Contribution to the knowledge of the fossil flora and fauna of the Douro Carboniferous Basin (NW of Portugal)

Pedro Alexandre Pereira Correia

Doutoramento em Geociências

Especialidade em Estratigrafia e Sedimentologia

Departamento de Geociências, Ambiente e Ordenamento do Território

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Orientador

Deolinda Flores, Professora Catedrática, Faculdade de Ciências da Universidade do Porto

Coorientadores

Artur Sá, Professor do Departamento de Geologia, Universidade de Trás-os-Montes e Alto Douro

Brendan Murphy, Professor do Departamento das Ciências da Terra, Universidade St. Francis Xavier

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ABSTRACT

The study of paleofloras and paleofaunas has played an important role in understanding the evolution of plant and animal communities and their ecosystems. In this sense, the study of Carboniferous flora and fauna contributes to the understanding of global-scale continental paleogeographic and paleoclimatic changes in the late Paleozoic time.

The paleobotany and paleozoology of continental Carboniferous strata in Portugal have been thoroughly documented by several authors. Among them, Carlos Teixeira (1910–1982) greatly contributed to the understanding of the paleontology of Carboniferous strata in Portugal, and his research has provided foundation for the current state of science knowledge.

The Douro Carboniferous Basin (DCB) is one of the best known continental Carboniferous intramontane basins in Portugal where a very important and diversified Late Pennsylvanian megaflora occurs. In this framework, the São Pedro da Cova and Ermesinde areas are the important fossil localities within the DCB, where exceptional paleontological, stratigraphic and structural features are preserved.

In this study, new paleontological occurrences were documented in the DCB. The new fossil specimens are from new outcrops that occur in the São Pedro da Cova and Montes da Costa regions. According the biostratigraphic data obtained, the new outcrops of both localities are assigned to early Gzhelian age.

The results obtained from systematic paleontology include the identification of 42 floral species documented for the first time in the DCB, and descriptions of 11 new species, and two new animal taxa. These new fossil data include the first record in the Iberian Massif of an enigmatic *Lesleya* dryland flora and the arachnid *Aphantomartus pustulatus*. Both occurrences provide significant floral and faunal affinities and paleogeographic, paleoenvironmental and paleoclimatic constraints between Laurentia and the Iberian Massif in the Late Pennsylvanian as Pangea amalgamated in the Late Pennsylvanian. Other floral elements with different stratigraphic ages, such as *Lobatopteris lamuriana* Heer, *Callipteridium jongmansi* Bertrand, *Pecopteris* cf. *miltonii* (Artis) Brongniart and aff. *Rhodeopteridium subpetiolatum* Potonié, are identified and represent controversial chronostratigraphic data for the DCB. The floral taxa described herein belong mainly to orders Sphenopsida, Pteridopsida and Pteridospermopsida, and these megafloral and faunal elements provide new insights into the paleobotanical diversity, paleoenvironment, paleoecology and paleoclimatic conditions of the Upper Pennsylvanian floras in the Iberian Massif. In this assessment, the new fossil data indicate that most of resident floral and faunal assemblages lived and evolved in mountain riparian environments within Variscan orogen during the Late Pennsylvanian during dry climatic intervals in the Late Pennsylvanian.

Key-words: Fossil flora and fauna, new outcrops, Douro Carboniferous Basin, lower Gzhelian, São Pedro da Cova, Montes da Costa, Portugal.

RESUMO

O estudo das floras e faunas fósseis do Carbónico (1) tem desempenhado um papel relevante na compreensão acerca das mudanças paleoclimáticas e paleogeográficas continentais, possibilitando assim um melhor entendimento sobre a evolução das comunidades vegetais e animais e seus ecossistemas à escala global no Paleozóico superior.

A paleobotânica e paleozoologia do Carbónico continental português foram exaustivamente documentadas por vários autores. Carlos Teixeira (1910–1982) foi um dos paleobotânicos portugueses do século XX que mais se destacou. O seu trabalho contribuiu para muito do nosso conhecimento atual, no que diz respeito à paleontologia do Carbónico de Portugal.

Uma das bacias carboníferas intramontanhosas mais conhecidas do Carbónico continental de Portugal é a Bacia Carbonífera do Douro (BCB). Esta preserva uma flora fóssil, diversificada, de idade do Pennsylvánico (2) Superior, constituindo por isso um importante objeto de estudo para a paleobotânica. São Pedro da Cova é o principal setor que compõe geologicamente a BCD, e destaca-se primordialmente, por se tratar de uma localidade com importantes afloramentos, reconhecidos pelas suas caracteristicas geológicas estruturais e pelos seus recursos paleontológicos singulares, com especial interesse científico. Os seus afloramentos contêm fósseis de vegetais e animais de idade do Gzheliano (Estefaniano C).

No presente trabalho, foram documentados novos elementos megaflorísticos e faunísticos na BCD. Os novos espécimes fósseis foram coletados em novos afloramentos das regiões de São Pedro da Cova e Montes da Costa. Esta última localidade insere-se na configuração geológica da BCD, e é detentora de uma megaflora fóssil bem preservada e diversificada. Os novos afloramentos foram atribuídos à idade do Gzheliano inferior com base nas espécies florísticas descritas.

Os resultados obtidos compreendem um total de 42 espécies documentadas pela primeira vez na BCD, com a descrição de 11 novas espécies, incluindo dois novos taxa de fauna. Estes dados fósseis incluem o primeiro registo na Península Ibérica da enigmática flora xeromórfica *Lesleya* e o aracnídeo *Aphantomartus pustulatus*, e

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(1, 2) According to the Portuguese version of the ICS International Chronostratigraphic Chart presented by Cohen *et al.* (2013) (http://www.stratigraphy.org/ICSchart/ChronostratChart2013-01Portuguese_PT.pdf).

representam importantes afinidades florísticos e faunísticos e restrições paleogeográficas, paleoambientais e paleoclimáticas entre o cratão norte-americano Laurentia e o Maciço (Hespérico) Ibérico dentro da configuração Pangeia no Pennsylvánico Superior. Outros elementos florísticos de diferentes idades estratigráficas, tais como as *Lobatopteris lamuriana* Heer, *Callipteridium jongmansi* Bertrand, *Pecopteris* cf. *miltonii* (Artis) Brongniart e aff. *Rhodeopteridium subpetiolatum* Potonié foram identificados e representam dados cronoestratigráficos controversos para a sequência estratigráfica da BCD. A maioria das espécies florísticas descritas neste trabalho pertence às ordens Sphenopsida, Pteridopsida e Pteridospermopsida, e fornece novos dados sobre a diversidade da flora fóssil da BCD e do Carbónico continental de Portugal. Estes elementos fornecem novos dados sobre as condições paleoecológicas e paleoclimáticas nas quais as floras e faunas residentes estavam inseridas. Nesta avaliação, os novos dados fósseis indicam que a maioria das floras e faunas residentes viveram e evoluíram em ambientes ribeirinhos montanhosos dentro do orógeno Varisco durante períodos de clima seco no Pennsylvánico Superior.

Palavras-chave: Flora e fauna fóssil, novos afloramentos, Bacia Carbonífera do Douro, Gzheliano inferior, São Pedro da Cova, Montes da Costa, Portugal.

Contents

CONTRIBUTION OF THE CO-AUTHORS

Professors Deolinda Flores and Ary Pinto de Jesus from Department of Geosciences, Environment and Spatial Planning of Faculty of Sciences of the University of Porto (Portugal) and Institute of Earth Sciences, Faculty of Sciences of the University of Porto Pole (ICT), Professor Artur Sá from Department of Geology, University of Trás-os-Montes and Alto Douro (Portugal) and Geosciences Center, University of Coimbra (Portugal), and Professor Brendan Murphy from Department of Earth Sciences, St. Francis Xavier University (Canada), as my PhD supervisors, with whom I discussed firsthand the results contributing to the improvement of the manuscripts.

Dr. Zbynek Šimůnek (Czech Geological Survey, Czech Republic) and Dr. Josef Pšenička (West Bohemia Museum in Pilsen, Czech Republic) contributed as experts in Paleobotany to the description and classification of the new paleobotanical material and delicate discussions in systematic paleontology.

Dr. Andre Nel (National Natural History Museum of Paris, France) contributed as expert in Paleoentolomology to the description and classification of the new insect specimens.

Rúben Domingos, André Carneiro and João Paulo Loureiro contributed in the field works (excavations) and fossil sample collection.

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PART I – INTRODUCTION

1. Overview

The knowledge of the paleobotany and paleozoology of the continental Carboniferous of Portugal is today quite deep documented in works authored by Carlos Ribeiro (Ribeiro *et al.*, 1853), Bernardino António Gomes (Gomes, 1865), Hugo Geinitz (Geinitz, 1867), Oswald von Heer (Heer, 1881), Wenceslau de Lima (Lima, 1983/1987, 1888), João Carrington Simões da Costa (Carríngton da Costa, 1931, 1938), Carlos Teixeira (Teixeira, 1937, 1938a, b, 1939a–e, 1940a–e, 1941a–d, 1942a–e, 1943, 1944a–c, 1945, 1946a, b, 1947, 1949, 1952, 1953, 1955, 1956, 1964, Teixeira and Medeiros, 1943; Teixeira and Fonseca, 1953; Teixeira and Pais, 1976), Rudolf Florin (Florin, 1940), Daniel Laurentiaux (Laurentiaux and Teixeira, 1948, 1950, 1958a, b), Neftali da Costa Fonseca (Fonseca, 1954, 1959), Paul Corsin (Corsin and Lemos de Sousa, 1972), João Pais (Pais, 1973), Richard Michael Cardwel Eagar (Eagar, 1983), Robert Wagner (Wagner, 1983; Wagner and Lemos de Sousa, 1982a, b, 1983, 1985) and Manuel João Lemos de Sousa (Lemos de Sousa and Wagner, 1983a, b, 1985a, b). However, the knowledge of the diversity of fossil flora and fauna of the continental Carboniferous of Portugal and their significance for paleoecology and paleoclimate need to be reappraised in the light of new fossil data.

The Douro Carboniferous Basin (DCB; lower Gzhelian [lower Stephanian C]; NW of Portugal) represents one of the most studied continental Carboniferous basins, concerning the fossil flora and fauna mainly carried out mainly by Carlos Teixeira and Daniel Laurentiaux during the decades of 1930–1950 (see aforementioned references). Additional studies focused on paleolimnology, performed by Carlos Teixeira and Neftali da Costa Fonseca in the 1940–50's, and later revised by Richard Michael Cardwel Eagar during the early 1980's, provide important insights about lacustrine-fluvial (limnic) environments described in DCB, based on the description of non-marine bivalves associated with fossil plant deposits.

The São Pedro da Cova region is one of the more complex structural-geologic areas inside the DCB, and one of better studied fossil localities with floras and faunas of the continental Carboniferous of Portugal described by several authors (see aforementioned references). Its Carboniferous strata include some relevant paleontological outcrops which preserve mainly a high diversity from early Gzhelian-age flora.

Fossil floral and faunal data of Permian–Carboniferous age have been used to gain a better understanding of the global-scale continental paleogeographic changes which led to variations in climate as expressed (i) within and among the different phytogeographic Pangean provinces such as Angara, Euramerica, Cathasia and Gondwana, (ii) the occasional mobility (migration) of their flora and fauna, and (iii) inferred of their paleoenvironments and paleoecologies (e.g., Alfred Wegener (Wegener, 1912), Richard Leary (Leary and Pfefferkorn, 1977; Leary and Trask, 1985), Maya M. Oshurkova (Oshurkova, 1996), Jörg Trappe (Trappe, 2000), Frédéric Fluteau (Fluteau *et al.*, 2001), Gian Battista Vai (Vai, 2003), Richard Michael Cardwel Eagar (Eagar and Belt, 2003), John L. Isbell (Isbell *et al.*, 2003), Hans Kerp (e.g., Kerp *et al.*, 2006), Robert H. Wagner (e.g., Wagner and Lyons, 1997; Wagner, 2004; Wagner and Mayoral, 2007), Hermann W. Pfefferkorn (e.g., Pfefferkorn *et al.*, 2008), Roy E. Plotnick (Plotnick *et al.*, 2009), Jason Hilton (Hilton and Cleal, 2007, 2011), Leonard Robert M. Cocks (e.g., Cocks and Torsvik, 2011), Rashmi K. Srivastava (Srivastava *et al.*, 2011), Howard Falcon-Lang (e.g., Falcon-Lang, 2003, 2004, 2006; Falcon-Lang and Bashforth, 2004; Falcon-Lang and DiMichele, 2010; Falcon-Lang *et al.*, 2009, 2011, 2012), William A. DiMichele (e.g., DiMichele *et al*., 2001, 2005, 2008, 2009, 2010, 2013), Nicholas A. Rosenau (Rosenau *et al.*, 2013) Arden Bashforth (Bashforth *et al.*, 2010, 2011, 2014), Christopher J. Ceal (Cleal, 2008a, b; Cleal and Thomas, 2004; Cleal *et al.*, 2015)).

The present work is the result of new paleontological studies on the DCB, conducted by the author, and this research focuses on the discovery and description of new macrofloral and faunal elements collected in newly discovered fossiliferous outcrops in the São Pedro da Cova (Gondomar) and Montes da Costa (Ermesinde) regions. Documentation of these new paleontological occurrences contributes (i) a better understanding of the paleontological diversity of the DCB, (ii) the attendant paleoenvironmental, paleoecological and paleoclimatic conditions, and (iii) to evaluate their significance for the local stratigraphy and continental paleogeography within the Variscan orogen for the Late Pennsylvanian.

2. Present research and objectives

The main objectives of this thesis are:

i) To update the published list of flora and fauna list of the Douro Carboniferous Basin;

ii) To provide a thorough taxonomic description and classification (systematic paleontology) of fossil flora and fauna from the new outcrops reported in the São Pedro da Cova and Montes da Costa regions;

iii) To compare the new fossil specimens with similar ones from paleobotanical reference collections;

iv) To upgrade the chronostratigraphic framework of the DCB based on the new biostratigraphical data;

v) To assess the significance of the new paleontological data for the paleogeography, paleoclimatology, paleoecology and paleoenvironment within Iberian Massif (Variscan orogen), expanding and refining the knowledge on the origin, and evolution of the DCB;

vi) To reconstruct the late Carboniferous landscape (paleoenvironment, paleoecology and paleoclimate) of the DCB, especially in the São Pedro da Cova region;

vii) To describe and characterize a set of new geosites for the framework “Carboniferous rocks” of the national inventory of Geological Heritage in the São Pedro da Cova and Montes da Costa regions.

3. Thesis structure

This thesis is presented in an article-based format and is comprised of five parts. The Part IV comprising the major part of this thesis was prepared as research papers published in national and international peer-reviewed journals, as well as in congress and conference extended abstracts. Their present status as follows:

Part I corresponds to the introduction that includes a general overview, present research and objectives of this work.

Part II provides a review the previous work on the geology and paleontology of the Douro Carboniferous Basin.

Part III comprises a description of the methods used and the materials studied. This part is divided in six sub-chapters, namely (i) fossil localities and sites and fossil sampling; (ii) methodology and sample preparation; (iii) preservation and taphonomy of the fossil samples studied; (iv) comparison with reference collections; (v) inventory of material placed in the depository; and, (vi) identification and characterization of the new outcrops.

Part IV includes the results and their respective discussion and conclusions. This part comprising papers published in national and international peer-reviewed journals, and congress and conference extended abstracts. The results provide new data concerning the fossil mega-fauna and flora of the DCB, including the description of new taxa, and implications for the paleogeography, paleoclimate, paleoecology and paleoenvironment in the Iberian Massif within the Variscan orogen. This part is divided in two main chapters. The first one is related to the new megaflora and the second to the megafaunal data. They comprise the following published and recently submitted papers:

New floral data

— Correia, P. A., Sá, A.A., Murphy, J.B., Šimůnek, Z., Flores, D. (2016). *Lesleya* Lesquereux from the Pennsylvanian of the Iberian Massif: part of a dryland megaflora from the Variscan orogen, northwestern Portugal. Canadian Journal of Earth Sciences 53, 883-895.

— Correia, P., Šimůnek, Z., Pšenička, J., Sá, A.A., Flores, D. The new plant species from the Upper Pennsylvanian of Portugal (Western Iberian Massif) (manuscript in preparation).

— Pšenička, J., Correia, P., Šimůnek, Z., Sá, A.A., Murphy, J.B., Flores, D. Revision of *Ilfeldia* and establishment of *Ovulepteris* gen. nov. from the Pennsylvanian of Europe, with a discussion on their concepts (accepted in Review of Palaeobotany and Palynology).

— Correia, P., Šimůnek, Z., Pšenička, J., Sá, A.A., Domingos, R., Carneiro, A., Flores, D. (2014). New paleobotanical data on the Portuguese Pennsylvanian (Douro Carboniferous Basin, NW Portugal). Comunicações Geológicas 101, Especial I, 409-414.

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New faunal data

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Part V is the last part of this thesis and, provides general conclusions and final remarks.

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PART II – PREVIOUS RESEARCH STUDIES ON THE GEOLOGY OF THE DOURO CARBONIFEROUS BASIN

1. Geologic setting

The continental Carboniferous of Portugal is exposed in intramountainous pull-apart basins along major tectonic troughs such as the Douro-Beiras Carboniferous Trough, and the Porto-Tomar and Ferreira-Ficalho Faults (e.g., Lemos de Sousa and Wagner, 1983a; Pinto de Jesus, 2001, 2003; Gama Pereira *et al.*, 2008; Flores *et al.*, 2010). Sedimentological facies distribution are profoundly influenced by the tectonic and include the development of alluvial fans at basin base cut by fluvial systems, passing upward into lacustrine and palustrine environments (e.g., Pinto de Jesus, 2001, 2003). These Carboniferous basins are located on the vicinity of Porto, in the North of Coimbra, and North of Alto Alentejo (e.g., Lemos de Sousa and Wagner, 1983a; Pinto de Jesus, 2001, 2003). To the north, the continental Carboniferous deposits are located between the regions of Criaz (northeast of Póvoa de Varzim) and Janarde (northwest of Castro Daire), comprising the Criaz-Serra de Rates, Casais-Alvarelhos, Ervedosa and Douro Basin, and southeastwards of Castro Daire, near Mioma two outcrops (Arco and S. Miguel) were also recognized (Ribeiro *et al.*, 1997; Pinto de Jesus, 2001). The Buçaco Basin is located to the north of Coimbra, and the Santa Susana Basin occurs in the Alto Alentejo region (e.g., Wagner, 1983; Lemos de Sousa and Wagner, 1983a; Pinto de Jesus, 2001, 2003; Figure 1).

The Douro Carboniferous Basin (DCB; Figure 2) is the major Carboniferous basin that occurs within the Douro-Beiras Carboniferous Trough (DBCT). The DBCT is located within the Central Iberian Zone of Variscan (= Hercynian) Chain in the Iberian Massif of NW Portugal. DBCT strikes approximately NW–SE, and extends about 85 km from the São Pedro Fins (NE Porto) to Janarde (E Arouca). The DCB is a narrow belt, typically less than 1 km wide (e.g., Lemos de Sousa and Wagner, 1983a; Pinto de Jesus, 2001, 2003). Within the DBCT there are several outcrops containing well-documented continental Carboniferous strata, with depositional ages ranging in age from middle Bashkirian–Moscovian (Westphalian, Early–Middle Pennsylvanian) to early Gzhelian (Stephanian C, Late Pennsylvanian; see chronostratigraphic classification for the Carboniferous System in Cohen *et al.*, 2013). The DBCT is generally interpreted as a pull-apart basin with a sinistral strike-slip component (Pinto de Jesus, 2001, 2003; Pinto de Jesus and Lemos de Sousa, 2003).

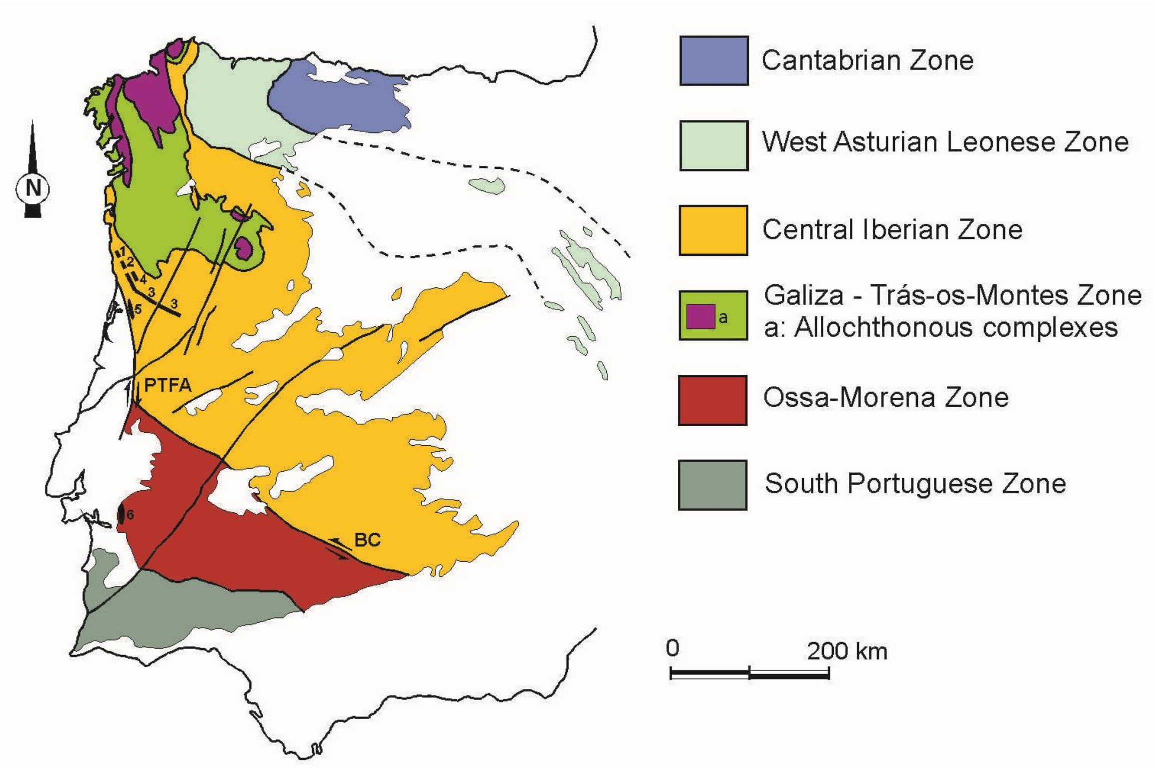

Fig. 1 - Locations of the continental Carboniferous strata in Portugal according to Wagner (1983) and Lemos de Sousa and Wagner (1983a): 1) Criaz-Serra de Rates (Moscovian [Westphalian]?); 2) Casais-Alvarelhos (lower Moscovian [middle Westphalian]?); 3) Douro Carboniferous Basin (lower Gzhelian [lower Stephanian C]); 4) Ervedosa (upper Moscovian [upper Westphalian D]); 5) Buçaco Basin (lower Gzhelian [upper Stephanian C]); 6) Santa Susana Basin (upper Moscovian [upper Westphalian D]). **BC** = “Badajoz-Córdoba” shear zone, **PTFA** = “Porto-Tomar-Ferreira do Alentejo” shear zone. Zonation of the Hesperian Massif adapted from Pérez-Estaún *et al.* (2004).

The DCB strata are continental intramontane syntectonic deposits (e.g., Schermerhon, 1956; Freire, 1981; Wagner, 1983; Domingos *et al.*, 1983; Pinto de Jesus, 2001, 2003). The strata are oriented approximately NW–SE (N130º±10ºE), with inclinations to NE that range between 45º up to vertical. Towards Southwest, the basal strata of the DCB unconformably overlie the Neoproterozoic–middle Cambrian sequence (*Schist-Greywacke Complex*; SGC). To the NE, the upper strata of the DCB are cuted by a reverse fault that placed the Silurian–Devonian sequence of the Valongo Anticline over the DCB strata (e.g., Domingos *et al.*, 1983; Lemos de Sousa, 1984; Wagner *et al.*, 1984; Pinto de Jesus, 2001, 2003; Pinto de Jesus and Lemos de Sousa, 2003; Lemos de Sousa *et al.*, 2010a, b).

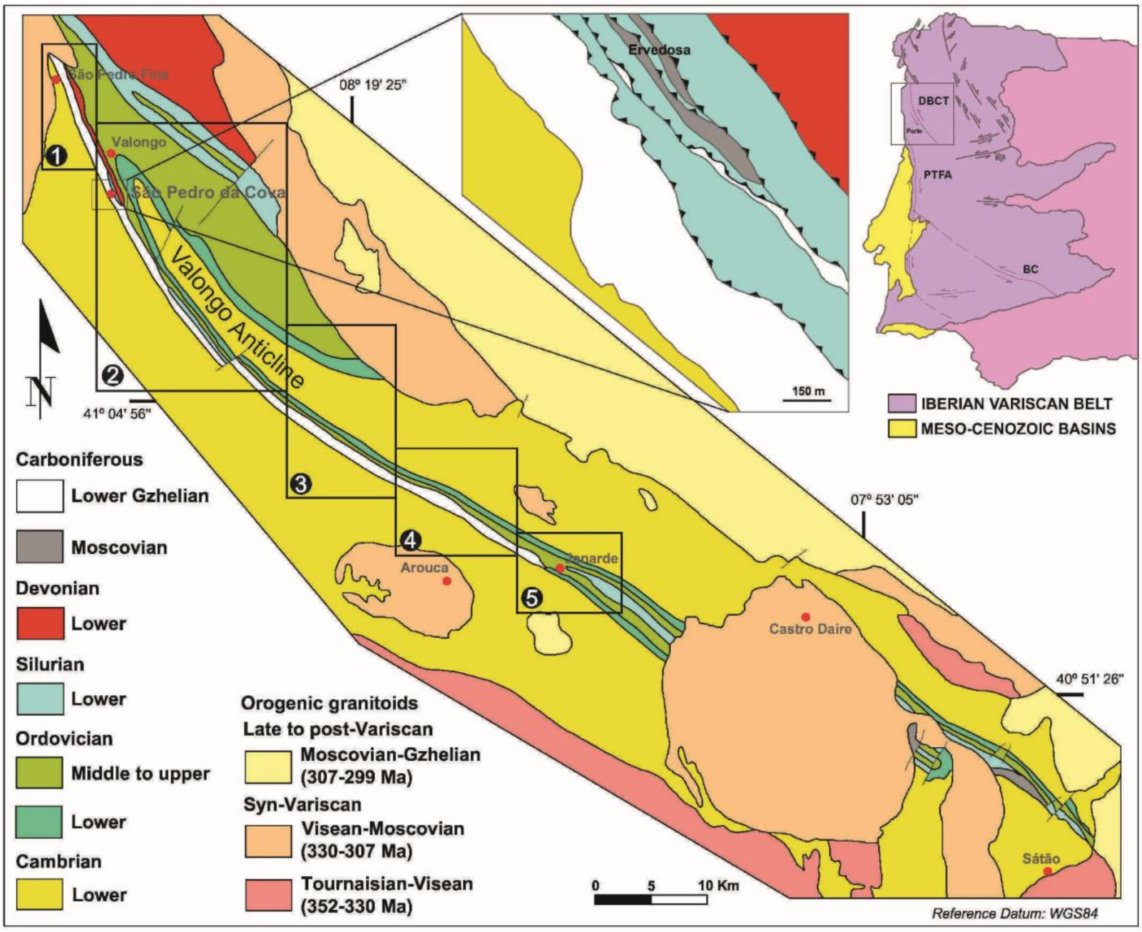

Fig. 2 - Regional geological setting of the DCB (lower Gzhelian, NW of Portugal). Geological map showing detailed geology of the São Pedro da Cova area and the different sectors (1. Sete Casais sector; 2. São Pedro da Cova–Midões sector; 3. Germunde sector; 4. Fojo–Pejão sector; 5. Janarde sector) that compose DCB. The ages of orogenic granitoids facies follow Oliveira *et al.* (1992) and Gradstein and Ogg (1996). **BC =** "Badajoz-Córdoba" shear zone, **DBCT** = Douro-Beiras Carboniferous Trough, **PTFA =** "Porto-Tomar-Ferreira do Alentejo" shear zone. Adapted from Pinto de Jesus (2001) and Correia *et al.* (2013).

2. Tectono-sedimentary units and depositional environments

The stratigraphic and sedimentological sequence of the DCB is comprised, from the base to the top, of eight tectono-sedimentary units (TSU), some of which are related by lateral facies variations. The TSU units A2, B2, C2 and D2 represent the lateral facies variations of TSU units A1, B1, C1 and D1, respectively (Pinto de Jesus, 2001, 2003; Lemos de Sousa *et al.*, 2010a, b; Figure 3). The following descriptions are summarized from Pinto de Jesus (1987), Pinto de Jesus and Lemos de Sousa (1998a, b) and Pinto de Jesus (2001, 2003).

TSU A1 consists of alluvial fan debris characterized by flow-dominated clastic rocks composed of red-brown or dark grey basal breccia deposits. These deposits include polymictic conglomerates characterized by a massive matrix-supported texture and, more rarely, a clast-supported texture without well-defined internal sedimentary structures. The clasts are typically angular and range from silt to block (up to 2 meters) in size. The clast lithologies are very variable (shale, greywacke, granite, greisen, gneiss, mica-schist, conglomerate and quartzite) and likely resulted from the erosion of adjacent mountainous regions such as Valongo Anticline and surrounding areas underlain by the Schist-Greywacke Complex. The basal breccia varies from metric to decametric in thickness. The top of the basal breccia is composed of dark grey to black mudstones, with small angular quartz clasts.

TSU B1 contains phytogenic and siliciclastic deposits that occur along the base of the DCB, and consist of alternating strata of shale, sandstone and coal beds. The shale strata display parallel lamination, along which the fossil plants occur. The fossiliferous strata preserve a highly diverse macroflora. At the top of the TSU B1 sequence, the phytogenic and siliciclastic strata are overlain by fluvial deposits.

TSU C1 is dominated by fluvial deposits with well-defined erosive lower contacts that cut the underlying strata including the phytogenic and siliciclastic deposits. These 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.

TSU D1 consists of phytogenic and siliciclastic deposits that occur at the top of the DCB sequence. They were deposited above the fluvial sequences of TSU C1, are very fossiliferous, consisting of alternating beds of coal, siltstone, mudstone and conglomerate. The more pelitic lithofacies generally display either a parallel internal lamination or a more massive texture. These sequences may also contain rare lenticular bodies composed of conglomerate or coarse sandstone.

TSU A2 characterized an intra-Carboniferous breccia that is in faulted contact (a reverse fault) with Carboniferous and Silurian strata (which contain graptolite fossils, likely *Monograptus*) within the DCB. Most breccia deposits exhibit a clast-supported texture, although a matrix-supported texture is locally observed. The breccia contains clasts of quartzite, shale, quartz and more rarely sandstone in a silty-clay matrix. The clasts can range up to 30 cm in length and they are typically subangular to subrounded. The deposits vary in thickness from one to about 50 meters.

