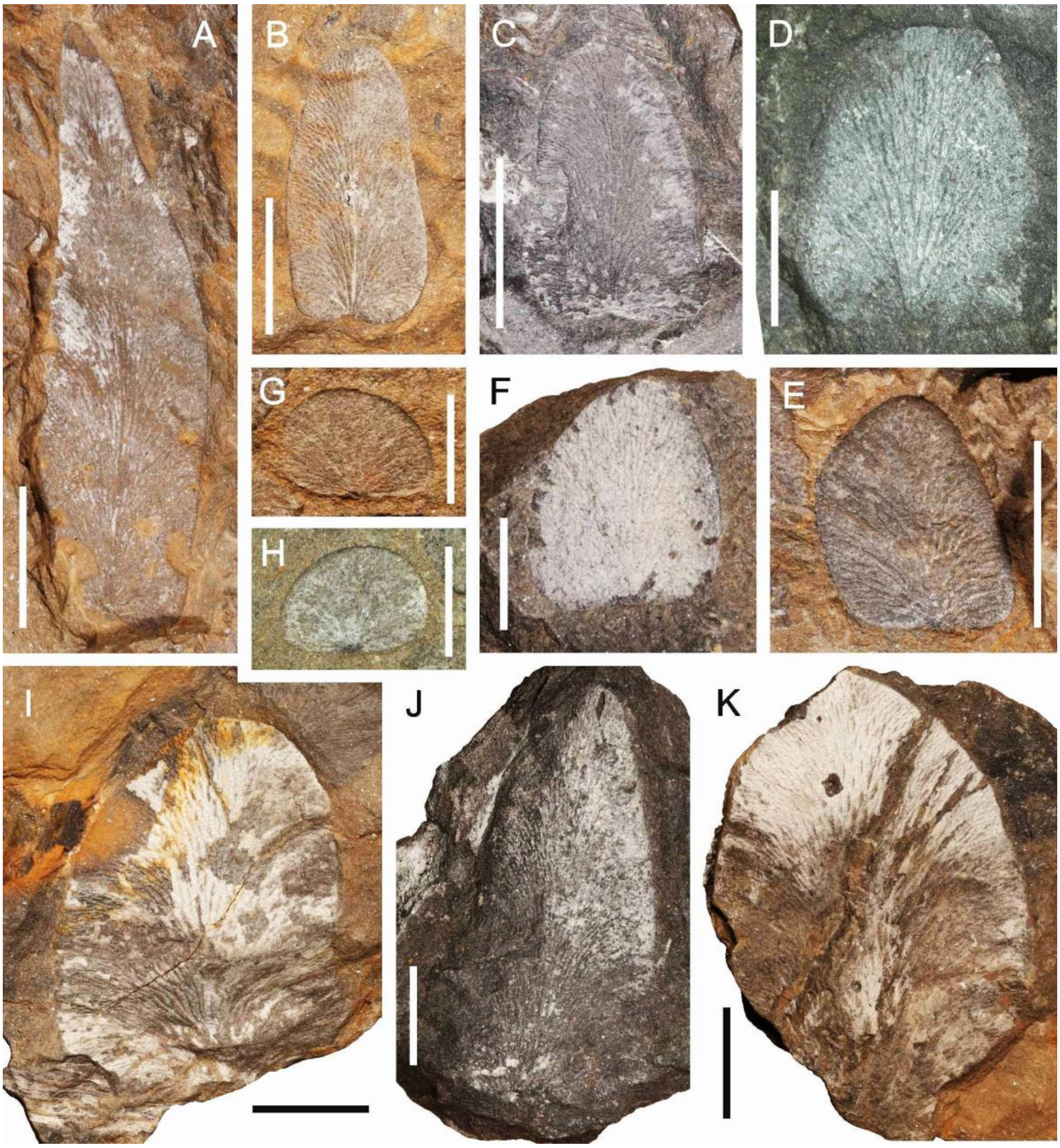

Plate 10 — Additional material of *Linopteris* cf. *neuropteroides* from the new fossil assemblage. Note the variation in morphology. Scale bars A-C, I-K: 10mm. Scale bars D-H: 5mm.

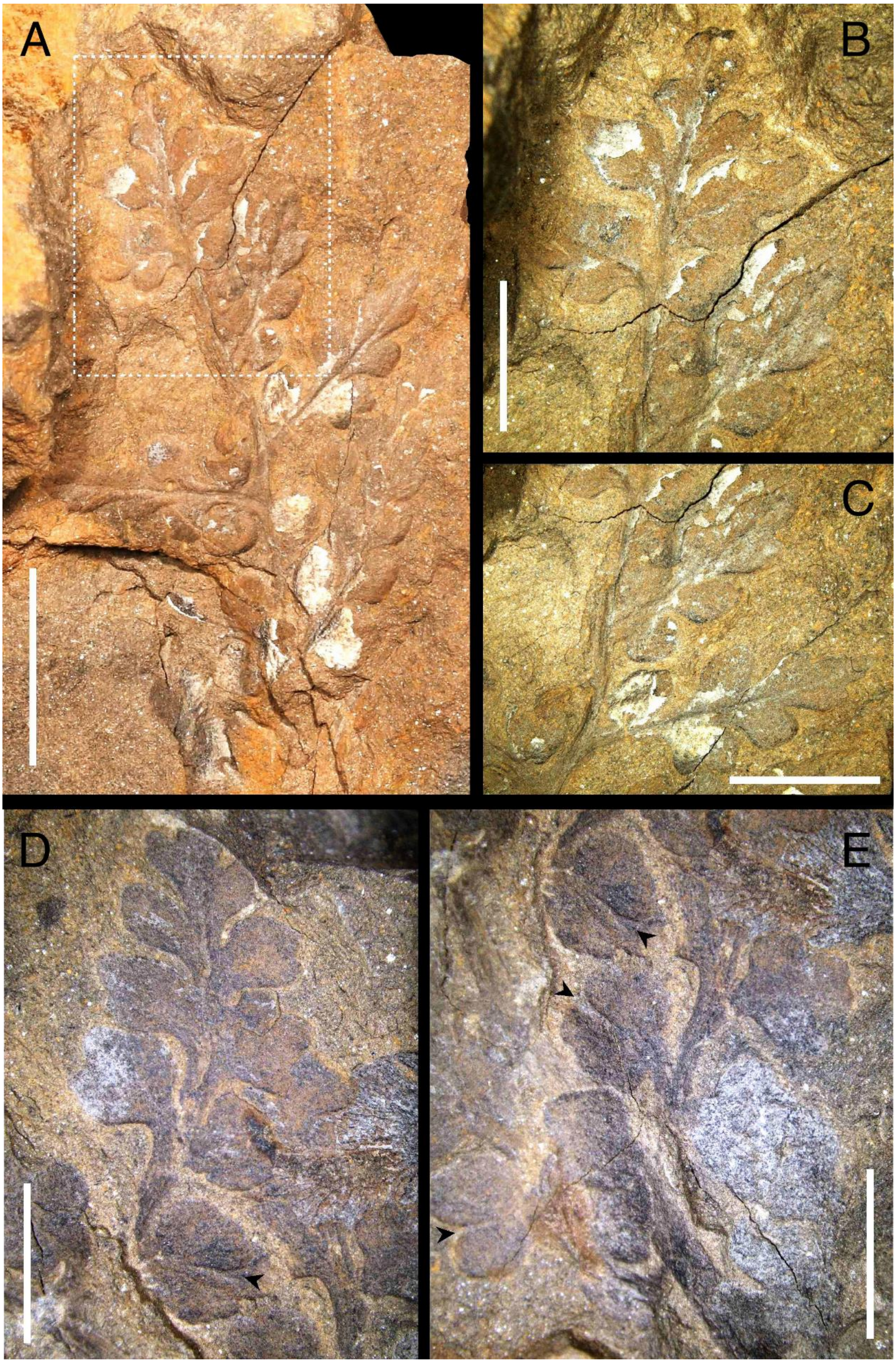

Plate 11 — Additional material of *Eusphenopteris nummularia* from the new fossil assemblage. A: *Eusphenopteris nummularia*, scale bar: 10mm.B: Detail of (A), scale bar: 5mm. C: Detail of (A), scale bar 5mm. D, E: Detail of pinnules *nummularia*, note the incised basal lobes (arrows), scale bars: 5mm. Plate by Pedro Correia and Catarina Barbosa.

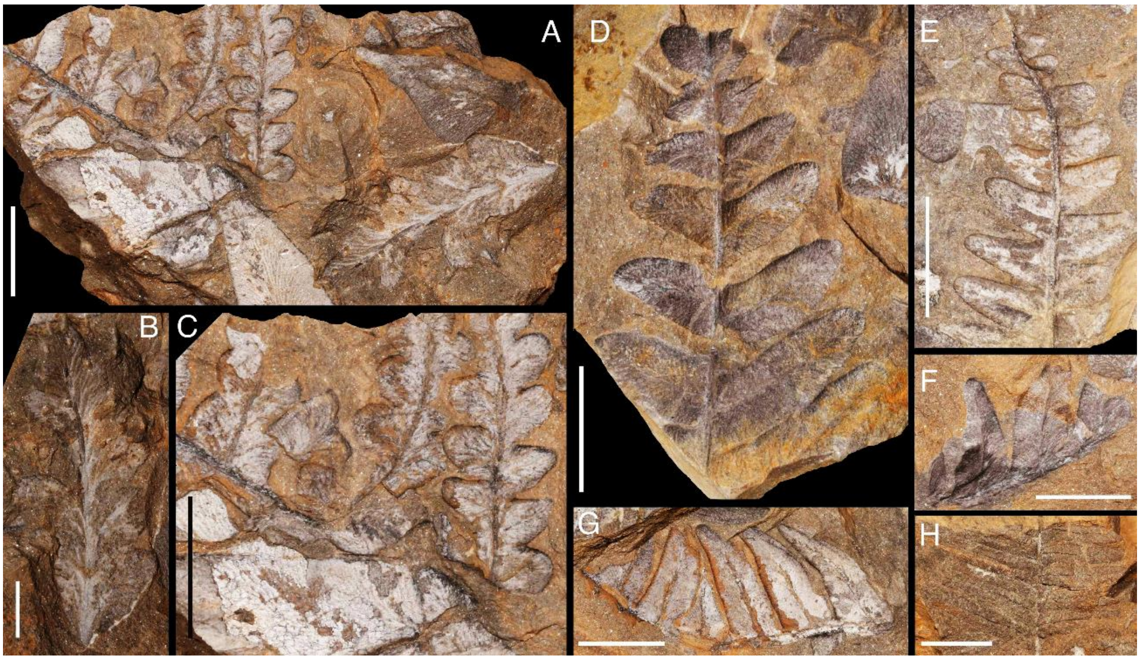

Plate 12 — Additional material of *Gondomaria* cf. *discreta* from the new floral assemblage. Scale bar A, C-H: 10mm. Scale bar B: 10mm. Plate by Pedro Correia and Catarina Barbosa.

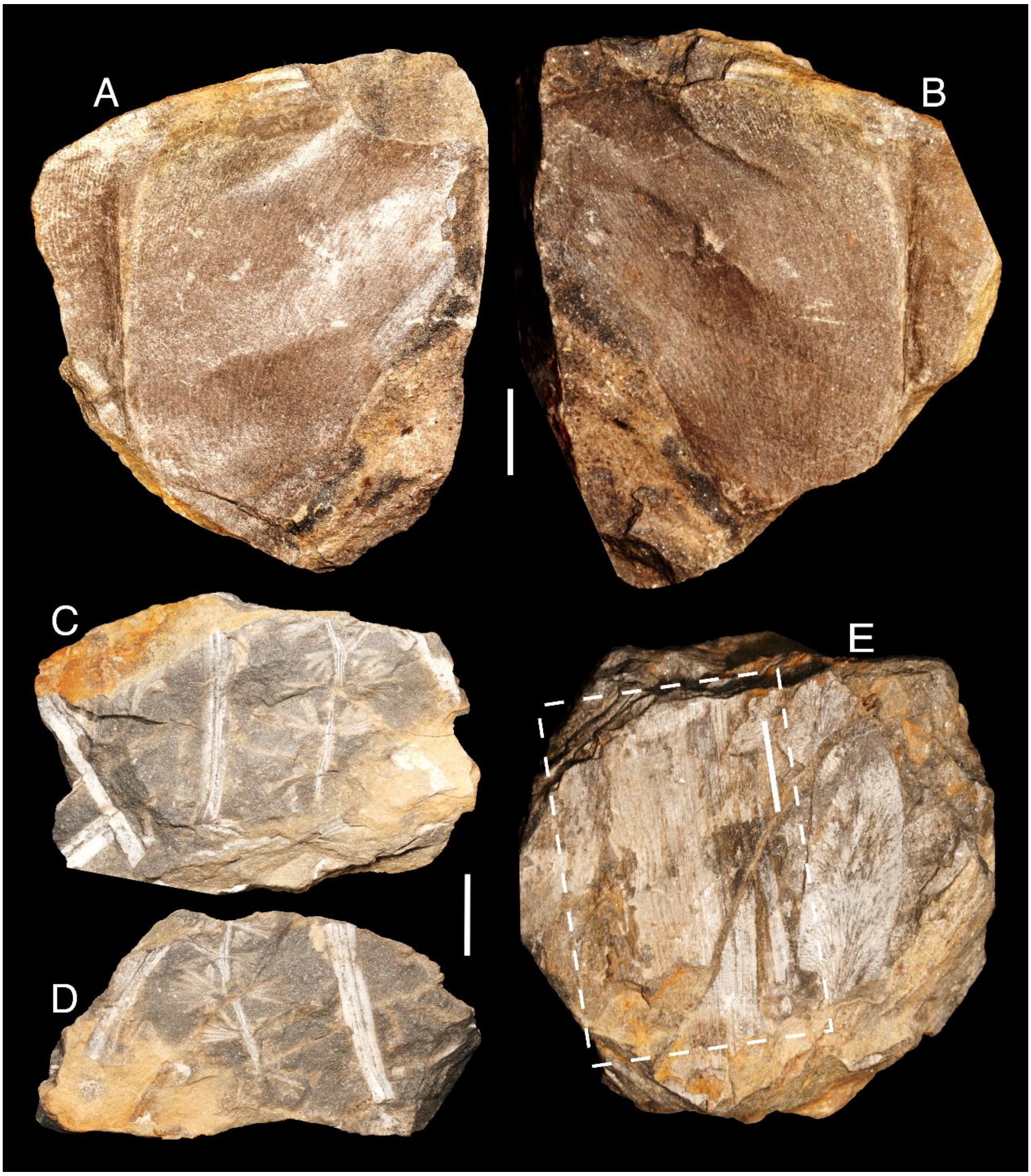

Plate 13 — Floral assemblage specimens, scale bars: 10mm. A: *Cordaites* sp., MHNCUP/PAB-463a, mould. B: *Cordaites* sp., MHNCUP/PAB-463b, counter mould. C: *Sphenophyllum costae*, MHNCUP/PAB-465a. D: *Sphenophyllum costae*, MHNCUP/PAB-465b. E: *Cordaites* sp. (white square) MHNCUP/PAB-460.

Plate 14 — Floral assemblage specimen MHNCUP/PAB-468, scale bars: 10mm. A: *Sphenophyllum majus.* B: Detail from (A). Plate by Pedro Correia.

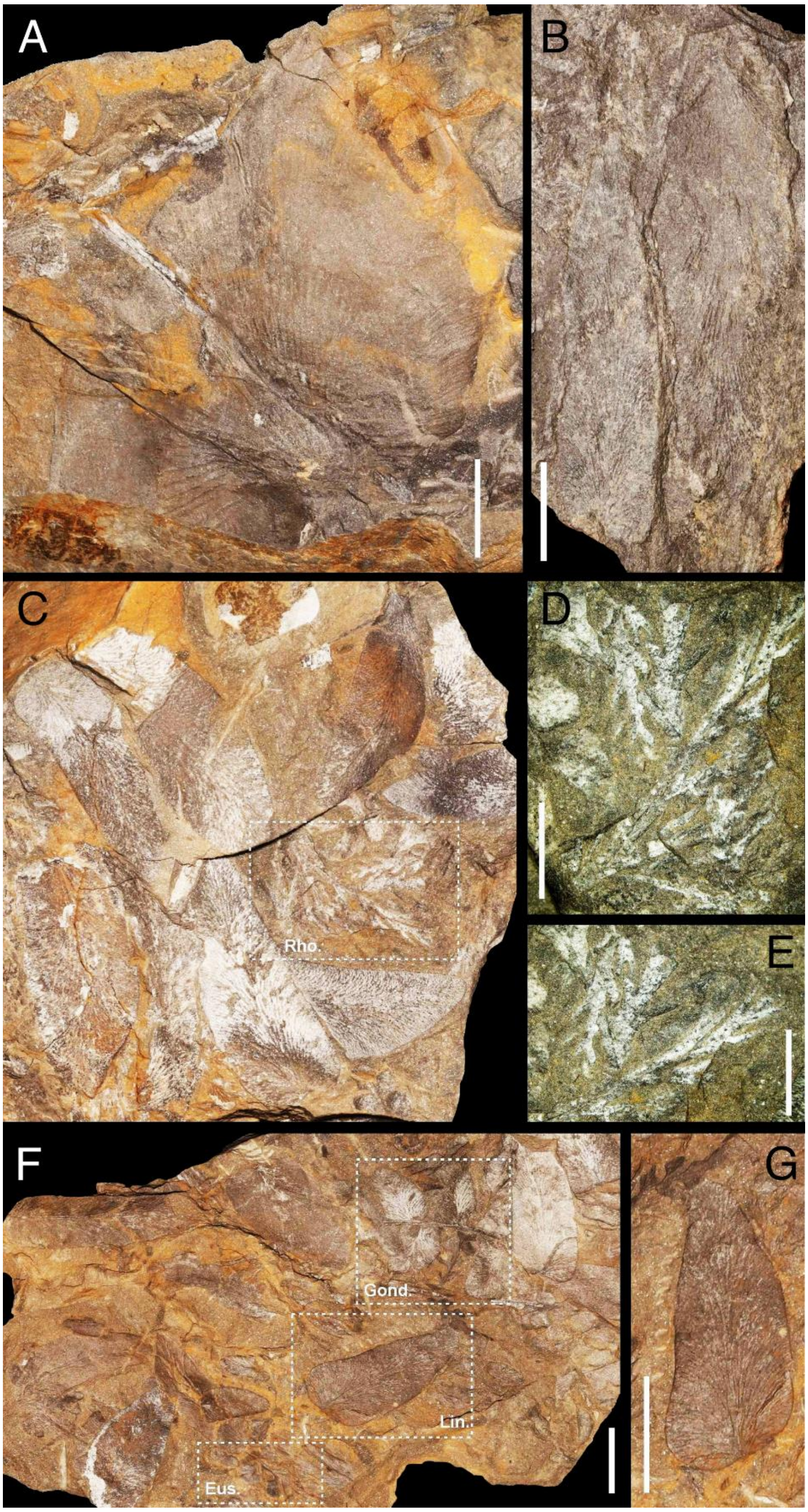

Plate 15 — Floral assemblage specimens. A: *Cyclopteris sp.,* scale bar: 10mm. B: *Linopteris* cf. *neuropteroides*, scale bar: 10mm. C: *Linopteris* cf. *neuropteroides*, includes *Rhodeopteridium* (Rho). D: Detail of (C), *Rhodeopteridium* sp., scale bar: 7,5mm. E: Detail of (D), scale bar: 5mm. F: *Gondomaria* cf. *discreta* (Gond.), *Linopteris* cf. *neuropteroides* (Lin.) and *Eusphenopteris* (Eus.). G: Linopteris cf. neuropteroides, detail from (F). Plate by Pedro Correia and Catarina Barbosa.