TSU B2 consists of phytogenic and siliciclastic deposits of the base of the DCB. Their characteristics are very similar to the observed in the TSU B1.

TSU C2 is dominated by fluvial deposits, whose structure and composition is very similar to that of TSU C1.

TSU D2 consists of phytogenic and siliciclastic strata that are the youngest deposits preserved in the DCB and have a stratigraphy similar to that of TSU D1. This unit is dominated by fluvial deposits, with structure and composition very similar to that of TSU C1.

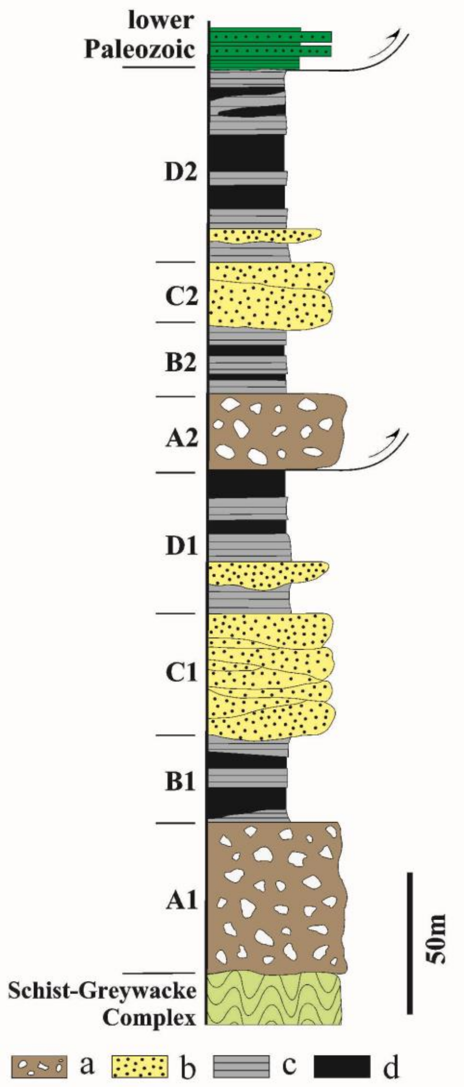

Fig. 3 - Stratigraphic and sedimentological column of DCB showing the different TSU units (modified after Pinto de Jesus, 2001). Geological materials illustrated in a, breccias; b, conglomerates and sandstones; c, siltstones and shales; d, coal beds.

The sedimentation in DCB was produced by alluvial systems with the development of debris flow-dominated alluvial fans derived from the adjacent SGC that are progradational towards NE, and feed longitudinal alluvial fans. The alluvial sedimentation is succeeded by a lacustrine-palustrine facies, which is overlain by strata deposited in a braided multistory-multichannel fluvial system. Strata near the top of the sequence were deposited in a lacustrine facies with local deltaic features (e.g., Pinto de Jesus, 2001, 2003; Lemos de Sousa *et al.*, 2010b).

These stratigraphic and sedimentological sequences are repeated in three tectonic panels (slices) resulting from the latest (Uralic and Saalic phases) stages of the Variscan orogeny (Lemos de Sousa, 1973, 1977, 1978a; Gradstein and Ogg, 1996; Oliveira and Pinto de Jesus, 1998; Pinto de Jesus, 2001, 2003; Pinto de Jesus and Lemos de Sousa, 2003). These tectonic panels are related with a set of reverse faults which occur in other sectors of the DCB (e.g., Pinto de Jesus, 2001; Figures 2, 5).

This tectonic framework is well represented in the São Pedro da Cova sector, which is structurally complex and tectonically divided in five tectonic panels (e.g., Lemos de Sousa, 1973, 1976, 1977, 1978a, b), separated by Silurian strata (Delgado, 1908; Fonseca, 1954, 1959; Teixeira, 1954, 1955a, b; Figures 4 and 5). This repetition of units is the result of the compressive tectonics that placed Silurian outcrops structurally above the Carboniferous strata through of thrust faults (Lemos de Sousa, 1973, 1977, 1978a, b; Domingos *et al.*, 1983; Wagner *et al.*, 1984; Pinto de Jesus, 2001; Figures 3–5). The Ervedosa outcrops are exposed in a fourth and fifth tectonic panel of early Moscovian (early Westphalian D of the Central/Western European regional scale) in age to NE (e.g., Lemos de Sousa, 1973, 1977, 1978a; Pinto de Jesus, 2001; Figures 4 and 5).

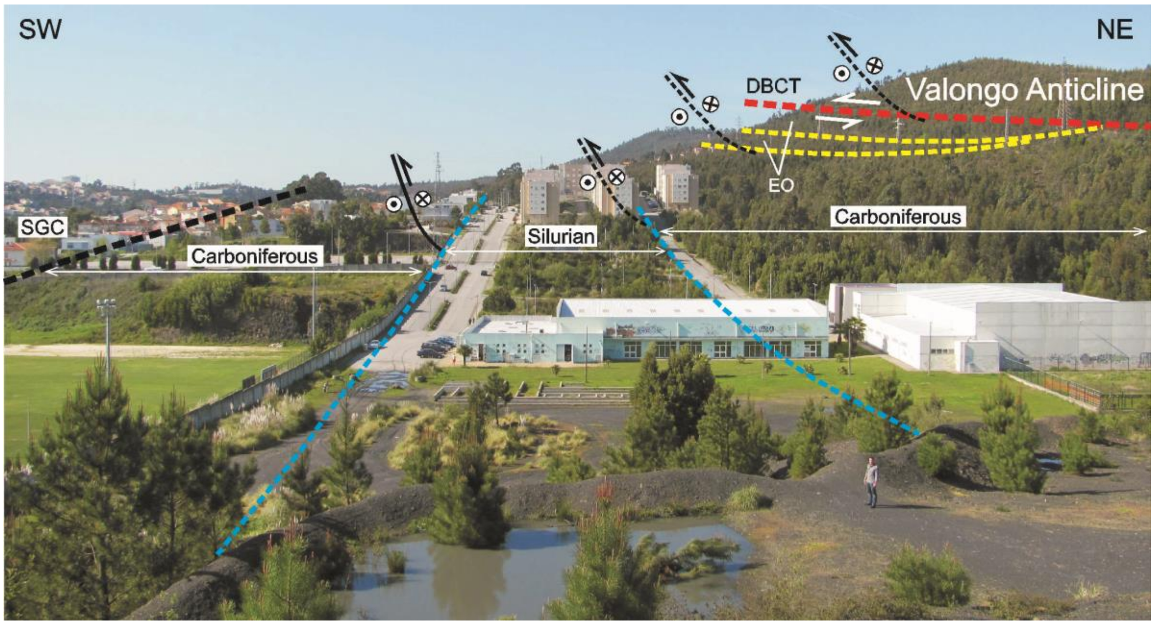

Fig. 4 - Panoramic view of the São Pedro da Cova region, Douro Carboniferous Basin. Abbreviations: **DBCT**, Douro-Beiras Carboniferous Trough; **SGC**, Schist-Greywacke Complex; **EO**, Ervedosa outcrops.

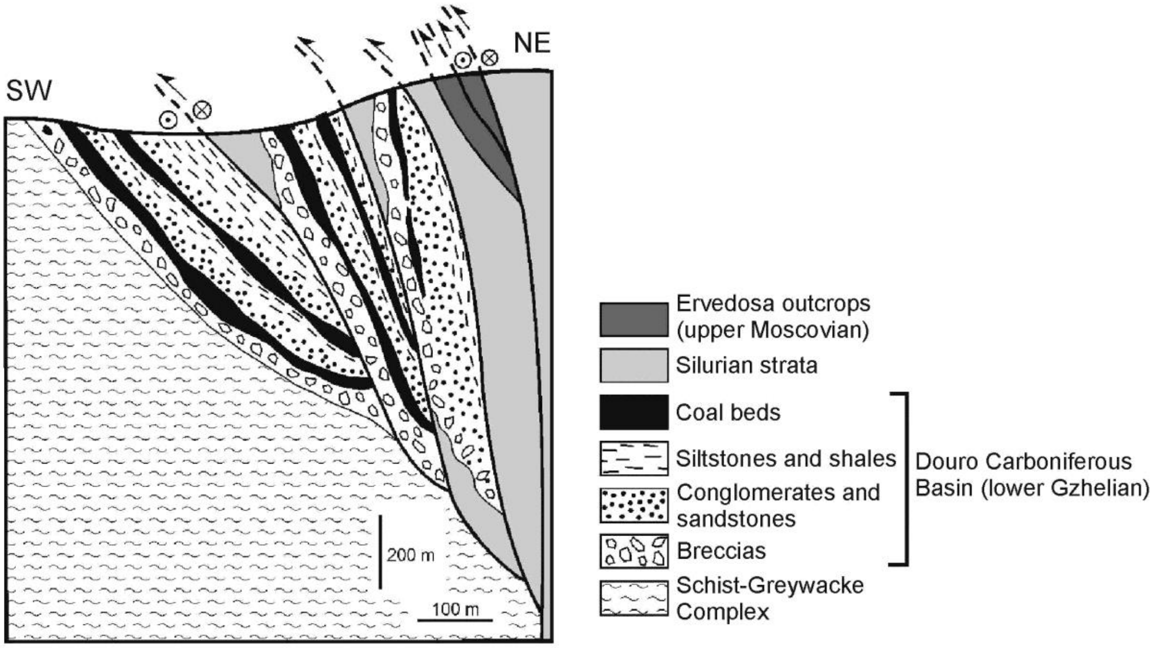

Fig. 5 - Current structural tectonics of São Pedro da Cova region (adapted from Pinto de Jesus, 2001).

3. Previous paleontological studies

3.1. Flora

Data from the 19th century on the continental Carboniferous strata authored mainly by Wenceslau de Lima, Bernardino António Gomes, Wilhelm Ludwig von Eschwege, Carlos Ribeiro, and Hugo Geinitz are summarized in Pinto de Jesus (2001). This research was also reviewed by Carríngton da Costa (1931, 1938), and by Teixeira (1937, 1938a, b, 1939a–d, 1940a, b, 1941a, b, 1944a, 1945, 1946a, 1949, 1953, 1955c, 1956; Teixeira and Medeiros, 1943; Teixeira and Pais, 1976). Teixeira`s research was particularly important to this study as it included a thorough review of the fossil flora of the DCB. These studies were reviewed later by Lemos de Sousa and Wagner (1983a, b), Wagner (1983), Wagner and Lemos de Sousa (1983), and Lemos de Sousa and Wagner (1985a, b). These works contain both an overview of previous research on the continental Carboniferous of Portugal, but also a synthesis of previous knowledge and a thorough review of the flora list of the DCB known at that time. In addition, this research provided detailed information about the stratigraphy, paleogeography, paleoenvironmental and paleoecological conditions, structural geology, and the paleobiodiversity in terms of paleobotanical elements. The last review of flora of the DCB offered a list of 65 species (3):

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(3) Floral species are grouped by systematic order. Systematic position is according to several authors (e.g., Cleal and Thomas, 1995; Taylor *et al.*, 2009; Bashforth *et al.*, 2016).

Lycopsida:

- *Cyperites* sp. (= *Lepidophyllum*)
- *Lepidodendron aculeatum* Sternberg
- *Lepidophylloides* sp.
- *Sigillaria brardi* Brongniart
- *Sigillariostrobus serreatus* Teixeira

Sphenopsida:

- Sphenophyllales:
  - *Sphenophyllum alatifolium* Renault
  - *Sphenophyllum costae* Sterzel
  - *Sphenophyllum longifolium* (Germar) Geinitz
  - *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger
  - *Sphenophyllum* cf. *thoni* var. *minor* Sterzel
  - (= *Lilpopia raciborskii* (Lilpop) Connor & Schaarschmidt)
- Equisetales:
  - *Annularia sphenophylloides* (Zenker) von Gutbier
  - *Annularia stellata* (von Schlotheim) Wood
  - *Asterophyllites equisetiformis* (von Schlotheim) Brongniart
  - *Calamites carinatus* Sternberg
  - *Calamites schuetzeiformis* forma *waldenburgensis* Kidston
  - *Calamites suckowii* Brongniart
  - *Calamites cisti* Brongniart
  - *Calamostachys tuberculata* Sternberg
  - *Equisetites zeaformis* Andrae
  - *Macrostachya carinata* (Germar) Zeiller

Pteridopsida (Polypodiopsida):

- Coenopteridales:
  - *Alloiopteris* sp.
  - *Nemejcopteris feminaeformis* (von Schlotheim) Barthel
- Marattiales:
  - *Acitheca polymorpha* (Brongniart) Wagner
  - *Lobatopteris viannae* (Teixeira) Wagner
  - *Pecopteris* cf. *ameromi* Stockmans & Willière
  - *Pecopteris candolleana* Brongniart
  - *Pecopteris cyathea* (von Schlotheim) Brongniart
  - *Pecopteris daubreei* Zeiller
  - *Pecopteris densifolia* Göppert
  - *Pecopteris gruneri* Zeiller

Pecopteris limae Teixeira
Pecopteris cf. *melendezi* Wagner
Pecopteris monyi Zeiller
Pecopteris unita Brongniart
Pecopteris sp. nov. (cf. *hemitelioides* Brongniart)
Pecopteris sp.

Filicales:
Oligocarpia leptophylla (Bunbury) Grauvogel-Stamm & Doubinger

Order uncertain:
Gondomaria discreta (Weiss) Wagner & Lemos de Sousa

Progymnospermopsida:

Noeggerathiales:
Rhacopteris gomesiana (Heer) Teixeira

Pteridospermopsida:

Trigonocarpales (Mesullosales):
Alethopteris zeilleri Ragot
Callipteridium (*Eucallipteridium*) *gigas* (von Gutbier) Weiss
Callipteridium (*Eucallipteridium*) *zeilleri* Wagner
Lescuropteris genuina (Grand'Eury) Remy
Linopteris neuropteroides (von Gutbier) Potonié
Neuropteris cordata Brongniart
Neuropteris gallica Zeiller
Neuropteris ovata var. *pseudovata* Gothan & Sze
Neuropteris zeilleri Lima
Neuropteris sp.
Odontopteris brardi Brongniart
Reticulopteris germari (Giebel) Gothan

Callistophytales:
Dicksoniites pluekenetii (von Schlotheim) Sterzel
Eusphenopteris rotundiloba (Němejc) Van Amerom
Pseudomariopteris ribeyroni (Zeiller) Danzé-Corsin
Pseudomariopteris cordato-ovata (Weiss) Gillespie *et al.*
(= *Pseudomariopteris corsini* (Teixeira) Wagner)
Pseudomariopteris cf. *busqueti* (Zeiller) Danzé-Corsin

Cordaitopsida (Spermatopsida):

Cordaitales (Cordaitanthales):
Cordaites sp.

<u>Ginkgopsida</u>:
  <u>Order uncertain</u>:
    Dicranophyllum gallicum Grand'Eury
    Dicranophyllum lusitanicum (Heer) Lima
<u>Coniferopsida (Pinopsida)</u>:
  <u>Voltziales</u>:
    Ernestiodendron filiciforme (von Schlotheim pars) Florin
    Culmitzschia (*Lebachia*) *parvifolia* Florin
    aff. *Culmitzschia* (*Lebachia*) *frondosa* var. *zeilleri* Florin
<u>Incertae sedis (Pteridophylla = Pteridospermopsida or Pteridopsida)</u>:
    Sphenopteris cf. *chaerophylloides* Brongniart
    Sphenopteris cf. *cremeriana* Potonié
    Sphenopteris cf. *germanica* Weiss
    Sphenopteris cf. *lenis* Zeiller
    Sphenopteris matheti Zeiller
    Sphenopteris mendescorreae Teixeira
    (? = *Sphenopteris sampaiana* Teixeira)
    Sphenopteris sp.
    Taeniopteris bertrandiana Teixeira
    Taeniopteris jejunata Grand'Eury
    aff. *Taeniopteris multinervis* Weiss

Previous research on DCB flora (Lemos de Sousa and Wagner, 1983a, b; Wagner, 1983; Wagner and Lemos de Sousa, 1983a; Lemos de Sousa and Wagner, 1985a, b; Wagner and Lemos de Sousa, 1985) provides a complete synthesis about the fossil flora of the late Carboniferous of Portugal. This syntheses includes flora of lower Gzhelian (= lower Stephanian C of the Central/Western European regional scale) for the Carboniferous strata in DCB. These strata correspond exclusively to continental fácies (e.g., Lemos de Sousa, 1973, 1978a; Wagner, 1983; Domingos *et al.*, 1983; Pinto de Jesus, 2001).

3.2. Fauna

Detailed studies on the fossil fauna, especially fossil insects, in the Carboniferous of Portugal were conducted mainly by Carlos Teixeira, Daniel Laurentiaux and colleagues (Teixeira, 1939e, 1941c, 1942, 1943, 1944a–c, 1946b; Laurentiaux and Teixeira, 1948, 1950, 1958a, b) and more recently by other researchers (Loureiro *et al.*, 2010). The works published by Teixeira (1939e, 1941c, 1942, 1943, 1944b, c, 1946b) documented the first discovery of insect fossils in the DCB (São Pedro da Cova, Valdeão and Pejão coalfields), with description of two Paleodictyoptera, *Homaloneura ribeiroi* Teixeira and *Valdeania medeirosi* Teixeira; four new Dictyoptera Phyloblattidae blattodeans, *Phyloblatta fonsecai* Teixeira, *P. carringtoni* Teixeira, *P. rosasi* Teixeira and *P. portuensis* Teixeira; and seven new taxa, *Lusitanomylacris pruvosti* Teixeira, *Stephanomylacris duriensis* Teixeira, *S. zbyszewskii* Teixeira, *Eneriblatta elegantissima* Teixeira, *E. insignis* Teixeira, *E. valonguesis* Teixeira and *E. lusitanica* Teixeira. The same author also reported indeterminate insect records of the orders Hadentomoidea and Protorthoptera, found in the Pejão region (Teixeira, 1944a–c). Similar studies were conducted in other Portuguese outcrops (brief summaries in Laurentiaux and Teixeira, 1948, 1950, 1958a, b), but no further insect fossils were documented in DCB until the work carried out by Loureiro *et al.* (2010).

Additional paleofaunal studies (Teixeira, 1944a) on the DCB documented non-marine (limnic) bivalves, such as *Estheria* (*Euestheria*) *cebennensis* Grand'Eury, *E. carneiroi* Teixeira and *Anthraconaia lusitanica* Teixeira, found in the Pejão, Lomba and Varziela regions. Other non-marine bivalve species such as *Anthraconaia*? *prolifera* Waterlot were documented by Teixeira and Fonseca (1953) and Fonseca (1959) in the São Pedro da Cova region. This research was updated by Eagar (1983) who documented *Anthraconaia lusitanica* Teixeira and *Anthraconaia*? *altissima* Eagar.

4. Biostratigraphy

Despite the detailed paleontological studies carried out on the Carboniferous outcrops along the DBT in Portugal (e.g., Bunbury, 1849; Ribeiro *et al.*, 1853; Gomes, 1865; Vasconcelos, 1877; Wenceslau de Lima, 1890, 1892, 1895; Fleury, 1923, 1936, 1937; Wattinson, 1926; Carríngton da Costa, 1931; Florin, 1940; Teixeira, 1944 with previous references) and Lemos de Sousa (1978a) *apud* Pinto de Jesus (2001), the first determinations of stratigraphic age based on flora composition of the Carboniferous were presented by Teixeira (1944a, 1945, 1954), Wagner (1966, 1979), Corsin and Lemos de Sousa (1972), Teixeira and Pais (1976) and Lemos de Sousa (1977, 1978a). These studies suggested an upper Kasimovian to early Gzhelian (Stephanian B and C of the Central/Western European regional scale) ages for the DCB strata.

Doubinger (1956) *in* Wagner and Lemos de Sousa (1983) assigned an early Gzhelian age for the DCB strata, comparing the floras from the Carboniferous of the Iberian Massif with the floristic elements from the Carboniferous Central Massif of South France. Subsequent studies of the flora of the DCB conducted by Wagner (1983, 1984), Wagner and Lemos de Sousa (1983, 1985) and Lemos de Sousa and Wagner

(1983a, b, 1985a, b), and additional faunal elements (Eagar, 1983) indicated an early Gzhelian (= early Stephanian C of the Central/Western European regional scale) age for the DCB strata. In the São Pedro da Cova sector, the early Gzhelian age was assigned to the strata in three tectonic panels, which contained similar flora (e.g., Fonseca, 1954, 1959; Lemos de Sousa, 1971, 1973, 1976; Lemos de Sousa and Wagner, 1983b; Pinto de Jesus, 2001; Lemos de Sousa *et al.*, 2010a; Figure 5).

More recent studies of the flora and stratigraphy of the DCB have confirmed the early Gzhelian age for the DCB strata (Correia *et al.*, 2009). These studies have yielded important index floral species for the Kasimovian–Gzhelian (Stephanian) stages established by Wagner (1966, 1983, 1984; Figure 6) such as *Sphenophyllum angustifolium* Germar, *Pecopteris arborescens* von Schlotheim, *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger, *Lobatopteris viannae* (Teixeira) Wagner, *Pecopteris cyathea* (von Schlotheim) Brongniart, *Pseudomariopteris cordato-ovata* (Weiss) Gillespie *et al.*, *Neuropteris ovata* ?var. *pseudovata* Gothan & Sze, *Eusphenopteris rotundiloba* (Němejc) Van Amerom, *Pseudomariopteris* cf. *busqueti* Zeiller, *Pecopteris* cf. *ameromi* Stockmans & Willière, and aff. *Taeniopteris multinervis* Weiss (Figure 6). Other studies on DCB flora have emphasized the occurrence of paleobotanical elements outside the basin, given the presence of walchian conifers (Voltziales) such as *Ernestiodendron filiciforme* von Schlotheim pars, aff. *Culmitzschia* (*Lebachia*) *frondosa* var. zeilleri Florin and *Culmitzschia* (*Lebachia*) *parvifolia* Florin, and dicranophylls (Ginkgopsida), *Dicranophyllum gallicum* Grand'Eury and *Dicranophyllum lusitanicum* Heer. These extrabasinal (dryland) elements are consistent with a paleoenvironmental interpretation that carachterizes DCB corresponds as an intramontane basin (Wagner, 1983; Lemos de Sousa and Wagner, 1983a, b; Wagner and Lemos de Sousa, 1983; Lemos de Sousa and Wagner, 1985a, b; Wagner and Lemos de Sousa, 1985; Lemos de Sousa *et al.*, 2010b).

Paleofaunal studies also indicate an early Gzhelian age for the DCB strata. For example, Eagar (1983) documents the occurrence of non-marine (limnic) bivalves such as *Anthraconaia lusitanica* Teixeira and *Anthraconaia*? *altissima* Eagar. Detailed studies on palynology (Fernandes *et al.*, 1997) also support an early Gzhelian age for the stratigraphic sequence of the DCB.

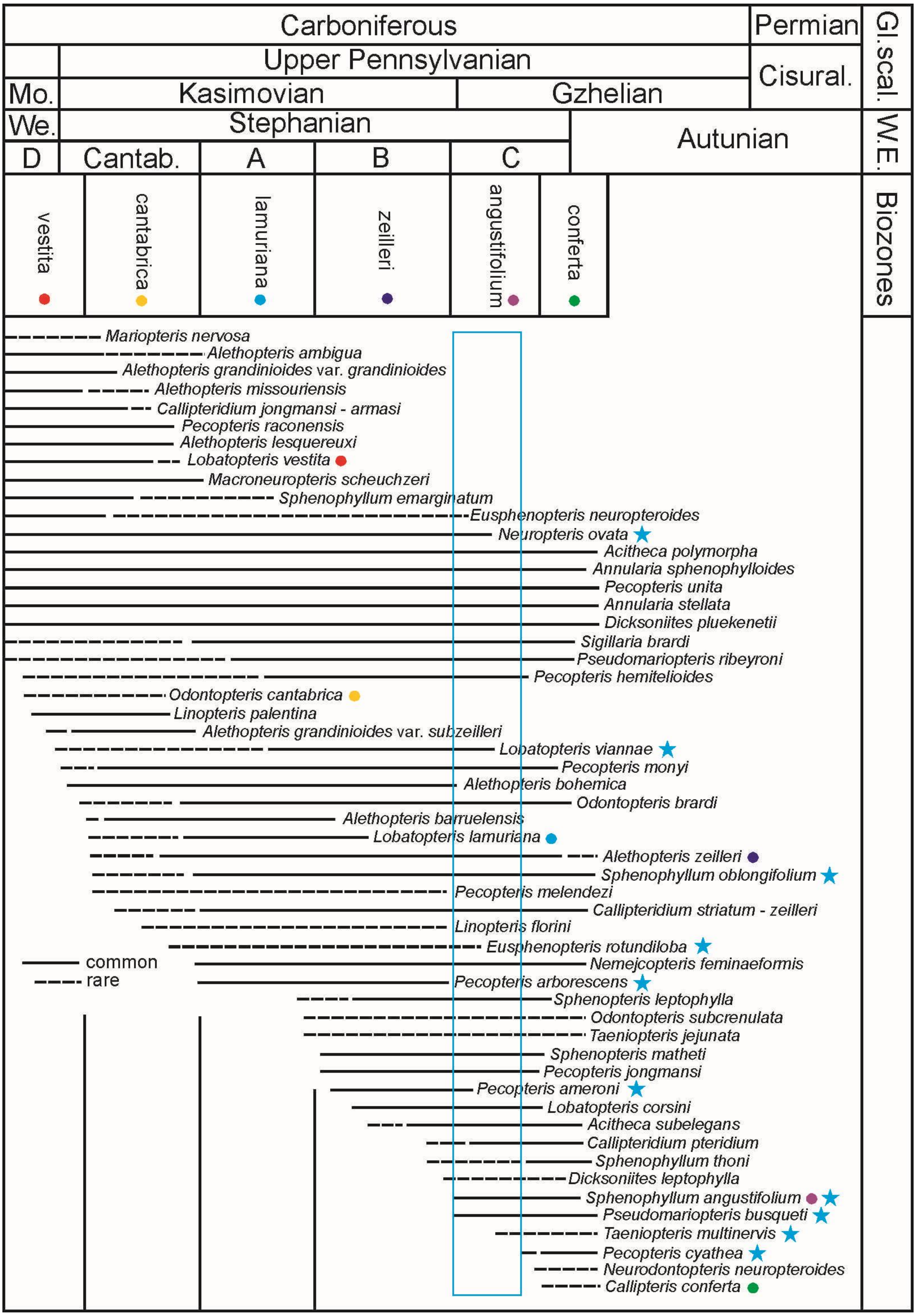

Fig. 6 - Stratigraphic ranges of the different megafloral species and biozones (marked with circles) for the Stephanian stage from the Iberian Massif. The species marked with "blue star" represent stratigraphic species described in DCB for the lower Gzhelian (lower Stephanian C). The blue rectangle represents an area where occur species which delimit the age-range for DCB. Adapted from Wagner (1984). Abbreviations: Mo., Moscovian; We., Westphalian; Cantab., Cantabrian; Cisural., Cisuralian; Gl.scal, Global scales; W.E., Central/Western European Regional Scale.

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PART III – MATERIAL AND METHODS

1. Data collection: Material and methods

1.1. Fossil localities and sites and fossil sampling

The new fossil specimens studied were collected in new lower Gzhelian (Upper Pennsylvanian) outcrops located in the São Pedro da Cova (Gondomar) and Montes da Costa (Ermesinde) regions (Figure 7). The field work on these fossil localities and sites was carried out during 2002–2015 and yielded many well-preserved specimens, particularly fossil flora samples. Within São Pedro da Cova region, the fossil sites comprise seven outcrops (Figures 4, 7).

The studied fossil material was selected comprising a total of 495 specimens, of which include 13 holotypes and 32 paratypes.

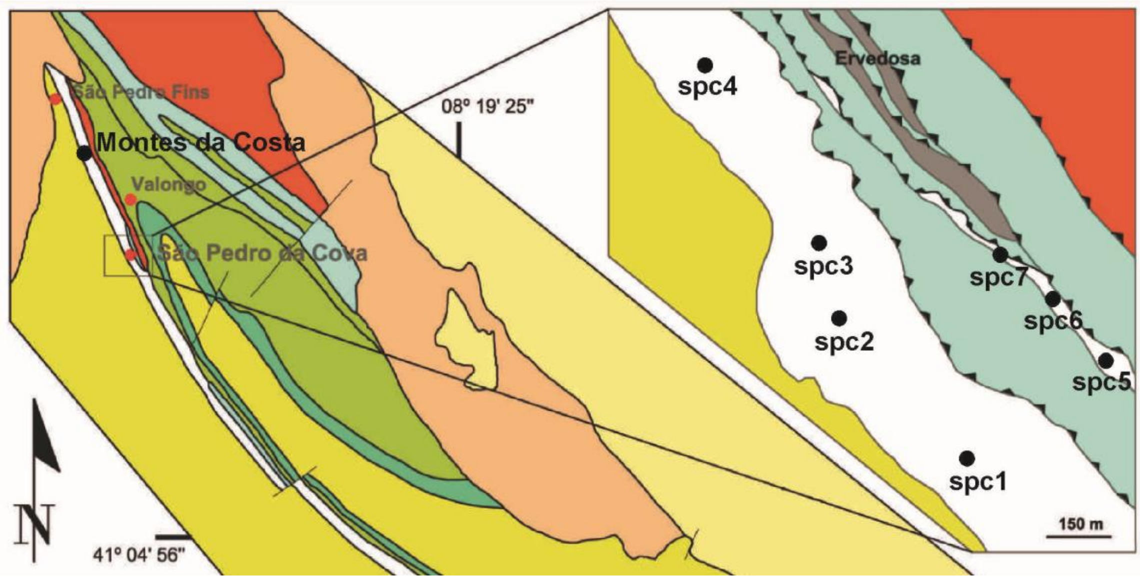

Fig. 7 - Map of the geographic spatial distribution of the new outcrops (fossil sites) reported in the São Pedro da Cova and Montes da Costa localities (adapted from Correia *et al.*, 2013). Abbreviations: **spc1–7**, São Pedro da Cova outcrops. Coordinates WGS84 of the outcrops: **spc1**, 41°09´18.20´´N, 08°30´05.81´´W; **spc2**, 41°09´44.65´´N, 08°30´25.73´´W; **spc3**, 41°09´44.60´´N, 08°30´23.10´´W; **spc4**, 41°10´29.66´´N, 08°30´41.51´´W; **spc5**, 41°09´36.81´´N, 08°30´10.71´´W; **spc6**, 41°09´42.56´´N; 08°30´14.68´´W; **spc7**, 41°09´42.21´´N; 08°30´15.43´´W; **Montes da Costa**, 41°12´49.86´´N, 08°32´05.70´´W. See Figure 2 for colours meaning.

1.2. Methodology and sample preparation

Classic paleobotany studies were made using comparative studies of well-preserved specimens. Modern identification of the fossil plants requires the use of mechanical equipment of cleaning and techniques of manufacturing of latex casts on the fossil specimens, as well as high resolution imaging for the detailed observation and recording fundamental features used correctly identify the fossil specimens, even those that are in advanced state of degradation or they are only small fragments.

The new fossil specimens described in this work were carefully prepared mechanically using chisels, hammers, needles and a compressed air and electric vibrotool equipment. On several occasions cleaning was performed using the support of a binocular magnifier. Several specimens were subjected to chemical treatment in boiling hydrochloric acid (10%) for the removal of oxidation crusts. Selected specimens were drawn in camera lucida, and later redrawn using CorelDRAW® for supporting in taxonomic description. The latex casts and several samples were coated with magnesium oxide prior to being photographed. In addition, specific samples (e.g., fertile pinnules/fronds) were tested by maceration process (through a small fragment of sample) and observed under SEM (*Scanning Electron Microscopy*) in order to ascertain the existence of spores, cuticles (epidermis), reproductive (e.g., pollen sacs) and respiratory structures (stomata). The study of high resolution microscopy allows obtain a more accurate taxonomic identification of the type fossil plant and identify higher taxa such as Division, Class, Order or Family.

1.3. Preservation and taphonomy of the studied fossil samples

The studied specimens in the DCB are preserved in fine-grained (silt-clay) clastic rocks in tectonically compressed (compact) shales. They underwent some taphonomic changes during their local/regional transport, deposition and preservation process. The specimens are preserved in a fragmentation state and are found in parautochthonous deposits which are associated with fluvial sandstone-lacustrine deposits. Most fossil samples are well-preserved and exhibit minimal effects of the compressive (Variscan) tectonics that characterizes the DCB. Some of the specimens are partially carbonized or coalified and oxidized by a hematite film.

1.4. Comparisons with reference collections

The new fossil occurrences include the recognition of several new taxa which were compared with specimens from reference collections such as those of the Czech Geological Survey (Prague, Czech Republic), West Bohemian Museum (Pilsen, Czech Republic), Botanical Garden of Cordoba (Spain), Museum of Natural History and Science of the University of Porto (Portugal), and National Natural History Museum of Paris (France).

1.5. Depository

The originals and latex casts of the holotypes and paratypes, as well as other materials published, are housed at the Museum of Natural History and Science of the University of Porto (NHMSUP — Museu de História Natural e da Ciência da Universidade do Porto), Czech Geological Survey of Prague and National Natural History Museum of Paris (France). The referenced specimens are kept in perfect conditions of preservation and safety, in accordance the international rules for the management and safeguard of paleontological collections.

FLORA

UP-MHNFCP-094951/-094952/-094954: holotype of ***Lesleya iberiensis* sp. nov.**
ZS 507: paratype of *Lesleya iberiensis* sp. nov.
ZS 508: paratype of *Lesleya iberiensis* sp. nov.
ZS 510: paratype of *Lesleya iberiensis* sp. nov.
UP-MHNFCP-130914a: holotype of ***Phyllotheca wegeneri* sp. nov.**
UP-MHNFCP-130914b: paratype of *Phyllotheca wegeneri* sp. nov.
UP-MHNFCP-154760: paratype of *Phyllotheca wegeneri* sp. nov.
UP-MHNFCP-154064a: holotype of ***Alloiopteris teixeirai* sp. nov.**
UP-MHNFCP-154064b: paratype *Alloiopteris teixeirai* sp. nov.
UP-MHNFCP-154065a: holotype of ***Annularia noronhai* sp. nov.**
UP-MHNFCP-154065b: paratype of *Annularia noronhai* sp. nov.
UP-MHNFCP-154066: holotype of ***Pecopteris alvarezii* sp. nov.**
UP-MHNFCP-154067: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154068: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154071: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154074: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154075: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154076: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154077: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154078: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154079: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154082: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154083: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154084: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154087: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-154761: paratype of *Pecopteris alvarezii* sp. nov.
UP-MHNFCP-130920a: holotype of ***Acitheca murphyi* sp. nov.**
UP-MHNFCP-130920b: paratype of *Acitheca murphyi* sp. nov.
UP-MHNFCP-130923: paratype of *Acitheca murphyi* sp. nov.
UP-MHNFCP-130924: paratype of *Acitheca murphyi* sp. nov.
UP-MHNFCP-130945: paratype of *Acitheca murphyi* sp. nov.
UP-MHNFCP-130947: paratype of *Acitheca murphyi* sp. nov.
UP-MHNFCP-130948: paratype of *Acitheca murphyi* sp. nov.

UP-MHNFCP-154758: paratype of *Acitheca murphyi* sp. nov.
UP-MHNFCP-154766: holotype of ***Ilfeldia gregoriensis* sp. nov.**
UP-MHNFCP-154767: paratype of *Ilfeldia gregoriensis* sp. nov.
UP-MHNFCP-154768: paratype of *Ilfeldia gregoriensis* sp. nov.
UP-MHNFCP-154769: paratype of *Ilfeldia gregoriensis* sp. nov.
UP-MHNFCP-154770: paratype of *Ilfeldia gregoriensis* sp. nov.

FAUNA
UP-MHNFCP-154771: holotype of ***Lusitaneura covensis* n. gen., n. sp.**
UP-MHNFCP-127180: holotype of ***Stenodictya*? *lusitanica* sp. nov.**

1.6. Identification and characterization of the new outcrops: lithological, paleontological and structural-tectonic aspects

The new outcrops (see detailed photos at following chapter: Part IV) herein described and presented are located in TSU units B1/B2 and D1/D2. Based on field observations, most of TSU units were identified in São Pedro da Cova region. These observations were based on lithological, paleontological and structural-tectonic aspects (Figures 8, 9).

Within the São Pedro da Cova region, most Carboniferous strata are steeply dipping, tectonically compressed and compact, and are composed of coal beds interbedded with sandstone (fluvial) deposits and laminated grey shales rich in fossil plants. The fossil plant-bearing shales preserve a very diversified megaflora which mainly comprise taxa belonging to genera and species of Pteridopsida, Pteridospermopsida, Sphenopsida, Cordaitopsida and Lycopsida. The fossil plant-bearing shales are associated with rare faunal elements such as arthropods, namely dictyoptera (roachoids) and palaeodictyoptera insects, and *Anthraconaia*-like non-marine (limnic) bivalves. The sandstone strata have variable thickness and are relatively oxidized. These strata correspond to the units TSU B1–D1/B2–D2 described in different tectonic panels exposed (Figure 8A). Basal strata consist of breccia deposits (TSU A1) (Figure 8E, F). Part of the Carboniferous strata of São Pedro da Cova has been displaced by reverse faults. One of reverse faults is a wide fault zone with a sinistral (left-lateral) strike-slip component, which placed Silurian strata over the Carboniferous strata (Figure 8A–C). The Silurian strata have a width of about 50 m and are composed of quartzite strata interbedded with shales and thin phthanites rich in iron sulphides (Figure 8D). The shales are striated and have colours ranging from light to dark grey. They contain rare monograptid graptolites (Figure 9C). Above the Silurian strata were tectonically placed the Carboniferous strata. These Carboniferous strata comprise the TSU units B2–D2 (Figure 9A, D, E). The TSU unit A2 (intra-Carboniferous breccia) has not been identified.

The new Carboniferous outcrops of the São Pedro da Cova region contain index species of Stephanian (Kasimovian–Gzhelian of the Global scale) age that were established by Wagner (1966, 1983, 1984; Figure 6). These species include *Sphenophyllum angustifolium* Germar, *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger, *Lobatopteris viannae* (Teixeira) Wagner, *Pecopteris cyathea* (von Schlotheim) Brongniart, *Pecopteris arborescens* von Schlotheim, *Pseudomariopteris cordato-ovata* (Weiss) Gillespie *et al.*, *Neuropteris ovata* ?var. *pseudovata* Gothan & Sze and *Eusphenopteris rotundiloba* (Němejc) Van Amerom, which indicate the early Gzhelian (early Stephanian C of the Central/Western European regional scale) age (see Wagner, 1984, chart 3).

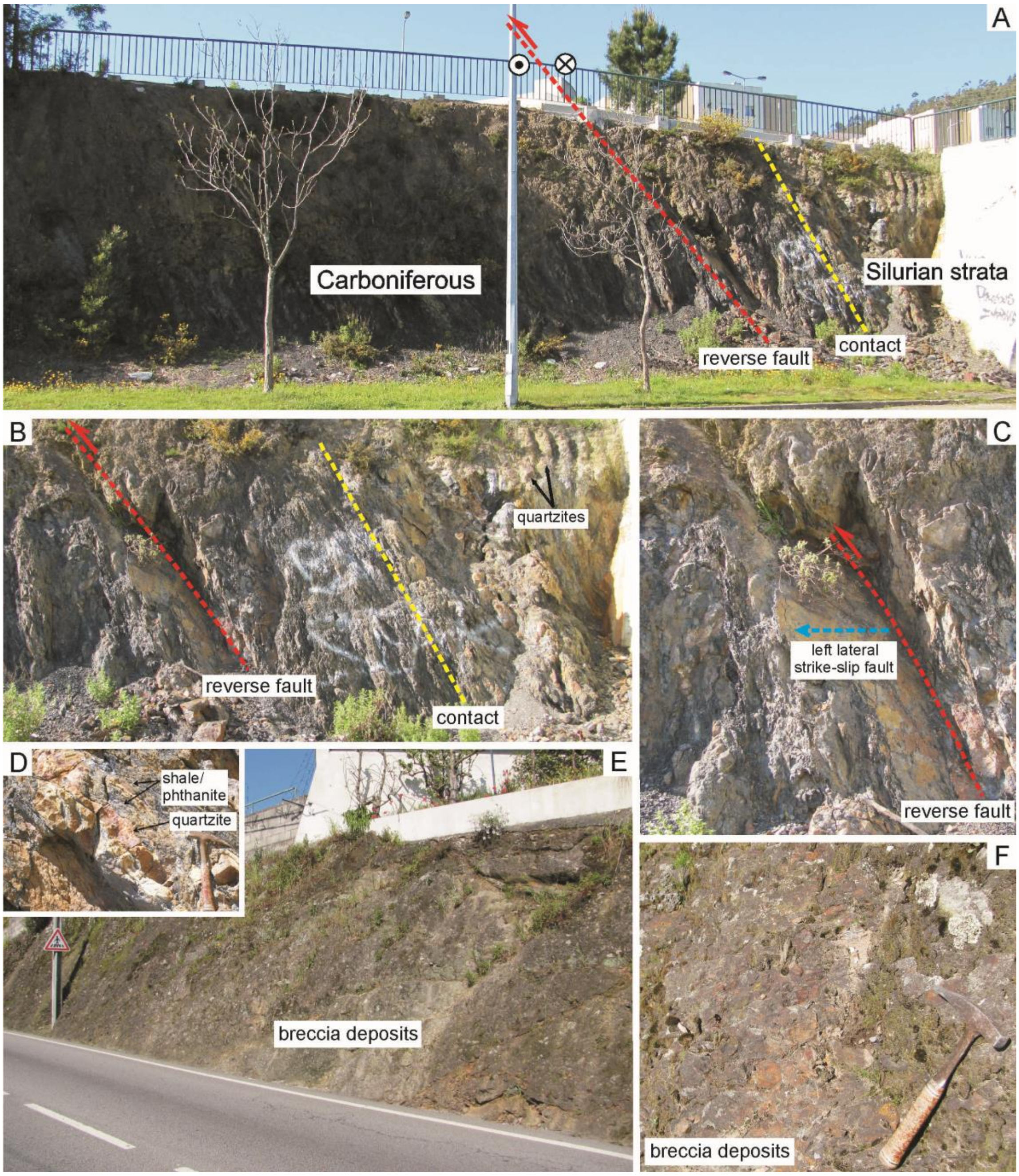

Fig. 8 - Lithologies and structural-tectonic aspects of the Carboniferous and Silurian strata in São Pedro da Cova (A–F).

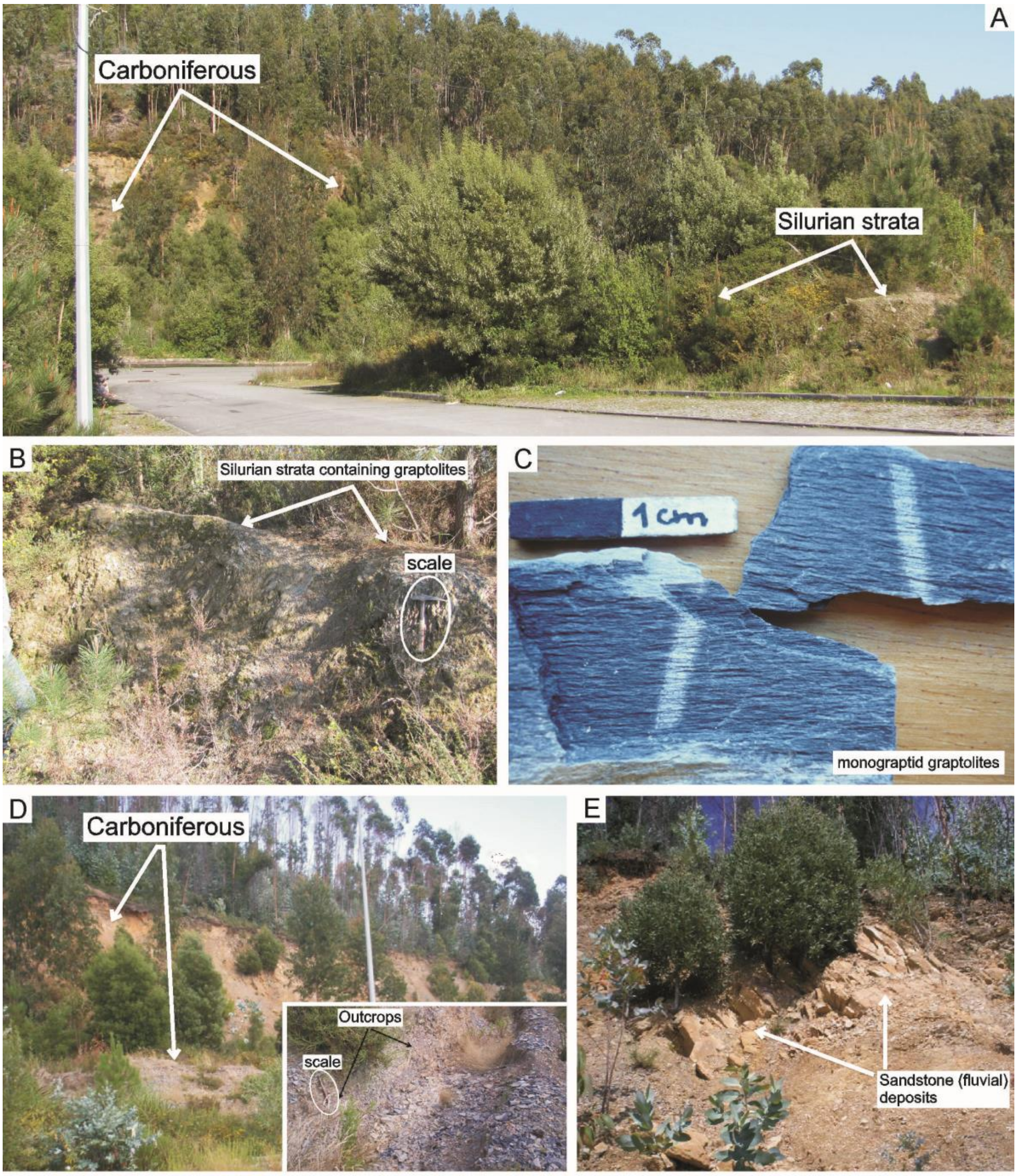

Fig. 9 - Lithology, paleontology and structural-tectonic aspects of the Carboniferous and Silurian strata in São Pedro da Cova (A–E).

In Montes da Costa region, stratigraphic-sedimentological sequences have also been described (Figures 10, 11) and are related with the TSU units studied in detail in São Pedro da Cova. The new outcrops of the Montes da Costa are steeply dipping strata resulting from the deformation associated with the Variscan Orogeny and they are mostly concordant with the regional NW–SE orientation established for the DCB (e.g., Pinto de Jesus, 2001, 2003 and references therein). The outcrops contain several floral remains preserved in compressed-compact shales that are interlayered with breccia, greywackes and sandstone deposits of variable thickness (Figures 10, 11). The fossiliferous lithology varies in color from light blue, yellow to grey, and also shows some oxidized levels. The greywackes preserve several sandstone lenses (or lenticles), typically 30 to 60 cm in length. The sandstones are relatively oxidized and were deposited in fluvial systems. This lithology occurs commonly in basal strata interlayered with levels of greywackes (Figure 11). The fossil beds are placed above repeated sequences of sandstone deposits and preserve several fossiliferous levels showing a high plant diversity composed of a number of documented genera taxa of pteridosperms/ferns, sphenopsids and cordaitopsids and by some rare faunal elements such as arthropods, namely palaeodictyoptera and blattodean insects, and non-marine bivalves that are probably *Anthraconaia lusitanica* Teixeira. The presence of floral species with Kasimovian–Gzhelian (Stephanian of the Central/Western European regional scale) age (see Wagner, 1966, 1983, 1984; Figure 6), such as *Sphenophyllum angustifolium* Germar, *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger, *Pecopteris cyathea* (von Schlotheim) Brongniart, *Pseudomariopteris cordato-ovata* (Weiss) Gillespie *et al.*, *Neuropteris ovata* ?var. *pseudovata* Gothan & Sze and *Eusphenopteris rotundiloba* (Němejc) Van Amerom, indicate a early Gzhelian (early Stephanian C) age for the new outcrops of Montes da Costa.

These outcrops are interpreted to correspond part of the units TSU C1 (repeated sequences of sandstone deposits) and TSU B1 and D1 (fossil macrofloral bed strata) which are overlain by conglomerate deposits (?top strata of TSU D1) at the top of the stratigraphic sequence (Figure 11). The conglomerate deposits present a clast-supported fabric, and the clasts are essentially heterometric fragments of quartzite (Figure 10D, E). On the top of this stratigraphic sequence, shale and greywacke strata contain exceptional trunks of *Calamites* preserved in growth/life position (i.e., autochthonous flora) (Figures 10F, G, 11).

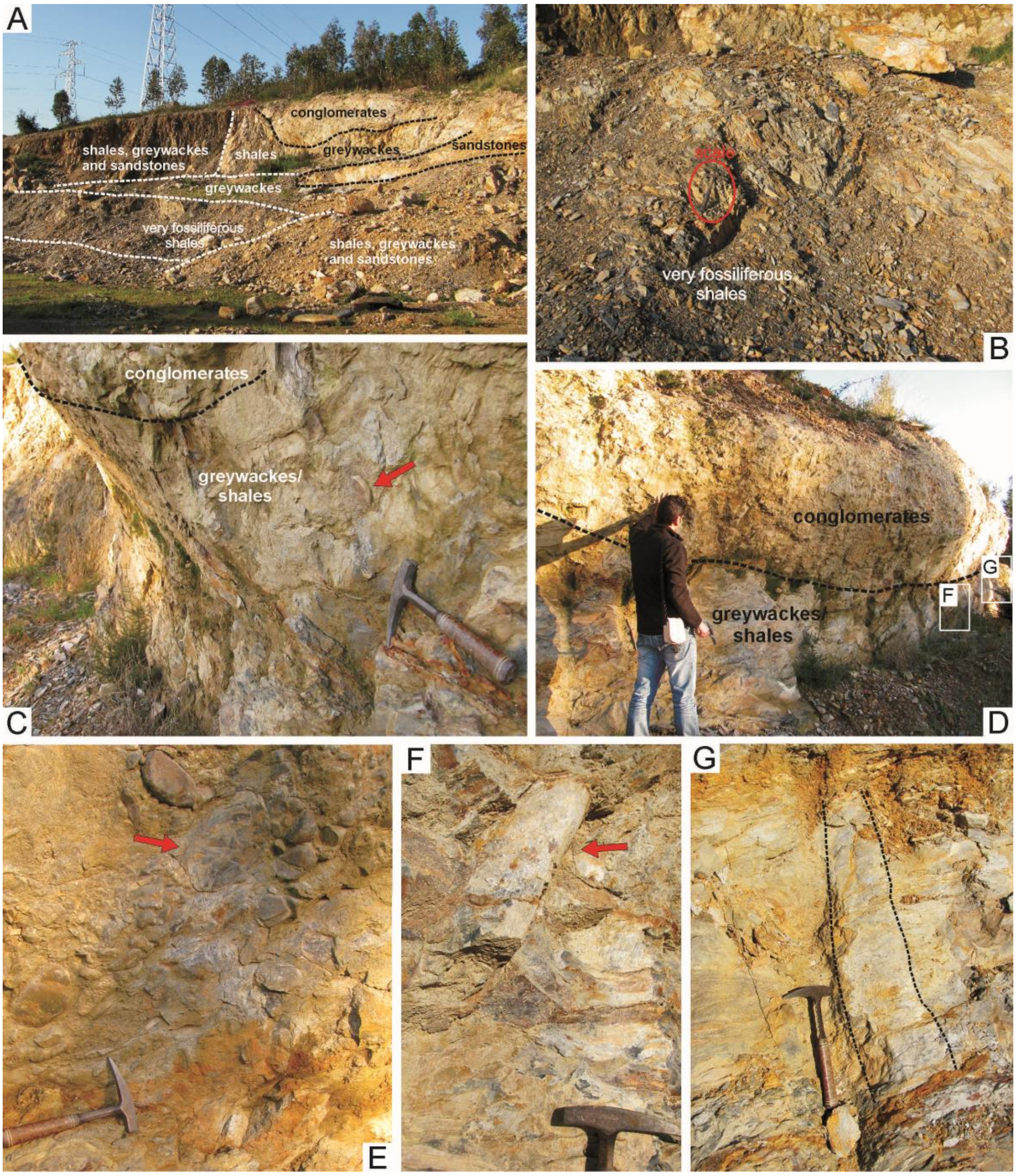

Fig. 10 - New outcrops of Montes da Costa (A–G). (A) The most representative strata exposed; (B) Very fossiliferous shales containing a high diversity of megaflora; (C) Stratigraphic contact between greywackes/shales and conglomerates, and strata of shale and greywacke showing some transverse sections of *Calamites* trunks preserved in growth position; (D) Stratigraphic contact between shales/greywackes and conglomerates; (E) Conglomerates containing *Calamites* trunks with transverse section exposed; (F, G) Shales and greywackes containing several *Calamites* trunks preserved in growth position. Red arrow indicating *Calamites* trunks.

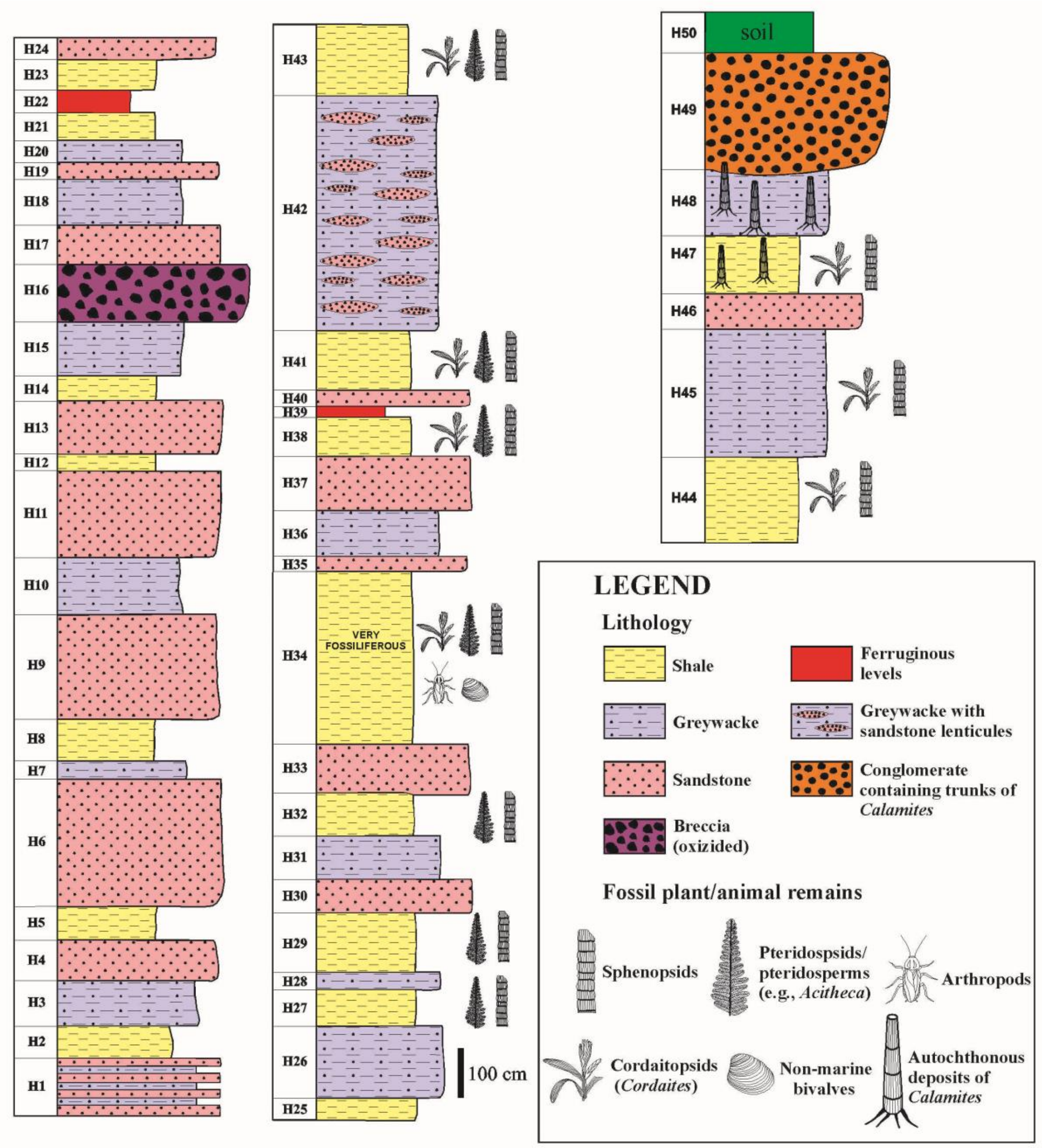

Fig. 11 - Stratigraphic log of the new lower Gzhelian outcrops of the Montes da Costa.

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PART IV – RESULTS

1. FLORA

1.1. New paleobotanical data on the Portuguese Pennsylvanian (Douro Carboniferous Basin, NW Portugal)

Adapted from Pedro Correia, Zbynek Šimůnek, Josef Pšenička, Artur A. Sá, Rúben Domingos, André Carneiro, Deolinda Flores
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Abstract

This paper describes nine new macrofloral taxa from Douro Carboniferous Basin (lower Gzhelian) of Portugal. The plant assemblage is mainly composed by pteridophylls (*Sphenopteriss arberi* Kidston, *Sphenopteris fayoli* Zeiller, *Sphenopteris tenuis* Schenk, *Odontopteris schlotheimii* Brongniart), sphenopsids (*Annularia spicata* von Gutbier, *Stellotheca robusta* (Feistmantel) Surange & Prakash, *Calamostachys grandis* Zeiller (Jongmans) and *Calamostachys calathifera* Sterzel) besides the gymnosperm *Cordaites foliolatus* Grand′Eury. The new data provide a better understating of the knowledge of late Carboniferous floras of Portugal, showing the high plant diversity of Gzhelian floras, when considerable changes in paleogeography and climate dynamics are evidenced in Euramerican floristic assemblages.

Resumo: Este trabalho descreve nove elementos megaflorísticos assinalados pela primeira vez no Carbónico (Gzeliano inferior) continental português. Os novos achados paleontológicos, *Sphenopteriss arberi* Kidston, *Sphenopteris fayoli* Zeiller, *Sphenopteris tenuis* Schenk, *Odontopteris schlotheimii* Brongniart, *Annularia spicata* von Gutbier, *Stellotheca robusta* (Feistmantel) Surange & Prakash, *Calamostachys grandis* Zeiller (Jongmans), *Calamostachys calathifera* Sterzel) e *Cordaites foliolatus* Grand′Eury, foram identificados em formações do Gzheliano da Bacia Carbonífera do Douro. Os novos dados permitem uma melhor compreensão do conhecimento da flora fóssil e da sua diversidade no Carbónico continental português, especialmente na Bacia Carbonífera do Douro, bem como a sua dinâmica em relação com as grandes mudanças na paleogeografia e no paleoclima aí ocorridas.

***Keywords*:** Fossil plant assemblage; São Pedro da Cova; Ermesinde; Douro Carboniferous Basin; Portugal.

1.1.1. Introduction

The fossil flora of Carboniferous of Portugal is still little known. The new megafloral occurrences recently found in the Upper Pennsylvanian strata of Douro Carboniferous

Basin (DCB) provide new and important data about paleobotanical richness and diversity of the Paleozoic floras of Portugal offering more information to previous researches reported from diverse localities and by different authors (e.g., Wenceslau de Lima, Bernardino António Gomes, Carlos Ribeiro, Carríngton da Costa, Carlos Teixeira, Robert Wagner). The main goal of the present study was to describe new paleobotanical occurrences of fossil taxa from the lower Gzhelian (Upper Pennsylvanian) outcrops in the São Pedro da Cova (Gondomar) and Ermesinde (Valongo) regions of the DCB (Figure 7).

1.1.2. Geological setting

Please, see PART II (pag. 21).

1.1.3. New paleobotanical data from Douro Carboniferous Basin

The new macrofloral taxa described in this paper were found in new outcrops of the DCB. These outcrops dated of the lower Gzhelian are located in the Montes da Costa (Ermesinde) and São Pedro da Cova (Gondomar) regions. Most specimens were found in light-todark gray shales (“insects level”: Loureiro *et al.*, 2010; Correia *et al.*, 2013, 2014) in the region of São Pedro da Cova. These shales are relatively compact, laminated and highly fossiliferous showing well-preserved plant fossils from a rich terrestrial flora-like Filicopsids and Pteridospermopsids (several genera: e.g., *Sphenopteris*, *Pecopteris*, *Lobatopteris*, *Callipteridium*, *Acitheca*, *Neuropteris*, *Cyclopteris* and *Oligocarpia*); Calamitales (e.g., *Calamites*, *Asterophyllites*, *Annularia* and *Calamostachys*); Sphenophytales (e.g., *Sphenophyllum*); Cordaitales (e.g., *Cordaites*); and some Lycophytales (lycophytes indet.). This flora is associated and/or interbedded with lacustrine deposits which are rich in non-marine bivalve fauna such as *Anthraconaia* cf. *lusitanica* Teixeira. This megaflora is typical from the Gzhelian (Late Pennsylvanian), when considerable changes in paleogeography and climate dynamics, evidencing a trend toward drier climate (e.g., Pfefferkorn and Thomson, 1982) are evidenced in Euramerican floristic assemblages. Paleofloras of this interval are characterized by the sudden decrease of arborescent lycophytes associated to the dominance of tree ferns/seed ferns and the representation of *Cordaites*.