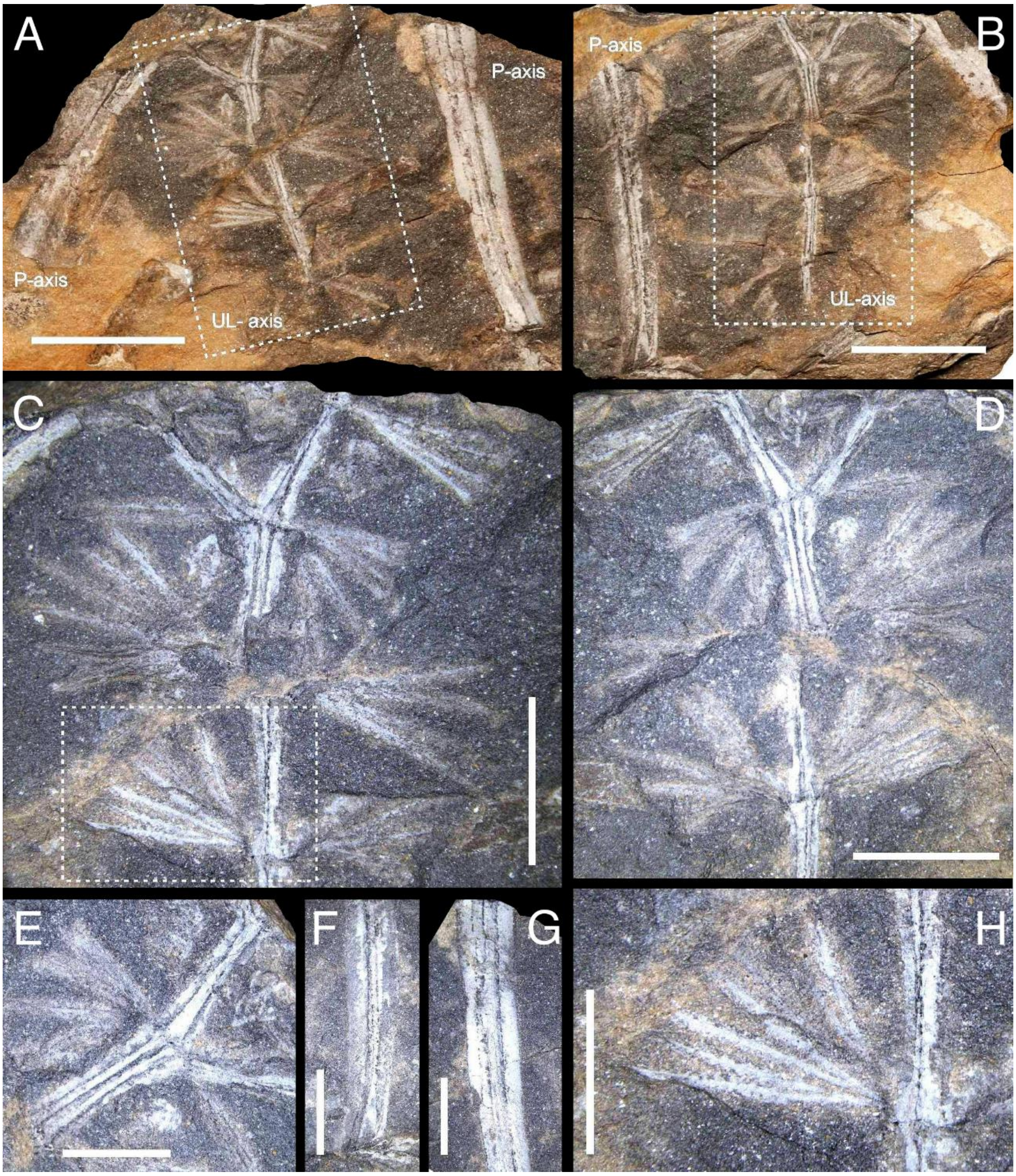

Plate 16 — Detail of *Sphenophyllum costae*, MHNCUP/PAB-465. A: MHNCUP/PAB-465b, two primary axis and one ultimate axis, scale bar: 10mm. A: MHNCUP/PAB-465a, one primary axis and one ultimate axis, scale bar: 10mm. C: Detail from (A), see well preserved whorl in white rectangle (H), scale bar: 5mm. D: Detail from (B), scale bar: 5mm. E: Detail from (B), note the difference in ribbing in the axis, scale bar: 3mm. F: Detail of (A). G: Detail of (B). H: Detail of (C), scale bar: 3mm. Plate by Pedro Correia.

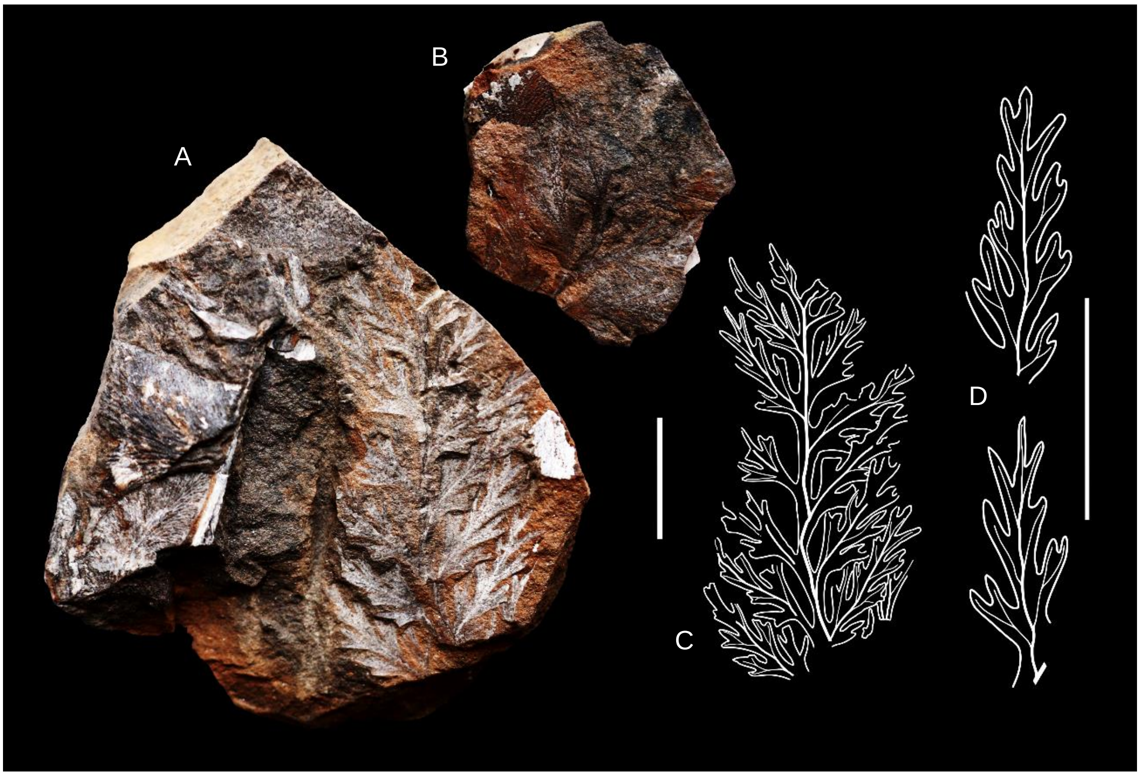

Plate 17 — Floral assemblage specimen. *Sphenopteris teixeirae* sp. nov. Scale bars: 10mm. A: Holotype MHNCUP/PAB-467a. B: Counter mould (paratype) MHNCUP/PAB-467b. C: Illustration of the specimen. D: Reconstruction of two pinnules.

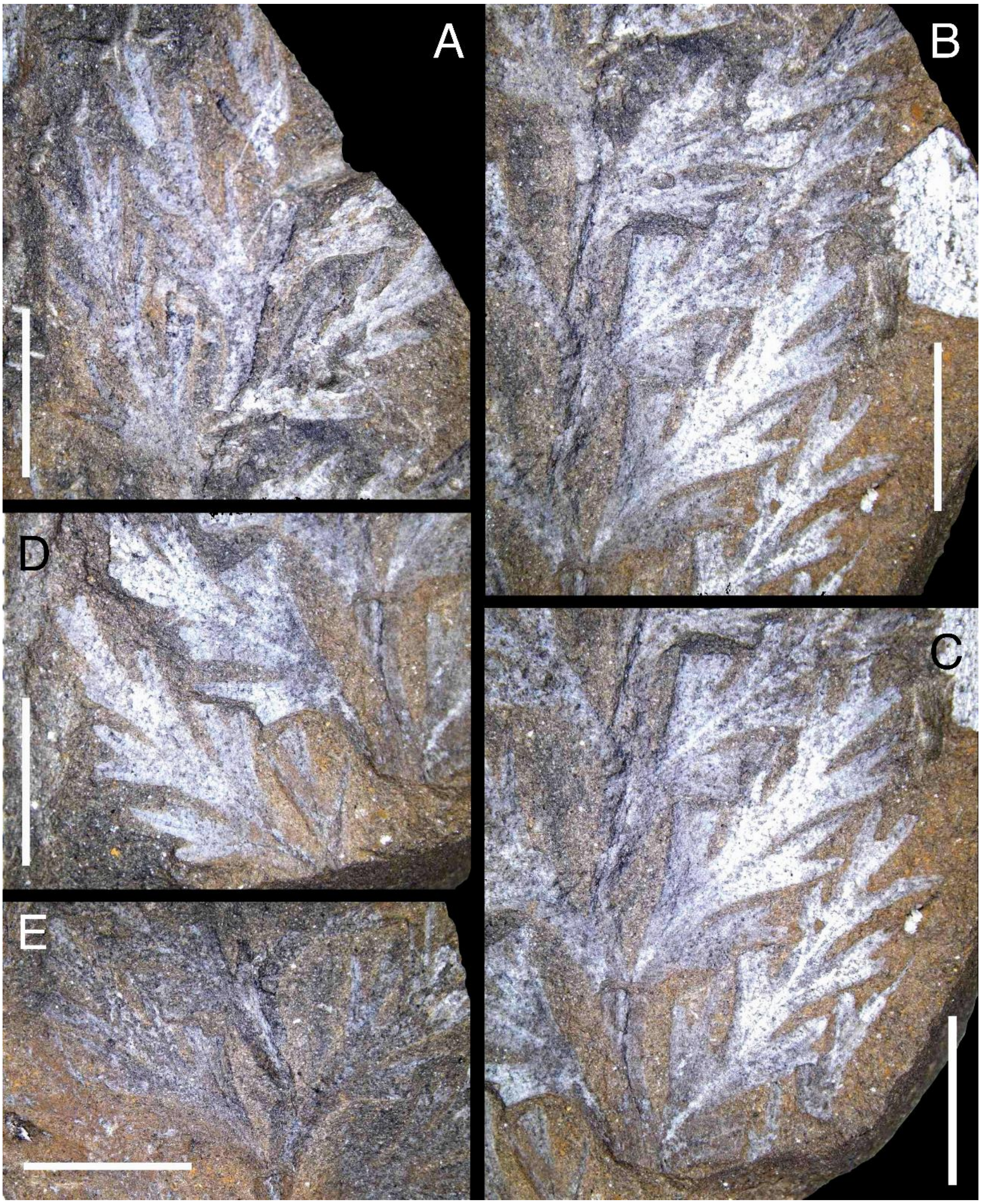

Plate 18 — Details of *Sphenopteris teixeirae* sp. nov., scale bars: 5mm. A-C: Details of holotype MHNCUP/PAB-467a. E: Detail of paratype MHNCUP/PAB-467b. Plate by Pedro Correia.

Annex 1 — *Lesleya* dichotomy key

1a — The margins are entire……………………………………2

1b — Margins not entire……………………………………9

2a — More than 40 veins per centimetre of margin……………………………………***L. doubingeria***

2b — Less than 40 veins per centimetre of margin……………………………………3

3a — Vein course strictly straight……………………………………***L. ensis***

3b — Vein course not straight……………………………………4

4a — number of veins per cm of the margin equal or lesser than 13……………………………………5

4b — Number of veins per cm of the margin is greater than 13……………………………………7

5a — Number of veins per cm of the margin equal or smaller than 8……………………………………***L. simplicinervis***

5b — Number of veins per cm of the margin greater than 8……………………………………6

6a — Leaf base cuneate……………………………………***L. iberiensis***

6b — Leaf base not cuneate……………………………………***L. gimmi***

7a — Leaf width equal or greater than 80mm……………………………………***L. grandis***

7b — Leaf width smaller than 80mm……………………………………8

8a — Number of veins per cm of margin greater than 20……………………………………***L. cheimarosa***

8b — Number of veins per cm of margin smaller than 20……………………………………9

9a — Veins fork only once……………………………………***L. angustai***

9b — Veins fork more than once……………………………………***L. cocchi***

10a — Margin strictly dentate……………………………………11

10b — Margin not strictly dentate……………………………………***L. ceriacoi sp. nov.***

11a — Vein course strictly straight……………………………………***L. delafondi***

11b — Vein course not straight……………………………………**L. weilerbachensis**

Annex 2 — Key morphological features of *Lesleya ceriacoi* sp. nov.

Table 1 — Comparison of the key morphological features of *Lesleya ceriacoi* sp. nov. with the other known species for the genus. Adapted from Correia *et al.* (2016, table 1), according to descriptions and illustrations provided in Remy and Remy (1975).

Characters	***Lesleya grandis* Lesquereux, 1880**	***Lesleya delafondii* Zeiller, 1890**	***Lesleya ensis* Zeiller, 1888**	***Lesleya weilerbachensis* Remy & Remy 1975**	***Lesleya iberiensis* Correia & al., 2016**	***Lesleya ceriacoi* sp. nov.**	***Lesleya gimmii* Remy & Remy, 1978**	***Lesleya angusta* Grand'Eury, 1877/1890**	***Cannophyllites (Lesleya) simplicinervis* Grand'Eury, 1890**	***Lesleya cocchii* De Stefani, 1901**	***Lesleya cheimarosa* Leary & Pfefferkorn, 1977**	***Lesleya microphylla* Lesquereux, 1884**
Leaf shape	Lanceolate	Lanceolate	Lanceolate	Lanceolate	Lanceolate	Lanceolate	Narrow–elliptical	Lanceolate	?Spatulate	?Lanceolate	Lanceolate	Oval–oblong
Leaf length	>190(220) mm	>200 mm	>155 mm	> 230 mm	>225 mm	550–600 mm	130 mm	235 mm	110-?300 mm	300-500 mm	200 mm	40 mm
Leaf width	83 (80) mm	70 mm	40 mm	66 mm	50 mm	64 mm	35 mm	27 mm	28-?80 mm	36 mm	40 mm	16 mm
Form of leaf apex	Obtuse	?obtuse	?obtuse	Obtuse	?	Acute (subacute)	?	Obtuse	Obtuse - rounded	?	Acute to attenuate	Obtuse
Form of leaf base	Cuneate	?	?	Cuneate	Cuneate	Narrowed (Acute)	Acute	Obtuse	Sub-cordate	?	Accuminate (acute)	Decurrent, shortly auriculate
Leaf margin	Entire to lacerate/ pinnatifid	Serrate	Entire	Dentate (serrate)	Entire	Serrate to deeply lacerated	Entire	Entire	Entire	Entire	Entire	Entire
Midrib width in the basis	2 mm	?	2 mm	?	1–3 mm	4 mm	5 mm	5 mm	> 3 mm	?	2.0	?
Midrib width in the middle	1 mm	1–2 mm	1 mm	1–2 mm	2–3 mm	2–3 mm	< 5 mm	2 mm	2.5–5 mm	2.0	0.7	?