1.1.4. Results

Identification of the new macrofloral elements in DCB (Plate I):

Stellotheca robusta **(Feistmantel, 1880) Surange & Prakash, 1962**

Description: Foliar whorl composed by 11–13 leaves, 14–19 mm long and 2.5–3.0 mm wide, widest point in the distal half, obtuse to acuminate apices. They are united at the base and display irregular margins. Midvein very strong (0.6–0.8 mm wide) and persists until the apex of leaf. It displays fine central vein.

Chronostratigraphical and geographical distribution: early Permian? of India (easthern Gondwana), (e.g., Boureau, 1964) and Gzhelian of Portugal.

Remarks: No preserved stem.

Sphenopteris tenuis **Schenk, 1883**

Description: Frond fragments of ultimate pinnae 22–60 mm long. Main rachis is 0.5–1.0 mm wide. Pinnules are 5 mm (upper pinnules) to 19 mm (lower pinnules) in length and 4–6 mm in width, lobed, retracted at the base and attached alternately on main rachis. Pinnules display seven lateral oval-triangular lobes. Flexuous midvein and lateral veins further divided.

Chronostratigraphical and geographical distribution: Carboniferous of Europe, ?America, China and Korea (e.g., Boureau and Doubinger, 1975) and Gzhelian of Portugal.

Remarks: Similarities with the species *Sphenopteris biturica* Zeiller.

Sphenopteris fayoli **Zeiller, 1888**

Description: Frond fragments of ultimate and penultimate pinnae 35–110 mm long. Ultimate pinnae attached alternately on main rachis and relatively spaced. Main rachis very strong, 3 mm wide, and secondary rachises are 1.5 mm in width. Pinnae consist of pinnules 6–22 mm long and 4–11 mm wide, strongly lobed. Pinnules display four lateral lobes, of ovate-triangular contour, attached by a large attachment base and decurrent. Pinnules of ultimate pinnae decurrent at the attachment base. Midvein strong and decurrent to the attachment base. Lateral veins divided twice to ?three times.

Chronostratigraphical and geographical distribution: Kasimovian–lower Gzhelian (Stephanian of the Central/Western European regional scale) of Europe (e.g., Boureau and Doubinger, 1975) and Gzhelian of Portugal.

Remarks: The material of *Sphenopteris fayoli* bears some similarities with the species *S. matheti* Zeiller and *S. biturica* Zeiller.

Sphenopteris arberi **Kidston, 1926**

Description: Ultimate pinnae 13–26 mm long composed by short lobed pinnules. Rachis very fine (0.5 mm wide). Pinnules 4–10 mm long and 3–5 mm wide, attached alternately on main rachis and relatively spaced. Pinnules display four lateral lobes, ovate, entire, which attached by a large attachment base and decurrent. Flexuous midvein and lateral veins further divided.

Chronostratigraphical and geographical distribution: Carboniferous strata of Great Britain (e.g., Kidston, 1923; Boureau and Doubinger, 1975) and Gzhelian of Portugal.

Remarks: The specimens display morphometric similarities with the species *Sphenopteris ovatifolia* Lillie.

Odontopteris schlotheimii **Brongniart, 1828**

Description: Terminal part of a penultimate order pinna preserved in 70 mm long and 50 mm wide. Sample displays two types of pinnules: large pinnules represent each undivided pinnule on the ultimate rachis order, in the terminal part of the frond, and small pinnules, growing on ultimate rachises. The largest pinnules are up to 21 mm long and 5 mm wide. They are slightly bent and of linguae shape. Its margin is smooth. Veins started obliquely from the midvein and reach the pinnule margin at angles of 70-80°. Vein density is approximately 30 veins per 1 cm of the pinnule margin. The smallest pinnules are more or less orbicular, oval, only 4–7 mm long and 3–4 mm wide. These pinnules are attached to the rachis by the whole base and several once or twice divided veins enter to the pinnules. The veins reach the pinnule margin at angles 75º–90°. The bigger pinnules occur again on the ultimate rachises on the right side, and they are 10–12 mm long. They display a midvein typical for *Neuropteris*. It is inferred that the atypical odontopterid pinnules found in the terminal part of the frond should be firstly odontopteridically divided on basal rachises, which were not preserved in the studied plant assemblage.

Chronostratigraphical and geographical distribution: upper Moscovian–lower Gzhelian (Stephanian of the Central/Western European regional scale) of North West Germany (e.g., van Waveren *et al.*, 2008) and Gzhelian of Portugal.

Remarks: Barthel (2006) described also large pinnules on terminal parts of *Odontopteris schlotheimii*. He discovered that some pinnules had lobate (or even dentate) margins similar to *Neuropteris pseudo-blissii* Potonié. Based on his observation, he assumed that *Neuropteris pseudo-blissii* is synonymous to *Odontopteris schlotheimii*. Portuguese material of *Odontopteris schlotheimii* pinnules has neither dentate margin, nor acute pinnule, so we think that *Neuropteris pseudo-blissii* corresponds to an independent species.

Cordaites foliolatus Grand'Eury, 1877

Description: Small leave, oval, narrowed to the base (6 mm wide). It is 51 mm long and 16 mm wide displaying abcordate leaf apex. Venation parallel, prominent and regular. Vein density about 30–32 per 1 cm. Veins arranged in pairs.

Chronostratigraphical and geographical distribution: Carboniferous of Central Bohemia (e.g., Ledran, 1966) and Gzhelian of Portugal.

Calamostachys grandis (Zeiller, 1888) Jongmans, 1911

Description: Fructification leafy shoots, 28–30 mm long and 2–4 mm wide, internodes about 1–1.5 mm long. Sterile bracts, 3–4 mm long, attached to the fructification cone axis nearly vertically and arlike bent upwards round the sporangiophores. Sporangiophores, 1–1.5 mm wide, located between the sterile bracts and attached to the internodes.

Chronostratigraphical and geographical distribution: Carboniferous of Central Bohemia (e.g., Němejc, 1953) and Gzhelian of Portugal.

Remarks: Cones of *Calamostachys grandis* represent fructification leafy shoots of species *Asterophyllites grandis* Sternberg (e.g., Němejc, 1953).

Annularia spicata von Gutbier, 1849

Description: Stem 30 mm long and 3.5 mm wide maximum, composed by four foliar whorls. Whorls consist of six narrow and slightly curved leaves, 5.5–10 mm long and 0.5–1.0 mm wide, widest point in the distal half, acuminate apices, no midvein. Leaves situated on its axis.

Chronostratigraphical and geographical distribution: Stephanian B and C of North West Germany (e.g., van Waveren *et al.*, 2008) and Gzhelian of Portugal.

Remarks: Some similarities are shown with the species *Annularia radiata* (Brongniart) Sternberg and *A. crassiscula* Halle (e.g., Boureau, 1964; van Waveren *et al.*, 2008).

Calamostachys calathifera Weiss, 1884

Description: Fertile articulated stem, 88 mm long and 2–4 mm wide, internodes about 5.5–11 mm long. Long sterile bracts, 15–25 mm long, attached on the whorls. They are few in number (3–4 leaves), narrow and display acuminate apices. Sporangiophores, 12–22 mm long and 3–4 mm wide, attached on the whorls arranged in acute angles.

Chronostratigraphical and geographical distribution: Carboniferous of Central Bohemia (e.g., Němejc, 1953) and Gzhelian of Portugal.

Remarks: *Calamostachys calathifera* bears similarities with *Volkmannia pseudosessilis* Grand′Eury (fructification of *Annularia sphenophylloides*), fructifications of *Annularia brevifolia* Schenk and *Calamites paleoceus* Stur (e.g., Němejc, 1953).

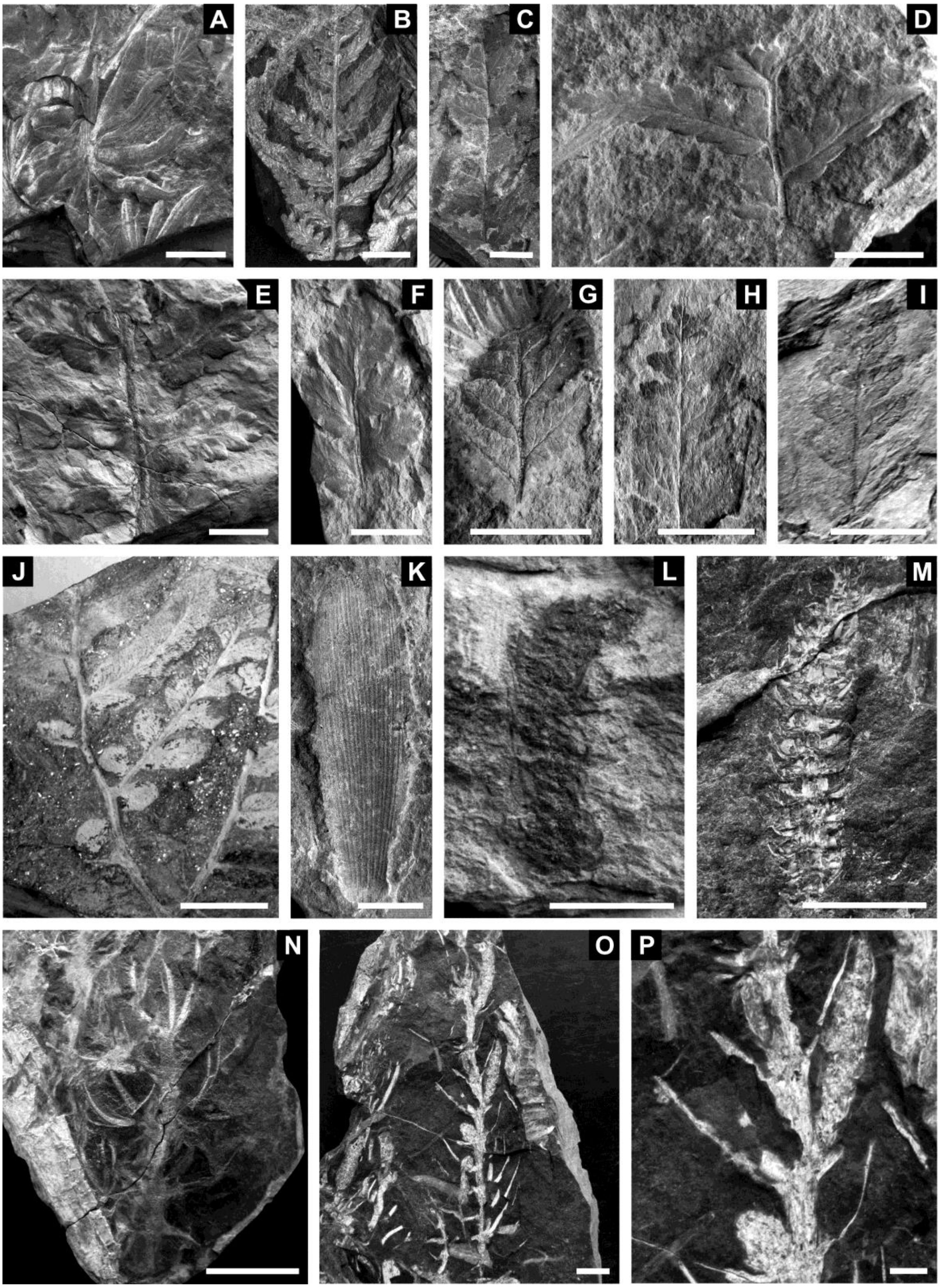

Plate I.

A. ***Stellotheca robusta* (Feistmantel) Surange & Prakash**

Locality—Montes da Costa, Ermesinde (TSU ?B1), DCB. Scale bar 10 mm.

B–D. ***Sphenopteris tenuis* Schenk**
Locality—São Pedro da Cova (outcrop spc2, TSU B1), DCB. Scale bar 10 mm.
E, F. ***Sphenopteris fayoli* Zeiller**
Locality—São Pedro da Cova (outcrop spc2, TSU B1), DCB. Scale bar 10 mm.
G–I. ***Sphenopteris arberi* Kidston**
Locality—São Pedro da Cova (outcrop spc2, TSU B1), DCB. G, H: scale bar 10 mm; I: scale bar 5 mm.
J. ***Odontopteris schlotheimii* Brongniart**
Locality—São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.
K. ***Cordaites foliolatus* Grand′Eury**
Locality—São Pedro da Cova (outcrop spc7, TSU B2), DCB. Scale bar 10 mm.
L, M. ***Calamostachys grandis* (Zeiller), Jongmans**
Locality—São Pedro da Cova (outcrop spc2, TSU B1), DCB. Scale bar 10 mm.
N. ***Annularia spicata* von Gutbier**
Locality—Montes da Costa, Ermesinde (TSU ?B1), DCB. Scale bar 10 mm.
O, P. ***Calamostachys calathifera* Sterzel**
Locality—Montes da Costa, Ermesinde (TSU ?B1), DCB. O: scale bar 10 mm; P: scale bar 2.5 mm.

1.1.5. Conclusions

A new fossil plant assemblage is identified on the late Carboniferous intramontane deposits of the Douro Carboniferous Basin, NW Portugal, composed mainly by Filicopsids and Pteridospermopsids (*Sphenopteris arberi* Kidston, *Sphenopteris fayoli* Zeiller, *Sphenopteris tenuis* Schenk, *Odontopteris schlotheimii* Brongniart), Sphenopsids (*Annularia spicata* von Gutbier, *Stellotheca robusta* (Feistmantel) Surange & Prakash, *Calamostachys grandis* (Zeiller) Jongmans, *Calamostachys calathifera* Sterzel) besides the gymnosperm *Cordaites foliolatus* Grand′Eury. Beyond the forms typically represented in the Gzhelian of the tropical Euramerica, during an interval of changing from humid to dry climate, the presence of *Stellotheca robusta*, previously described from the lower Permian of Eastern Gondwana (India) is a new evidence that must be investigated in future studies.

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1.2. *Lesleya* Lesquereux from the Pennsylvanian of the Iberian Massif: part of a dryland megaflora from the Variscan orogen, northwestern Portugal

Adapted from Pedro Correia, Artur A. Sá, J. Brendan Murphy, Zbyněk Šimůnek, Deolinda Flores

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Abstract

The Carboniferous–early Permian plant genus *Lesleya* is a characteristic component of 'dryland floras' that occupied a wide range of moisture-stressed, well-drained environments in tropical regions of Euramerica. Fossil records of *Lesleya* are almost exclusively found in basinal lowlands. For example, occurrences in Early Pennsylvanian-age, seasonally-dry, parautochthonous deposits in basinal lowlands of North America (e.g., Illinois Basin, USA), indicate that *Lesleya* lived in that region in low altitude (lowland) paleoenvironments during dry climatic intervals. In this paper, we document the first occurrence of *Lesleya* during the Carboniferous on the Iberian Massif, in lower Gzhelian (Upper Pennsylvanian) strata of the Douro Carboniferous Basin, in northwestern Portugal. This newly discovered occurrence includes a new species, *Lesleya iberiensis* sp. nov., recognized on the basis of natural molds of leaves. The Portuguese *Lesleya* fossils are from upland intramontane deposits and they occur between coal-beds. Their fossil remains are preserved in mica-rich shales which were deposited between sandstone-dominated fluvial and shale-dominated lacustrine deposits, suggesting that this megaflora was deposited near freshwater bodies. These new data provide evidence that this megaflora grew in mountain riparian environments within the Variscan orogen, either in localized, well-drained areas or during drier climatic intervals in the Late Pennsylvanian.

Keywords**:** *Lesleya*; megaflora; Iberian Massif; Variscan orogen; drylands; riparian environments; intramontane basins.

1.2.1. Introduction

Pennsylvanian-age 'dryland floras' include a diversity of terrestrial plants that occupied a wide range of moisture-deficient and well-drained environments within the Euramerican Floristic Province (here called Euramerica) (e.g., Falcon-Lang, 2003; DiMichele *et al.*, 2009, 2010; Falcon-Lang *et al.*, 2009, 2011a, b; Bashforth *et al.*, 2014). These dryland floras flourished wherever favorable climatic and edaphic conditions existed, particularly where habitats became dry enough to support such biomes during dry climate intervals (e.g., DiMichele *et al.*, 2009, 2010; Falcon-Lang *et al.*, 2011b; van Hoof *et al.*, 2013; Bashforth *et al.*, 2014). Pennsylvanian-age dryland plant communities are still poorly understood compared to biomes that colonized tropical wetland ecosystems (Falcon-Lang, 2003; Falcon-Lang *et al.*, 2011a). Fossil records for dryland plant communities are almost exclusively found in basinal lowlands (e.g., Leary and Pfefferkorn, 1977; Leary and Trask, 1985; DiMichele *et al.*, 2009, 2010; Falcon-Lang *et al.*, 2009; Bashforth *et al.*, 2014).

Lesleya is an enigmatic member of 'dryland (xerophilous–mesophilous) floras' (generally xeromorphic) and is one of the indicator taxa used to assess soil dryness conditions in Pennsylvanian-age deposits (e.g., DiMichele *et al.*, 2010; Falcon-Lang *et al.*, 2011a; Bashforth *et al.*, 2014). Fossils of *Lesleya* are mainly found in seasonally-dry basinal lowlands (e.g., Leary and Pfefferkorn, 1977; Leary and Trask, 1985; DiMichele *et al.*, 2008, 2010; Falcon-Lang *et al.*, 2011a; Bashforth *et al.*, 2014). In North America, paleoecological studies on Pennsylvanian-age parautochthonous deposits have examined seasonally-dry floral assemblages containing conifers, cordaitaleans, and pteridosperms including foliage of *Lesleya* (e.g., Leary and Pfefferkorn, 1977; Leary and Trask, 1985; Plotnick *et al.*, 2008, 2009; DiMichele *et al.*, 2010). These floral assemblages occur in basin-margin settings developed on drought-prone limestone substrates in basinal lowlands and are preserved in clastic rocks deposited between coal-beds (e.g., Plotnick *et al.*, 2008, 2009; DiMichele *et al.*, 2008, 2010). *Lesleya* is restricted to the equatorial regions of Euramerica, where it occurs in Carboniferous and lower Permian strata (e.g., Sellards, 1908; Leary and Pfefferkorn, 1977; Leary, 1981; Wagner, 2004; Leary and Trask, 1985; Šimůnek, 1996; Cleal and Thomas, 2004; DiMichele *et al.*, 2008, 2010). The megaflora containing *Lesleya* is limited to lower Bashkirian (Lower Pennsylvanian) strata in North America (e.g., Illinois Basin, USA), but it has a wider paleogeographical distribution in Carboniferous–lower Permian strata of Europe (e.g., Leary and Pfefferkorn, 1977; Leary and Trask, 1985; Šimůnek, 1996; DiMichele *et al.*, 2008, 2010).

In this paper, we document the first occurrence of *Lesleya* in the Iberian Massif, on the basis of leaf fossils recently found in lower Gzhelian (Upper Pennsylvanian) strata of the Douro Carboniferous Basin (DCB), in northwestern Portugal (Figure 2). The DCB is an intramontane basin located adjacent to the Valongo Anticline in the Central Iberian Zone of the Variscan orogen (e.g., Wagner, 1983; Domingos *et al.*, 1983; Correia *et al.*, 2013). The development of intramontane basins such as the DCB was common during the Variscan orogen (e.g., Wagner, 2004; Cleal, 2008; Wagner and Álvarez-Vázquez, 2010; Bashforth *et al.*, 2011) and such basins are well-documented in the Iberian Massif (e.g., Wagner, 1983; Pinto de Jesus, 2001). While recognizing that our results do not preclude the occurrence of *Lesleya* in a wide range of moisture-stressed environments, in this paper we provide a better understanding of the 'dryland floras' in the Iberian Massif, and we assess its significance for interpreting the paleoclimate, paleoecology and paleoenvironment in that region during the Late Pennsylvanian.

1.2.2. Geological background

Please, see PART II (pag. 21).

1.2.3. Dryland megafloral assemblages and non-marine faunal associations previously described in DCB

In previous studies of the DCB fossil megaflora, Lemos de Sousa and Wagner (1983b) emphasized the occurrence of *Pseudomariopteris* cf. *busquetii* (Zeiller) Danzé-Corsin, aff. *Taeniopteris multinervia* Weiss and *Neuropteris ovata* Hoffmann var. *pseudovata* Gothan & Sze. Those author's interpretations of the paleoenvironmental, paleoecological and paleogeographic conditions for the DCB strata were based on the strata being adjacent to mountainous regions, such as Valongo Anticline, and on the occurrence of dryland (xerophilous–mesophilous) floras in the Iberian Massif. Previous descriptions of the DCB dryland floras also identified the conifers *Ernestiodendron filiciforme* (von Schlotheim pars) Florin, aff. *Culmitzschia frondosa* (Renault) var. *zeilleri* (Florin) Clement-Westerhof and *Culmitzschia parvifolia* (Florin) Clement-Westerhof and the cordaitales *Dicranophyllum gallicum* Grand'Eury and *Dicranophyllum lusitanicum* (Heer) Lima (Wagner, 1983; Wagner and Lemos de Sousa, 1983; Domingos *et al.*, 1983).

In addition to these floras, paleozoological studies (Eagar, 1983) documented occurrences of the non-marine bivalves *Anthraconaia lusitanica* Teixeira and *Anthraconaia*? *altissima* Eagar in the DCB. These bivalves indicate freshwater conditions, which are common in intramontane limnic basins (e.g., Eagar, 1983, 1987; Eagar and Belt, 2003; Pleijel *et al.*, 2004; Racheboeuf *et al.*, 2002, 2008; Charbonnier *et al.*, 2008; Schultze, 2009; Tibert *et al.*, 2011).

1.2.4. Portuguese material of *Lesleya*

The *Lesleya* fossils reported herein are natural molds of leaves collected from recently discovered, early Gzhelian-age (Late Pennsylvanian) outcrops in the DCB, located within the São Pedro da Cova region of northwestern Portugal (outcrop spc6; Figures 2, 7).

These outcrops correspond to the upper part of TSU B2 in transition to TSU C2 of the DCB stratigraphy (Figure 3). The fossils of *Lesleya* are fragmentary in nature and commonly occur at various stratigraphic levels, within compressed grey shales that are interbedded with sandstone deposits of variable thickness (Figures 12–14). The grey shales are composed of two distinct lithofacies: mica-rich shales that contain abundant detrital muscovite and clay-rich shales with more pelitic features. Both lithofacies are reasonably well exposed and contain a variety of fossils: the mica-rich shales contain various macrofloral elements (e.g., *Lesleya* and *Cordaites*), whereas the clay-rich shales contain non-marine bivalves (*Anthraconaia*) and insects (blattodeans) (Figures 12–14).

Fig. 12 - Outcrop where the specimens of *Lesleya* were collected (unpublished picture taken in 2007 by P. Correia).

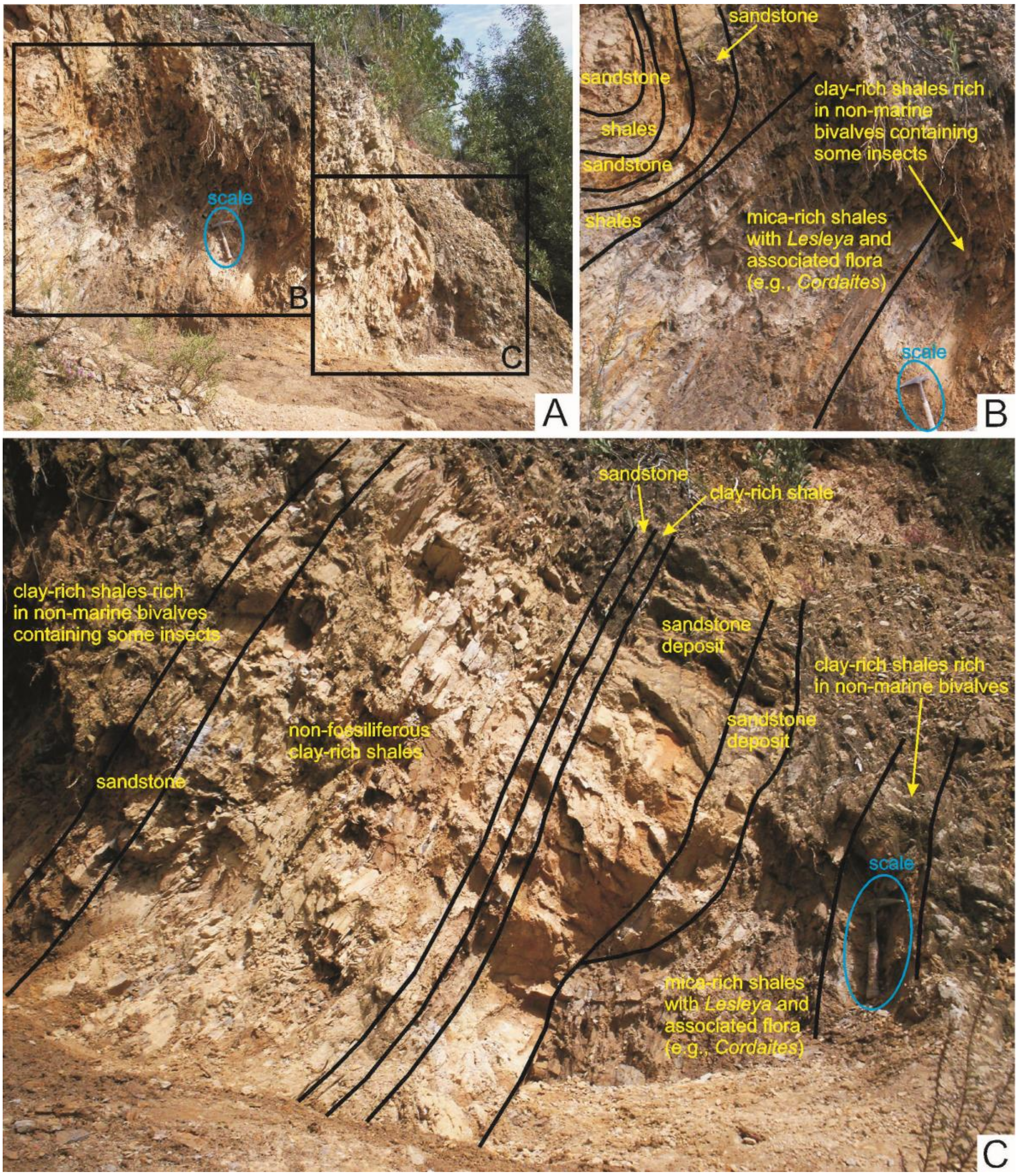

Fig. 13 - Photographs of the *Lesleya* outcrop in the São Pedro da Cova region, northwestern Portugal. (A) View of fossiliferous portion of outcrop, consisting of siliciclastic deposits (mica-rich shale lithofacies) containing *Lesleya* and associated flora (e.g., *Cordaites*) interlayered with pelitic deposits (clay-rich shale lithofacies) rich in non-marine bivalves (*Anthraconaia*) and some insects. (B, C) Closer views of the upper (B) and lower (C) parts of the fossiliferous sequence showing interlayered shale and sandstone strata.

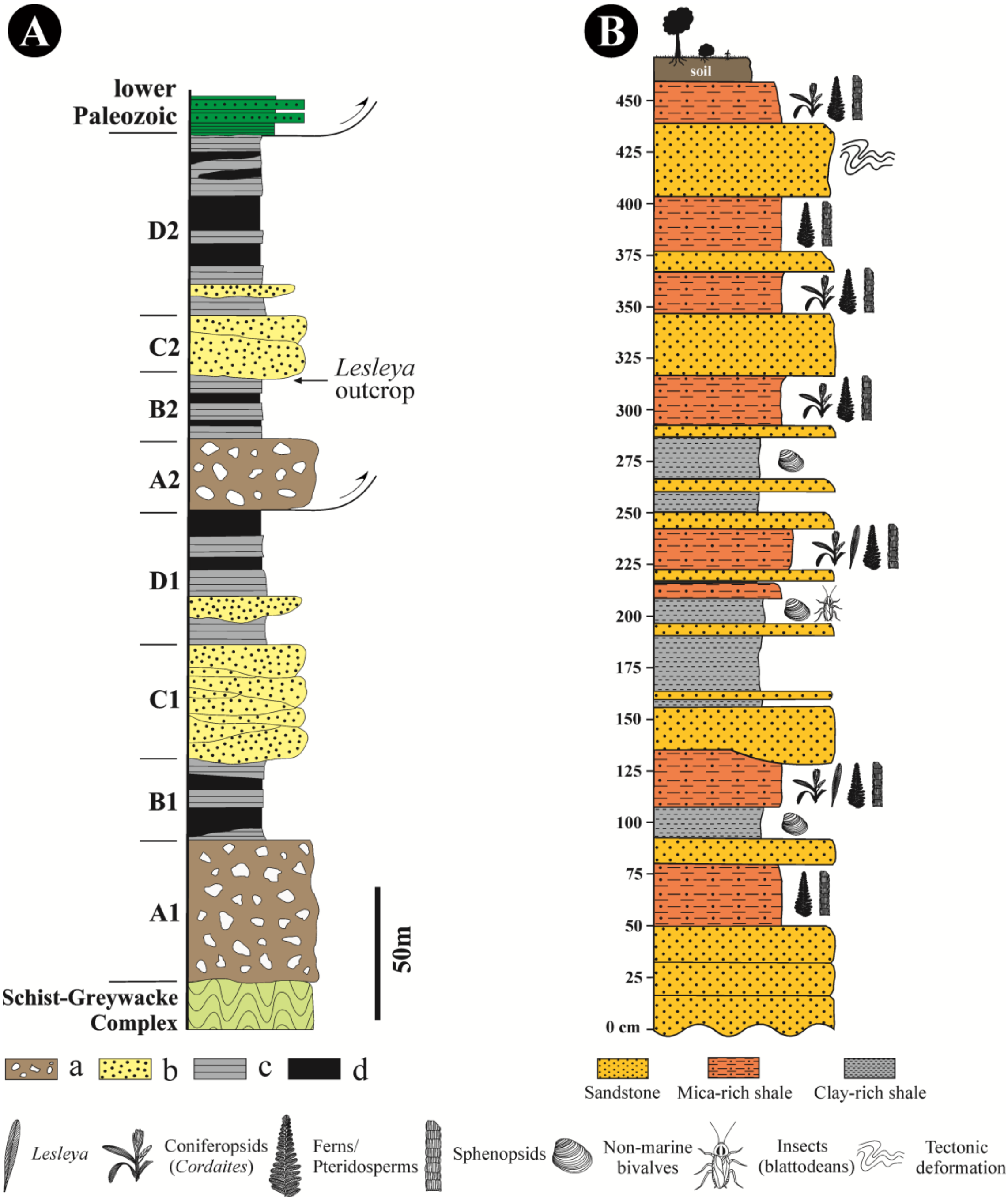

Fig. 14 – (A) Generalized stratigraphic and sedimentologic column for the Douro Carboniferous Basin, northwestern Portugal, showing the eight tectono-sedimentary units (TSU) recognized in the sequence (adapted from Pinto de Jesus 2001) and the position of the *Lesleya* outcrop. Key for lithologies: a, breccias; b, conglomerates and sandstones; c, siltstones and shales; d, coal beds. (B) Detailed stratigraphic and sedimentologic column for the *Lesleya* outcrop, in the São Pedro da Cova region, showing positions of fossiliferous layers.

The *Lesleya* leaves were found in association with leaves of *Cordaites*. An associated flora, consisting of species such as *Neuropteris ovata* ?var. *pseudovata* Gothan & Sze, *Linopteris neuropteroides* (von Gutbier) Potonié, *Dicksoniites pluekenetii* (Sternberg) Sterzel, *Pecopteris cyathea* (von Schlotheim) Brongniart, *Pseudomariopteris cordato-ovata* (Weiss) Gillespie *et al.* ex Krings & Kerp, *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger, *Calamites suckowii* Brongniart, *Callipteridium* (*Eucallipteridium*) *gigas* (von Gutbier) Weiss, *Acitheca polymorpha* (Brongniart) Schimper and *Asterophyllites equisetiformis* (von Schlotheim) Brongniart, as well as faunal species *Anthraconaia* cf. *lusitanica* Teixeira, were collected together with specimens of *Lesleya* and *Cordaites*. This fossil plant assemblage occurs in association with lacustrine deposits containing non-marine bivalves that are probably *Anthraconaia lusitanica* Teixeira and *Anthraconaia*? sp. nov. (Figures 13, 14; Plate II).

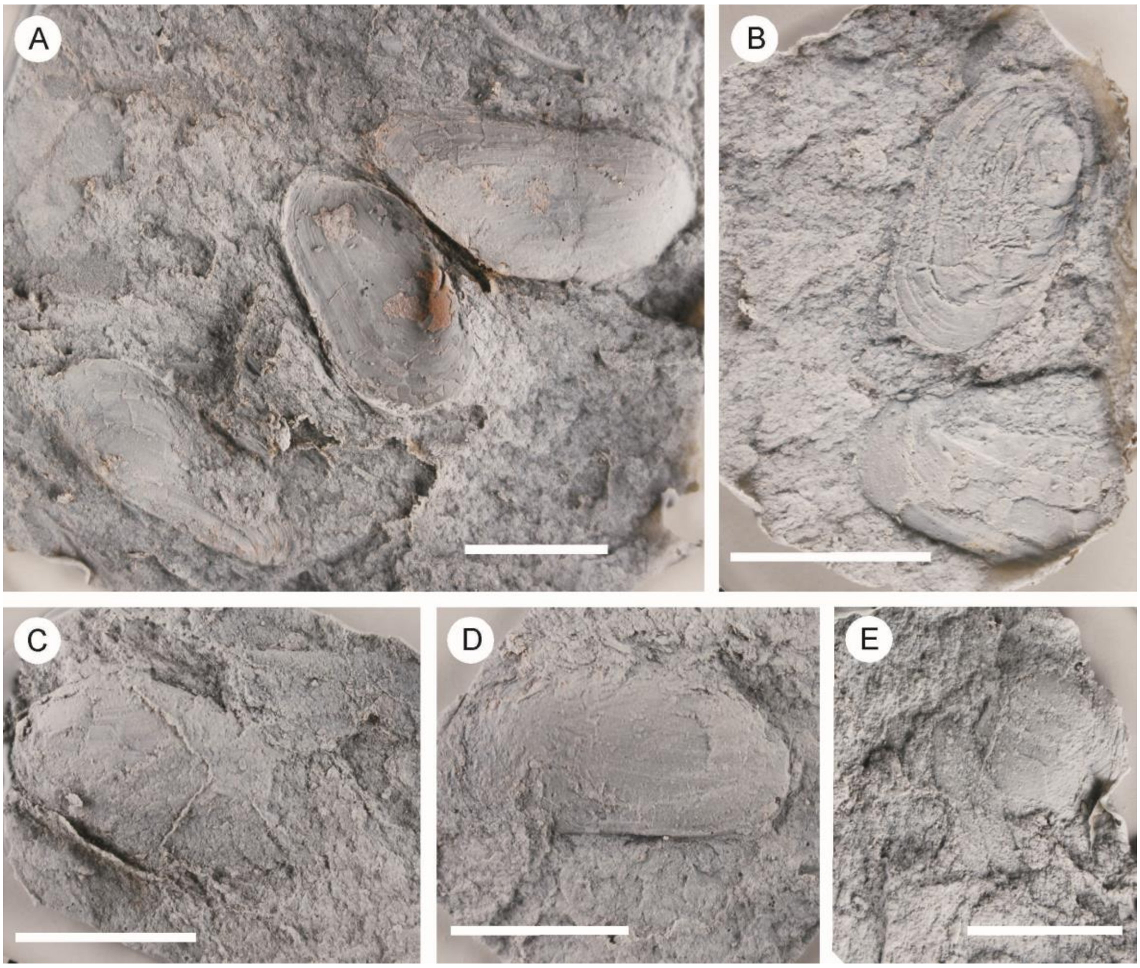

Plate II - Non-marine (limnic) bivalves (latex casts). (A–D) *Anthraconaia* cf. *lusitanica* Teixeira. (E) *Anthraconaia*? sp. São Pedro da Cova (TSU B2), DCB. Scale bar 10 mm. (plate unpublished)

The associated flora and fauna were previously identified and described by Wagner (1983, 1984) and Eagar (1983) in the lower Gzhelian strata of the Iberian Massif and in the DCB (Wagner, 1983; Eagar, 1983; Lemos de Sousa and Wagner, 1983a, b; Wagner and Lemos de Sousa, 1983; Lemos de Sousa and Wagner, 1985a, b).

1.2.5. Systematic paleontology

Division: Gymnospermophyta
Class: Pteridospermopsida Oliver & Scott, 1904
(or Class Cycadopsida Brongniart, 1843)
Order and Family unknown
Genus: *Lesleya* Lesquereux, 1880

Comments: *Lesleya* is restricted to equatorial regions of Euramerica where it ranges from the Carboniferous to early Permian (Table 1, Figure 15). The geographic distribution of *Lesleya* is more widespread in Europe, where occurs mainly in Upper Pennsylvanian and lower Permian strata. In North America, *Lesleya* is found mainly in Lower Pennsylvanian strata, but some occurrences in lower Permian deposits have been documented (e.g., Leary and Pfefferkorn 1977; Leary and Trask, 1985; Šimůnek, 1996; DiMichele *et al*., 2008, 2010).

Lesleya contains 11 previously described species (e.g., Šimůnek 1996; Figure 15, Table 1). Most species were established on the basis of fragmentary material (e.g., Lesquereux, 1879 [atlas: pl. 25, figs. 1–3], 1884; Zeiller, 1890; Remy and Remy, 1975, 1978). Species are differentiated mainly on the basis of leaf characters (see Table 2), such as: leaf shape including type of apex and base shape; type of margin (e.g., entire or undulate margin); and venation pattern, including type of venation (e.g., simple/pinnate or dichotomous; curved or sinuous), number of lateral veins per cm on margin, and angles between midvein/lateral vein and lateral vein/margin (e.g., Leary and Pfefferkorn, 1977; Leary, 1980; Šimůnek, 1996). Where organically preserved material is available, cuticular features also are useful for differentiating species of *Lesleya* and assessing their phylogenetic relationships (e.g., Florin, 1933; Šimůnek, 1996). Here, we describe a new species of *Lesleya* recognized on the basis of leaf fossils from lower Gzhelian (Upper Pennsylvanian) deposits in Portugal. The new Portuguese species is most similar to *Lesleya cheimarosa*, a geologically older congener described by Leary and Pfefferkorn (1977) from lower Bashkirian (Lower Pennsylvanian) deposits in the Illinois Basin, USA, and known by very complete leaf specimens, including the holotype (see Leary and Pfefferkorn, 1977, pl. 8, figs. 1, 2; Leary and Trask, 1985, pl. 1, fig. 2).

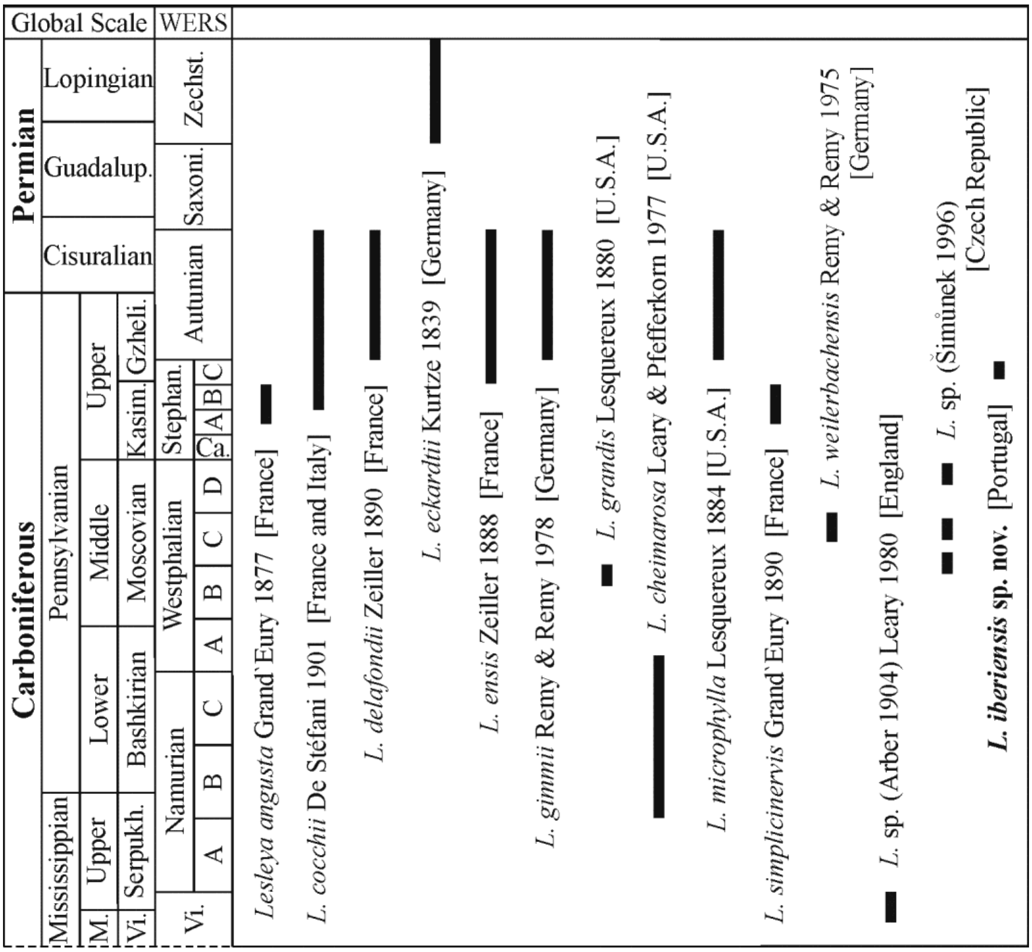

Fig. 15 - Stratigraphic ranges and geographic distributions of *Lesleya* species in Euramerica. Adapted from Šimůnek (1996, table 1). Abbreviations: Ca., Cantabrian; Guadalup., Guadalupian; Gzheli., Gzhelian; Kasim., Kasimovian; M., Middle; Saxoni., Saxonian; Zechst., Serpukhovian; Stephan., Stephanian; Vi., Visean; WERS, Western Europe Regional Scale; Zechstein; Serpukh.

The higher level affinities of *Lesleya* are uncertain. Its familial and ordinal affinities are unknown (e.g., Taylor *et al.*, 2009), whereas at the class level *Lesleya* variously has been assigned to, or allied with, both the Cycadopsida and Pteridospermopsida (Remy and Remy, 1977, 1978; Leary, 1990). A relationship between *Lesleya* and Permian–Mesozoic cycads has been suggested on the basis of their similar foliage (e.g., Florin, 1933; Remy and Remy, 1978; Leary, 1990, 1993, 1998; Wagner, 2004; Taylor *et al.*, 2009). *Lesleya* also has been suggested as a probable ancestor to cycads (Remy and Remy, 1978; Leary, 1990; Taylor *et al.*, 2009). Florin (1933) regarded *Lesleya* as a primitive gymnosperm, however, it is not closely related to Permian seed ferns or Mesozoic gymnosperms based on morphological and epidermal features. In addition, Wagner (2004) proposed *Lesleya* as the tropical ancestor of the south temperate, Permian *Glossopteris* Brongniart. That ancestral affinity seems unlikely considering differences between the two groups in their venation patterns (anastomosed/reticulated venation in *Glossopteris* versus pinnatifid/pinnate venation in *Lesleya*) and reproductive organs (e.g., Leary, 1990, 1993, 1998).

Lesleya iberiensis **sp. nov.**

Plates III and IV

Etymology: The specific epithet refers to the discovery of this species in the Iberian Massif.

Holotype: Natural mold of a nearly complete, large leaf broken in three pieces (separately numbered as UP-MHNFCP-094951/-094952/-094954) and preserved in grey shales (Plate III). The specimen is stored in the NHMSUP.

Paratypes: The three paratypes also are natural molds of leaves preserved in grey 324 shales (Plate IV): ZS 507 and ZS 508 are the lower parts of two different leaves, whereas ZS 510 is a nearly complete, but poorly preserved leaf. The specimens are are stored in the Czech Geological Survey of Prague.

Type locality: Outcrop (spc6) located in DCB, São Pedro da Cova region, northwestern Portugal (Figure 7).

Type horizon and age: Compressed dark grey, mica-rich shale lithofacies; TSU B2 (Figure 14). Early Gzhelian or Late Pennsylvanian in age.

Diagnosis: Simple leaves, maximum dimensions about 225 mm long and 50 mm wide; margins strongly arched towards the leaf base; base long and narrow (cuneate); margin entire; midvein broad, 1.0 to 3.0 mm wide; lateral veins fork once or twice; lateral veins oblique, slightly curved (arched) with a 7° to 15° angle at the midvein and 5º to 35º angle on margin; 10–13 veins per cm on margin. See Table 1 for more detailed comparisons with other named congeners.

Description: The holotype (Plate III) is a nearly complete leaf missing its tip and an irregular portion midway along its length. The leaf has a maximum width of 50 mm and its preserved length is 225 mm; when intact, its total length would have been about 250 mm. The lateral veins are widely spaced (11–13 veins per cm on margin) and fork once or twice. They are oblique, slightly curved or arched from the midvein to the margin and, as measured along the mid-length of the leaf, form angles of 7° to 15° with the midvein and 30° to 35° with the margin. The midvein is broad (1.0–2.5 mm wide) and bears several longitudinal striations. The paratypes ZS 507a, b (Plate IV, A, B) and ZS 508 (Plate IV, D) are lower parts of two leaves, with preserved dimensions of 100 mm long and 44 mm wide for ZS 507 and 70 mm long and 23 mm wide for ZS 508. In both specimens, the lateral veins are oblique, curved from the midvein to the margin, spaced 10–12 veins per cm on margin and fork once or twice, forming angles of 9º to

14º with the midvein and 5º to 18º with the margin. The midveins are 1–3 mm wide. The third paratype, ZS 510 (Plate IV, C), is a nearly complete, but poorly preserved leaf, >170 mm long and 44 mm wide. The lateral veins are oblique, slightly curved from the midvein to the margin, spaced 10–12 veins per cm on margin and fork once or twice, forming angles of 8°–12° with the midvein, and 16°–27° with the margin. The midveins are 2–3 mm wide.

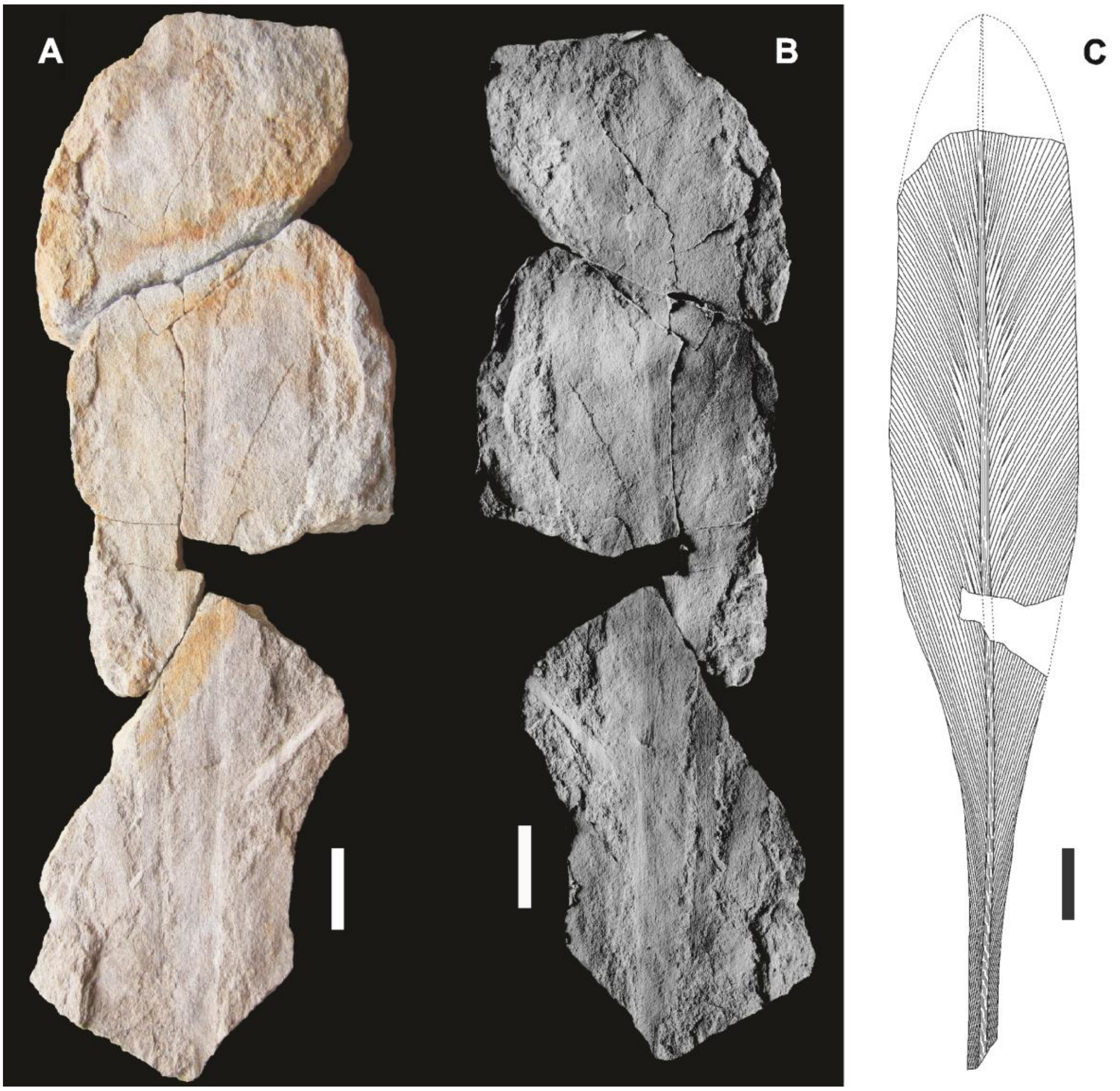

Plate III - Holotype leaf (UP-MHNFCP-094951/-094952/-094954) of ***Lesleya iberiensis* sp. nov.**, from the Late Pennsylvanian (early Gzhelian) of the Douro Carboniferous Basin, Sao Pedro da Cova region, northwestern Portugal. (A) Photograph of original specimen, preserved as a natural mold in grey shale, missing its tip, base, and a small piece midway along leaf, and broken in three pieces. (B) Latex cast of original specimen, showing positive relief. (C) Interpretive drawing of original specimen, showing reconstructed leaf margins (dotted lines) based, in part, on paratypes and comparisons with other congeners. Images at different magnifications; scale bars = 20 mm.

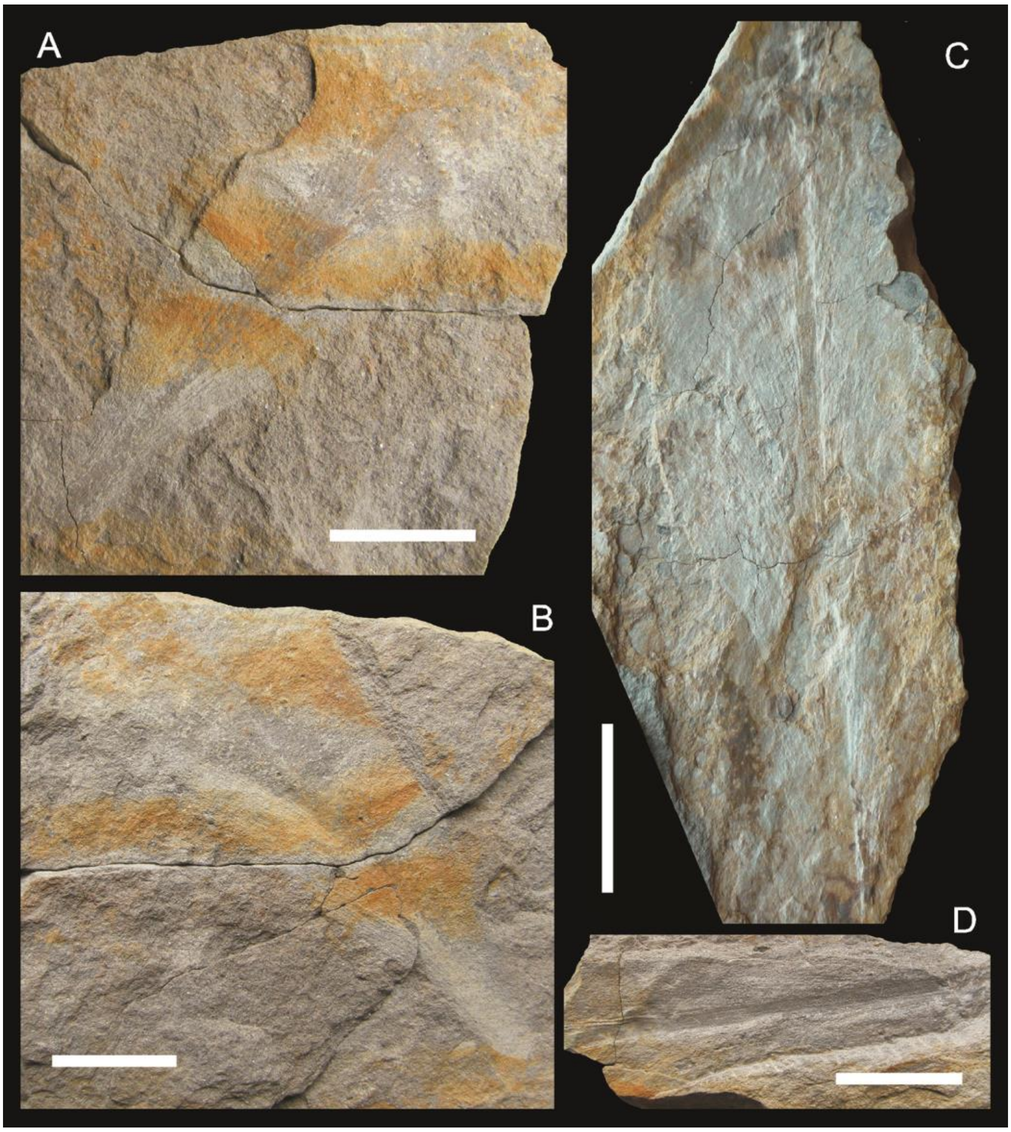

Plate IV - Paratype leaves of ***Lesleya iberiensis* sp. nov.**, from the Late Pennsylvanian (early Gzhelian) of the Douro Carboniferous Basin, Sao Pedro da Cova region, northwestern Portugal. All are photographs of uncoated, original specimens preserved as natural molds in grey shale. (A, B) Paratype ZS 507, lower part of leaf; part (A) and counterpart (B) slabs. (C) Paratype ZS 510, nearly complete, but poorly preserved leaf. (D) Paratype ZS 508, lower part of leaf. Images at different magnifications; scale bars = 20 mm.

All four examples of *Lesleya iberiensis* sp. nov. display strongly arched margins with a narrowing at the leaf base (i.e., cuneate-shaped leaf base; see different types of leaf bases in Hickey, 1977: appendix fig. 4), a long base, and a broad midvein that increases in width towards the leaf base and is longitudinally striated. Although the apex is missing from all four specimens, we restore it as having a lanceolate outline (see reconstruction drawing of holotype in Plate III, C).

Remarks and comparisons: The Portuguese material displays morphological features typical of the genus *Lesleya*. According to the original generic diagnosis from Lesquereux (1880, p. 142), *Lesleya* is characterized by the following combination of features: “*Pinnae simple, very entire, sublanceolate, gradually narrowing towards the base, traversed by a thick costa effaced under the apex; veins oblique, curved, equal, repeatedly dichotomous*”. Subsequent treatments by Leary and Pfefferkorn (1977) and Leary and Trask (1985) described *Lesleya* foliage as simple, large and wide leaves, generally 10 cm in width and with a length that can exceed 30 cm (although there also are some smaller forms from the Czech Republic; e.g., Šimůnek, 1996), having a lanceolate/sublanceolate apex and arched margins with a narrowing at the well-developed leaf base, a broad midvein, and oblique lateral veins that are curved, and equally repeatedly dichotomous.

The Portuguese material also is comparable to *Megalopteris* (Dawson) Andrews, 1875. This is due to the fact that *Megalopteris* and *Lesleya* foliage look very similar, especially when preserved in a fragmentary state. Lesquereux (1880, p. 142) stated: “*This genus [Lesleya] is related by some of its characters to Neuropteris and by its nervation of its fine species especially to Megalopteris*”. *Megalopteris* and *Lesleya* both have large and wide foliage, lanceolate/sublanceolate apexes and arched margins, a broad midvein, and oblique lateral veins that are curved and equally repeatedly dichotomous. Upper pinnules of *Megalopteris* fronds can display arched margins with a narrowing at the pinnule base (e.g., Zeiller, 1900, fig. 85) reminiscent of leaf bases in *Lesleya*. Leary (1980, p. 30) characterized *Megalopteris* as follows: “*Frond rugose, rachis thick, striated, broadly winged, pinnae alternate, very oblique, acute at apex, often an inch wide and six inches long, margin undulate; midrib disappearing before reaching apex, veins numerous, very oblique, curved, forking thrice very obliquely*”. According to Leary (1980), *Lesleya* differs from *Megalopteris* in that *Lesleya* foliage consists of simple leaves, whereas *Megalopteris* is a compound leaf or pinnae comprised of three or more lobes or pinnules (see Leary and Pfefferkorn, 1977, fig. 8; pls. 6–8; Leary and Trask, 1985, pl. 1; see also additional descriptions by Leary and Pfefferkorn, 1977 and Cross *et al.*, 2005). Leary (1980, p. 30) also stated, “…*when a complete leaf or frond is preserved, or even a fragment sufficient to observe the division into two or more lobes, generic separation is quite simple*”. The Iberian leaf fossils reported herein are sufficiently intact to demonstrate the absence of any *Megalopteris*-like division; that supports our assignment of these specimens to *Lesleya*. Florin (1933) was able to distinguish stomata of two genera based on cuticular material. Cuticular features are uninformative for establishing the generic identity of *Lesleya iberiensis* sp. nov., because no organically preserved (cuticular) material is available.

Table 1 - Comparison of leaf features among ***Lesleya iberiensis* sp. nov.** and the other 11 named species in the genus. Data compiled from descriptions and figures in papers cited in "Authors" column.

Lesleya species	Authors	Pinna (leaf shape)	Width [mm]	Length [mm]	Leaf base	Leaf apex	Midvein width [mm]	Margin shape	Venation	Nº bifurcations of lateral veins	Angle between lateral vein/ margin	Angle between lateral vein/ midvein	Nºveins per 1 cm on the leaf margin
delafondii	Zeiller 1890	lanceolate	70	>200	?	obtuse	?	denticulate? to entire	slightly curved	3–?4	30°–32°	26°	8–12
grandis	Lesquereux 1880	lanceolate	80	220	?cuneate	obtuse	strong	entire to lobate/lancerate	some sinusoidal effect	3–4	20°–82°	56°–60°	25–30
cheimarosa	Leary & Pfefferkorn 1977	lanceolate	40	200	long and narrow (cuneate)	sub/lanceolate to accute	broad 0.7–2	entire	S-shaped (sinuous)	1–2	40°–70°	10°–70°	24–36
angusta	Grand'Eury 1877	lanceolate	17	170	obtuse	blunt	?	entire	slighty curved to margin	0–1	45°–55°	±35°	±10
*cocchii**	De Stéfani 1901	?lanceolate	16	?	?	?	2	entire	curved to margin	1–2 near base	±50°	±15°	±20
ensis	Zeiller 1888	lanceolate	40	>115	?	?blunt	1	entire	slighty curved	2–3	35°–40°	10°–12°	8–12
gimmii	Remy & Remy 1978	narrow-elliptical	30–40	>200	acute	?	6 at base	entire	slightly S-shaped	2–3	28°–53°	06°	10–13
*microphylla***	Lesquereux 1884	oval-oblong	16	40	decurrent, shortly auriculate	obtuse	?	entire	?	?	50°	very acute	40
simplicinervis	Grand'Eury 1890	?spatulate	27	110	rounded	rounded	?	entire	slighty curved to margin	0 (simple veins)	±35°	15°–20°	8–10
weilerbachensis	Remy & Remy 1975	lanceolate	65	>250	cuneate	acute	1.5–2	dentate	slighty curved	3–?4	09°–10°	13°–14°	12–20
*eckardtii****	Kurtze 1839	lanceolate	23–30	>200	acute	blunt	2	entire to ?lobate	straight	0 (simple veins)	±60°	60°	8–9
***iberiensis* sp. nov.**	**in this paper**	**lanceolate**	**50**	**>225**	**long and narrow (cuneate)**	**?lanceolate**	**broad 1–3**	**entire**	**slighty curved (arched)**	**1–2**	**05°–35°**	**07°–15°**	**10–13**

*According Zeiller (1906);
** According to the description;
***This species still be assigned to genus *Taeniopteris* Brogniart by some authors - *Taeniopteris eckardtii* Kurtze 1839 (see Halle, 2014).