Midrib width in the apex	Decurrent until the end of apex?	Divided in individual veins? (missing tip)	Divided in individual veins	Divided in individual veins	?	Divided in individual veins	?Into veins	1 mm; spread into veins	Divided into veins	?	divided into veins	?
Lateral veins per 1 cm of the margin	16–20; 25–30	8–12	8–12	12–20	10–13	10–12	10–13	15–17	7–8	circa 18	24–36	40
Angles of lateral veins and leaf margin	?	?	?	9–10°; basis 13	variable depending on position (5°–35°)	20–23°	34–52°	55–60°	34–38°	40–45°	40–70°	50°
Angles of lateral veins and midrib	50–60°	26°	10–22°	13–14°; apex 11°	7°–15°	5°–14°	Nearly parallel (6°)	25–30°	13–25°*	15–30°*	10–20°	Very acute
Number of vein forking	2–3x	3–?4x	2–3x	3–(4)x	1–2x	3x	3x (near midrib)	1x (near midrib)	0–(1)x	2–3x	1–2x	?
Vein course	Till 1/3 equally to the margin bent, but apically more straight	Straight	Straight	Straight, only near the margin slightly bent	slightly curved	slightly curved	Oblique course from midrib and then straight to the margin	Slightly oblique from midrib to the margin	Very slightly obliquely from midrib to the margin	Obliquely from midrib slightly curved and nearly straight to the margin	Slightly S-shaped	?
Tooth length	No	0.5–1.0 mm	No	1.5–2.5 mm	No	1.5–5.5 mm	No	No	No	No	No	No

Number of teeth per 1 cm	No	8	No	4.-5	No	2	No	No	No	No	No	No
							15 ribs on midrib	According to Grand'Eury (1890)	*25° smaller pinnule	Zeiller, 1906 - small fragment		
										*slightly different angle on both sides of midrib		
Locality	USA	Autun, France	France	Weilerbach, Germany	Douro Basin, Portugal	Douro Basin, Portugal	Germany	Gard, France	Gard, France	Italy; Blanzy, France	Illinois, USA	USA
Age	Duckmantian	Asselian	Gzhelian - Asselian	Bolsovian	Gzhelian	Gzhelian	Asselian	Barruelian - Stephanian B	Barruelian - Stephan B	Stephanian B - Asselian	Namurian B-C	late Stephanian C to late Autunian

Annex 3 — Barbosa *et al.*, in press. “*Phyllotheca douroensis* sp. nov., a new equisetalean fossil-species from the Douro Carboniferous Basin (Upper Pennsylvanian; NW Portugal): palaeobiogeographical, systematic and evolutionary implications”

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ARTÍCULO ORIGINAL

Phyllotheca douroensis sp. nov., a new equisetalean fossil-species from the Douro Carboniferous Basin (Upper Pennsylvanian; NW Portugal): palaeobiogeographical, systematic and evolutionary implications

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ABSTRACT

The first occurrence of the fossil-genus *Phyllotheca* (Equisetales) from the Carboniferous of Portugal is documented and its palaeobiogeographical, systematic and evolutionary significance is assessed. In this paper, we described this new equisetalean fossil as new species, *Phyllotheca douroensis* sp. nov., found in the Douro Carboniferous Basin (lower Stephanian C/lower Gzhelian, Upper Pennsylvanian), in northwestern Portugal. *P. douroensis* sp. nov. represents a convergent form of Phyllothecaceae sensu lato (comprises the Angaran Tchernoviaceae and the Gondwanan Gondwanostachyaceae) with closer affinities to Euramerican floral province.

KEYWORDS

Phytogeographic provinces (Floral Realms); Convergent evolution; *Phyllotheca*; Equisetales; Douro Carboniferous Basin; Lower Gzhelian (Upper Pennsylvanian)

1 Introduction

The global-scale changes in the Earth's climate of the late Palaeozoic due to the formation of supercontinent Pangaea had a key role for the global distribution of floras. These late Palaeozoic floras were segregated into four major phytogeographic provinces (Floral Realms) – Angara, Euramerica, Cathaysia and Gondwana (e.g., Oshurkova, 1996; Vai, 2003; Wagner, 2004; Sunderlin, 2010; Cocks & Torsvik, 2011; Pfefferkorn & Wang, 2016; Correia & Murphy, 2020; Correia *et al.*, 2021). The different "Floral Realms" show clear differences in their terrestrial plants which colonized in different palaeoclimates (e.g., Oshurkova, 1996; Wagner, 2004). Although they shared similar palaeoecologies, these palaeoprovinces developed different floral assemblages and coal forming plants (e.g., Oshurkova, 1996; Wagner, 2004). More conclusive floral signatures are based on a large number of species and genera replaced by endemic taxa in each of four floristic provinces (e.g., Oshurkova, 1996; Vai, 2003; Wagner, 2004; Srivastava & Agnihotri, 2010; Correia & Murphy, 2020; Correia *et al.*, 2021).

However, several convergent plant forms with strong morphological similarity have been documented among the different palaeoprovinces (e.g., Boureau, 1964; Naugolnykh, 2002; Boardmann & Iannuzzi, 2010; Srivastava & Agnihotri, 2010; Boardman *et al.*, 2016; Correia *et al.*, 2021). The late Palaeozoic equisetalean *Phyllotheca* (sensu Brongniart, 1828) is a fossil-genus that has been described for several plant groups of the Equisetales of similar foliage (*Phyllotheca*-type) with different phylogenetic affinities (e.g., Meyen, 1967, 1969, 1971, 1982, 1987; Cúneo & Escapa, 2006; Naugolnykh, 2002; Taylor *et al.*, 2009; Boardmann & Iannuzzi, 2010; Srivastava & Agnihotri, 2010; Boardman *et al.*, 2016; Correia *et al.*, 2021). *Phyllotheca* is a cosmopolitan taxon that was widespread across the Angaran and Gondwanan floral provinces during Carboniferous and Permian times (e.g., Townrow, 1955; Boureau, 1964; Meyen, 1969, 1971, 1982; Oshurkova, 1996; Mcloughlin *et al.*, 2005; Cúneo & Escapa, 2006; Taylor *et al.*, 2009; Srivastava & Agnihotri, 2010; Prevec *et al.*, 2010; Boardman *et al.*, 2016; Correia *et al.*, 2021). By contrast, there are other equisetaleans that occur only in restricted regions or in a specific province because of the restricted environmental, climatic and ecological conditions in which these plants lived. Such conditions led to origin to many endemic forms with singular morphological characteristics (e.g., Boureau, 1964; Verbitskaya & Radchenko, 1968; Oshurkova, 1996; Naugolnykh, 2002; Weber, 2008; Correia *et al.*, 2021).

In this paper, we report an enigmatic equisetalean fossil from Euramerican province with similar floral (morphological) characteristics to Gondwanan and Angaran provinces, found in the Douro Carboniferous Basin (DCB; lower Stephanian C/Gzhelian, Upper Pennsylvanian) in northwestern

Portugal (Fig. 1). Here, we describe this new fossil as *Phyllotheca*-like and assess its palaeobiogeographical, systematic and evolutionary significance with the potential floral endemism present in the DCB.

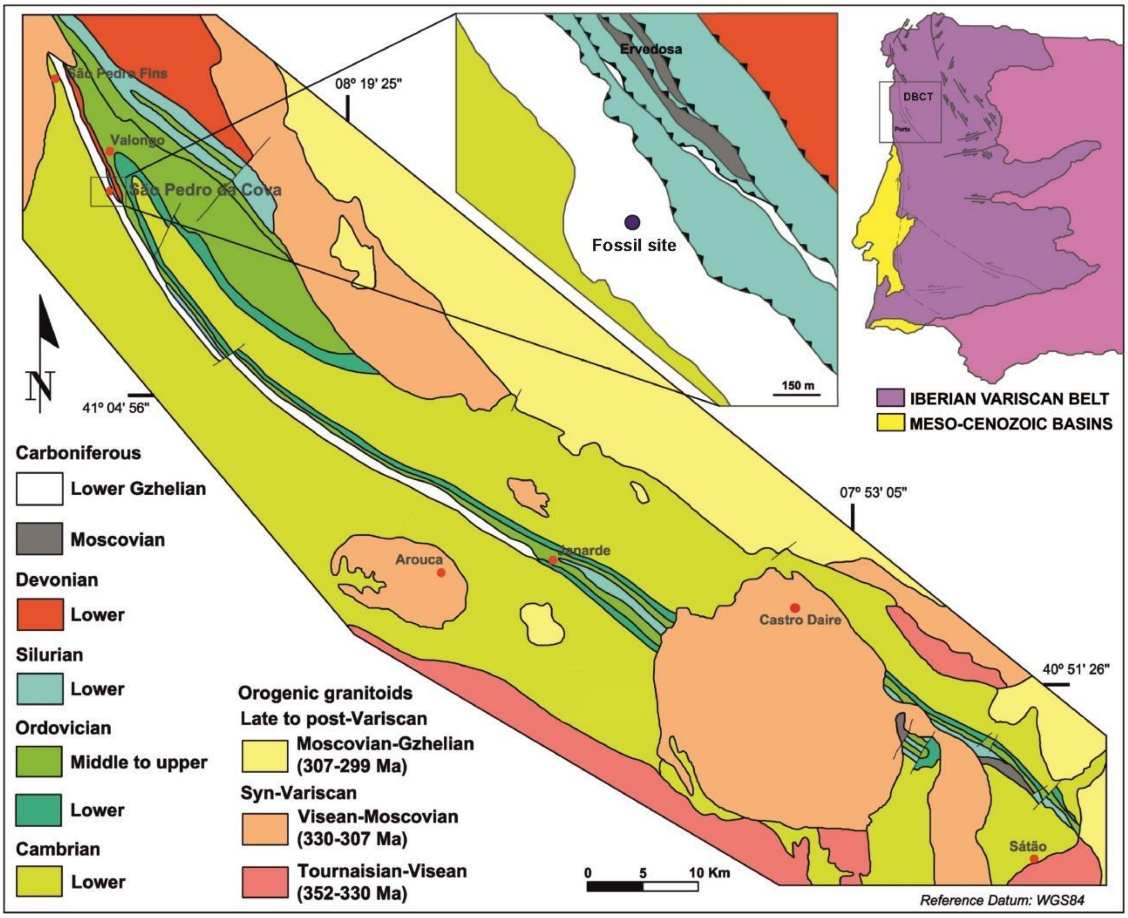

Figure 1. Regional geological setting of the Douro Carboniferous Basin (lower Stephanian C/lower Gzhelian, NW of Portugal). Geological map showing detailed geology of the São Pedro da Cova region with fossil site where was found *Phyllotheca douroensis* sp. nov. Modified from Correia *et al.* (2016, fig. 1).

2 Geological and palaeontological background

The DCB is a narrow (typically less than 1 km wide) sedimentary basin that occurs within the Douro-Beira Carboniferous Trough (DBCT), which is located within the Central Iberian Zone of the Variscan (or Hercynian) Chain of the Iberian Massif in northwestern Portugal (Fig. 1). The DBCT strikes approximately in a northwest to southeast direction and extends about 85 km from the localities of São Pedro Fins (Maia, NE Porto) to Janarde (Arouca). The DBCT is generally interpreted as a narrow pull-apart basin with a sinistral strike-slip component (Pinto de Jesus, 2001, 2003). Within the DBCT, there are several, well-documented exposures of terrestrial strata that were deposited during the Carboniferous. These deposits range in age from middle Bashkirian to Moscovian (equivalent to Westphalian in regional chronostratigraphy) to upper Gzhelian (equivalent to Stephanian C/lower Autunian in regional chronostratigraphy).

Strata in the intramontane DCB consist of terrestrial, syntectonic deposits of early Stephanian C (early Gzhelian) age (Lemos de Sousa & Wagner, 1983; Wagner, 1983; Domingos *et al.*, 1983; Pinto de Jesus, 2001, 2003). Toward the southwest, the basal strata unconformably overlie a Neoproterozoic to middle Cambrian sequence known as the Schist-Greywacke Complex. Toward the northeast, the upper strata of the DCB are truncated by a reverse fault that placed the Silurian to Devonian sequence of the Valongo Anticline over the DCB strata (Domingos *et al.*, 1983; Pinto de Jesus, 2001, 2003).

The context for interpreting the new equisetalean fossil reported herein is provided by associated flora and fauna that occur in deposits with intramontane characteristics. These deposits are described in detail by Wagner and Lemos de Sousa (1983) and Correia *et al.* (2016, 2018) who documented dryland floral elements in the DCB such as walchian conifers *Ernestiodendron filiciforme* (Schlotheim ex Sternberg) Florin, cf. *Culmitzschia frondosa* (Renault) var. *zeilleri* (Florin) Clement-Westerhof and

Culmitzschia parvifolia (Florin) Kerp et Clement-Westerhof, dicranophyllaleans *Dicranophyllum gallicum* Grand'Eury and *Dicranophyllum lusitanicum* Heer, cordaitalean *Cordaites,* and the cycadopsid *Lesleya iberiensis* Correia *et al.* The intramontane deposits of DCB are also characterised by the presence of the non-marine and limnic bivalves *Anthraconaia lusitanica* (Teixeira) Eagar and *Anthraconaia*? *altissima* Eagar (Eagar, 1983).

3 Material and methods

3.1 Locality and fossil material

The *Phyllotheca*-like fossil (Fig. 3A) was discovered in an excavation (outcrop location: 41°09´44.65´´N, 08°30´25.73´´W) during fieldwork in 2010 in the São Pedro da Cova region, in the DCB (Fig. 1). Here, we describe it as a new species of *Phyllotheca*. The fossil material consists of a single specimen (holotype) and is preserved as adpression (compression/impression; sensu Shute & Cleal, 1996) in a laminated shale bed. This lithology contains several layers very rich in fossils with well-preserved plant and animal remains (Fig. 2B).

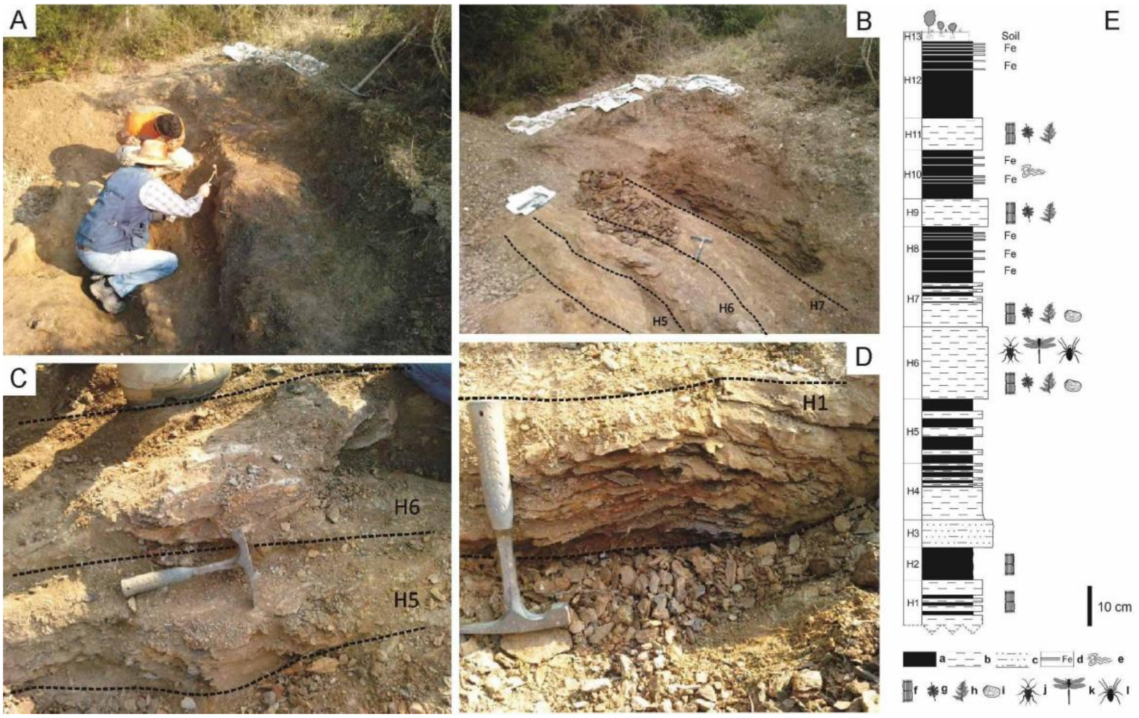

Figure 2. Lower Gzhelian outcrops of the Sao Pedro da Cova region, Douro Carboniferous Basin, northwestern Portugal. (**A**) Description of the different horizons of the log; (**B**) Samples collection of the different horizons; (**C**). H5 and H6 horizons rich in plant fossils, containing some very rare faunal fossils such as non-marine bivalves, insects and arachnids; (**D**). Shale levels containing trunks of *Calamites* interlayered with oxidised iron levels. Excavation works during fieldwork in 2010. (**E**) Stratigraphic log of the lower Gzhelian outcrops of the occurrence of *Phyllotheca douroensis* sp. nov., in Sao Pedro da Cova region. (a) Coal-bearing shale. (b) Fossil-bearing shale. (c) Silt-rich shale. (d) Ferruginous (clay with oxidised iron) shale. (e) Levels with tectonic deformation. (f) *Calamites*-rich levels. (g) *Annularia*-rich levels. (h) Pteridosperms and ferns. (i) Non-marine bivalves. (j) *Lusitaneura covensis* Loureiro *et al.*, 2010. (k) Palaeodictyoptera (e.g., *Stenodictya lusitanica* Correia *et al.*, 2014

and Dictyoptera (blattodeans) insects). (l) *Aphantomartus pustulatu*s (Scudder) Rössler. Modified from Correia *et al.* (2013, fig. 2).

The fossil site (Fig. 2A) preserves various fossiliferous levels containing many remains of plant and animal fossils. The new *Phyllotheca* species was found together with a diverse flora with several fossil-taxa belonging to ferns (e.g., *Cyathocarpus* Weiss, *Lobatopteris* Wagner, *Acitheca* Schimper, *Oligocarpia* Göppert, *Asterotheca* Presl ex Corda, *Stellatheca* Danzé, *Spiropteris* Schimper), pteridosperms (e.g., *Douropteris* Correia *et al.*, *Eusphenopteris* Gothan ex Simson-Scharold non Kidston, *Callipteridium* (Weiss) Zeiller, *Pseudomariopteris* Danzé-Corsin, *Neuropteris* (Brongniart) von Sternberg, *Sphenopteris* (Brongniart) von Sternberg, *Dicksoniites* Sterzel, *Telangium* Benson, *Cyclopteris* Brongniart), and calamitaleans (e.g., *Calamites* Suckow, *Asterophyllites* Brongniart, *Annularia* von Sternberg, *Calamostachys* Schimper, *Sphenophyllum* Brongniart (Correia *et al.*, 2019a, b). The *Phyllotheca*-like fossil (Fig. 3A) occurs in association with other equisetaleans (e.g., *Annularia noronhai* Correia *et al.*, 2019b) and many fern and pteridosperm taxa (e.g., *Douropteris alvarezii* Correia *et al.*, 2019a) found in the H6 horizon (Fig. 2B, C, E).

The faunal assemblage is also composed of rare animal elements, such as myriapods, arachnids (*Aphantomartus pustulatus* (Scudder) Rössler), eurypterids (*Adelophthalmus* sp.) and insects (dictyoptera and palaeodictyoptera), and includes non-marine bivalves likely belonging to the species *Anthraconaia lusitanica* Teixeira (e.g., Loureiro *et al.*, 2010; Correia *et al.*, 2013, 2014a, b; Correia *et al.*, 2019a, b; Fig. 2B). The occurrence of these non-marine bivalves indicates that the plants and arthropods lived at the interface between fluvio-lacustrine freshwater environments within an intramontane basin (Correia *et al.*, 2016, 2019a, b).

3.2 Sample preparation and repository

The holotype specimen was cleaned either manually or mechanically with a compressed air and electric vibrotool, and drawn using a camera lucida to help with the taxonomic evaluation. It is stored in the Museu de História Natural e da Ciência da Universidade do Porto (MHNC-UP; Portugal).

4 Systematic palaeobotany

Division **Sphenophyta**

Class **Equisetopsida** Agardh, 1825

(Subclass **Equisetidae**)

Order **Equisetales** DC. ex Berchtold & Presl, 1820

Family **Phyllothecaceae** sensu lato Brongniart, 1828

(**Phyllothecaceae** sensu stricto ≡ **Gondwanostachyaceae** Meyen, 1969)

Genus ***Phyllotheca*** Brongniart, 1828 emend. Townrow, 1955

1828 *Phyllotheca* Brongniart, p. 152.

1955 *Phyllolheca* Brongniart emend. Townrow, p. 39–40.

Type species: *Phyllotheca australis* Brongniart, 1828 emend. Townrow, 1955; type horizon unknown, Hawkesbury River, Sydney Basin, New South Wales, Australia (McLoughlin, 1992; McLoughlin *et al.*, 2005).

Generic diagnosis: See Townrow (1955, p. 39–40; see also Boureau, 1964, p. 392–396).

Distribution of the genus: Cosmopolitan genus; late Carboniferous to Early Cretaceous (e.g., Boureau, 1964; Maheshwari, 1974; Anderson & Anderson, 1985; McLoughlin, 1992).

Phyllotheca douroensis sp. nov.

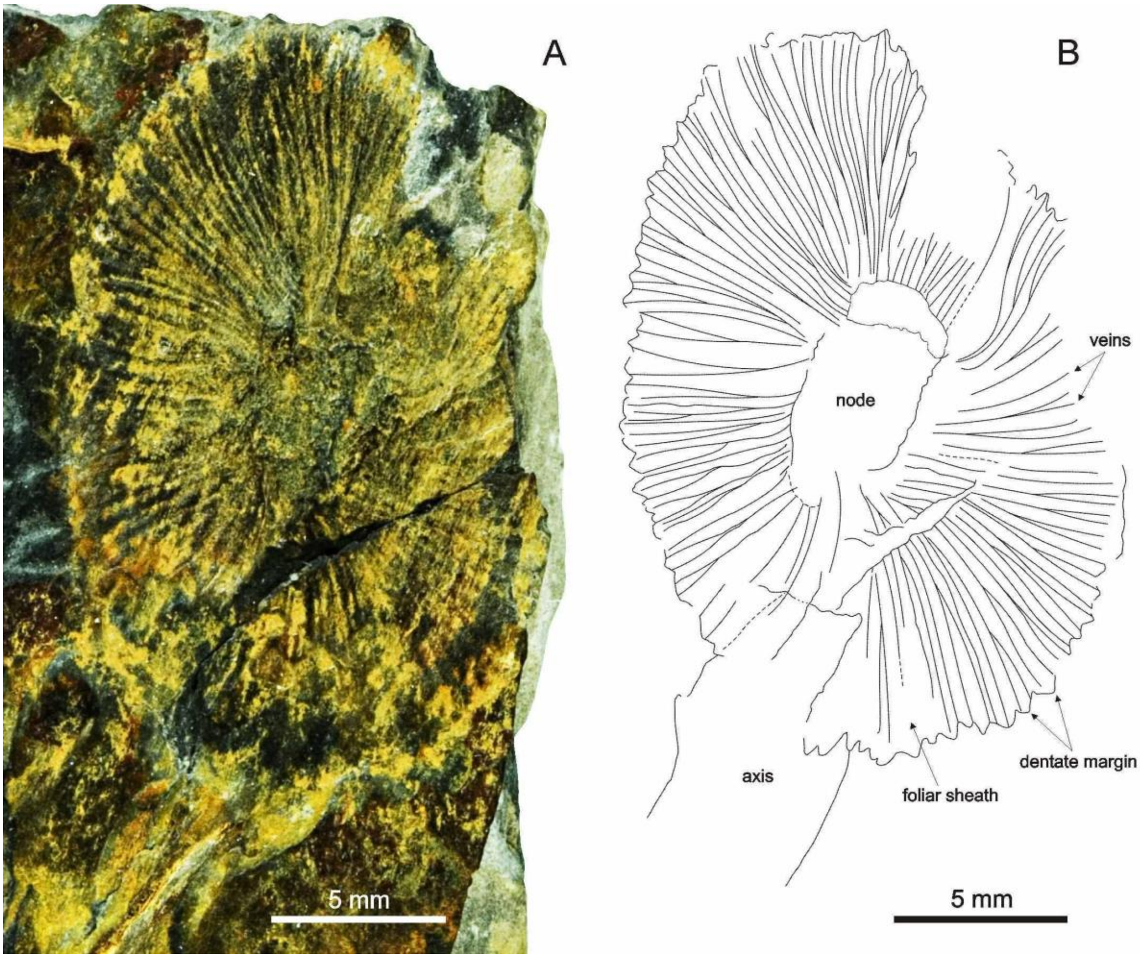

Figure 3. *Phyllotheca douroensis* sp. nov., São Pedro da Cova region, Douro Carboniferous Basin, northwestern Portugal. (**A**) Holotype specimen (MHNCUP/PAB-130919) characterised by a basal? leaf whorl attached to a broad axis. (**B**) Camera-lucida hand drawing of holotype highlighting the large and well-developed disc shaped foliar sheath of the new species.

Holotype: MHNCUP/PAB-130919 (Fig. 3A).

Type locality: São Pedro da Cova region, DCB, northwestern Portugal (Fig. 1).

Stratigraphic age: Early Stephanian C (middle Gzhelian, ca. 303 Ma), Late Pennsylvanian.

Type horizon: Compressed and laminated grey shales; horizon H6 (Fig. 2B, C, E).

Etymology: The specific epithet "*douroensis*" refers to the Douro Carboniferous Basin from which the fossil was collected.

Diagnosis: Leaf whorl with a single, large and well-developed foliar sheath, totally opened in disc shape, and basally attached to a broad axis; densely covered with simple to divided veins; veins mainly divided two times (rarely thrice); sheath margins irregular and entirely dentate; small and asymmetrical dentate margins.

Description of the holotype: The holotype MHNCUP/PAB-130919 (Fig. 3A) consists of a nearly complete leaf whorl, partially fused into a single, large and well-developed disc shaped foliar sheath which is attached to a broad axis. The leafy axis has a width of about 5 mm and is poorly preserved. The foliar sheath is large of 4.5–7.5 mm in width and has a total length of about 22 mm. The foliar sheath is densely covered with simple to divided veins, mostly divided twice to rarely thrice. The sheath margins are irregular and entirely dentate, with small and asymmetrical teeth.

5 Discussion

5.1 Taxonomic assignment and comparisons

The new equisetalean fossil from the DCB, *Phyllotheca douroensis* sp. nov. (Fig. 3A), displays a large and well-developed foliar sheath totally released from the stem from the node (or distally opened), cup-shaped, which are diagnostic features of the fossil-genus *Phyllotheca* described by Brongniart (1828) (see summary of the morphological characters of the genus in Correia *et al.*, 2021, table 1; see also McLoughlin, 1992).

Among all known species of *Phyllotheca*, *Phyllotheca douroensis* sp. nov. is most similar to the Gondwanan *Phyllotheca etheridgei* Arber, 1905 from the late Permian of Newcastle Series, New South Wales, Australia (Saksena, 1952, 1954; Boureau, 1964). Basal leaf whorls of *P. etheridgei* show a large and well-developed disc shaped foliar sheath with dentate margins (Fig. 4) and size comparable to that of *P. douroensis* sp. nov. However, they differ from the venation pattern in foliar sheaths. The veins of the foliar sheath of *P. douroensis* sp. nov. are divided at least twice to thrice (Fig. 3B), while veins of the foliar sheaths of *P. etheridgei* are simple, without any divisions (Fig. 4). Furthermore, there are some dissimilarities in the sheath margins of both species; *P. etheridgei* shows regular dentate margins, while the dentate margins of *P. douroensis* sp. nov. are relatively irregular or asymmetrical. The preservation state of the fossil material by compression can, however, have had some taphonomic influence on apparent asymmetrical shape of the foliar sheath of *P. douroensis* sp. nov. In addition, *P. douroensis* sp. nov. has similar foliar sheaths to those of the *Iberisetum* Correia *et al.*, 2021, an endemic-like taxon from the Late Pennsylvanian of DCB, although they present structural differences especially in the shape of the foliar sheaths.

Only a single leaf whorl is described for the *P. douroensis* sp. nov., but based on its broad axis it is likely that it corresponds to a basal leaf whorl from a leafy axis with similar foliar polymorphism to that of *P. etheridgei* (Fig. 4).

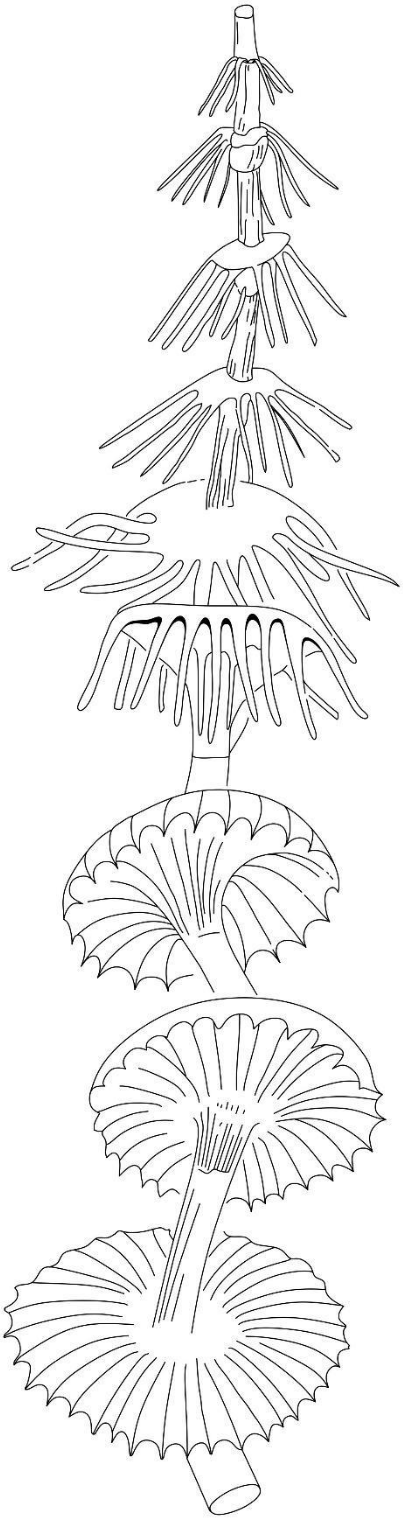

Figure 4. *Phyllotheca* (*Raniganjia*?) *etheridgei* Arber, 1905 from the late Permian of Newcastle Series, New South Wales, Australia (Gondwana) showing foliar polymorphism. Reconstruction according to Saksena (1954; see Boureau, 1964, fig. 366).

5.2 Morphological similarity with the foliage of Gondwanan and Angaran floras and its palaeobiogeographical significance

The floras of the DCB are described as typical Euramerican floral elements. They were deposited and preserved in an intramontane environment within central tropical Pangaea in seasonal conditions during an interval of wet to dry climate transition in the Gzhelian (Late Pennsylvanian, ca. 304–299 Ma) (Correia & Murphy, 2020; Correia *et al.*, 2016, 2018). These restricted environmental, climatic and ecological conditions led to origin to many plant forms with endemic morphological characteristics in this Euramerican region (e.g., *Lesleya iberiensis* Correia *et al.*, 2016, *Acitheca murphyi* Correia *et al.*, 2018, *Douropteris alvarezii* Correia *et al.*, 2019a, *Annularia noronhai* Correia *et al.*, 2019b, *Annularia paisii* Correia *et al.*, 2020, *Iberisetum wegeneri* Correia *et al.*, 2021). However, some unusual floral elements outside of the intramontane basin, such as the Gondwanan *Stellotheca robusta* (Feistmantel) Surange & Prakash, have been documented in the lower Gzhelian strata of DCB (Correia *et al.*, 2014a, 2018).

The new equisetalean fossil (Fig. 3A) from DCB described herein shows a strong morphological similarity with the *Phyllotheca*-type foliage. The fossil-genus *Phyllotheca* has an extensive geographic and stratigraphic range which has been globally recognized in upper Carboniferous–Early Cretaceous strata (e.g., Boureau, 1964). Several late Palaeozoic equisetaleans with *Phyllotheca*-type foliage have been reported in both Gondwanan and Angaran provinces (e.g., Boureau, 1964; Meyen, 1971;

Naugolnykh, 2002, 2004, Taylor *et al.*, 2009; Elgorriaga *et al.*, 2018). Rare Palaeozoic equisetalean records with endemic characteristics to Angaran floral province have also been occasionally reported in the upper Carboniferous of Iberian Massif (e.g., Broutin, 1974). For example, the first record of the Angaran endemic genus *Koretrophyllites* Radczenko outside of the Angara was documented by Broutin (1974) who described the *Koretrophyllites crassinervis* found in upper Gzhelian (Autunian–Stephanian, Upper Pennsylvanian) strata of the Guadalcanal Basin, Sevilla, in Spain. These occurrences suggest floral exchanges between Euramerica, Angara and Gondwana. Large-scale floral migrations have been documented among the different phytogeographic provinces (e.g., Naugolnykh & Uranbileg, 2018). The presence of *Phyllotheca* in DCB may indicate a distant migration of typical Gondwanan or Angaran floras to the Euramerican province. Such a possible scenario may mean that these floral migrations occurred when the different provinces shared similar climatic conditions for the same time intervals.

5.3 Systematic and evolutionary considerations

Once the type species (*Phyllotheca australis*) comes from the Gondwanan floral province (e.g., Boureau, 1964, McLoughlin, 1992; Mcloughlin *et al.*, 2005; Srivastava & Agnihotri, 2010; Roesler & Iannuzzi, 2012), the attribution of the new equisetalean fossil (*P. douroensis* sp. nov.) from DCB to the fossil-genus *Phyllotheca* raises some questions from the systematic and evolutionary point view.

When Brongniart (1828) described *Phyllotheca*, he established the fossil-family Phyllothecaceae (sensu lato) based on the vegetative parts attributed to this fossil-genus (Correia *et al.*, 2021). Phyllothecaceae sensu lato comprises two families: Gondwanostachyaceae sensu stricto and Tchernoviaceae sensu stricto, two biologically and phytogeographically distinct groups (e.g., Meyen, 1967, 1969; Coreia *et al.*, 2021). The two families have very distinct reproductive structures but have similar foliage, i.e. *Phyllotheca*-type (Meyen, 1967, 1969, 1971, 1987; Cúneo & Escapa, 2006; Weber, 2008; Srivastava & Agnihotri, 2010; Boardman & Iannuzzi, 2010). Since both groups arose in places with similar ecological conditions, this homoplasy (in the foliage) is due to convergent evolution (Meyen, 1967, 1987; Roesler & Iannuzzi, 2012; see also Naugolnykh, 2002). Foliage of *P. douroensis* sp. nov. is closely related to foliage of Phyllothecaceae sensu lato, but has no preserved reproductive organs that link either to Gondwanostachyaceae or to Tchernoviaceae.

The close resemblance to the endemic Australian *Phyllotheca etheridgei* is very interesting, because it could indicate phylogenetic affinities between the Portuguese and Gondwanan species, i.e. with Gondwanostachyaceae. *P. etheridgei* has been renamed as *Raniganjia etheridgei* (Arber) Rigby, 1962a (De *et al.*, 2003). *Raniganjia* Rigby, 1962b corresponds to a rare equisetalean member from the late Permian beds (Raniganj, Kamthi and Pachwara Formations) of Indian Gondwana, and equivalent Formations in Australia and Brazil (De *et al.*, 2003). Later, McLoughlin (1992) considered *P. etheridgei* as an intermediate form in which leaves are variously fused or free, having pointed apices typical of *Phyllotheca* but also showing transverse striae characteristic of the genus *Raniganjia*. It is not possible to relate these intermediate forms to *P. douroensis* sp. nov. because only a single leaf whorl is described for the Portuguese species. However, it is very likely that *P. douroensis* sp. nov. corresponds to a convergent form of *Phyllotheca*-type foliage to the Euramerican floral province.