Among the 11 previously described species in the genus, *Lesleya cheimarosa* Leary & Pfefferkorn, 1977 from the early Bashkirian (Early Pennsylvanian) of the Illinois Basin, USA (see Leary and Pfefferkorn, 1977, pl. 8, figs. 1, 2; Leary and Trask, 1985, pl. 1, fig. 2) is most similar to *Lesleya iberiensis* sp. nov. Both species are known by very complete leaves that have entire margins, are similar in size and shape (i.e., large and wide leaves, have strongly arched margins that narrow towards a cuneate-shaped base) and have dichotomous venation. The holotype leaf of *L. cheimarosa* was described by Leary and Pfefferkorn (1977, p. 25) as follows: "*Simple leaf of considerable size, about 20 cm long and 4 cm wide, lanceolate with acute to attenuate tip. Base long and narrow (acuminate). Margin entire, venation pinnate, midrib thick, 0.7 to 2.0 mm wide; lateral veins fork once or twice; lateral veins S-shaped with a 10º to 20º angle at the midvein, 30º to 70º angle in center, and 40º to 70º angle on margin; 24 to 36 veins per cm on margin*". Based on that description, *L. iberiensis* sp. nov. differs from *L. cheimarosa* in details of the lateral veins. Specifically, *L. cheimarosa* displays S-shaped (sinuous) and numerous (24–36) lateral veins (see Leary and Pfefferkorn, 1977, fig. 8C, F, pp. 22, 23; pl. 6, fig. 5; pl. 8, figs. 1, 2; see also description of Leary, 1980), whereas *L. iberiensis* sp. nov. has lateral veins that are slightly curved and fewer in number (10–13) and more widely spaced (see Table 1). More detailed comparisons among all 12 congeners are presented in Table 1.

1.2.6. Discussion

1.2.6.1. Living habitat, deposition and preservation of *Lesleya* in intramontane basins from the Iberian Massif

In Early Pennsylvanian-age rocks of North America (e.g., Illinois Basin), *Lesleya* occurs in parautochthonous deposits in seasonally-dry basinal lowlands (e.g., Plotnick *et al.*, 2008, 2009; DiMichele *et al.*, 2008, 2010), indicating living habitats in low altitude environments during intervals of relatively dry climate (e.g., DiMichele *et al.*, 2008, 2009, 2010). In the Iberian Massif, the Late Pennsylvanian-age *Lesleya* described herein is preserved in immature shales that are in gradational contact with sandstone deposits (Figures 13, 14B). These DCB strata represent a depositional area with typically upland elevations and occur in areas adjacent to mountainous regions such as Valongo Anticline located in the Central Iberian of the Variscan orogen (e.g., Wagner, 1983; Domingos *et al.*, 1983; Correia *et al.*, 2013). These strata have previously been shown to be syntectonic siliciclastic intramontane deposits resulting from the erosion of surrounding areas (e.g., Wagner, 1983; Domingos *et al.*, 1983; Pinto de Jesus, 2001; Figure 16). Moreover, the frequent and cyclic occurrence of sandstone deposits in the DCB (described as TSU C1/C2), including those occurring between the *Lesleya* deposits within TSU B2 (Figure 14A), indicate that this megaflora was associated with fluvial-dominated (systems) environments (Figure 16). This evidence indicates that *Lesleya* grew in riparian environments in mountainous regions within Variscan orogen during the Late Pennsylvanian (Figure 16).

In Lower Pennsylvanian rocks in the Illinois Basin, USA, *Lesleya* occurs in parautochthonous deposits in seasonally-dry, basinal lowlands (e.g., Plotnick *et al.*, 2008, 2009; DiMichele *et al.*, 2008, 2010). In that region, *Lesleya* lived in low altitude environments during intervals of relatively dry climate (e.g., DiMichele *et al.*, 2008, 2009, 2010). In the Iberian Massif, the Late Pennsylvanian-age *Lesleya* described herein is preserved in immature shales that are in gradational contact with sandstone deposits (Figures 13, 14B). These DCB strata represent deposition at more upland elevations and occur in areas adjacent to mountainous regions, such as the Valongo Anticline located in the Central Iberian of the Variscan orogen (e.g., Wagner, 1983; Domingos *et al.*, 1983; Correia *et al.*, 2013). These strata previously have been shown to be syntectonic, siliciclastic, intramontane deposits resulting from the erosion of surrounding areas (e.g., Wagner, 1983; Domingos *et al.*, 1983; Pinto de Jesus, 2001; Figures 2, 16). Moreover, the frequent and cyclic occurrence of sandstone deposits in the DCB (described as TSU C1/C2), including those occurring between the *Lesleya* deposits within TSU B2 (Figure 14A), indicate that this megaflora was associated with fluvial-dominated environments (Figure 16). This evidence indicates that *Lesleya* grew in riparian environments in mountainous regions within the Variscan orogen during the Late Pennsylvanian.

1.2.6.2. Interpretation of the climate, vegetation ecology and lacustrine depositional environments in DCB

In lower Bashkirian (Lower Pennsylvanian) strata of North America, *Lesleya* has been interpreted as part of a seasonally-dry (= dryland) flora (e.g., DiMichele *et al.*, 2010; Falcon-Lang *et al.*, 2011a; Bashforth *et al.*, 2014). The Portuguese *Lesleya* outcrops occur between coal-bed strata in TSU B2 (Figure 14A). The presence of *Lesleya* in discrete horizons in the Iberian Massif may indicate those plants were growing in localized, drier or well-drained conditions. An alternative interpretation to this scenario is that deposition and preservation of *Lesleya* and possibly other components of the associated flora in the DCB occurred during intervals of drier and less humid climate within the region.

In the Portuguese outcrops that contain *Lesleya*, the abundance of pteridosperms/ferns (the most common genera are *Pecopteris*, *Sphenopteris* and *Callipteridium*) and cordaitopsids (e.g., *Cordaites*) indicates that the latter taxonomic groups dominated the resident floral assemblages. Other groups, such as sphenopsids (e.g., *Sphenophyllum*, *Calamites* and *Asterophyllites*) occur less frequently, although they are locally common in the DCB strata, whereas lycopsids and *Lesleya* are very rare. The voltziales *Ernestiodendron* and *Culmitzschia* and the dicranophyll *Dicranophyllum* have not been documented in the new *Lesleya* outcrops, but they occur commonly in the DCB, in particularly in São Pedro da Cova region.

The *Lesleya* deposits are interlayered with lacustrine deposits rich in *Anthraconaia*-like non-marine (limnic) bivalves (Plate II), which suggests the associated megaflora grew in or adjacent to marginal lacustrine environments.

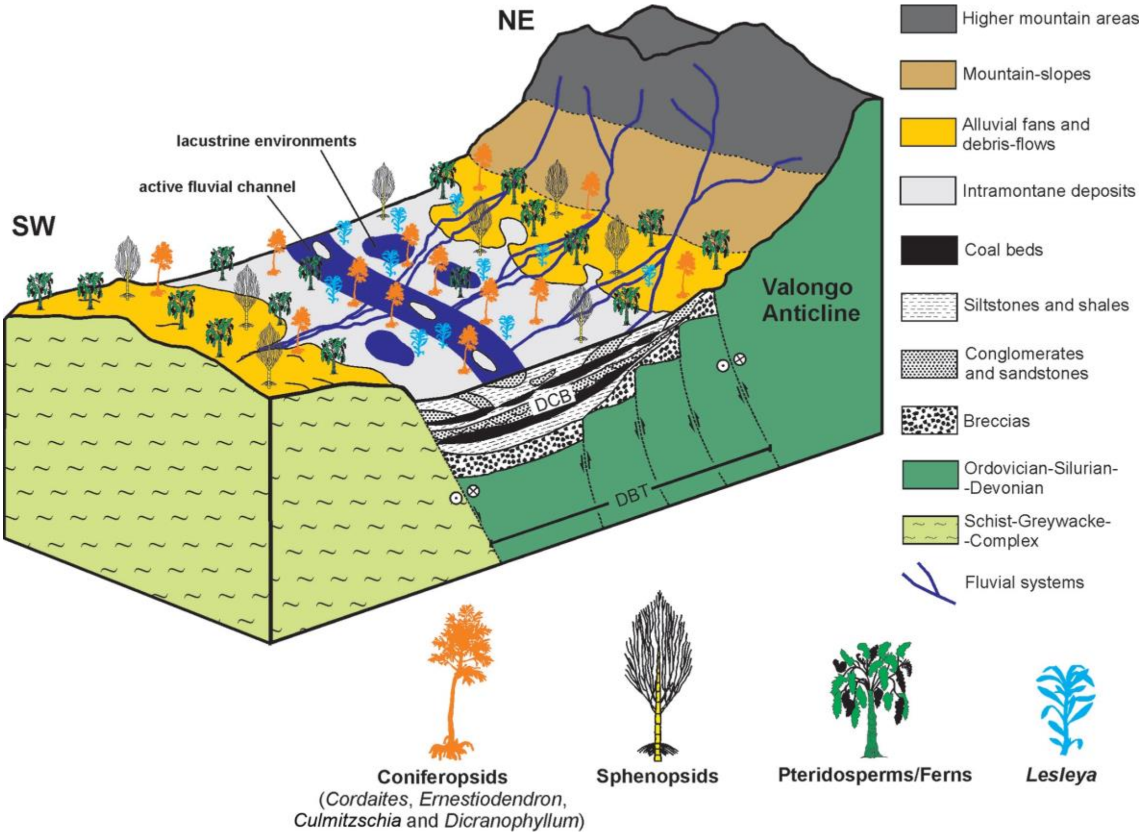

Fig. 16 - Proposed interpretive model of the living habitat of *Lesleya* and associated flora in riparian environments during the Late Pennsylvanian within the intramontane basin Douro Carboniferous Basin, Variscan orogen, northwestern Portugal. Adapted from Pinto de Jesus (2001). Abbreviations: DCB, Douro Carboniferous Basin; DBT, Douro-Beiras Carboniferous Trough. No vertical or lateral scales implied.

1.2.7. Conclusions

In this paper, we document the first occurrence of *Lesleya* within the Iberian Massif of northwestern Portugal (Figure 17). We also describe a new Late Pennsylvanian species, *Lesleya iberiensis* sp. nov., on the basis of leaf impressions. Similarities in leaf structures noted for *L. iberiensis* sp. nov. and *L. cheimarosa* (Early Pennsylvanian, USA) may indicate a close relationship between the two congeners, perhaps with the younger *L. iberiensis* sp. nov. having descended from the older *L. cheimarosa* lineage. Although a possible relationship between those congeners is intriguing, it remains conjecture pending a rigorous analysis of relationships within the genus.

The discovery of *Lesleya* within the Iberian Massif offers the opportunity to examine relationships among its megaflora, environmental and climatic conditions, and geological-tectonic setting (Figure 16). The context for the interpreting the paleoenvironmental and paleoecological conditions of *Lesleya* as part of the 'dryland flora' in intramontane basins within the Variscan orogen is based on stratigraphic, sedimentological, lithological and geological-tectonic evidence previously presented for the DCB as well as on paleontological data provided by its associated flora and fauna.

Fig. 17 - Artistic reconstruction of ***Lesleya iberiensis*** **sp. nov.** This reconstruction was drawn by Andrey Atuchin, based on line drawings (camera lucida) of original specimens and supplementary pictures provided by P. Correia.

Previous studies have demonstrated that *Lesleya* preferred seasonally-dry (= dryland) and well-drained environments within Euramerica. In North America, the occurrence of *Lesleya* in Lower Pennsylvanian parautochthonous deposits in seasonally-dry basinal lowlands of the Illinois Basin, USA, indicates *Lesleya* grew there in low altitude (lowland) environments during dry climatic intervals (see e.g., DiMichele *et al.*, 2008, 2009, 2010). Our report of *Lesleya* in an intramontane basin within the Iberian Massif is an example of this genus also living at higher elevations, where its preferred growing conditions (i.e., seasonally dry and well drained) were present. Those conditions within the Iberian Massif may have been localized or the result of longer term and more widespread, dry climatic intervals in the region during the Late Pennsylvanian.

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1.3. The new plant species from Late Pennsylvanian of Portugal (Western Iberian Massif)

Adapted from Pedro Correia, Zbyněk Šimůnek, Josef Pšenička, Artur A. Sá, Deolinda Flores

(manuscript in preparation)

Abstract

The Douro Carboniferous Basin (lower Gzhelian/lower Stephanian C, Upper Pennsylvanian; NW Portugal) is one of richest continental sedimentary basins in fossil floras of late Carboniferous in Portugal. There, you can find places of great interest and potential for paleobotany research. New field works were carried out on Douro Carboniferous Basin allowed to describe a new fossil plants assemblage. Based on this knowledge a significant revision of the DCB fossil flora is required. The new plant assemblage comprises a well-preserved and very diversified macroflora belonging to genera and species of Pteridopsida, Pteridospermopsida, Sphenopsida, Cordaitopsida and Lycopsida, including the new taxa, *Annularia noronhai* sp. nov., *Phyllotheca wegeneri* sp. nov., *Alloiopteris teixeirai* sp. nov., *Pecopteris alvarezii* sp. nov. and *Acitheca murphyi* sp. nov. The new paleobotanical material was obtained in new outcrops dated of early Gzhelian and are preserved in tectonized (compressed) intramontane deposits. The fossil sites are located in São Pedro da Cova and Ermesinde regions, within the Douro Carboniferous Basin. Rare associated fossil remains of arthropods and non-marine bivalves also have been reported in both localities.

***Keywords*:** Megaflora; new species; São Pedro da Cova; Montes da Costa; lower Gzhelian; Douro Carboniferous Basin, Portugal.

1.3.1. Introduction

The fossil floras of the continental Carboniferous of Portugal are still in a low level knowledge stage. Douro Carboniferous Basin (DCB; lower Gzhelian; NW of Portugal; Figure 2) represents one of the basins more studied about the Carboniferous floras of Portugal. DCB is a major Carboniferous basin within the Douro-Beira Carboniferous Trough, which is located within the Central-Iberian Zone of the Iberian Massif in the NW Portugal. The DCB strata corresponds to the continental intramontane syntectonic deposits occurring within a narrow range, and showing 85 km length NW–SE-striking lineament extending from São Pedro Fins (E Porto) to Janarde (E Arouca) (Pinto de

Jesus, 2001, 2003; Correia *et al.*, 2013, 2014a, b). Historically, the majority of the works carried out in these materials were developed by the Portuguese geologist and paleobotanist Carlos Teixeira (1910–1982), mainly during the decades 1930–40 (e.g., Teixeira, 1937, 1938a, b, 1939a, b, 1940a, b, 1941, 1944, 1945). Carlos Teixeira described several new taxa of fossil flora and fauna, especially documented in rocks of Douro Carboniferous Basin.

One of more structural-geologic areas inside the DCB (e.g., Pinto de Jesus, 2001, 2003; Figures 2, 7) crops out in Sao Pedro da Cova village. At the same time is one of better studied fossil localities with continental floras of the Carboniferous of Portugal. These excellent paleontological outcrops preserve a diverse plant assemblage from the early Gzhelian-age (e.g., Teixeira, 1937, 1938a, b, 1939a, 1940a, b, 1941, 1944, 1945; Teixeira and Pais, 1976; Wagner, 1983; Wagner and Lemos de Sousa, 1983; Lemos de Sousa and Wagner, 1983b; Lemos de Sousa and Wagner, 1985a; Correia *et al.*, 2009, 2010, 2014a). The previous works on DCB flora have emphasized the occurrence of *Pseudomariopteris* cf. *busquetii* (Zeiller) Danzé-Corsin, cf. *Taeniopteris multinervia* Weiss or *Neuropteris ovata* var. *pseudovata* Gothan & Sze. Wagner and Lemos de Sousa (1983) based their interpretations of the paleogeography and the deposition of the intramontane strata of DCB on the occurrence of dryland (xerophilous–mesophilous) floras such as walchian conifers (Voltziales) *Ernestiodendron filiciforme* (von Schlotheim pars) Florin, cf. *Culmitzschia frondosa* (Renault) var. *zeilleri* (Florin) Clement-Westerhof and *Culmitzschia parvifolia* (Florin) Clement-Westerhof, and also the dicranophylls (Ginkgopsida) *Dicranophyllum gallicum* Grand'Eury and *Dicranophyllum lusitanicum* Heer (e.g., Lemos de Sousa and Wagner, 1983b; Wagner and Lemos de Sousa, 1983; Correia *et al.*, 2016). More recently, new records of dryland floras have been documented in DCB, in São Pedro da Cova region, with description of the new cycadopsid species *Lesleya iberiensis* Correia *et al.* (Correia *et al.*, 2016).

In this paper, we describe a new floral taxa from new lower Gzhelian outcrops recently discovered in São Pedro da Cova region (outcrop spc2, TSU B1). And more recently, additional new outcrops show a very rich flora and include new taxa were also found in the Montes da Costa (Ermesinde) region and are documented in this paper. This last locality is framed within the geological setting of the DCB (Figures 7, 10). Based on the identified floral species from the Carboniferous outcrops of the Iberian Massif and in the DCB (e.g., Wagner, 1983; Lemos de Sousa and Wagner, 1983a, b; Wagner and Lemos de Sousa, 1983; Lemos de Sousa and Wagner, 1985a, b) has been assigned to early Gzhelian age for the Montes da Costa outcrops. The fossil flora of both studied localities is represented by several species belonging to Pteridopsida, Pteridospermopsida, Sphenopsida, and Cordaitopsida and Lycopsida (Plates V–XVIII, Table 2). Associated fossil remains of arthropods consisting of insects, arachnids, eurypterids and myriapods, as well as the occurrence of *Anthraconaia*-like non-marine bivalves (Plate XIX), have also been recently discovered in both localities (e.g., Loureiro *et al.*, 2010; Correia *et al.*, 2013, 2014b). The new taxa are here described and presented in systematic paleontology.

1.3.2. Geological setting

Please, see PART II (pag. 21).

1.3.3. Systematic paleobotany

Division: Equisetophyta Scott, 1900
Class: Equisetopsida Agardh, 1825
(= Sphenopsida Scott, 1909)
Order: Equisetales Berchtold & Presl, 1820
Family: Calamitaceae (= Calamostachyaceae) Unger, 1840
Genus: *Annularia* Brongniart, 1828

***Annularia noronhai* sp. nov.**
Plate V, 1–3

Etymology: The species name "*noronhai*" honors Professor Fernando Noronha from the Department of Geosciences, Environmental and Spatial Planning, Faculty of Sciences of University of Porto (Portugal).
Holotype: Specimen UP-MHNFCP-154065 designated here on Plate V, 1–3 is stored at the NHMSUP.
Type locality: Outcrop located close to the Rua da Associação Desportiva, São Pedro da Cova, outcrop spc2, DCB (Figure 7).
Type horizon: Horizon is composed by light-to-dark grey shales; TSU B1. These shales are compressed/compact, laminated and show an excellent conservation of fossilization. Lower Gzhelian, Upper Pennsylvanian.
Diagnosis: Linear-lanceolate leaves bilaterally symmetrical, terminating distally in a strongly developed aristate-caudate mucro.
Description: Stem 80 mm in length and 5–6 mm in maximum diameter, with nodes 8–11 mm in width and spaced about 32 mm (Plate V, 1–3). The sheath of nodes where the leaves are attached has a width of 1.5 to 2 mm. The leaves are bilaterally symmetrical, long (25–30 mm in length), linear to lanceolate, and are in number from

18–20 per whorl (verticil). The width of leaves ranges between 1 and 2 mm. The midrib (central vein) of leaves is very visible that ranges between 0.3 and 0.5 mm in width. The leaf apex displays a very developed aristate-caudate mucro, extending out of leaf about 2.5 to 5.0 mm in length (see also Figure 18a, b).

Discussion and comparisons: Among all known species of *Annularia*, *Annularia stellata* (von Schlotheim) Wood, *Annularia spinulosa* Sternberg, *Annularia carinata* von Gutbier and *Annularia radiata* (Brongniart) Sternberg are most similar to *Annularia noronhai* sp. nov.

Annularia noronhai sp. nov. displays a set of characters that occur within the morphological variation of leaves of *Annularia stellata* (von Schlotheim) Wood. The leaves of *A. stellata* are spatulate-lanceolate to linear-oblanceolate that range from 14 to 75 mm (especially 25 to 30 mm) in length and its width ranges between 0.5 and 3 mm; the leaves are generally 16 to 32 per whorl; the central vein of leaves has a width ranges between 0.3 and 0.5 mm; the sheath has a width of 1.5 to 2 mm; and the nodes are spaced between 12 and 35 mm, and 2 to 5 mm in width (e.g., Boureau, 1964, pp. 181–183; Crookall, 1969, pp. 721; Castro, 2005, pl. 53, figs. 1, 2, 5). However *A. noronhai* sp. nov. differs from *A. stellata* which has leaves showing a very short mucro (about 1 mm long) with an acute shape, or lack thereof (see Crookall, 1969, fig. 209; Castro, 2005, pl. 53, pp. 1, 2, 5; Plate V, 4–5, Figure 18c). *A. stellata* is a common and widespread species occurring in rocks range in age from middle Bashkirian/Moscovian (Westphalian of the Central/Western European regional scale) to Permian of Europe and Asia and Pennsylvanian of the North America (e.g., Crookall, 1969; Boureau, 1964).

Annularia noronhai sp. nov. resembles to *Annularia carinata* von Gutbier (= *A. mucronata* Schenk, 1883; e.g., Barthel, 1976, 2009; DiMichele *et al.*, 2013). *A. carinata* shows 10–24 long radially symmetrical arranged lanceolate to mucronate leaves. The leaves of *A. carinata* are 4–25 mm long and 1.5–3.5 mm wide. The leaf midrib is strong (0.35 mm wide) and penetrated in an apical mucro or an acute apex (e.g., Geinitz, 1849, pl. II, figs. 4–8; Boureau, 1964, fig. 153, p. 174; Castro, 2005, pl. 51, figs. 2, 3; Gómez-Alba, 2007, pl. 28, fig. 2; Barthel, 2009, figs. 19, 20; Leven *et al.*, 2011, fig. 3A, B; pl. 3, figs. 2–4; D; Bashforth *et al.*, 2011, pl. I, fig. 4; DiMichele *et al.*, 2013, fig. 4.3). However, *A. noronhai* sp. nov. differs from *A. carinata* which can display spatulate leaves showing a very short mucro or lack thereof (e.g., Boureau, 1964; Castro, 2005, pl. 51, figs. 2, 3; Leven *et al.*, 2011, fig. 3A, B; pl. 3, figs. 2–4; D; Bashforth *et al.*, 2011, pl. I, fig. 4; Figure 18e). *Annularia carinata* have been described in the Pennsylvanian of the North American, Kasimovian/lower Gzhelian (Stephanian of the Central/Western

European regional scale) to Permian of the Chine and Korea, and Carboniferous of the Europe (e.g., Boureau, 1964; DiMichele *et al.*, 2013).

Annularia noronhai sp. nov. also shows some similarities with *Annularia radiata* (Brongniart) Sternberg. The leaves *A. radiata* are 7 to 30 mm in length and 0.5 to 2 mm in width; they are 8 to 20 in number per whorl and display a relatively developed mucro, i.e. an acute-acuminate apex; they have relatively parallel margins; the nodes are 0.5–3.0 mm in width and spaced between 15–30 mm (internodes). However leaves of *A. radiata* are linear-lanceolate and its mucro is significantly shorter (about 0.5–1.0 mm long; see Crookall, 1969, figs. 213, 214; Boureau, 1964, p. 177, 178) compared to that observed in *A. noronhai* sp. nov. (Figure 18f). *A. radiata* occurs commonly in Sepukhovian–lower Bashkirian (Namurian of the Central/Western European regional scale) rocks from Belgian and Moscovian (Westphalian of the Central/Western European regional scale) strata of United Kingdom, but it has a widespread distribution in the Pennsylvanian and Permian of North America and Europe (e.g., Boureau, 1964; Crookall, 1969).

Comparisons with *Annularia spinulosa* Sternberg also were performed, with differences in the mucro type observed (Figure 18). *A. spinulosa* has been synonymized as *A. stellata* (e.g., Barthel, 2000, 2004; DiMichele *et al.*, 2013). However, *A. spinulosa* seems to belong to a different species from *A. stellata*. The leaves of *A. spinulosa* show large acute-acuminate apexes (features observed in the holotype E 39 from Sternberg′s collection stored in the National Museum of Prague; Figure 18d). *A. spinulosa* has been described in Saxony (Lower Rotliegend of Döhlen Basin [Germany], Late Pennsylvanian? to early Permian) rocks (e.g., DiMichele *et al.*, 2013).

Family: Phyllothecaceae Brongniart, 1828
Genus: *Phyllotheca* (Brongniart) Townrow, 1955

***Phyllotheca* (*Calamariophyllum*?) *wegeneri* sp. nov.**
Plate VII, 1–4

Etymology: The specific name “*wegeneri*” honors the meteorologist Alfred Wegener for his famous and controversy theory of continental drift and supercontinent Pangea during the 1910s.

Holotype: Specimen UP-MHNFCP-130914a is stored at the NHMSUP (Plate VII, 1).

Paratypes: Specimens UP-MHNFCP-130914b and UP-MHNFCP-154760 (Plate VII, 2-4).

Type locality: Outcrop located close to the Rua da Associação Desportiva, São Pedro da Cova, outcrop spc2, DCB (Figure 7).

Type horizon: Horizon is composed by light-to-dark grey shales; TSU B1. Compressed/compact and laminated shales. Lower Gzhelian, Upper Pennsylvanian.

Diagnosis: Wide and articulated stem covered by strong vertical ribs widely spaced, disposing oval and large scars arranged laterally close to nodes. Lanceolate leaves, relatively short and rigid, and strongly welded to stem from the nodes forming a fused (closed) leaf sheath.

Description: Holotype UP-MHNFCP-130914a (Plate VII, 1) is composed of a sterile and intercalary growth stem (branch). The stem is 85 mm long and 22–30 mm wide and is covered by strong longitudinal ribs which are spaced between 1.0 and 1.5 mm wide. The scars are rounded, having 6.6–7.3 mm in length. The vertical ribs can be confused with the margins and midrib of the leaves. The leaves are lanceolate, relatively rigid and short (15–20 mm long and 1.5–2.0 mm wide), and are few in number (10–12 leaves per node or verticil). The leaves are oriented towards to the top of the stem, strongly welded or appressed to stem from the node, forming a leaf sheath fused (closed) to stem. They are loose approximately of its mid-length; they display a single midrib. The leaf sheath has a length of about 20 mm. The midrib of leaves is strong, 0.5–1.0 mm in width. The internodes are 32–36 mm in length. Each internode displays individually a scar which is placed laterally (and alternately) close to upper node. The paratype UP-MHNFCP-154760 represents a small fragment which preserves lateral part of a leaf sheath with very short and rigid leaves (Plate VII, 4).

Discussion and comparisons: Based on articulated stems showing leaves attached from the nodes and leaf sheaths on the Portuguese samples allowed us to classify them to the genus *Phylotheca* (Brongniart) Townrow (e.g., Boureau, 1964; Meyen, 1971; Broutin, 1974). This material also shows some similarities with genus *Koretrophyllites* Radczenko (Radczenko, 1955). *Koretrophyllites* displays articulated stems and leaves attached to nodes grouped in verticils (e.g., Radczenko, 1955; Boureau, 1964; Meyen, 1971; Broutin, 1974). Various forms of *Phyllotheca* have an identical morphology as *Koretrophyllites* (Meyen, 1971; Broutin, 1974). Meyen (1971) suggested that all the species of *Koretrophyllites* should be included in genus *Phyllotheca* (Taylor *et al.*, 2009). This author refers that numerous species assigned to the genus *Koretrophyllites* represent lateral or terminal branches, often fertile, of *Phyllotheca* (Broutin, 1974). According to descriptions from Radczenko (1955), Boureau (1964) and Broutin (1974), *Phyllotheca* is mainly diagnosed by its well-developed leaf sheath and flexible leaves, and *Koretrophyllites* is described as a genus of form of articulated sterile branches with verticils, simple and loose leaves from the base or weakly welded to stem but without forming leaf sheath. *Koretrophyllites* includes fertile forms with elongated leaves that are not fused into a cup at the node (Boureau, 1964; Taylor *et al.*, 2009). UP-MHNFCP-130914a, b and UP-MHNFCP-154760 preserve most critical features assigned to genus *Phyllotheca* such as leaf sheath (although fused to stem) and leaves strongly welded to the stem.

Compared with known species of genus *Phyllotheca*, species *Phyllotheca griesbachi* Zeiller is most similar to *Phyllotheca wegeneri* sp. nov. *P. griesbachi* shows a very narrow leaf sheath showing leaves 20–25 mm long relatively welded or appressed to stem. However, *P. wegeneri* sp. nov. differs from *P. griesbachi* in the following characters. *P. griesbachi* displays a leaf sheath opened in top part in horizontal disc-shaped and 30–40 flexible leaves per verticil (e.g., Boureau, 1964), while *P. wegeneri* sp. nov. shows a leaf sheath significantly fused (closed) to stem and short and rigid leaves (see Figure 19). *P. griesbachi* also displays significantly smaller stems compared that of *P. wegeneri* sp. nov. (see Boureau, 1964). In addition, the large scars of *P. wegeneri* sp. nov. represent an another distinctive character for the taxonomic separation between the Portuguese species and *P. griesbachi*. The scars of *P. wegeneri* sp. nov. resulted likely of the insertion of sporangiospores or lateral or terminal branches. *P. griesbachi* occurs in early Permian rocks of Gondwana Flora (e.g., Boureau, 1964).

Division: Pteridophyta Schimper, 1879
Class: Pteridopsida
(= Polypodiopsida Smith *et al.*, 2006)
Order: Zygopteridales Corsin, 1960
Family: Zygopteridaceae Corsin, 1960
Genus: *Alloiopteris* Potonié, 1897

***Alloiopteris* (*Sphenopteris*?) *teixeirai* sp. nov.**

Plate IX, 1–3

Etymology: The species name "*teixeirai*" honors Portuguese paleobotanist Professor Carlos Teixeira (1910–1982).

Holotype: Specimen UP-MHNFCP-154064a is stored at the NHMUP (Plate IX, 1).

Paratype: UP-MHNFCP-154064b (Plate IX, 2, 3).

Type locality: Outcrop located close to the Rua da Associação Desportiva, São Pedro da Cova, outcrop spc2, DCB (Figure 7).

Type horizon: Horizon is composed by light-to-dark grey shales. These shales are compressed/compact, laminated and shows an excellent conservation of fossilization. Lower Gzhelian, Upper Pennsylvanian.

Diagnosis: Ultimate pinna composed of asymmetrical pinnules. Pinnule margins bearing sucessive teeth or lobes, slightly irregular and well-developed with very deep apical and basal sides. Teeth showing small indentations on the marginal lamina. Basal teeth subtriangular and relatively more developed. Distal teeth shorter without indentations. Midvein strong basally and decurrent at the pinnule apex. Lateral veins generally divided twice.