6 Conclusions

In this work, we report the first occurrence of the equisetalean fossil-genus *Phyllotheca*, named *Phyllotheca douroensis* sp. nov., in the Portuguese Carboniferous and it is more an element of strong morphological convergence between distantly related floras. This new finding indicates that Phyllothecaceae sensu lato was not restricted only to Angaran and Gondwanan floral provinces, suggesting that late Palaeozoic equisetaleans with *Phyllotheca*-type foliage occurred in Euramerican floral realm.

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Author contributions

P.C. and C.B. wrote the manuscript. P.C. and A.A.S. prepared the figures. J.M. helped in the preparation of fossil sample and photographic documentation. P.C., C.B. and A.A.S. were involved in the taxonomic study of the new equisetalean fossil and corrected the text of manuscript. All authors discussed and approved the final manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

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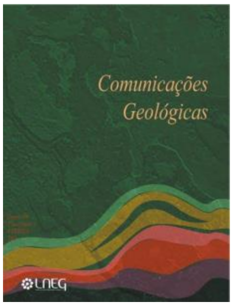
Annex 4 — Barbosa & Muchagata, in press. “The use of latex moulds as a complement for studying paleobotanical specimens”

O uso de moldes de latex como complemento ao estudo de espécimes paleobotânicos

The use of latex moulds as a complement for studying paleobotanical specimens



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Resumo: Neste trabalho, apresentamos a história dos moldes de latex em Paleontologia e o seu uso no ramo. Também discutimos a metodologia e as vantagens de moldes de fósseis em latex. Os moldes látex em fósseis são usados desde a primeira metade do século XIX e continua a ser usado até hoje. A metodologia sofreu poucas alterações mas algumas inovações foram introduzidas. Também discutimos as vantagens do uso generalizado desta técnica no estudo de compressões paleobotânicas. Este método é útil no estudo de espécimes mal preservados em Paleobotânica e Paleontologia, dado que o látex permite uma melhor visualização ou destaque de certos caracteres diagnósticos importantes para identificação. O uso generalizado desta técnica aumentaria a quantidade de fósseis viáveis para estudo.

Palavras-chave: Preparação, Método de Látex, Paleobotânica, compressões/impressões, MHNC-UP

Abstract: In this paper, we present the history of latex in Paleontology and its role in the field today. We discuss the methodology and advantages of latex fossil moulds, while also presenting examples of moulds of compressions/impressions of plant fossils. Latex rubber has been used to create moulds of fossils since the first half of the 20th century and it is still used in various branches of Paleontology. While the methods have stayed largely unchanged, some innovations have been introduced. We also discuss the virtues of large scale adoption of latex in the study of paleobotanical compressions/impressions, a technique not widely used in that branch, but in which latex can provide better visualization of certain key diagnostic characters for identification. Furthermore, widespread use of latex would increase the amount of viable fossils for study.

Keywords: Preparation techniques, Latex method, Paleobotany, fossil compressions/impressions, MHNC-UP

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1. Introduction

The use of latex in Paleontology began in the first half of the 20th century. Ever since its introduction in 1938 (von Fuehrer, 1938), this replication method has seen many applications in various areas of the field and is still in use (Baird, 1955; Goodwin and Chaney, 1994; Davis *et al.*, 1998; Green, 2001). However, as Green (2001) points out, the technique has barely changed over the years, evidenced when comparing the methodologies from Fischer (1939) and Parsley (1989).

Latex casting and moulding can serve three main purposes: curating original material, research and/or teaching. Moulds or casts help in curation in museums, since holotypes and additional type material can be replicated in high detail so other researchers can study the material from replicas, preventing deteriorating the original specimens; furthermore it can be used as a way of safekeeping in the event of the destruction of the original material. Moulds produced for research require very fine detail; meanwhile replicas produced for teaching purposes, whether in a classroom environment or an exhibit can be less detailed. Another distinction that should be made is between moulds (negatives) made with the intention of casting a positive replica of a fossil and moulds where the mould itself is the final product. This paper focuses heavily on the latter, as it is the most pertinent to the study of paleobotanical compressions/impressions. While casts and replicas are copies of the fossil itself, the latex moulds used here are just a copy of the internal or external relief of the specimen.

Resins like latex and other materials like silicone, which is an artificial inorganic polymer, have been widely used in the creating moulds of type specimens. Even though, in a research environment, latex rubber is most commonly used to create casts/moulds of smaller invertebrate fossils, i.e. trilobites, brachiopods, crinoids, insects, etc. (Angiolini *et al.*, 2003; Ausich *et al.*, 2007; Pereira, 2017; Domingos *et al.*, 2020; Correia *et al.*, 2019, as exemplified in Figure 1c–f, it can also be applied to other groups such as vertebrates (Garner, 1953; Swanson & Carlson, 2002; Leite *et al.*, 2007) or even plants (Boersma, 1985; Taylor *et al.*, 2009), see Figure 1 a–b. The use of this technique in the study of plant fossils is the primary focus of this work.

According to Green (2001), there are some drawbacks to the use of latex, such as the shrinkage the moulds are bound to suffer over time. This can lead to distortion of the specimen if the changes are not equal in all dimensions (Monge & Mann, 2005). According to Heaton (1980), the constitution of the latex affects the "shelf life" of the mould. Latex with a high ammonia content leads to moulds that are more prone to lose their elasticity and become brittle, and finer details will degrade over time; higher quality latex is much more stable and can last up to 15 years without degrading (Heaton, 1980). Ideally the cast is photographed (or 3d modelled, using photogrammetric techniques), and so, if and when the latex cast degrades, there is already a photographic record to be analysed without having the need to make another mould, which might, in time and if done too often, damage the fossil.

One of the advantages of this material is the absence of emission of toxic fumes. It is also easily cleaned from tools (Green, 2001). Another advantage of the technique is that after the removal of a latex cast, any impurities that might be present on the surface of the fossil are peeled away with the latex leaving the specimen completely clean. Latex is also cheaper than silicone, has exceptional tensile strength and, if stored in an airtight container, has a fairly long shelf life (Stanley, 1975).

In this paper, we discuss latex moulding methodology as well as the history of its use in the field of Paleontology and its many branches, with a focus on the application of this technique in the study of paleobotanical impressions/compressions (sensu Shute and Cleal, 1996). It sometimes can be difficult to find bibliographic support for paleontological techniques and methodologies, due to the organic way these tend to pass from colleague to colleague. This may lead to some difficulties for students or researchers looking to learn more techniques. With this paper, our aim was to offer an overview of one of those techniques and a jumping off point for further research.

1.1. Latex in Paleobotany

Even though latex moulds have been used in Paleontology for about 80 years, they continue to provide additional insights to researchers everywhere. Next, two different applications of this material in the field of Paleobotany are discussed.

The first, most common use of the technique, already widespread in other fields, is the use of casts to highlight anatomical characters of specimens. The use of latex moulds in Paleobotany has been reported before – such as Boersma (1985) – and especially in the study of cuticles, but its use in Portuguese Paleobotany was pioneered by Correia *et al.* (2016) (see Fig. 1a). In this particular case, the method was chosen due to poor preservation of the holotype (see Correia *et al.*, 2016, fig. 5). The whitened latex mould allowed for a high degree of contrast, which emphasized anatomical features. As such, the use of latex moulding to analyse plant impressions can be useful for reproducing the original morphology of an external mould and/or for studying internal “hidden” structures. Using latex can also, in some cases, help clean the specimen of some extra sediment.

The second is a preparation method that the authors have dubbed latex peeling. While working on another specimen, a plant adpression from the Douro Carboniferous Basin preserved in compressed grey shales and part of the botanical collection of the *Museu de História Natural e da Ciência da Universidade do Porto* (MHNC–UP), the authors intended to use latex moulding to produce images for taxonomic studies. When the moulds were removed from the fossil, a lot of oxides and matrix particles were removed alongside them. This had two consequences: the moulds were not usable but the fossil was exceptionally clean.

However, the usage of latex is not recommended as the moulding might compromise the fossil and future cuticular analysis (Stankiewicz *et al.*, 1998; Zodrow *et al.*, 2000); however, since our studies focus primarily on the general morphology of the leaf, the latex casts highlight characters that would otherwise be very hard to perceive, such as venation and leaf margins (Correia *et al.*, 2016).

2. Creating latex moulds

When choosing to produce a mould of a specimen there are many important factors to consider. The first is whether the specimen in question can be cast without suffering irreparable damage, as this is obviously counterproductive. The methodology discussed here will focus on latex moulds made for the purpose of taxonomic studies, in other words, the moulds need to be highly detailed and well photographed but do not need to be especially durable.

It should be taken into consideration that, when the fossil is delicate or the matrix it is in is not consolidated there are several consolidating techniques (such as using diluted resins) that have to be made before attempting a latex cast, since they penetrate the fossil and matrix pores creating a surface coating and protecting the fossil (Goodwin and Chaney, 1994).

2.1. Methodology

The first step is making sure the fossil is clean (see Fig. 2a). As mentioned before, a preliminary cast – a latex peel – can be made to clean the fossil. However, we should stress that specimen cleaning can be accomplished simply by washing the specimen, or by using mechanical or chemical techniques, before considering latex as a viable option.

The next step is to prepare the latex mixture (see Fig. 2b). The liquid rubber is poured into a container and mixed with drops of Chinese ink, which serves the purpose of dyeing the transparent rubber in order to enhance contrast (Green, 2001). The raw latex is slightly translucent and white/yellowish in colour, which does not photograph well: the translucency hides details and surface topography of the mould, and the colour of raw latex reflects too much light, which reduces contrast and obscures details (Heaton, 1980). The optimal tone should be dark and even (Parsley *et al.* 2018).

After the mixture is prepared, it is very carefully applied in a thin layer to the surface of the fossil, making sure no air bubbles are formed, since these would diminish the quality of the final mould. It is common practice to humidify the surface of the specimen with soapy water for optimum surface contact, which prevents the formation of air bubbles (Baird, 1955). In this case, the latex was applied with a standard glass rod (see Fig. 2c). An alternative method of spreading is with a compressed air hose (Heaton, 1980). The specimen is then placed in a dehydrator or oven, at a temperature between 70–80ºC, until the latex has dried (see Fig. 2d). It is possible for the mould to air dry, however this may take longer.

The process of spreading a layer of latex and curing it (in an oven or at room temperature) is repeated until the mould is sufficiently thick (see Fig. 2e).

The proper removal of the latex cast is very important, as demonstrated by Saleh *et al.* (2020): the authors identify a specimen in which the incorrect/incomplete removal of the latex after numerous moulds led to the remnants of the mould mimicking morphological structures, which were mistakenly identified as soft tissue.

This example highlights the need to be aware of any given specimen’s previous history as well as the danger of submitting a fossil to too many interventions, so recording the history of a specimen within an institution is vital (Saleh *et al.*, 2020).

After the removal, it is customary to glue – using latex or diluted resins like Paraloid B-72 – the mould to a piece of cardboard to give it more structural stability and make it easier to handle (see Fig. 2f).

The next step is whitening the mould, which increases contrast and emphasizes details (Parsley *et al.*, 2018), making the specimen easier to photograph. There are many ways to do this, here we approach two. Virtual whitening is also possible and shows great promise for bigger specimens (Hammer & Spocova, 2013; Parsley *et al.*, 2018).

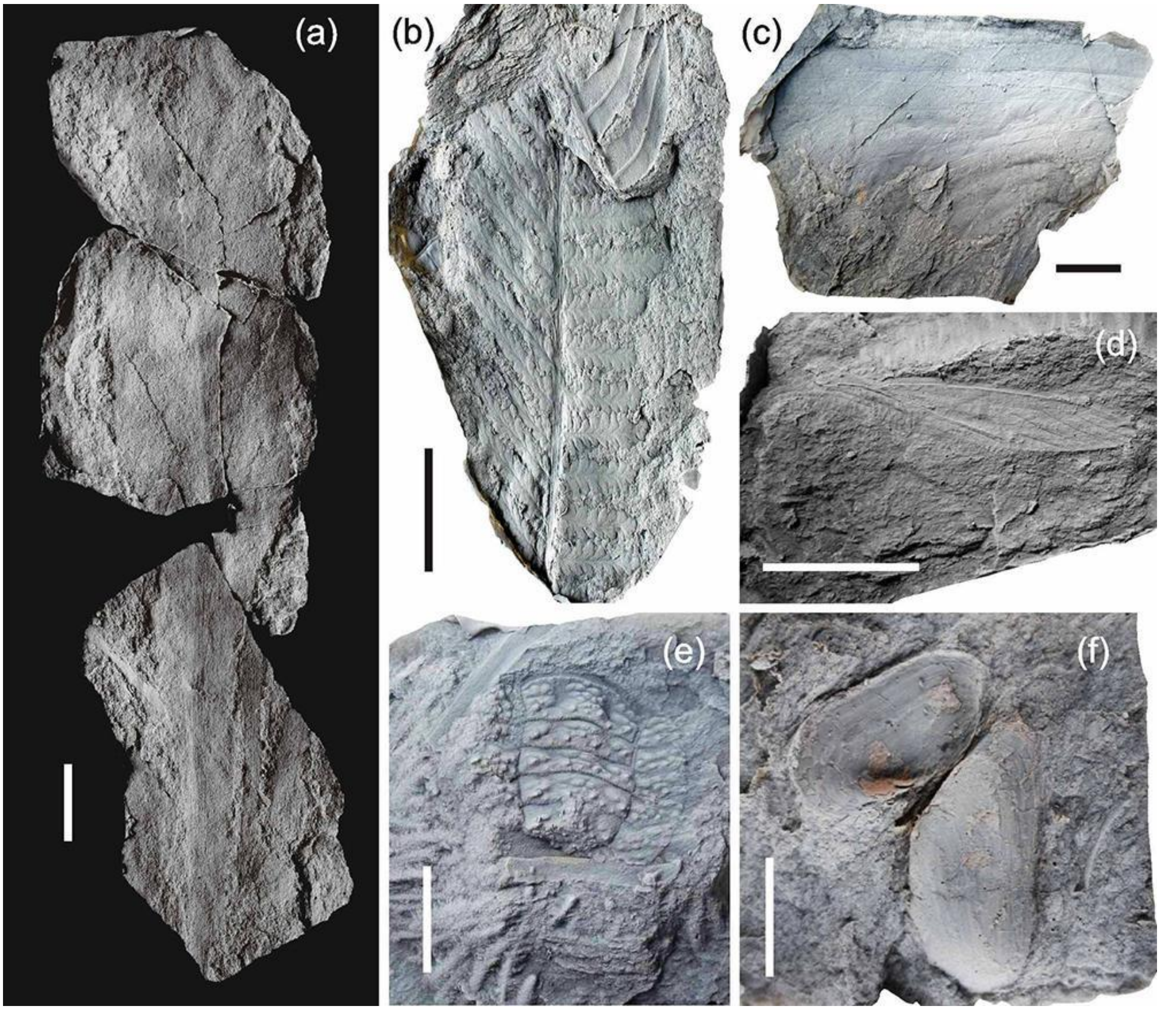

Figura 1. Exemplos de moldes de latex de fósseis de plantas, artrópodes e bivalves de São Pedro da Cova, Bacia Carbonífera do Douro (Gzeliano inferior, Pensilvaniano Superior; noroeste de Portgual). (a) *Lesleya iberiensis* (Gymnospermophyta); (b) *Sphenopteris* sp. (Pteridospermophyta); (c) *Stenodyctia lusitanica* (Insecta); (d) *Lusitaneura covensis* (Insecta); (e) *Aphantomartus pustulatus* (Arthropoda); (f) *Anthraconaia* sp. (Bivalvia). Escalas: 5 mm (e); 10 mm (c, d, f); 20 mm (a, b). Figura por P. Correia.

Figure 1. Examples of latex casts of plant, arthropod and bivalve fossils from S. Pedro da Cova, Douro Carboniferous Basin (lower Gzhelian, Upper Pennsylvanian; NW Portugal). (a) *Lesleya iberiensis* (cycad–like gymnosperm); (b) *Sphenopteris* sp. (pteridosperm); (c) *Stenodyctia lusitanica* (insect); (d) *Lusitaneura covensis* (insect); (e) *Aphantomartus pustulatus* (spider–like arthropod); (f) *Anthraconaia*–like non marine bivalves. Scale bars: 5 mm (e); 10 mm (c, d and f); 20 mm (a and b). Figure by P. Correia.

Dry application of ammonium chloride (NH4Cl) is by far the most common way to whiten fossils (Parsley *et al.*, 2018). There are a few different configurations (Branson and Mehl, 1933 in Parsley *et al.*, 2018, p239; Cooper, 1935; Teichert, 1948; Sakamoto, 1970; Feldmann, 1989; Green, 2001) but they all converge on the basic concept: ammonium chloride is heated inside a glass tube over a flame and the vapour is blown (with a squeeze bulb, compressed air or even by breath) into the fossil. Whitening with ammonium chloride is fairly safe and controllable and allows for more consistent results (Parsley *et al.*, 2018).

One other method is to burn a strip of magnesium ribbon and hold the mould above it, in the direction of the billowing smoke (see Fig. 2g). This should be done carefully since the magnesium oxide burns very hot and can completely cover the mould, leaving it completely white and rendering it useless. Luckily, the magnesium oxide is easy to remove from the mould so another attempt can be made. Even though it can be used successfully (Correia *et al.*, 2016), the highly reflective nature of magnesium oxide and the difficulty in obtaining an even coat are clear disadvantages of this method.

The final step, and ultimate goal of the technique, is photography. Traditional specimen lighting techniques dictate that the primary light come from the upper left corner and secondary light come from the lower right to act as a bounce light (see Fig. 2h).

After the photographs are taken, it is important to rinse the ammonium chloride or magnesium oxide off the mould to prevent it from being damaged or corroded: clear running water will do.

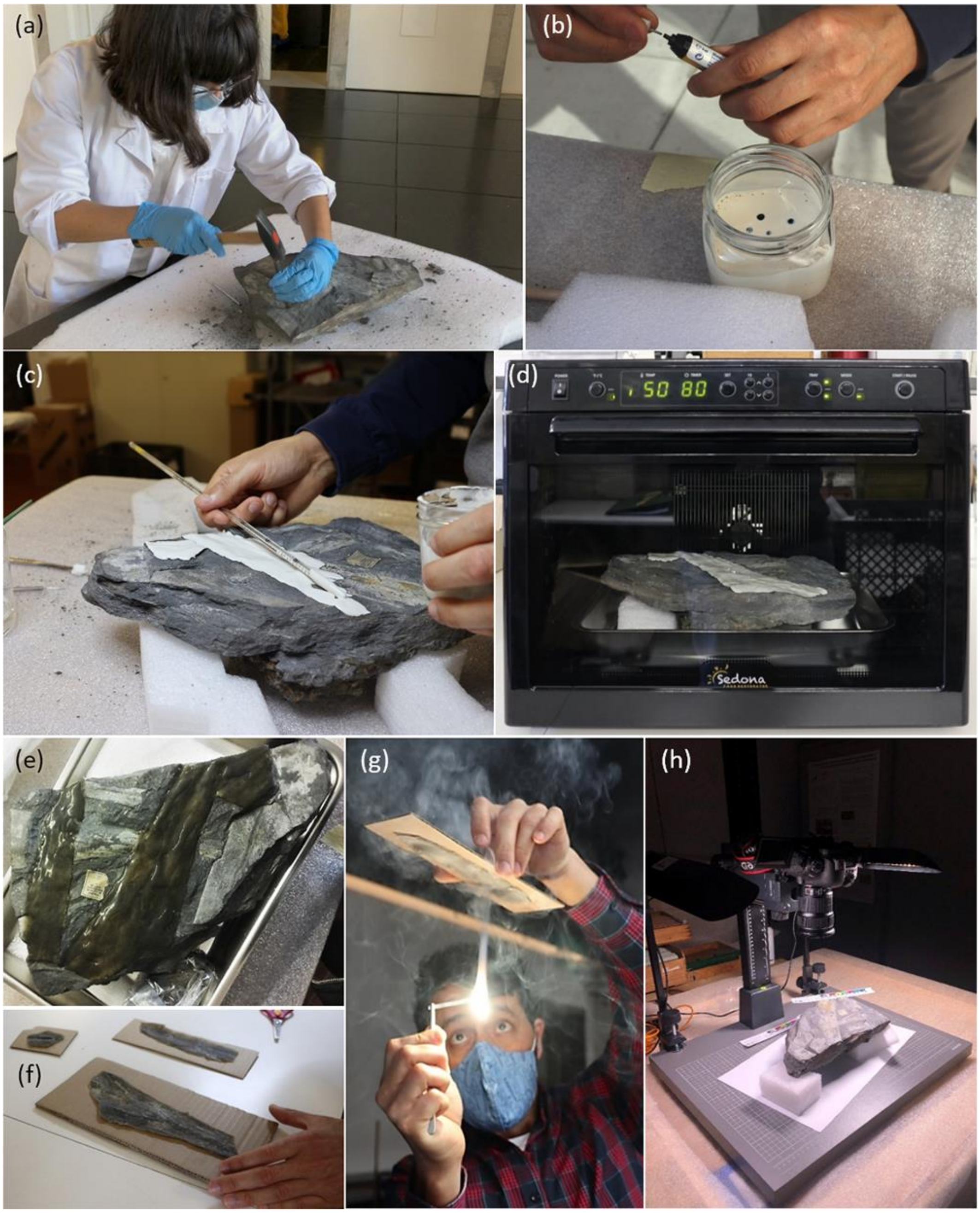

Figure 2. Passos do processo de moldagem em latex, fotograpfias por JMD. (a) Limpar o fóssil (fóssil a ser preparado por CB); (b) misturar látex com um corante (p.e. tinta da china ou grafite); (c) aplicar camada fina de látex, com cuidado para evitar formação de bolhas de ar; (d) deixar o látex curar à temperatura ambiente ou numa estufa; (e) Repetir o processo para as camadas seguintes, descolar o látex do fóssil cuidadosamente; (f) colar o molde a um cartão; (g) branqueamento (látex a ser branqueado por PC); (h) fotografar o molde (exemplo de copy stand do Herbário PO, no MHNC–UP.

Figure 2. Steps of the latex moulding process, photographs by João Muchagata Duarte. (a) Make sure the fossil is clean, fossil being prepared by one of the authors (Catarina Barbosa); (b) mix latex with a dye; (c) apply thin layer of latex on the fossil, careful not to create air bubbles; (d) allow to cure either at room temperature or in an oven; (e) Apply the next layers and allow to cool, carefully peel the mould from the fossil, starting from the edges and progressing inward; (f) glue the mould to a piece of cardboard; (g) whitening (latex mould being whitened by PC); (h) photographing the mould: example of copy stand setup from the PO Herbarium, at the MHNC–UP.

3. Closing remarks

Latex moulding in Paleontology can take many forms, depending on the purpose of the mould. While not a necessary process for the study of plant fossils, it can be especially useful for reproducing the original morphology of an external mould and/or for observing/studying internal structures hidden in pits. These are especially important when taxonomic descriptions, especially in potential type specimens, are being made.

However, it is critical to consider the impact latex moulds can have on a fossil: from the mould peeling process taking away part of the cuticle, to poor removal of the mould leaving behind traces of latex, there are many ways in which a latex mould can negatively impact a specimen. When deciding whether or not to employ this technique (or any other) the conservation of the fossil should be foremost. While it is common practice to whiten fossil specimens directly, the use of latex moulds for photography those reduces the interventions done on the specimen.

Further studies on the subject would include systematizing the density of the latex rubber in relation to the quality of preservation and type of matrix of a fossil specimen. Although, like any method, they have their drawbacks, latex moulds are a valuable asset to any palaeobotanist's arsenal of techniques.

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Annex 5 — Correia *et al.*, 2022. “A new species of *Lesleya* (Spermatopsida) from the Carboniferous of Iberia and its palaeoecological and evolutionary significance”

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A new species of *Lesleya* (Spermatopsida) from the Carboniferous of Iberia and its palaeoecological and evolutionary significance

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ABSTRACT

Plant adaptations to environmental and climatic changes in Pangaean intramontane basins are poorly understood. Here, we document a previously unknown primitive gymnosperm species, *Lesleya ceriacoi* sp. nov., from the Douro Carboniferous Basin (DCB; lower Gzhelian, Upper Pennsylvanian; NW Portugal) of the Variscan Iberian Massif (Iberia). This new species is described from a 303 million-years-old fossil rediscovered at the U.Porto's Herbarium PO, stored at the Museu de História Natural e da Ciência da Universidade do Porto (MHNC-UP; Portugal). *L. ceriacoi* sp. nov. displays an exquisite leaf shape with morphological traits adapted to specific ecological conditions of the DCB. These leaf morphological traits comprise toothed and dissected margins, which represent specialised adaptations to drier (xerophytic) conditions of the DCB during the Gzhelian (ca. 304–299 Ma), at the end of the Late Pennsylvanian. The xeromorphic traits of the new species represent an evolutionary novelty for the Pennsylvanian Euramerican dry-climate adapted floras, and are evidence of evolutionary adaptation to environmental and climatic change in intramontane basins like DCB within central tropical Pangaea. Such an adaptation occurred during an interval of wet to dry climate transition after the end of one late Palaeozoic Gondwana Ice Age (glaciation) in Gzhelian time.

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Introduction

A general rise in the sea level and the subsequent decrease of humid conditions due to the waning of a late Palaeozoic Ice Age interval in southern Gondwana, a major glaciation of the Phanerozoic, led to significant climatic and environmental changes within the central tropical Pangaea (e.g., Isbell et al. 2003; Wagner 2004; Fielding et al. 2008; DiMichele et al. 2010; Correia and Murphy 2020). These greenhouse conditions resulted in a significant widespread aridification that occurred in the interior of the Pangaean supercontinent during its final amalgamation (fusion) in the Late Pennsylvanian–early Permian (Correia and Murphy 2020; Figure 1a). As a result, parts of the tropical regions of western and central Pangaea became drier and less humid during that time interval (Wagner and Lyons 1997; Wagner 2004; Cecil 2013; Correia and Murphy 2020; see also Bashforth et al. 2021).

The Douro Carboniferous Basin (DCB) of the Variscan Iberian Massif (= Iberia), in northwestern Portugal, is one of many places that were located within central tropical Pangaea in the late Palaeozoic (Correia and Murphy 2020; Figure 1b). The floras of the DCB were deposited and preserved in an intramontane environment during an interval of wet to dry climate transition in the Gzhelian (Late Pennsylvanian, ca. 304–299 Ma) (Correia et al. 2016, 2018; Correia and Murphy 2020). The DCB was characterised by a relatively seasonal climate during Gzhelian time (Correia et al. 2020; Bashforth et al. 2021). A drier climate led to the appearance of several species with xeromorphic characteristics and, at the same time, to the disappearance of typical wetland and coal-forming floras (the so-called 'ever-wet floras'), such as lycophytes, in this region during that time period (Correia et al. 2016, 2018; Correia and Murphy 2020). The Carboniferous–early Permian genus *Lesleya* is a xeromorphic plant (mesophyte to xerophyte) that has been recently documented in lower Gzhelian strata of the DCB (Correia et al. 2016). *Lesleya* is an element of Euramerican floras that was adapted to seasonally dry environments of the western and central tropical Pangaea (DiMichele et al. 2010, 2016; Bashforth et al. 2014, 2016, 2021; Correia et al. 2016; Correia and Murphy 2020). This plant, a member of the larger dry-climate adapted flora, commonly known as 'drought-tolerant flora', has tentatively been considered as a primitive gymnosperm and possible ancestor of the modern cycads (Florin 1933; Remy and Remy 1978; Leary 1990; Taylor et al. 2009).

The diversity and climatic and environmental conditions of the Pennsylvanian Euramerican dry-climate adapted floras, that include the genus *Lesleya*, have been extensively studied (e.g., DiMichele et al. 2010, 2016; Bashforth et al. 2014, 2016, 2021; Correia et al. 2016; Correia and Murphy 2020). However, their morphological and ecological adaptations to intramontane environments are poorly understood. In this paper, we describe a new *Lesleya* species from the DCB, with leaf morphological traits adapted to xerophytic conditions. Here, we assess the morphological and ecological aspects of this fossil and how these aspects provide additional constraints for plant adaptations to changing environments in intramontane basins within central tropical Pangaea in Late Pennsylvanian time.

Material and methods

The Portuguese museums have a large repository of palaeontological collections. In their historical collections, there are many fossils that remained unstudied for several decades, and that have become new and important discoveries in recent years (e.g., Ausich et al.

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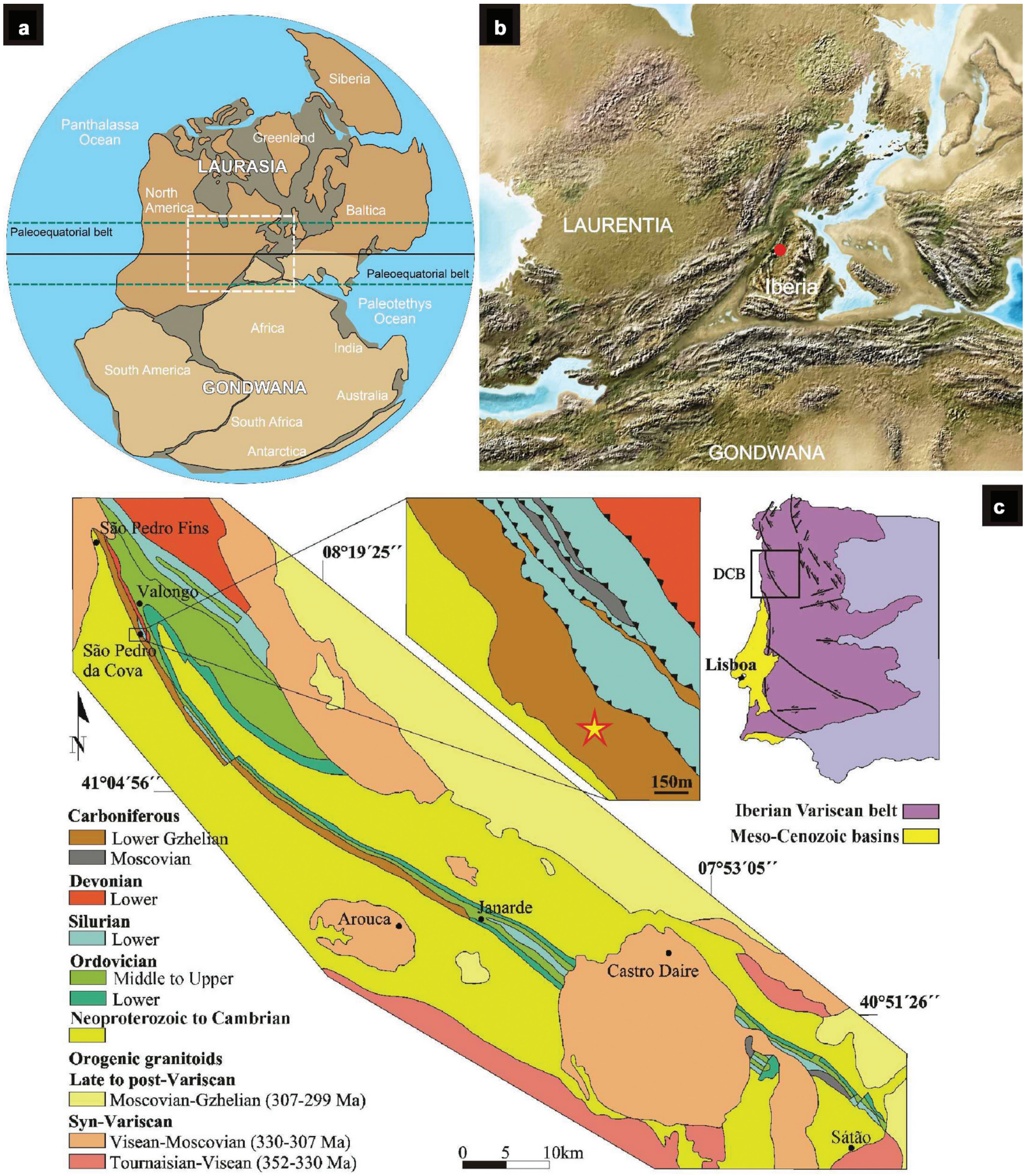

Figure 1. Geographical and geological setting of the Douro Carboniferous Basin (DCB) located within central tropical Pangaea in the late Palaeozoic. (a) Pangaean supercontinent formed during the Late Pennsylvanian–early Permian. Adapted from Correia and Murphy (2020; Figure 1). (b) Panoramic view of the central tropical Pangaea (white dashed rectangular box) in a, highlighting Variscan Iberian Massif (= Iberia) amalgamated to landmasses Laurentia (North America) and Northern Africa (Gondwana) with the location of the DCB (red dot), in northwestern Portugal. Modified from Correia and Murphy (2020, Figure 5). (c) Map showing regional geology of the DCB in northwestern Portugal and the detailed geology and location of the supposed fossil site (star) of ***Lesleya ceriacoi*** sp. nov. in the São Pedro da Cova region. Adapted from Correia et al. (2016; Figure 1).

2007; Smith et al. 2012). In this work, we document a fossil of a new plant species that was stored at the MHNC-UP herbarium for over 100 years without ever having been studied.

The plant fossil was found in lower Stephanian C (lower Gzhelian, upper Pennsylvanian) strata of the region of São Pedro da Cova in the DCB (northwestern Portugal), located in the Variscan Iberian Massif (e.g., Wagner 1983; Domingos et al. 1983; Correia et al. 2016; Figure 1b, c). The outcrop site where the fossil specimen was found is unknown. Nevertheless, given the sedimentological features of the rock strata, it is very likely that the specimen was collected at the plant-fossil-bearing siliciclastic strata that are described for the stratigraphic sequences of the DCB (Correia et al. 2016). These fossiliferous strata occur within a succession of shale, sandstone and coal, which are overlain by fluvial sequences. The fluvial deposits represent a fluvial system complex with vertical accretion composed of interbedded conglomerates, sandstones, and siltstones, with pelitic layers more prevalent near the top of the sequence (Pinto de Jesus 2001, 2003; Correia et al. 2016).

The fossil (Figure 2) contains five leaf fragments that form the holotype (Figure 3) and four paratypes (Figures 4 and 5) of the new species of *Lesleya*. The fossils are preserved as adpressions (compressions/impressions; sensu Shute and Cleal 1996) in laminated and compact (compressed) grey shales, rich in quartz clasts. MHNCUP/PAB-29a (Figure 3) was selected as the holotype because it represents the best-preserved and largest specimen and shows the greatest number of diagnostic characters.