Description: Frond fragment of the last order with length above 115 mm and 33 mm wide maximum (Plate IX, 1–3). The frond rachis is 1–2 mm in width. The pinnules are 13–17 mm long and 4–7 mm wide, relatively asymmetrical, closely spaced but non-decurrent, strongly retracted at the base, and perpendicularly attached on rachis. The pinnules margins have lobed to dentate shape (see different types of leaf margin in Hickey, 1977, appendix fig. 4), converging to a rounded apex. The teeth are 8–10 in number per pinnule margin, well-developed (1–2 mm long and 1–1.5 mm wide) and slightly irregular. The apical and basal sides of teeth/lobes are very deep, showing one to three small indentations (of second and third order?; see Hickey, 1977, appendix fig. 4; Figure 20a). The basal teeth are subtriangular and relatively more developed. The distal teeth are shorter and without indentations. The midvein is strong (mainly at the base; 0.8–0.9 mm wide maximum), parallel or subparallel to the pinnule margin, and decurrent at the pinnule apex. The lateral veins are inclined on the midvein (with angles range between the 25° and 50°), curved until the marginal lamina, generally divided twice, and grouped by lobe/tooth (Plate IX, 1–3; Figure 20a).

Discussion and comparisons: The diagnosis of Portuguese material (holotype UP-MHNFCP-154064a is based on the particular morphological features similar to those assigned to genus *Alloiopteris* and features related to sphenopterid-type pinnules (*Sphenopteris*). The *Sphenopteris* pinnules are generally symmetrical, spaced, retracted at the base (i.e., in a petiolate insertion), showing scalloped to lobed margins. The pinnules of *Alloiopteris* are generally asymmetrical, long and narrow, and closely spaced. The pinnules margins of *Alloiopteris* are serreate or coarsely toothed (dentate). Each tooth displays some small indentations on the marginal lamina. The lateral veins are inclined when started from the midvein, curved, simples or more or less ramified (e.g., Andrews *et al.*, 1970; Brousmiche, 1983). Unlike pinnules of *Alloiopteris*, pinnules of holotype UP-MHNFCP-154064a are not long and narrow (pinnule sphenopterid type?). Nevertheless, we provisionally attributed the Portuguese material to genus

Alloiopteris, although an assignment to genus *Sphenopteris* (Brongniart) Sternberg could be considered later.

In comparison with similar species of *Alloiopteris*, *Alloiopteris teixeirai* sp. nov. can be compared to *Alloiopteris erosa* (von Gutbier) White. Distal and proximal pinnules of ultimate pinnae of *A. erosa* display a venation pattern and limbic morphology very similar to that of *A. teixeirai* sp. nov. However, *A. teixeirai* sp. nov. is clearly a different species from the *A. erosa*. Proximal and distal pinnules of ultimate pinnae of *A. erosa* show basal teeth with deep indentations (of second and third order; see orders of teeth in Hickey, 1977, appendix fig. 4) and they appear to be reduced becoming in small anadromous-aphlebia-shaped teeth (see Brousmiche, 1983, text-fig. 20 and tabl. 9; Figure 20b–f). Additionally, *A. teixeirai* sp. nov. shows pinnules significantly more shorter compared to those of the *A. erosa*. *A. erosa* is known from middle Bashkirian to Moscovian (Westphalian) rocks of Germany, France, United States and of Kasimovian–lower Gzhelian (Stephanian of the Central/Western European regional scale) of France and Spain (e.g., Wagner, 1966; Andrews *et al.*, 1970; Brousmiche, 1983).

Alloiopteris teixeirai sp. nov. also displays some similarities with *Corynepteris similis* (Sternberg) Kidston. *C. similis* shows distal pinnules bearing the same limbic morphology and venation pattern preserved in *A. teixeirai* sp. nov., however, proximal pinnules of *C. similis* display one of basal teeth highly developed showing a long narrow lanceolate shape (see Brousmiche, 1983, tabl. 8; Figure 20g, h) while basal teeth of *A. teixeirai* sp. nov. are subtriangular and relatively developed (Figure 19a). The genus *Corynepteris* described by Potonié (1897) has been erected for fertile organs belonging to (sterile) pinnules of *Alloiopteris* species (e.g., Brousmiche, 1983; Galtier, 2004). *Corynepteris similis* occurs in rocks that range in age from Serpukhovian–lower Bashkirian (Namurian of the Central/Western European regional scale) to middle Bashkirian–Moscovian (Westphalian of the Central/Western European regional scale) of East Europe (e.g., Andrews *et al.*, 1970; Brousmiche, 1983).

Order: Marattiales Engler & Prantl, 1902
Family: Psaroniaceae Unger in Endlicher, 1842
(= Asterothecaceae Engler & Gilg, 1919)
Genus: *Pecopteris* Brongniart, 1828

Pecopteris alvarezii sp. nov.
Plates XI

Etymology: The specific name "*alvarezii*" that honors the American geologist Walter Alvarez, from the Earth and Planetary Science Department at the University of California, Berkeley (USA), for the controversy theory of the extinction of the dinosaurs (known as "K-Pg extinction event").

Holotype: Specimen UP-MHNFCP-154066 is stored at the NHMSUP (Plate XI, 1).

Paratypes: UP-MHNFCP-154067, UP-MHNFCP-154068, UP-MHNFCP-154071, UP-MHNFCP-154074, UP-MHNFCP-154075, UP-MHNFCP-154076, UP-MHNFCP-154077, UP-MHNFCP-154078, UP-MHNFCP-154079, UP-MHNFCP-154082, UP-MHNFCP-154083, UP-MHNFCP-154084, UP-MHNFCP-154087, UP-MHNFCP-154761 (Plate XI, 2–15).

Type locality: Outcrop located close to the Rua da Associação Desportiva, São Pedro da Cova, outcrop spc2, DCB (Figure 7).

Type horizon: Horizon is composed of compressed/compact and laminated shales; TSU B1. These shales show an excellent conservation of fossilization. Lower Gzhelian, Upper Pennsylvanian.

Diagnosis: Fronds at least bipinnate. Pinnules spaced, well-individualized, mostly large and slightly asymmetrical bilaterally; lobed/pinnately lobed at the lower parts of pinnae tapering gradually towards smaller and non-lobed or entire margined pinnules at distal parts of the pinnae. Lobed pinnules bearing 4–8 lobes, generally poorly developed and asymmetrical; basal lobes more developed and asymmetrical bilaterally. Midvein very strong and basally decurrent. Lateral veins generally divided once to rarely three-times, with two or three ramified veins entering in each lobe of lobed pinnules.

Description: Frond fragments consisting of pinnae of ultimate and penultimate orders. The compound fronds are sterile and showing pinnules very variable in shape (Plate XI, 1; Figure 21a). The penultimate pinnae are more than 110 mm long and ultimate pinnae are 60–100 mm long and 22–32 mm wide. The rachises of the penultimate orders are 3–6 mm wide and those of ultimate ones are 1–2 mm wide (Plate XI, 1–3). The ultimate pinnae are inserted obliquely from the penultimate rachis about 40º to 75º and are closely spaced, often touching laterally, and tapering gradually towards small pinnules in the distal parts of pinnae (Plate XI, 1, 3). The pinnules are 4–25 mm long 2–5 mm wide, well-individualized and very spaced (non-decurrent) with a rounded-obtuse apexes, obliquely attached to rachis forming angles between 45º and 65º, sometimes almost perpendicularly, and are slightly retracted at the base (i.e., in a petiolate insertion) (Plate XI; Figure 21).

Larger pinnules located in the middle and lower parts of pinnae (intermediate and proximal pinnules) are lobed to pinnately lobed and slightly asymmetrical bilaterally

(Plate XI, 1; Figure 21a, pinnules “P1”). The lobes are 4–8 in number, rounded, generally poorly developed and asymmetrical. Lobes are more accented at the lower parts of pinnules, where one lobe (or rarely two) is significantly more developed on one side of pinnules (basal lobes called here as “BL1” and “BL2”; BL2 correspond to the basal lobe more developed) (Plate XI, 1, 4–11, 13–15; Figure 21).

Smaller pinnules located in the upper parts of pinnae (distal pinnules) are very spaced (non-decurrent) and generally non-lobed or entire margined (Plate XI, 3, 12, pinnules “P4”).

Midvein is well-marked, very strong (0.5–1.0 mm) and basally decurrent, particularly well-pronounced at the base, with a small attenuation at the pinnule apex. Lateral veins generally once forked shortly after coming off of the midvein, second fork approximately at half the length of vein and a rarely third fork is near the pinnule margin (detail observed in distal [non-lobed] pinnules; Figure 21h). Groups of bifurcated lateral veins occur frequently between groups of two-pronged (i.e., with a second order of bifurcation) veins development in lobed and non-lobed pinnules. Vein density ranges from about 25 to 30 or more per 10 mm on the pinnule margin/border (detail observed in lobed pinnules).

Discussion and comparisons: The pinnules of *Pecopteris alvarezii* sp. nov. are lobed/pinnately lobed tapering gradually to smaller and non-lobed pinnules, a morphological character that has been usually described for the *Lobatopteris* group or formgenus established by Wagner (1959a). The pecopterid species of the *Lobatopteris* group generally display a gradual transition between lobed/lobate pinnules in basal parts of ultimate pinnae and non-lobed or entire margined pinnules tapered gradually in size towards smaller pinnules at distal (terminal) parts of pinnae. Lobed pinnules are normally retracted at the base (e.g., Lemos de Sousa and Wagner, 1985b; Wagner *et al.*, 1985). Nevertheless, this character is not decisive for taxonomic separation because it is common in several pecopterid species (e.g., Wagner and Álvarez-Vázquez, 2016) attributed to the genus *Pecopteris* sensu Brongniart (1828). In sterile pecopterid pinnules, the venation pattern represents a decisive taxonomic character used to distinguish between closely related genera morphologically such as *Lobatopteris* and *Pecopteris* (e.g., Wagner, 1959b; Lemos de Sousa and Wagner, 1985b; Wagner and Álvarez-Vázquez, 2016). The lobatopteroid venation comprises of three or four orders of bifurcation of the lateral veins (so-called as lobatopteroid vein pattern). This venation pattern corresponds to a simple vein ramified in three or four-pronged (i.e., veins with three or four orders of bifurcation) (e.g., Wagner, 1959b; Lemos de Sousa and Wagner, 1985b; Pšenička *et al.*, 2009).

Pecopteris alvarezii sp. nov. shows several veins (mostly ramified in two to three-pronged) entering in each lobe of lobed pinnules (Plate XI, 1; Figure 21a). This feature is clearly different from lobatopteroid venation pattern which displays only one ramified vein (become dichotomous towards the margin pinnule) in both lobed and non-lobed pinnules (e.g., Wagner, 1959b, fig. 6; Wagner *et al.*, 1985, pl. 3, 1; pl. 4, 3; pl. 5, 5; Pšenička *et al.*, 2009, figs. 2, 3A), whereas up to 3 lateral veins generally in two to three-pronged that can enter to each lobe at *Pecopteris alvarezii* sp. nov. (Figure 21).

Pecopteris alvarezii sp. nov. also shows some similarities with the genus *Margaritopteris* (sensu Gothan, 1913) which bears lobed pinnules with several veins to enter to each lobe (e.g., Taylor *et al.*, 2009). However, *Margaritopteris* pinnules are strongly lobed to tongue-shaped and broadly attached to rachis (e.g., Taylor *et al.*, 2009), while lobed pinnules of *Pecopteris alvarezii* sp. nov. are retracted at the base (Figure 21).

Similarities with the fern (Marattiales) *Crenulopteris* (sensu Wittry *et al.*, 2014) is also analyzed. In this analysis, sterile lobed/pinnatifid pinnules and venation pattern of the Portuguese material and newly erected *Crenulopteris* are compared. However, the definition of the genus *Crenulopteris* is based mainly on predominantly pinnatifid or pinnately lobed pinnules (see complete diagnosis proposed by Wittry *et al.*, 2014, p. 7), unlikely *Pecopteris alvarezii* sp. nov. that shows pinnately lobed pinnules tapering gradually to entire margined/non-lobed pinnules. Differences in the pinnule type also were reported. Pinnules of *Crenulopteris* are linguaeform or elongate subtriangular and lobed pinnules show well-developed and symmetrical lobes (Wittry *et al.*, 2014, figs. 2D, 3B), whereas pinnules of *Pecopteris alvarezii* sp. nov. are very variable in shape, mostly large and slightly asymmetrical bilaterally or marginally, with majority lobes poorly developed and asymmetrical in lobed pinnules (Plate XI, 4–11, 13–15; Figure 21).

The closely similar species *Lobatopteris geinitzii* (von Gutbier) Wagner shows very variable pinnules with gradual passages between lobed pinnules and non-lobed pinnules; pinnules are generally with rounded apexes and slightly retracted bases; lobed pinnules are slightly asymmetrical bilaterally; lobed margins smoothed out toward the top pinnules (pinnule apex); midvein is relatively decurrent at the base; two to four-pronged veins grouped in each lobe of the lobed pinnules and slightly lobed pinnules (Geinitz, 1849, pl. IX, 1, 2, 8; pl. XI, 5, 6; Barthel, 2009, figs. 101, 102; Figure 22a, b). However, *P. alvarezii* sp. nov. clearly differs from *L. geinitzii* in the venation pattern. Pinnules of *L. geinitzii* display a midvein faintly decurrent at the base in comparison with the well-pronounced and very strong midvein of *P. alvarezii* sp. nov. Furthermore, distal pinnules of *L. geinitzii* are decurrent (see Geinitz, 1849, pl. IX, 1, 2, 8; pl. XI, 5, 6), while distal pinnules of *P. alvarezii* sp. nov. are well-individualized and very spaced (non-decurrent). In addition, pinnules of *L. geinitzii* are characterized by absence of basal lobes "BL2", and their lateral veins are rarely once bifurcated and groups three to four orders of bifurcation occur from a simple vein (e.g., Geinitz, 1849, pl. IX, 1, 2, 8; pl. XI, 5, 6; Barthel, 2009, figs. 100–102; Figure 22a, b). *L. geinitzii* occurs in lower Stephanian (Kasimovian–lower Gzhelian of the Global scale [E. Europe]) to Permian rocks of Germany (e.g., Geinitz, 1849; Barthel, 2009).

P. alvarezii sp. nov. also closely resembles *Pecopteris saraefolia* var*. lobata* Corsin. *P. saraefolia* var. *lobata* shows pinnules of similar size and dimensions (9–15 mm long) to those of *P. alvarezii* sp. nov., and they are lobed (with relatively more developed basal lobes and lobed margins attenuated towards the upper parts of pinnules) and converging to a rounded apex, slightly asymmetrical bilaterally, slightly retracted at the base; midvein strong, in relief at the pinnule base, and significantly attenuated at the pinnule apex (e.g., Corsin, 1951; Andrews *et al.*, 1970; Langiaux, 1984, figs. 147, 148, 151, 152; see also Figure 22c–e). However, pinnules of *P. saraefolia* var. *lobata* are distinguished by the non-pronounced midvein (mainly at the pinnule base), venation with three to four orders of bifurcation, and by ?absence of the basal lobe "BL2" (see Langiaux, 1984, figs. 147, 148, 151, 152). In addition, the pinnules of *P. saraefolia* var. *lobata* are significantly more narrow (approximately 2 mm wide, rarely 3 mm) (e.g., Corsin, 1951; Andrews *et al.*, 1970; Figure 22c–e). *P. saraefolia* var. *lobata* is known in middle–upper Moscovian (Westphalian D of the Central/Western European regional scale) rocks from France (e.g., Andrews *et al.*, 1970; Langiaux, 1984).

The smaller (non-lobed) pinnules of *P. alvarezii* sp. nov. (Plate XI, 3) also can be compared with the pinnules of ultimate pinnae of *Pecopteris saraefolia* Bertrand, which show rounded-obtuse apexes and groups of bifurcated veins to three orders of bifurcation. However, distal pinnules of *P. alvarezii* sp. nov. are well-individualized (entire) and very spaced (non-decurrent) and display groups of veins with three orders of bifurcation, while pinnules of *P. saraefolia* are decurrent (e.g., Andrews *et al.*, 1970; fig. 116, pp. 146; Langiaux, 1984, figs. 145, 146, 149, 150; Germer and Engel, 1986, fig. 42; Figure 22f, g). *P. saraefolia* is known in middle–upper Moscovian (Westphalian D of the Central/Western European regional scale) rocks of France (e.g., Andrews *et al.*, 1970; Langiaux, 1984).

Pecopteris miltonii (Artis) Brongniart is another species with strong similarities to *P. alvarezii* sp. nov. *P. miltonii* shows pinnules of very variable shape, similar morphometric characteristics (pinnules of ultimate pinnae are 10–25 mm long) compared to *P. alvarezii* sp. nov., inclined on the rachis, mostly lobed converging to a rounded-obtuse apex, retracted at the base, and similar venation pattern (midvein decurrent at the base and groups of three-pronged veins preserved in more lobed pinnules; e.g., Kidston, 1924, pl. CXXI, 1, 4a; Brongniart, 1828; Andrews *et al.*, 1970, fig. 79; Pšenička *et al.*, 2009, p. 141, fig. 3; Figure 22h–k). However, *P. alvarezii* sp. nov. differs from the *P. miltonii* in following characteristics: *P. miltonii* generally displays symmetrical pinnule margins and smaller (non-lobed) pinnules decurrent (in distal parts of pinnae), non-pronounced midvein (mainly at the pinnule base) in comparison with the well-pronounced midvein of *P. alvarezii* sp. nov., groups of veins with four orders of bifurcation, and absence of the basal lobe "BL2" (e.g., Kidston, 1924, pl. CXXI, 1, 4a; Brongniart, 1828; Andrews *et al.*, 1970, fig. 79; Germer and Engel, 1986, figs. 18, 19; Figures 21, 22h–k; Plate XVII, 11). *P. miltonii* has been revised and its name was transferred for the genus *Lobatopteris* (sensu *Lobatopteris miltonii* (Artis) Wagner) by some authors (e.g., Shute and Cleal, 1989; Pšenička *et al.*, 2009; Wittry *et al.*, 2014). However, it does not show a characteristic pattern of development of the lobatopteroid venation (Wagner and Álvarez-Vázquez, 2016). *P. miltonii* occurs in middle Bashkirian–middle Moscovian (Westphalian A–C of the Central/Western European regional scale) rocks of Europe and North America (e.g., Andrews *et al.*, 1970; Germer and Engel, 1986).

P. alvarezii sp. nov. also resembles to *Pecopteris volkmannii* Sauveur. *P. volkmannii* shows relatively lobed pinnules with rounded apexes, spaced (non-decurrent), and slightly retracted at the base (Figure 22l, m). However, pinnules of *P. volkmannii* are considerably smaller (10–13 mm long and 2.5–3.0 mm wide) compared to the *P. alvarezii* sp. nov., *P. volkmannii* shows symmetrical margins and smaller (non-lobed) pinnules decurrent, non-pronounced midvein (except at the base) or not as broad as that of the *P. alvarezii* sp. nov., only one simple vein ramified (with three or four orders of bifurcation) enters in each lobe, and absence of basal lobes "BL2" (e.g., Andrews *et al.*, 1970, figs. 141, 142; Germer and Engel, 1986, fig. 27; Figures 21, 22l, m). *P. volkmannii* occurs in middle Bashkirian–middle Moscovian (Westphalian A–C of the Central/Western European regional scale) rocks of Europe (e.g., Andrews *et al.*, 1970; Germer and Engel, 1986).

Genus: *Acitheca* Schimper, 1879 emend. Zodrow *et al.*, 2006

Acitheca murphyi **sp. nov.**

Plates XII, XIII

Etymology: The specific name “*murphyi*” honors Professor James Brendan Murphy, from St. Francis Xavier University, Nova Scotia (Canada), a world expert in studies on plate tectonic processes of the ancient Earth and paleocontinental reconstructions.

Holotype: Specimen UP-MHNFCP-130920a designated here is stored at the NHMSUP (Plate XII, 1).

Paratypes: Fertile specimens (No. Collection: UP-MHNFCP-130920b, UP-MHNFCP-130923, UP-MHNFCP-154758, UP-MHNFCP-130924; Plate XII, 2–8) and sterile specimens (No. Collection: UP-MHNFCP-130945, UP-MHNFCP-130947, UP-MHNFCP-130948; Plate XII, 9–13).

Type locality: The holotype was found in lower Gzhelian outcrops located in the Montes da Costa area, DCB (Figures 7, 10).

Type horizon: Compressed shales, very fossiliferous, interspersed with sandstones, conglomerates and greywackes. Lower Gzhelian, Upper Pennsylvanian.

Diagnosis: Large pecopterid fertile pinnules, synangia arranged on both sides of midvein. Fertile pinnules with 10 synangia on each side of the midvein and pinnule margin. Synangia consist of 4 very elongated and narrow sporangia 6–9 mm long terminated by very acute apex.

Description: Frond fragments (Plate XII, 1, 2) represent terminal part of pinnae of the last order with lengths exceeding 40 mm and showing large fertile pinnules (13–22 mm long and 2.5–5.0 mm wide), which are relatively spaced in both sides of the rachis. The rachis of the pinnae is very strong with 3–4 mm wide, where the fertile pinnules are inserted obliquely. Additional material (Plate VII, 3–8) is composed by isolated fertile pinnules 21–26 mm long and 4–5 mm wide. The sporangia of the isolated fertile pinnules are 6–8 mm long and 0.5–1.0 mm wide. Some isolated fertile pinnules of lateral compression display well-preserved sporangia 9 mm long (Plate XII, 3, 4). One of the isolated pinnules (Plate XII, 6, 8) has a row of 10 synangia preserved that occur in parallel on one side of the pinnule, between the midvein and pinnule margin. Each synangia is composed of 4 sporangia (Figure 23d).

All material shows pinnules with parallel margins, slightly arched and rounded apices. Midvein of the pinnules is visible despite its poor preservation. The lateral veins of fertile pinnules are not discernible. Most pinnules are preserved in lateral compression and their sporangia are partly covered by lamina (about 2 mm wide). The sporangia display a very elongate shape and acute apices.

Discussion and comparisons: *Acitheca murphyi* sp. nov. shows some similarities with two Pennsylvanian species of *Acitheca*: *Acitheca polymorpha* (Brongniart) Schimper and *Acitheca ambigua* (Sternberg) Němejc.

A. murphyi sp. nov. resembles to fertile ultimate and penultimate pinnae of *A. polymorpha* from the upper Kasimovian (Stephanian B of the Central/Western European regional scale) of the Czech Republic which are preserved in lateral compression (Zodrow *et al.*, 2006, pl. XI, 1–5, pl. XII, 1, 2, 4). The reproductive structures of *A. murphyi* sp. nov. and *A. polymorpha* are comparable: synangia of the Czech *A. polymorpha* material consists of 4 (rarely three) elongate sporangia with acute apex (Zodrow *et al.*, 2006, see table 3; pl. XI, 2, 5). However, sporangia fertile pinnules of Czech *A. polymorpha* specimens are significantly smaller in length (2–5 mm long/0.4–0.8 wide; Zodrow *et al.*, 2006, table 2, p. 249) compared with those of *A. murphyi* sp. nov. (6–9 mm long/0.5–1.0 mm wide; Plate XIV, 1–4). The pinnule length also can be comparable, i.e., compressed fertile pinnules of *A. polymorpha* are relatively smaller (9.5–15 mm long; Zodrow *et al.*, 2006, table 3, p. 260, and plate XI, XII) (see summary in Table 3), although this feature is not a decisive distinguishing criterium for minor differences in length, because size of pinnule can be result of ecological adaptation.

A. murphyi sp. nov. also closely resembles to fertile specimens of *A. ambigua* from Coalfield upper Moscovian (upper Asturian in the regional scale) of Czech Republic. Czech fertile penultimate and ultimate pinnae of *A. ambigua* have pinnules 14–20 mm long and 4–7 mm wide, with rounded apices and parallel margins. Their pinnules have 10–15 synangia that occur in parallel on either side of the midvein and the pinnule margin. Each synangia consists of 4 sporangia (Zodrow *et al.*, 2006, pl. XVI, 1–9, pp. 267, 273). However, their sporangia differ from the *A. murphyi* sp. nov. The sporangia of the Czech fertile *A. ambigua* specimens are 3–4 mm long and 0.5–1.0 mm wide (Zodrow *et al.*, 2006) (see summary in Table 3).

Spores identified by SEM analyses in the paratypes UP-MHNFCP-130923 (Plate XII, 3, 4) and UP-MHNFCP-130924 (Plate XII, 6, 7) were assigned to two genera palynomorphs, compared with *Convolutispora* and *Knoxisporites* (Plate XIII, 3–7). However, they seem do not belong to genus *Acitheca*, probably come from different plants, i.e., contamination before fossilization. The *Verrucosisporites* and *Punctatisporites* palynomorphs represent the more spore-type attributed to fertile specimens of *Acitheca* (e.g., Zodrow *et al.*, 2006).

Sterile pinnules of *Acitheca murphyi* sp. nov.

In this paper, we also discussed sterile specimens collected in the same horizon (H34 horizon; Figure 10) in outcrops of the Montes da Costa where fertile specimens assigned to *A. murphyi* sp. nov. has been established. The debatable material shows morphometric features that can be compared with *A. murphyi* sp. nov. This material consists of ultimate pinnae with large sterile pinnules (Plate XII, 9–13; Figure 23f), which are preserved in compressed gray shales. The ultimate pinnae have lengths ranging between 50 to 90 mm. The rachis of the pinnae is 1–2 mm wide. The pinnules are 10–22 mm long and 2–7 mm wide. They have more or less parallel margins, rounded apices, slightly contracted at base and are inserted obliquely to rachis. The lateral veins fork one to twice with a vein density of 11–17 veins per 10 mm on the pinnule margin.

In comparison with similar species, sterile pinnules of *Acitheca murphyi* sp. nov. closely resembles to sterile pinnules of *A. ambigua* specimens from Czech Republic (see Zodrow *et al.*, 2006, fig. 2, p. 247). Both species displays similar pinnule-type/variability, attachment to rachis, and venation pattern. Sterile pinnules of *A. ambigua* are 11–18 mm long and 4–6 mm wide. The lateral veins of the sterile pinnules of *A. ambigua* display one or two bifurcations and there are 18–22 veins per 10 mm at pinnule margin (Zodrow *et al.*, 2006, p. 273), whereas *A. murphyi* sp. nov. shows 11–17 veins per 10 mm.

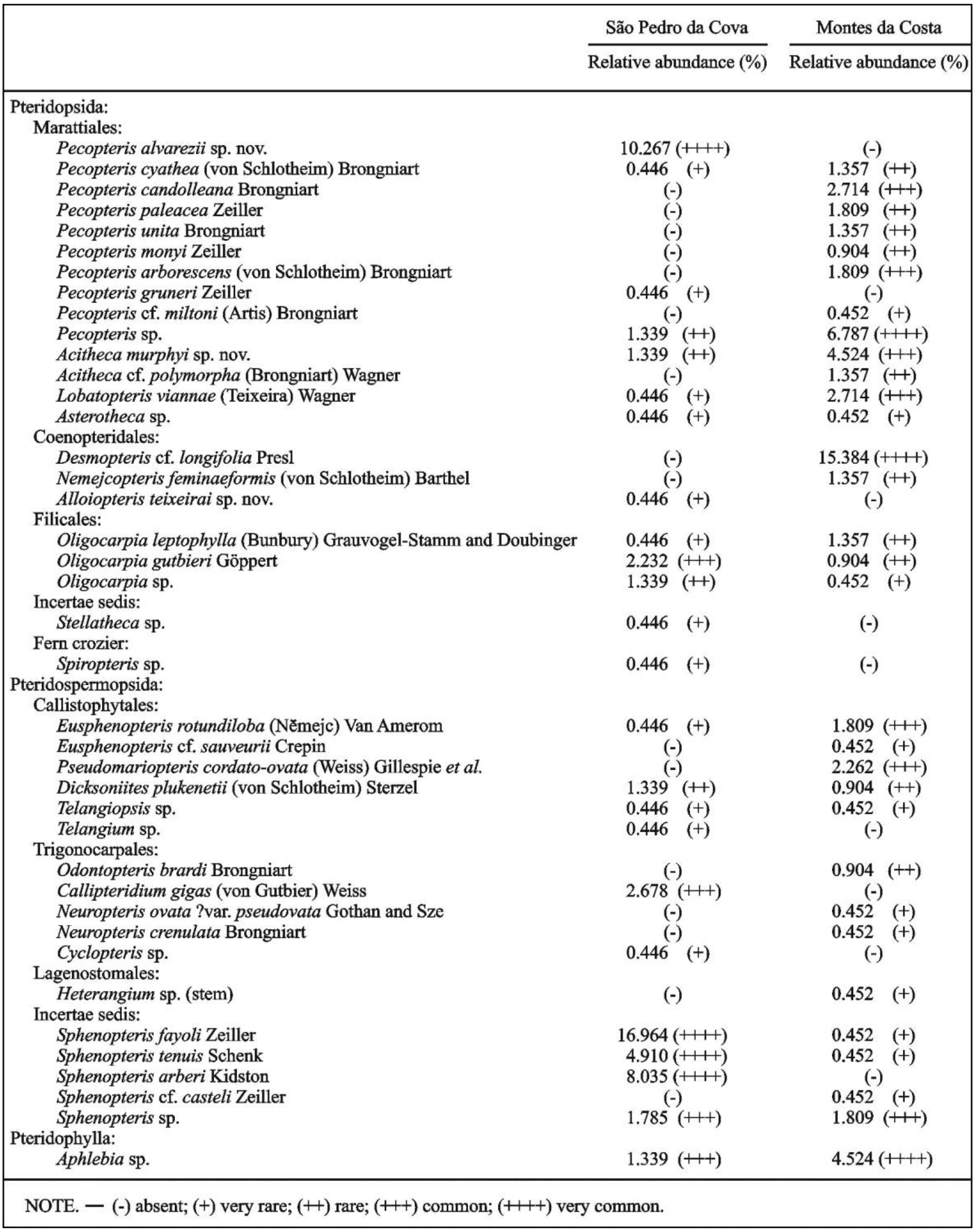
1.3.4. Conclusions

The new paleontological sites of the São Pedro da Cova and Montes da Costa (Ermesinde) regions preserve a high diversity of early Gzhelian-age paleofloras and their plant assemblages recently described implies a significant revision of the taxa list of the DCB. Within these plant assemblages, we described five new species, *Annularia noronhai* sp. nov., *Phyllotheca wegeneri* sp. nov., *Alloiopteris teixeirai* sp. nov., *Pecopteris alvarezii* sp. nov. and *Acitheca murphyi* sp. nov.

The two fossil localities show similar faunal and floral assemblages (Table 3) and paleoecological-environmental similarities also were recognized. The high percentage of samples of pteridopsids (ferns) and sphenopsids (equisetopids) collected in Montes da Costa suggest that these taxonomic groups dominated the plant assemblages that lived and evolved in this area (Table 3). The sphenopsids are also predominantly found in the new outcrops of São Pedro da Cova, but other plant groups such as pteridopsids occur infrequently (Table 3). Cordaitopsids and lycopsids occur rarely in both fossil localities. Animal fossils such as non-marine bivalves and arthropods remains also have been described in both fossil localities although they occur very rarely. The occurrence of non-marine bivalves associated with sandstone deposits indicates the development of local fluvial-lacustrine environments. However, both outcrops studied here show different depositional and preservation records. The newly discovered paleontological site of Montes da Costa contains several autochthonous *Calamites* trunks (conserved in growth position) preserved mainly in the top strata of the stratigraphic sequence (Figures 10, 11). These *Calamites* trunks are preserved in the conglomeratic deposits and they indicate a sudden catastrophic flooding. In addition, the surprising occurrence of typically Westphalian (Moscovian–middle Bashkirian)-age floral species such as *Desmopteris* cf. *longifolia* and *Pecopteris* cf. *miltonii* (Table 3) in the outcrops of Montes da Costa (Figure 10) represent controversial implications for the stratigraphic age established for the DCB.