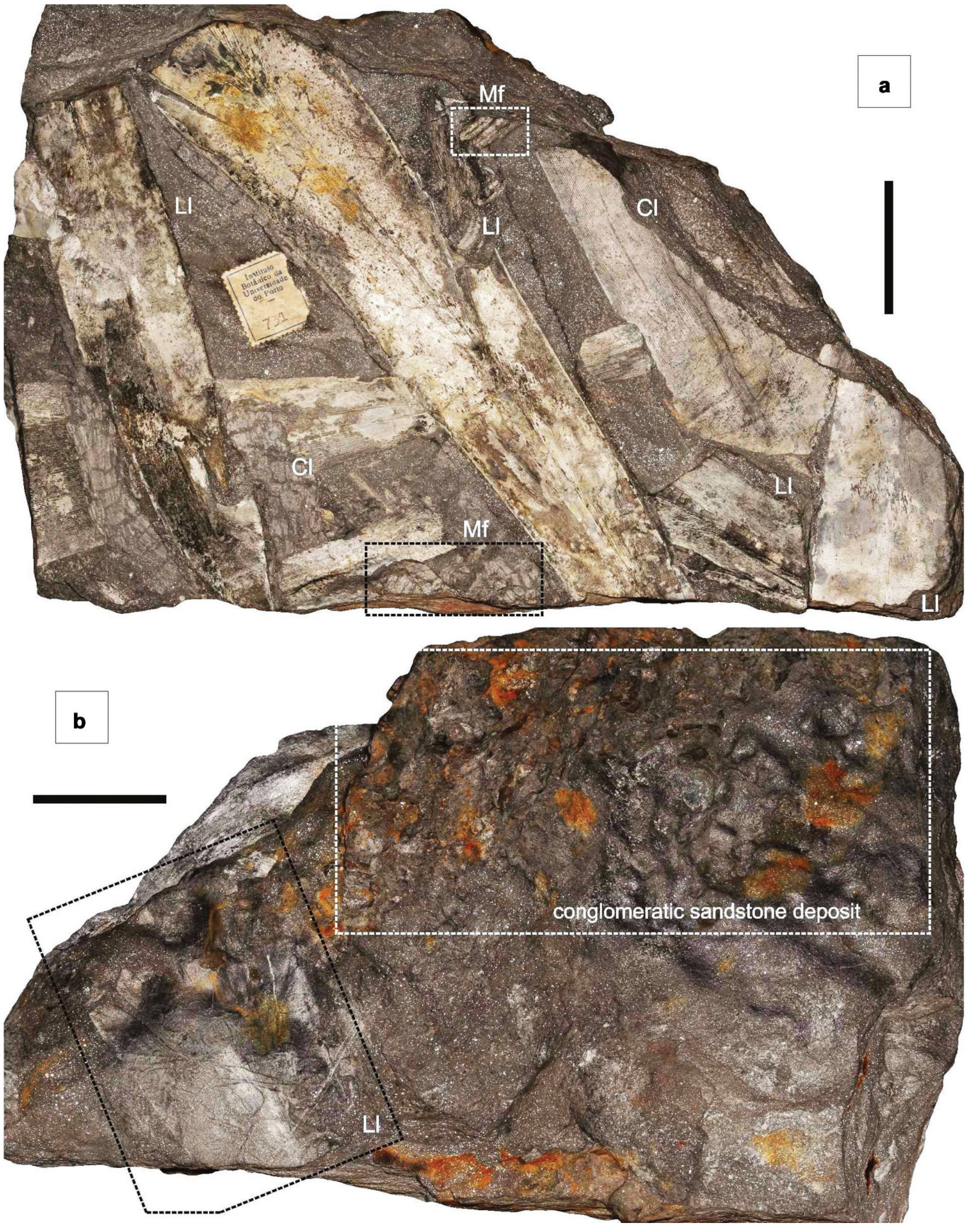

Figure 2. Overview of the studied fossil containing the different type specimens of ***Lesleya ceriacoi*** sp. nov. (a) Frontal side of the fossil displaying the main type specimens associated with *Cordaites* leaves and marattialean foliage remains. (b) Back side of the fossil showing a wide *Lesleya* leaf deeply lacerated in both margin sides, preserved in a siltstone interlayered with a conglomeratic sandstone deposit. Abbreviations: Ll, *Lesleya* feaf; Cl, *Cordaites* leaf; Mf, marattialean ferns. Scale bars: 40 mm.

The fossil was manually prepared with chisels, hammers, and needles. Photographs for the plates were taken with a Canon EOS 6d Mark II camera with an EF 24–105 mm f/3.5–5.6 IS STM lens, a Kaiser RS10 Camera stand with RTP camera arm and RB 5020 ds2 LED lighting unit. The images were processed using Adobe Photoshop CC 2018 and CorelDRAW Graphics Suite.

The fossil that contains the type specimens is stored in the palaeobotany collection of the MHNC-UP (MHNCUP/PAB; Portugal) and is formerly part of the PO Herbarium collection.

Palaeobotanical history of the genus *Lesleya*

The genus *Lesleya* is relatively common in some localities in the United States of America (USA), whereas it is rare in European localities. It was erected by Lesquereux (1879–1880); the type species is *Lesleya grandis* Lesquereux. Lesquereux (1884) described a second species, *L. microphylla*, based on two specimens from Kansas. Since 1884, nine additional species have been described from Pennsylvanian and Permian strata of Illinois, England, France, Germany, and Italy. These species are based only on one or a few specimens. Zeiller (1888, 1890) described *L. ensis* Zeiller (1888) from the Stephanian of Commentry in France and *L. delafondii* Zeiller (1890) based on one single specimen. Florin (1933) later studied the cuticles of this species. Based on haplocheilic stomata, he considered *Lesleya* to be a primitive gymnosperm.

Grand'Eury (1890) revised *L. angusta* Grand'Eury (1877) and described a new species *L. simplicinervis* Grand'Eury (1890). Both species are from the Stephanian of Saint Etienne, France. De Stefani (1901) described *L. cocchii* De Stefani from Italy and this species was also subsequently described from France, Le Crusot and Puits Saint-Paul localities of the Stephanian age (Zeiller 1906).

Figure 3. Holotype MHNCUP/PAB-29a of ***Lesleya ceriacoi*** sp. nov. from the early Gzhelian (Late Pennsylvanian) of the Douro Carboniferous Basin, northwestern Portugal. (a) Lower-to-middle part of a leaf with straight margins towards leaf base, showing a deep laceration on the lamina (white dashed rectangular box). (b) Enlargement of top part of the specimen in a, displaying margins with discrete to deep lacerations (white/black dashed rectangular boxes). (c) Enlargement of lower/middle part of the specimen in a, exhibiting a deep laceration on blade (white dashed rectangular box). Scale bars: 20 mm.

Remy and Remy (1977) transferred *Taeniopteris eckardtii* to *Lesleya* (*L. eckardtii*). This should be the youngest representative of *Lesleya* known from the late Permian of Germany, although its taxonomic assignment to the genus remains doubtful. These authors described another two species of *Lesleya* – *L. weilerbachensis* Remy and Remy (1975) and *L. gimmii* Remy and Remy (1978). *L. weilerbachensis* comes from the Westphalian and *L. gimmii* is from the Stephanian of Germany.

L. cheimarosa Leary and Pfefferkorn (1977) was first discovered in Brown County, Illinois. Subsequently, many further specimens were found in Rock Island County (Leary 1981). This species is known from the middle to late Namurian (Early Pennsylvanian). Remy and Remy (1978) suggest a relationship of *Lesleya* to primitive cycads (DiMichele et al. 2016). Leary (1990) found ovules on the basal part of a petiole of a *Lesleya* leaf, interpreted it as similar to some modern cycads, and suggested that *Lesleya* could be the possible ancestor of these cycads (see also Taylor et al. 2009, p. 669).

Šimůnek (1996) studied cuticles of Bohemian *Lesleya*. The cuticles conformed to features of pteridosperms and cycads. Leary (1998) suggested a relationship with the Gondwanan genus *Glossopteris* Brongniart (DiMichele et al. 2016; see also Wagner 2004, p. 36).

Álvarez-Ramis (1997) described '*L. doubingeria*' from the Puertollano Basin (Stephanian C) in the province of Ciudad Real, south-central Spain. However, according to Wagner and Álvarez-Vázquez (2010, p. 289), this is an unacceptable record in view of the dubious generic identification and the spurious species description. It is based on a single fragment of a possible broad-leaved *Taeniopteris* (cf. *T. abnormis* Gutbier). The first representative from Iberia was described as *L. iberiensis*. The fossils of this species were found in lower Gzhelian (Upper Pennsylvanian) strata of the region of São Pedro da Cova, in DCB (Correia et al. 2016).

Additionally, there are other *Lesleya*-like specimens of doubtful classification in need of taxonomic revision. A good example of this are the long leaves '*Taeniopteris* spp.' from the early Permian (Kungurian) Colwell Creek Pond locality, north-central Texas described by Schachat et al. (2014). The oblique veins of these specimens are *Lesleya*-like. *Lesleya* has usually oblique or s-shaped veins, whereas the lateral veins of *Taeniopteris* Brongniart are generally orthogonal to the midvein or very slightly oblique (often with slight curvature at both the insertion point and the margin). Most of the *Taeniopteris* species have angles between veins and pinnule margins of 60–90°, whereas *Lesleya* has angles usually less than 60° (see further explanations about the genus *Lesleya* in 'Taxonomic assignment and comparisons' in the section 'Discussion').

Systematic description

Division

Tracheophyta

Subdivision

Spermatophyta Willkomm 1854

Class

Spermatopsida Willkomm 1854

Order and Family

uncertain

Genus

Lesleya Lesquereux, 1879–80

Type species

Lesleya grandis Lesquereux 1879–1880 (syntype, ISM 8654 – Soft shaly sandstone, base of the Chester Limestone). Two remaining specimens were cited by Watt (1974) as being at Harvard. However, no catalogue numbers were given. The type specimens were assigned to Lesquereux by Prof. A. H. Worthen; Lendemer 2002).

Systematic remarks and diagnostic characters used for species differentiation

The taxonomic classification of the genus *Lesleya* for order and family levels still remains uncertain (e.g., Taylor et al. 2009; DiMichele et al. 2016). Bashforth et al. (2016) have placed *Lesleya* within Phasmatocycadales and Phasmatocycadaceae, in accordance with Doweld (2001) and Anderson et al. (2007). However, this attribution to order and family levels is obscure or unclear. In relation to the higher taxonomic ranks, it seems that most authors tend to place *Lesleya* within Gymnospermophyta, with affinities to the Cycadopsida and Pteridospermopsida (e.g., Florin 1933; Leary 1974, 1990, 1993, 1998; Leary and Pfefferkorn 1977; Remy and Remy 1977, 1978; Wagner 2004; Taylor et al. 2009). However, both the Gymnospermophyta and the Pteridospermopsida are not monophyletic groups and, therefore, can not be considered as valid taxonomic ranks. Moreover, raising 'seed plants' to a divisional rank is basically taxonomic inflation and obscures phylogenetic relationships. As for the Cycadopsida, Leary (1990) found similarities with the seed habit of the modern cycadopsid gymnosperms (cycads), but this systematic affinity is quite uncertain because it is based on one single, very incomplete and poorly preserved leaf specimen of *Lesleya* – only the species *L. cheimarosa* has seeds on petioles (Leary 1990, fig. 1). Fructifications of other *Lesleya* species are unknown. A formal classification of the gymnosperms and pteridosperms for higher ranks is Spermatopsida within the division Tracheophyta, which form part of the same monophyletic or natural group – the 'spermatophytes' (seed-producing plants *sensu lato*) (e.g., Kenrick and Crane 1997; Crane et al. 2004; Pryer et al. 2004; Anderson et al. 2007).

Due to the fragmentary nature of most *Lesleya* material (Lesquereux 1879–1880, 1884; Zeiller 1890; Remy and Remy 1975, 1978), the different species of *Lesleya* are classified using leaf characters such as the leaf shape, type of margin and the venation pattern (Leary and Pfefferkorn 1977; Leary 1980; Šimůnek 1996; Correia et al. 2016; see Table 1).

In addition, only leaves (that include the ovules attached to leaf petioles) are known for the genus *Lesleya*, then this generic name is treated here as a 'fossil-genus' of foliage, not a genus of whole plant.

Lesleya ceriacoi

Correia, Barbosa, Šimůnek, Muchagata et Sá, sp. nov.
Figures 2–6

Diagnosis

Large lanceolate leaf with serrate margins in the apical part, broad at the middle with straight margins gradually tapering into a narrow base. Teeth widely spaced (ca. 2 teeth/cm), asymmetrical and with irregular arrangement. Broad midvein divided into a spray of separate veins in the leaf apex. Oblique lateral veins arise in very acute angle from midrib, curve slightly, dividing twice to thrice, reaching the margin in acute angle. Vein density 10–12 veins/cm on the leaf margin.

Etymology

The new species is named after the Head of Collections and Research of the MHNC-UP Luis Ceríaco, for his important contribution as a herpetologist and explorer to the knowledge of the biodiversity of Africa, where he has led several expeditions and has discovered many new endemic species.

Holotype

Specimen MHNCUP/PAB-29a designated here is stored at the MHNC-UP (Figures 3 and 6a).

Paratypes

Specimens with numbers MHNCUP/PAB-29b, MHNCUP/PAB-29c, MHNCUP/PAB-29d and MHNCUP/PAB-29e (Figures 4, 5 and 6b–e).

Type locality

São Pedro da Cova region, Douro Carboniferous Basin, northwestern Portugal (Figure 1c).

Type horizon and age

Compressed (compact) and laminated grey shales, rich in quartz clasts. The age is early Gzhelian (ca. 303 Ma) of the Late Pennsylvanian Epoch.

Table 1. Comparison of the key morphological features of *Lesleya ceriacoi* sp. nov. with the other known species for the genus. Adapted from Correia et al. (2016, table 1) and according to descriptions and illustrations provided of Remy and Remy (1975).

Characters	*Lesleya grandis* Lesquereux (1879–1880)	*Lesleya delafondii* Zeiller (1890)	*Lesleya ensis* Zeiller (1888)	*Lesleya weilerbachensis* Remy and Remy (1975)	*Lesleya iberiensis* Correia et al. (2016)	*Lesleya ceriacoi* sp. nov.	*Lesleya gimmii* Remy and Remy (1978)	*Lesleya angusta* Grand'Eury 1877/ Grand'Eury (1890)	*Cannophyllites (Lesleya) simplicinervis* Grand'Eury (1890)	*Lesleya cocchii* De Stefani (1901)	*Lesleya cheimarosa* Leary and Pfefferkorn (1977)	*Lesleya microphylla* Lesquereux (1884)
Leaf shape	Lanceolate	Lanceolate	Lanceolate	Lanceolate	Lanceolate	Lanceolate	Narrow–elliptical	Lanceolate	?Spatulate	?Lanceolate	Lanceolate	Oval–oblong
Leaf length	>190(220) mm	>200 mm	>155 mm	> 230 mm	>225 mm	550–600 mm	130 mm	235 mm	110-?300 mm	300–500 mm	200 mm	40 mm
Leaf width	83 (80) mm	70 mm	40 mm	66 mm	50 mm	64 mm	35 mm	27 mm	28-?80 mm	36 mm	40 mm	16 mm
Form of leaf apex	Obtuse	?obtuse	?obtuse	Obtuse	?	Acute (subacute)	?	Obtuse	Obtuse – rounded	?	Acute to attenuate	Obtuse
Form of leaf base	Cuneate	?	?	Cuneate	Cuneate	Narrowed (Acute)	Acute	Obtuse	Sub-cordate	?	Acuminate (acute)	Decurrent, shortly auriculate
Leaf margin	Entire to lacerate/ pinnatifid	Serrate	Entire	Dentate (serrate)	Entire	Serrate to deeply lacerated	Entire	Entire	Entire	Entire	Entire	Entire
Midrib width in the base	2 mm	?	2 mm	?	1–3 mm	4 mm	5 mm	5 mm	> 3 mm	?	2.0	?
Midrib width in the middle	1 mm	1–2 mm	1 mm	1–2 mm	2–3 mm	2–3 mm	< 5 mm	2 mm	2.5–5 mm	2.0	0.7	?
Midrib width in the apex	Decurrent until the end of apex?	Divided in individual veins? (missed tip)	Divided in individual veins	Divided in individual veins	?	Divided in individual veins	?Into veins	1 mm; spread into veins	Divided into veins	?	divided into veins	?
Lateral veins per 1 cm of the margin	16–20; 25–30	8.–12	8.–12	12.–20	10.–13	10.–12	11.-13	15–17	7.-8	cca 18	24–36	40.
Angles of lateral veins and leaf margin	?	?	?	9.–10°; base 13	variable depending on position (5°–35°)	20°–23°	34–52°	55–60°	34–38°	40–45°	40–70°	50°
Angles of lateral veins and midrib	50–60°	26°	10–22°	13–14°; apex 11°	7°–15°	5°–14°	Nearly parallel (6°)	25–30°	13–25°*	15–30°*	10–20°	Very acute
Number of vein forking	2–3x	3–?4x	2–3x	3–(4)x	1–2x	3x	3x (near midrib)	1x (near midrib)	0-(1)x	2–3x	1–2x	?
Vein course	Till 1/3 equally to the margin bent, but apically more straight	Straight	Straight	Straight, only near the margin slightly bent	slightly curved	slightly curved	Oblique course from midrib and then straight to the margin	Slightly oblique from midrib to the margin	Very slightly obliquely from midrib to the margin	Obliquely from midrib slightly curved and nearly straight to the margin	Slightly S-shaped	?
Tooth length	No	0.5–1.0 mm	No	1.5–2.5 mm	No	1.5–5.5 mm	No	No	No	No	No	No
Number of teeth per 1 cm	No	8	No	4.-5	No	2	No	No	No	No	No	No
							15 ribs on midrib	According to Grand'Eury (1890)	*25° smaller pinnule	Zeiller 1906 – small fragment *slightly different angle on both sides of midrib		
Locality	USA	Autun, France	France	Weilerbach, Germany	Douro Basin, Portugal	Douro Basin, Portugal	Germany	Gard, France	Gard, France	Italy; Blanzy, France	Illinois, USA	USA
Age	Duckmantian	Asselian	Gzhelian – Asselian	Bolsovian	Gzhelian	Gzhelian	Asselian	Barruelian – Stephanian B	Barruelian – Stephan B	Stephanian B – Asselian	Namurian B–C	late Stephanian C to late Autunian

Detailed description

The holotype MHNCUP/PAB-29a (Figures 3 and 6a) is the lower-to-middle part of a leaf with preserved length of 218 mm and width of 49 mm. The leaf margins are lacerated, having discrete lacerations in the top and lower regions of specimen (Figure 3b) and a deep laceration at the middle that reaches almost the midvein, dividing the lamina into two separate segments (Figure 3a, c); the lacerations occur through the lateral veins. The margins remain relatively straight, becoming gradually narrower towards the basal part of the leaf (Figure 3a). The lateral veins are closely spaced (10–12 veins/cm on leaf margin) and divided two or three times, forking two times close the midvein with a later (third) bifurcation occurring near the margin. They are oblique, slightly curved from the midvein to the margin, forming angles of 5°–14° with the midvein, and 20°–23° with the margin. The midvein is broad (2.5–4.0 mm wide) with irregular margin at its base, bearing several longitudinal striations.

Paratype MHNCUP/PAB-29b (Figure 4 and 6b) is an upper part of a leaf with a nearly complete acute leaf apex. The leaf has a preserved length of 165 mm and a maximum width of 37 mm. Its leaf margins are serrate in the apical part and slightly to deeply lacerated at the middle and basal parts of specimen (Figure 4b). The teeth of the serrate parts of the margins are 1.5–5.5 mm in length, widely spaced with two teeth per cm on the margin (an average of 2–6 leaf teeth on the apex margins), asymmetrical, and irregularly arranged (Figure 4b, c). The midvein is relatively thin (0.5–2.0 mm wide) and terminates by dividing into multiple arching smaller veins in the leaf apex. Paratype MHNCUP/PAB-29c (Figures 2b, 5a and 6c) is a middle-to-upper part of a leaf with a preserved length of 94 mm and a maximum width of 63 mm. Its leaf margins are deeply lacerated, and midvein is relatively thin, having a width of 2.0–2.2 mm. Paratype MHNCUP/PAB-29d (Figure 5b and 6d) is a middle/lower part of a leaf of 59 mm in length and 41 mm in width. Its leaf margins are substantially entire and straight, and midvein is thin with a width of 1.2 mm. Paratype MHNCUP/PAB-29e (Figure 5c and 6e) is an incomplete part of a leaf base of 52 mm in length and 28 mm in width. Its leaf margins are entire, relatively straight and asymmetrical. The midvein is broad with a width of about 4.0 mm and longitudinally striated. All four

Figure 4. Paratype MHNCUP/PAB-29b of ***Lesleya ceriacoi*** sp. nov.; early Gzhelian, Douro Carboniferous Basin (Portugal). (a) Upper part of a leaf with a nearly complete acute leaf apex, showing serrate and lacerate margins. (b) Enlargement of top part of the specimen in a, displaying serrate margins on leaf apex (black dashed rectangular boxes) and deep/discrete lacerations on the lamina (white dashed rectangular boxes). (c) Enlargement of serrate margin on leaf apex in b, showing six leaf teeth (white dashed rectangular boxes). (d) Enlargement of serrate margin on leaf apex in b, showing two leaf teeth (white dashed rectangular boxes) and one discrete laceration (black dashed rectangular box). Scale bars: 20 mm (a and b); 10 mm (c and d).

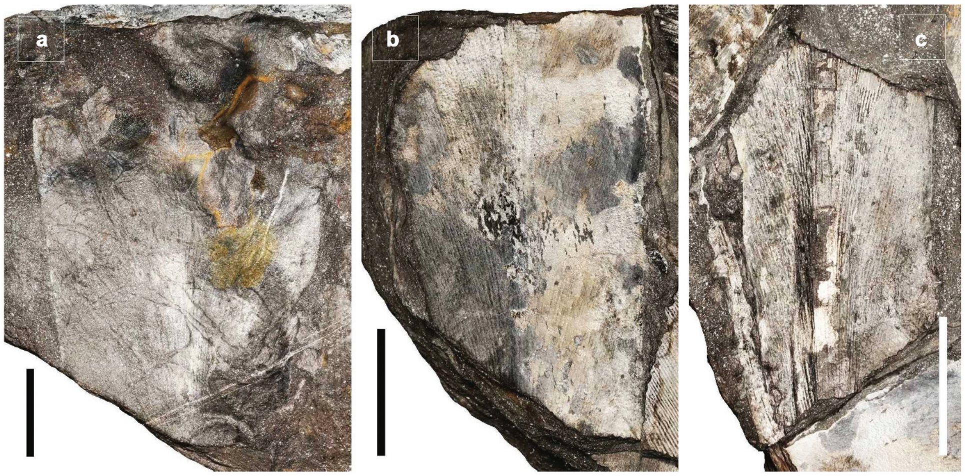

Figure 5. Paratypes of ***Lesleya ceriacoi*** sp. nov.; early Gzhelian, Douro Carboniferous Basin (Portugal). (a) Middle-to-upper part of a leaf showing deeply lacerated margins (MHNCUP/PAB-29c); specimen preserved on the back side of the fossil (Figure 1b). (b) Middle/lower part of a leaf (MHNCUP/PAB-29d). (c) Lower part of a leaf (MHNCUP/PAB-29e). Scale bars: 20mm.

paratypes display oblique lateral veins, closely spaced, and slightly curved from the midvein to the margin, forming very acute angles with the midvein.

The reconstruction of an entire leaf of the new ***Lesleya* species** is in Figure 7. It is based on the different preserved leaf parts (Figure 6), which compose a nearly complete leaf. Its total length is estimated to about 60 cm.

Discussion

Taxonomic assignment and comparisons

The five specimens described herein (Figures 2–6) display typical morphological features of the genus *Lesleya. Lesleya* leaves are described as simple, large and wide, of lanceolate and sublanceolate shape, with entire to pinnatifid margin, gradually narrowing towards the base, and having very oblique veins, curved, sinuous or s-shaped, equal, simple/pinnate to repeatedly dichotomous (e.g., Lesquereux 1879–1880, p. 142; Leary and Pfefferkorn 1977; Remy and Remy 1978; Leary 1980; Leary and Trask, 1985; Šimůnek 1996; Correia et al. 2016).

In comparison with all known species of *Lesleya* (Table 1), *Lesleya ceriacoi* sp. nov. bears the closest resemblance to *Lesleya grandis* Lesquereux 1879–1880 from the upper Mississippian (‘Chesterian’) of the USA. *L. grandis* has wide leaves with deeply pinnatifid (dissected?) margins in both apical and lower leaf parts (the nature of the dissected margins is discussed further in subsection ‘Adaptation strategies of the leaf morphological traits of *Lesleya ceriacoi* sp. nov.’). However, leaves of *L. grandis* display a cuneate base with arched margins and obtuse apex (Lesquereux 1879–1880, pl. XXV, figs. 1–3), whereas *L. ceriacoi* sp. nov. shows an acute/subacute and serrate apex and straight margins that gradually taper into a narrow base. Furthermore, the leaves of *L. ceriacoi* sp. nov. are significantly larger and show more inclined lateral veins than those of *L. grandis* having a lower vein density, and a midvein divided into a spread of separate veins in the leaf apex (see summary of comparative features in Table 1).

L. ceriacoi sp. nov. also bears some similarities to *L. weilerbachensis* Remy and Remy (1975) from the Westphalian C–D (Bolsovian–Asturian/Moscovian) of Germany (e.g., Remy and Remy 1975, 1978; Correia et al. 2016). *L. weilerbachensis* has wide leaves with serrate margins and bears strongly inclined lateral veins and a midvein divided into veins at the apex. However, *L. weilerbachensis* shows straight lateral veins, an obtuse apex and cuneate base and its serrate margins have symmetrical teeth with a regular arrangement. In contrast, *L. ceriacoi* sp. nov. shows slightly curved lateral veins, an acute/subacute apex and straight margins that gradually narrow towards the base. In addition, leaves of *L. ceriacoi* sp. nov. are substantially larger and have an irregular tooth arrangement, with asymmetrical teeth, widely spaced, and few in number (an average of 2–6 leaf teeth on apex margins) (see Table 1).

L. ceriacoi sp. nov. also shows a superficial similarity to *L. iberiensis* Correia et al. (2016), a Portuguese congener of the same age (early Stephanian C/early Gzhelian) and found in the DCB (Correia et al. 2016). Both species display very inclined and slightly curved lateral veins with a similar vein density, and have a broad midvein. However, they differ greatly in the form of leaf margins. The margins of *L. Iberiensis* are entire and arched towards the base, forming a cuneate and long base. In addition, they also are distinguished by the leaf size (see Table 1).

L. delafondii Zeiller (1890) from the upper Autunian (Asselian/lower Permian) of France (e.g., Correia et al. 2016) has wide and serrate leaves with a venation pattern similar to that of *L. ceriacoi* sp. nov. However, *L. ceriacoi* sp. nov. differs from *L. delafondii* in the tooth size and arrangement. Serrate margins of *L. delafondii* have substantially smaller and more numerous teeth, with a regular arrangement on leaf margin (see Florin 1933, text-fig. 1, p. 4; see also Table 1). The holotype of *L. delafondii* does not have a leaf base or apex (Zeiller 1890, fig. 2), so comparison of these features is not possible.

Adaptation strategies of the leaf morphological traits of **Lesleya ceriacoi** *sp. nov*

Lesleya ceriacoi sp. nov. exhibits an exquisite leaf morphology in showing a very long and relatively narrow leaf that is broadly dissected (lacerated) with a serrate apex. A number of factors could explain this complex leaf shape. Leaf form is closely associated with climate (e.g., Xu et al. 2008, 2009; Guerin et al. 2012; Schmerler et al. 2012). The leaf form tends to become narrower during intervals of drought, as narrow leaves can reduce transpiration during drier periods (e.g., Farris 1984; Xu et al. 2008, 2009). Other aspects of leaf form, such as toothed margins, evolve along an environmental gradient (Schmerler et al. 2012). As the principal photosynthetic

Figure 6. The different preserved leaf parts of ***Lesleya ceriacoi*** sp. nov. (a) holotype MHNCUP/PAB-29a. (b) Paratype MHNCUP/PAB-29b. (c) Paratype MHNCUP/PAB-29c. (d) Paratype MHNCUP/PAB-29d. (e) Paratype MHNCUP/PAB-29e. Scale bar to all specimens: 50 mm.

organ of most plants, leaves are organs that are sensitive to environmental changes in the process of evolution and adaptation (e.g., Xu et al. 2008). Xeromorphic traits, like those of *Lesleya*, are thought to be ecological adaptations to seasonally dry environments (e.g., DiMichele et al. 2010, 2016; Bashforth et al. 2014, 2016, 2021; Correia et al. 2016; Correia and Murphy 2020). *L. ceriacoi* sp. nov. provides novel 'xeromorphic' morphological traits for the genus in Euramerican drought-tolerant floras. They evidence evolutionary adaptation to a changing environment in DCB within central tropical Pangaea during the Late Pennsylvanian. This adaptation to environmental change is consistent with the appearance of *Lesleya* in the early Gzhelian (Late Pennsylvanian) of Iberia immediately after a transition from glacial to interglacial (humid-to-dry) conditions in central tropical Pangea during the Kasimovian–Gzhelian (ca. 303.7 Ma) interval (Correia et al. 2016; Correia and Murphy 2020).

On the other hand, some adaptive morphological traits, such as toothed margins, may be the result of a plant response to a more seasonal environment, or even to biotic factors, such as herbivory (Schmerler et al. 2012; see also Givnish and Kriebel 2017). Plant fossil assemblages of the DCB have demonstrated that climatic conditions were at least somewhat seasonal during the depositional history of this intramontane basin (Correia et al. 2020; Bashforth et al. 2021). In addition, plant–insect interactions of galling documented in the fossil record of the DCB (Correia et al. 2020) suggest that the resident plant species could have developed some antagonistic traits, like leaf teeth, as a defence mechanism against attacks from herbivorous insects. The insect-induced plant galls are known to become more prevalent on modern vegetation as climate shifts to drier conditions (Price et al. 1987; Raman et al. 2005; Correia et al. 2020). Such a response in the DCB is consistent with sedimentological indicators of seasonal precipitation (Correia et al. 2020) at the time that the *L. ceriacoi* sp. nov. appeared.

The leaf lacerations of the *L. ceriacoi* sp. nov., may result from several factors. They may be features of old leaves or result when a leaf became dry and fissures started to occur along the veins after its death. Laceration may also be a taphonomic result after leaf burial. On the other hand, these lacerations could indicate something about leaf stiffness or even thickness of the lamina.

Nevertheless, degree of blade dissection is correlated with climate in modern plants (Royer et al. 2005; Xu et al. 2008). The deep lacerations taking place simultaneously on both leaf margins of *L. ceriacoi* sp. nov. (see Figures 5a and 6c) suggest that this species may have developed dissected leaf margins as adaptive traits to the specific climatic conditions of the DCB. It is also interesting to note the entire leaf margins of the Portuguese congener *L. iberiensis*, which coexisted with *L. ceriacoi* sp. nov. in the region of São Pedro da Cova. This coexistence could suggest that laceration is a phenotypic trait variation (intraspecific variation) within a single species – *L. iberiensis*. However, this seems unlikely given the significant differences between the two species, especially in the apex margins (see Table 1 for the morphological differences among the known species of the genus).

Palaeoecology

The leaf fossils of *Lesleya ceriacoi* sp. nov. are associated with fragmented cordaitalean leaves of the genus *Cordaites* Unger – a coniferopsid gymnosperm, and also with some fragments of marattialean fern foliage (Figure 2a). Recent studies (Correia et al. 2016; Correia and Murphy 2020) have demonstrated that *Lesleya* and *Cordaites* preferred moisture-deficient (seasonally dry) environments within DCB. The occurrence of these plants together with other xerophytes, such as walchian conifers, taeniopterids, and dicranophyllalean conifers in the fossil record of DCB (Wagner and Lemos de Sousa 1983; Correia et al. 2016, 2018; Pšenička et al. 2017), suggests that seasonally dry climatic conditions prevailed in this region during Gzhelian time, at the end of the Late Pennsylvanian. These dry seasonal conditions comprised a dry subhumid to semiarid climate (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; see also Cecil 2013, table 2). Similar biomes have been documented in Lower and Middle Pennsylvanian deposits of the Illinois Basin, USA (DiMichele et al. 2016; Bashforth et al. 2016, 2021). Their taphocoenoses are composed mainly of the gymnosperms *Lesleya, Cordaites* and *Taeniopteris* and walchian conifers, indicating that drought-tolerant floras colonised various tropical regions of the central Pangaea throughout Pennsylvanian time. The dispersion of these plants into central tropical Pangaea occurred when new dryland (seasonally dry) environments appeared (Correia and Murphy 2020).

Interestingly, the presence of associated remains of marattialean ferns (Figure 2a) suggests that drought-tolerant floras, such as *L. ceriacoi* sp. nov., coexisted with relict mesophytes–hygrophytes (see Bashforth et al. 2021, table 1), possibly from a wetland vegetation reduced to small and scattered (riparian?) refugia within a predominantly dryland setting. A mixture of wetland and drought-tolerant taxa may also indicate that the resident floras lived in different soil moisture conditions, and they were transported and preserved to the same sites of deposition under a regime of seasonal precipitation. The floras of the DCB grew in siliciclastic environments adjacent to fluvial and limnic habitats within an intramontane region (Correia et al. 2016, 2020; Bashforth et al. 2021). *L. ceriacoi* sp. nov. occurs in a siltstone interlayered with a conglomeratic sandstone deposit (Figure 2b). Such a sedimentological record suggests that this plant lived near fluvial environments, the same environmental interface described for the habitat of *L. iberiensis* in the São Pedro da Cova region, where this species was also found together with leaves of *Cordaites* (Correia et al. 2016, Figure 7). Similar ecological conditions have been

Figure 7. Suggested reconstruction of an entire leaf of ***Lesleya ceriacoi*** sp. nov. on the basis of the different leaf parts (Figure 6) preserved on the matrix of the fossil. Artwork of Vitor Silva, based on pencil drawing and plates of the original specimens provided by P. Correia.

documented in Early Pennsylvanian-age macrofloral deposits from New Brunswick, in Canada, where leaves of *Lesleya* and *Cordaites* are found together in seasonally dry habitats associated with marginal fluvial depositional environments (Bashforth et al. 2014). This also is essentially the same flora reported by Bashforth et al. (2016) from the margin of the Illinois Basin, in Indiana, USA, in the late Bolsovian (early/middle Moscovian), where *Lesleya* was found in association with *Cordaites* and marattialean fern foliage.

Conclusions

In this work, we document a 303 million-years-old fossil of a previously unknown gymnosperm species, *Lesleya ceriacoi* sp. nov., from the Upper Pennsylvanian of Portugal, rediscovered in the historical (herbarium) collections of the Museu de História Natural e da Ciência da Universidade do Porto (MHNC-UP). *L. ceriacoi* sp. nov. displays a sophisticated leaf shape with novel xeromorphic morphological traits for the genus (*Lesleya*) and provides valuable insights on the morphological and ecological adaptations of the Euramerican drought-tolerant floras to the intramontane environments within central tropical Pangaea. These adaptations occurred during a climate transition interval from icehouse to greenhouse conditions at the end of Late Pennsylvanian (Gzhelian) time. Furthermore, the discovery of this new species indicates that the genus was much more diverse than presently understood from its spotty fossil record.

Museums are a treasure trove of many new species. The description of this new species based on museum material also highlights the importance of natural history museums and their collections for the advancement of science.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Author contributions

P.C. and Z.Š. wrote the manuscript. P.C. and A.A.S. prepared the figures. J. M. helped in the preparation of fossil sample and photographic documentation. P.C., Z.Š., C.B. and A.A.S. were involved in the taxonomic study of the new *Lesleya* fossil and corrected the text of manuscript. All authors discussed and approved the final manuscript.

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