In conclusion, the results obtained of this work provide a better understanding the knowledge of the late Carboniferous floras of Portugal. The new paleontological outcrops of São Pedro da Cova and Montes da Costa offer excellent opportunities to develop further studies on the Late Pennsylvanian flora and fauna.

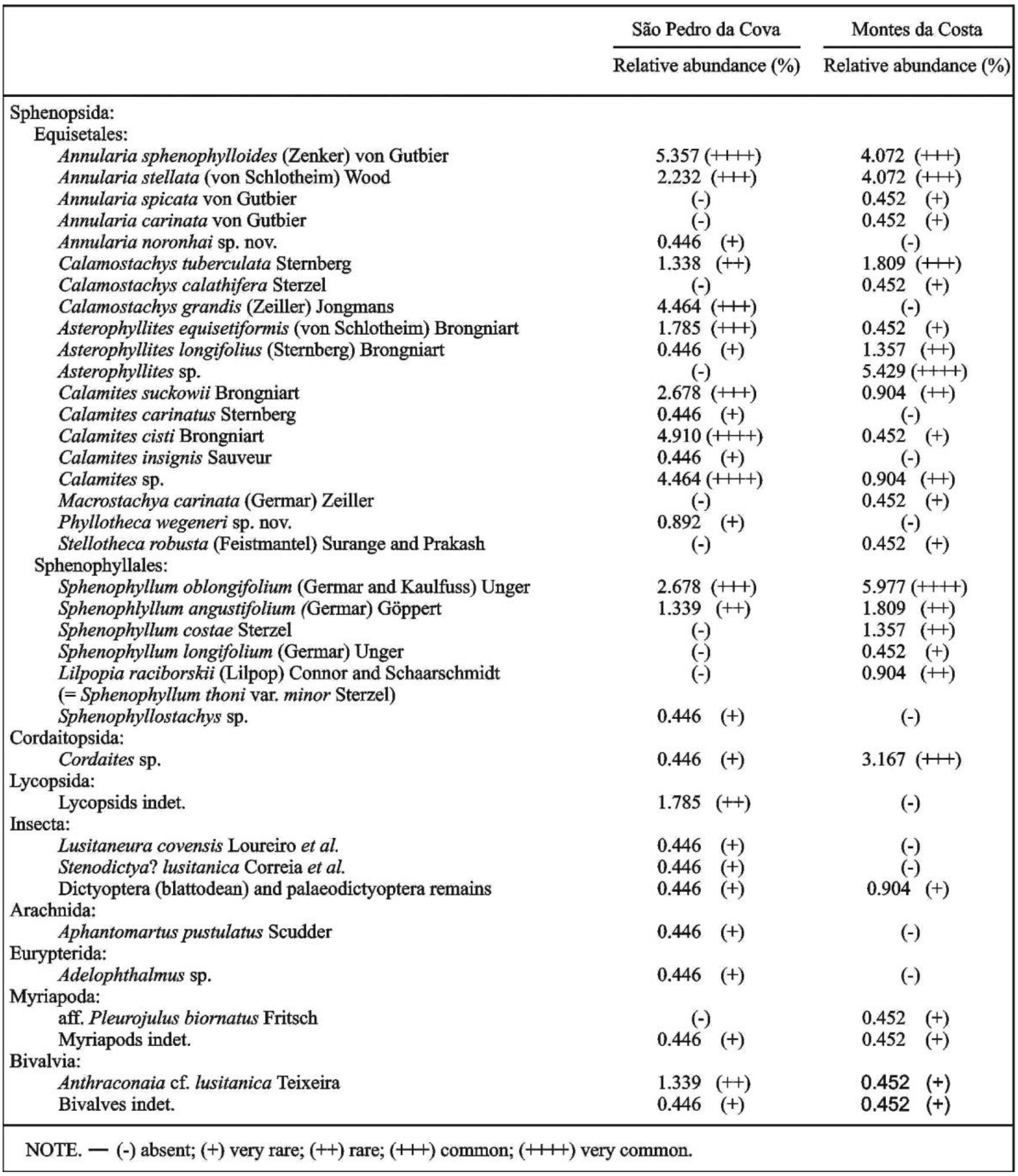
Table 2 - Species taxa list and relative abundance of species that composes the floral and faunal assemblages of the new lower Gzhelian outcrops of São Pedro da Cova and Montes da Costa.



	São Pedro da Cova	Montes da Costa
	Relative abundance (%)	Relative abundance (%)
Pteridopsida:		
Marattiales:		
Pecopteris alvarezii sp. nov.	10.267 (++++)	(-)
Pecopteris cyathea (von Schlotheim) Brongniart	0.446 (+)	1.357 (++)
Pecopteris candolleana Brongniart	(-)	2.714 (+++)
Pecopteris paleacea Zeiller	(-)	1.809 (++)
Pecopteris unita Brongniart	(-)	1.357 (++)
Pecopteris monyi Zeiller	(-)	0.904 (++)
Pecopteris arborescens (von Schlotheim) Brongniart	(-)	1.809 (+++)
Pecopteris gruneri Zeiller	0.446 (+)	(-)
Pecopteris cf. *miltoni* (Artis) Brongniart	(-)	0.452 (+)
Pecopteris sp.	1.339 (++)	6.787 (++++)
Acitheca murphyi sp. nov.	1.339 (++)	4.524 (+++)
Acitheca cf. *polymorpha* (Brongniart) Wagner	(-)	1.357 (++)
Lobatopteris viannae (Teixeira) Wagner	0.446 (+)	2.714 (+++)
Asterotheca sp.	0.446 (+)	0.452 (+)
Coenopteridales:		
Desmopteris cf. *longifolia* Presl	(-)	15.384 (++++)
Nemejcopteris feminaeformis (von Schlotheim) Barthel	(-)	1.357 (++)
Alloiopteris teixeirai sp. nov.	0.446 (+)	(-)
Filicales:		
Oligocarpia leptophylla (Bunbury) Grauvogel-Stamm and Doubinger	0.446 (+)	1.357 (++)
Oligocarpia gutbieri Göppert	2.232 (+++)	0.904 (++)
Oligocarpia sp.	1.339 (++)	0.452 (+)
Incertae sedis:		
Stellatheca sp.	0.446 (+)	(-)
Fern crozier:		
Spiropteris sp.	0.446 (+)	(-)
Pteridospermopsida:		
Callistophytales:		
Eusphenopteris rotundiloba (Němejc) Van Amerom	0.446 (+)	1.809 (+++)
Eusphenopteris cf. *sauveurii* Crepin	(-)	0.452 (+)
Pseudomariopteris cordato-ovata (Weiss) Gillespie *et al.*	(-)	2.262 (+++)
Dicksoniites plukenetii (von Schlotheim) Sterzel	1.339 (++)	0.904 (++)
Telangiopsis sp.	0.446 (+)	0.452 (+)
Telangium sp.	0.446 (+)	(-)
Trigonocarpales:		
Odontopteris brardi Brongniart	(-)	0.904 (++)
Callipteridium gigas (von Gutbier) Weiss	2.678 (+++)	(-)
Neuropteris ovata ?var. *pseudovata* Gothan and Sze	(-)	0.452 (+)
Neuropteris crenulata Brongniart	(-)	0.452 (+)
Cyclopteris sp.	0.446 (+)	(-)
Lagenostomales:		
Heterangium sp. (stem)	(-)	0.452 (+)
Incertae sedis:		
Sphenopteris fayoli Zeiller	16.964 (++++)	0.452 (+)
Sphenopteris tenuis Schenk	4.910 (++++)	0.452 (+)
Sphenopteris arberi Kidston	8.035 (++++)	(-)
Sphenopteris cf. *casteli* Zeiller	(-)	0.452 (+)
Sphenopteris sp.	1.785 (+++)	1.809 (+++)
Pteridophylla:		
Aphlebia sp.	1.339 (+++)	4.524 (++++)

NOTE. — (-) absent; (+) very rare; (++) rare; (+++) common; (++++) very common.

Table 2 (continued).



	São Pedro da Cova	Montes da Costa
	Relative abundance (%)	Relative abundance (%)
Sphenopsida:		
Equisetales:		
Annularia sphenophylloides (Zenker) von Gutbier	5.357 (++++)	4.072 (+++)
Annularia stellata (von Schlotheim) Wood	2.232 (+++)	4.072 (+++)
Annularia spicata von Gutbier	(-)	0.452 (+)
Annularia carinata von Gutbier	(-)	0.452 (+)
Annularia noronhai sp. nov.	0.446 (+)	(-)
Calamostachys tuberculata Sternberg	1.338 (++)	1.809 (+++)
Calamostachys calathifera Sterzel	(-)	0.452 (+)
Calamostachys grandis (Zeiller) Jongmans	4.464 (+++)	(-)
Asterophyllites equisetiformis (von Schlotheim) Brongniart	1.785 (+++)	0.452 (+)
Asterophyllites longifolius (Sternberg) Brongniart	0.446 (+)	1.357 (++)
Asterophyllites sp.	(-)	5.429 (++++)
Calamites suckowii Brongniart	2.678 (+++)	0.904 (++)
Calamites carinatus Sternberg	0.446 (+)	(-)
Calamites cisti Brongniart	4.910 (++++)	0.452 (+)
Calamites insignis Sauveur	0.446 (+)	(-)
Calamites sp.	4.464 (++++)	0.904 (++)
Macrostachya carinata (Germar) Zeiller	(-)	0.452 (+)
Phyllotheca wegeneri sp. nov.	0.892 (+)	(-)
Stellotheca robusta (Feistmantel) Surange and Prakash	(-)	0.452 (+)
Sphenophyllales:		
Sphenophyllum oblongifolium (Germar and Kaulfuss) Unger	2.678 (+++)	5.977 (++++)
*Sphenophlyllum angustifolium (*Germar) Göppert	1.339 (++)	1.809 (++)
Sphenophyllum costae Sterzel	(-)	1.357 (++)
Sphenophyllum longifolium (Germar) Unger	(-)	0.452 (+)
Lilpopia raciborskii (Lilpop) Connor and Schaarschmidt (= *Sphenophyllum thoni* var. *minor* Sterzel)	(-)	0.904 (++)
Sphenophyllostachys sp.	0.446 (+)	(-)
Cordaitopsida:		
Cordaites sp.	0.446 (+)	3.167 (+++)
Lycopsida:		
Lycopsids indet.	1.785 (++)	(-)
Insecta:		
Lusitaneura covensis Loureiro *et al.*	0.446 (+)	(-)
Stenodictya? *lusitanica* Correia *et al.*	0.446 (+)	(-)
Dictyoptera (blattodean) and palaeodictyoptera remains	0.446 (+)	0.904 (+)
Arachnida:		
Aphantomartus pustulatus Scudder	0.446 (+)	(-)
Eurypterida:		
Adelophthalmus sp.	0.446 (+)	(-)
Myriapoda:		
aff. *Pleurojulus biornatus* Fritsch	(-)	0.452 (+)
Myriapods indet.	0.446 (+)	0.452 (+)
Bivalvia:		
Anthraconaia cf. *lusitanica* Teixeira	1.339 (++)	0.452 (+)
Bivalves indet.	0.446 (+)	0.452 (+)

NOTE. — (-) absent; (+) very rare; (++) rare; (+++) common; (++++) very common.

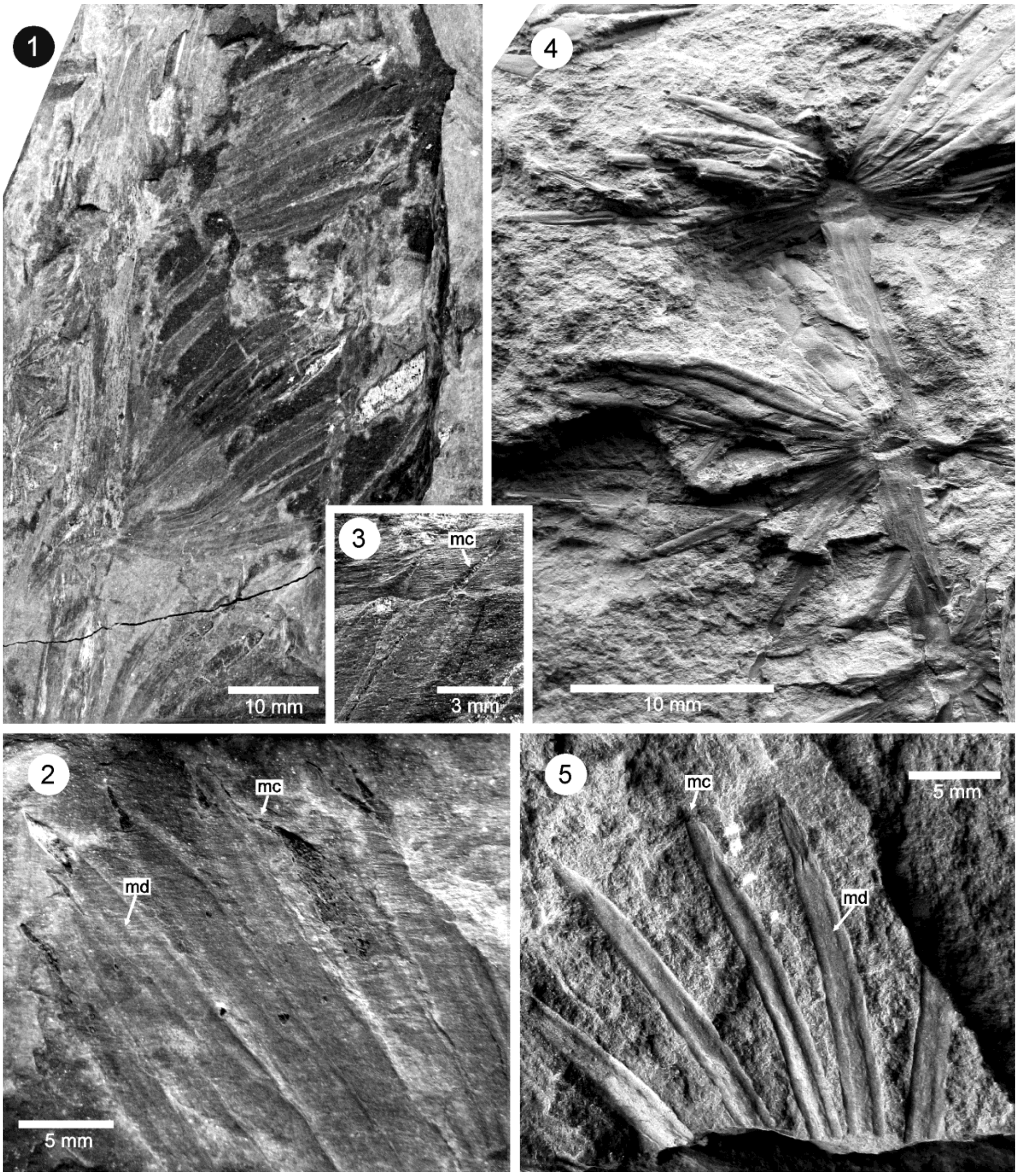


Plate V - New sphenopsid species and comparative species from the new lower Gzhelian outcrops of São Pedro da Cova, DCB, Portugal; 1–3. ***Annularia noronhai* sp. nov.** (holotype UP-MHNFCP-154065; 2, 3. Detail of 1). 4, 5. *Annularia stellata* (von Schlotheim) Wood. Abbreviations: mc, mucro; md, midrib.

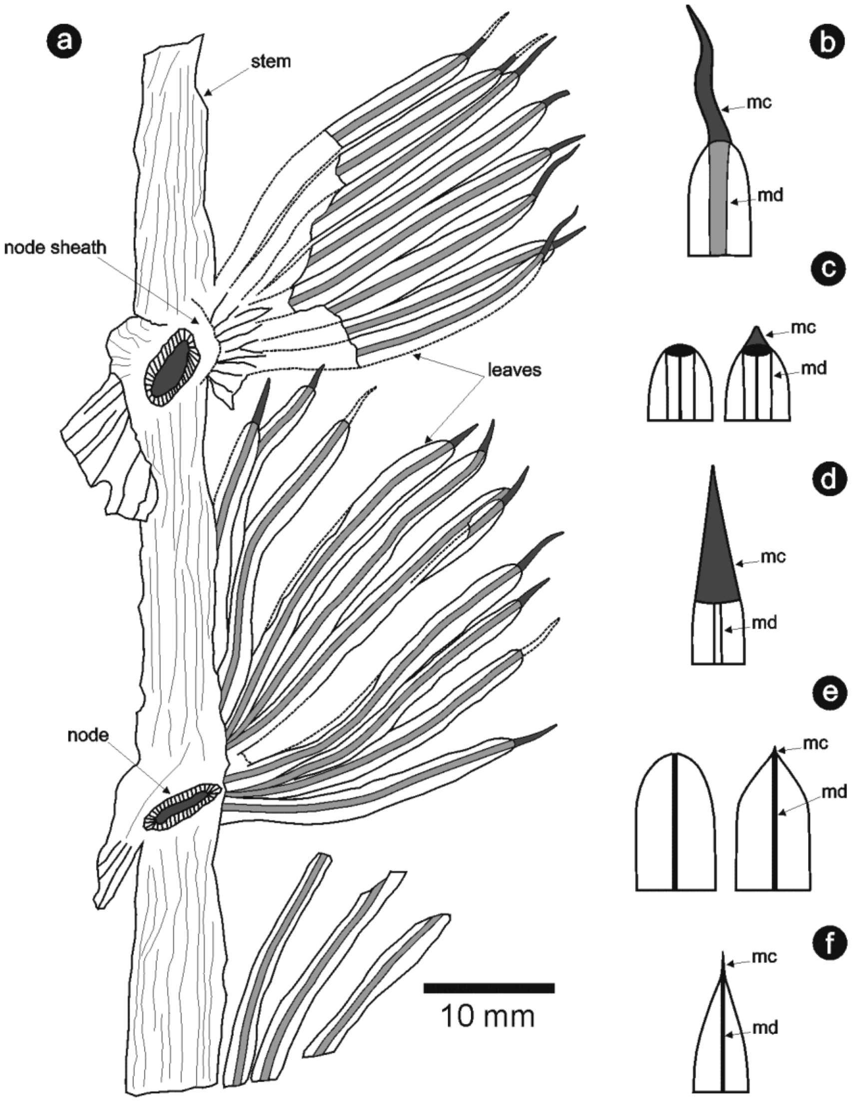


Fig. 18 - Schematic drawings of ***Annularia noronhai*** **sp. nov.** (drawn in camera lucida) and the most similar species (adapted from Boureau, 1964; Crookall, 1969; Gómez-Alba, 2007; Bashforth *et al.*, 2011). (a, b) *Annularia noronhai* sp. nov., (c) *Annularia stellata* (von Schlotheim) Wood, (d) *Annularia spinulosa* Sternberg (from holotype E 39), (e) *Annularia carinata* von Gutbier, (f) *Annularia radiata* (Brongniart) Sternberg. Abbreviations: mc, mucro; md, midrib.

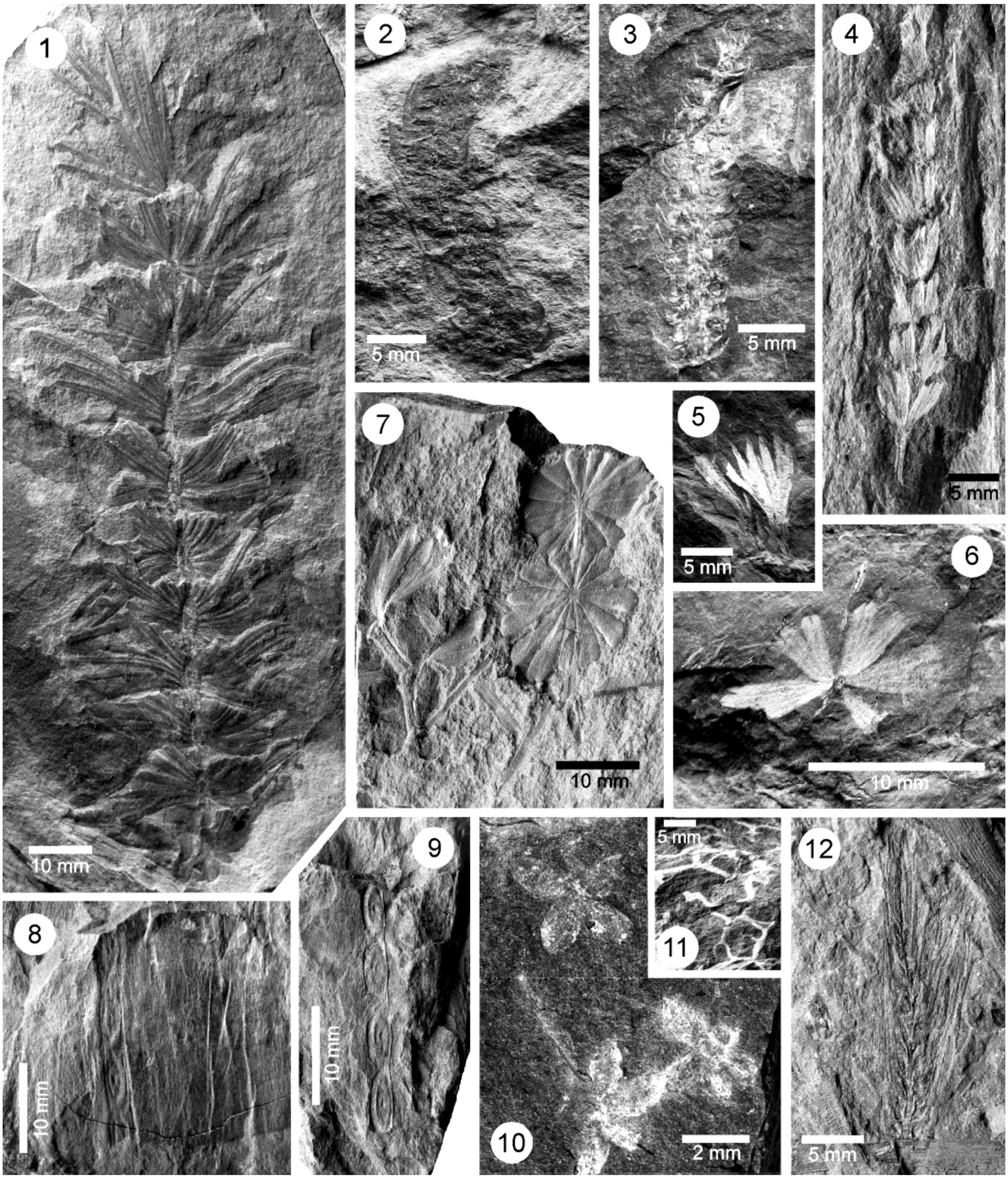


Plate VI - Representative sphenopsids and licopsids in new lower Gzhelian outcrops of São Pedro da Cova, DCB, Portugal; 1. *Asterophyllites equisetiformis* (von Schlotheim) Brongniart, 2, 3. *Calamostachys grandis* (Zeiller) Jongmans, 4, 5. *Sphenophyllum angustifolium* Germar, 6. *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger, 7. *Annularia sphenophylloides* (Zenker) von Gutbier and *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger, 8, 9. Lycopsids indet., 10. Reproductive organs of *Sphenophyllum*, 11. Probably roots of sphenopsids, 12. *Sphenophyllostachys* sp.

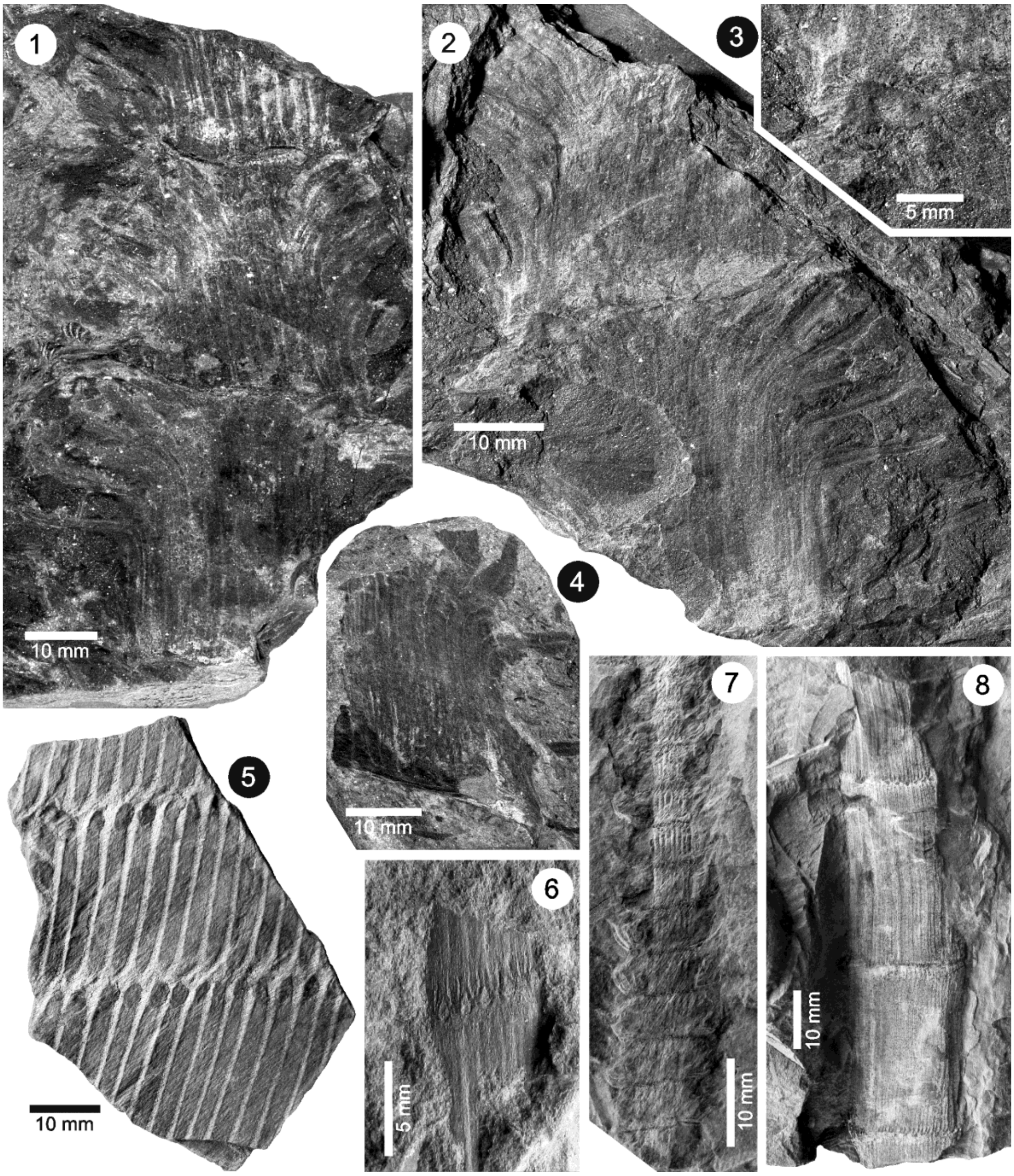


Plate VII - Additional sphenopsids from the new lower Gzhelian outcrops of São Pedro da Cova, DCB, Portugal; 1–4. ***Phyllotheca wegeneri* sp. nov.** (1. Holotype UP-MHNFCP-130914a; 2, 3. Paratype UP-MHNFCP-130914b; 3. Detail of 2; 4. Paratype UP-MHNFCP-154760), 5. *Calamites suckowii* Brongniart, 6. *Calamites insignis* Sauveur, 7. *Calamostachys tuberculata* Sternberg, 8. *Calamites cisti* Brongniart.

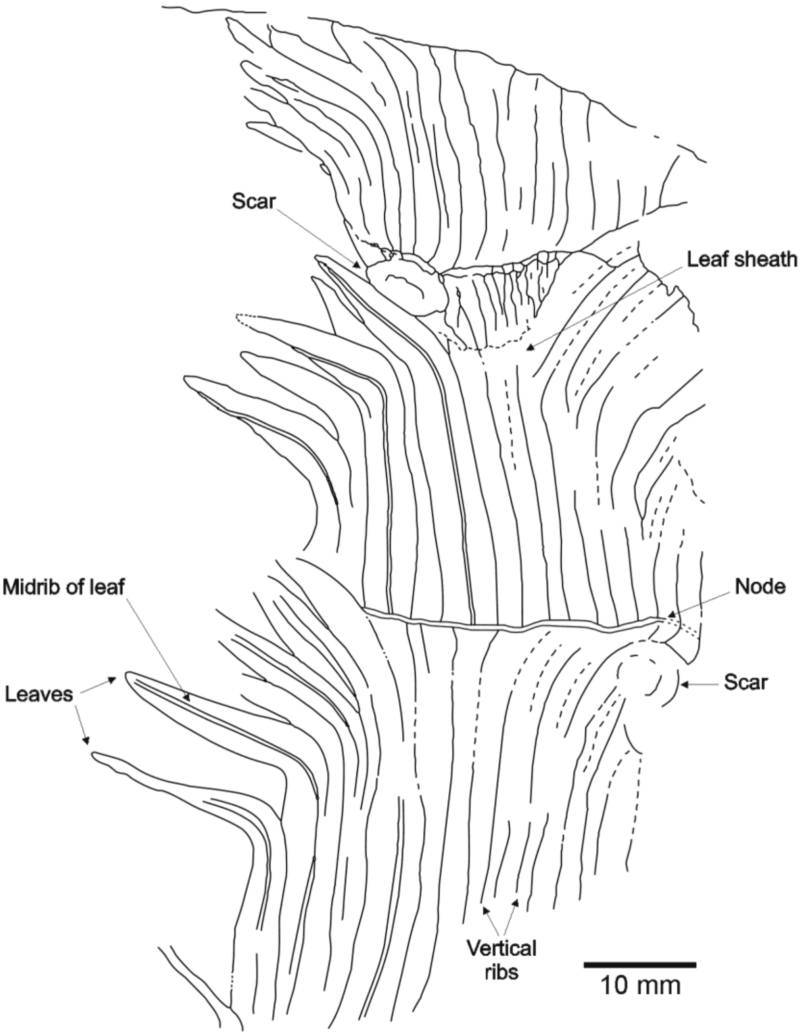


Fig. 19 - Camera lucida drawing holotype of ***Phyllotheca wegeneri* sp. nov.**

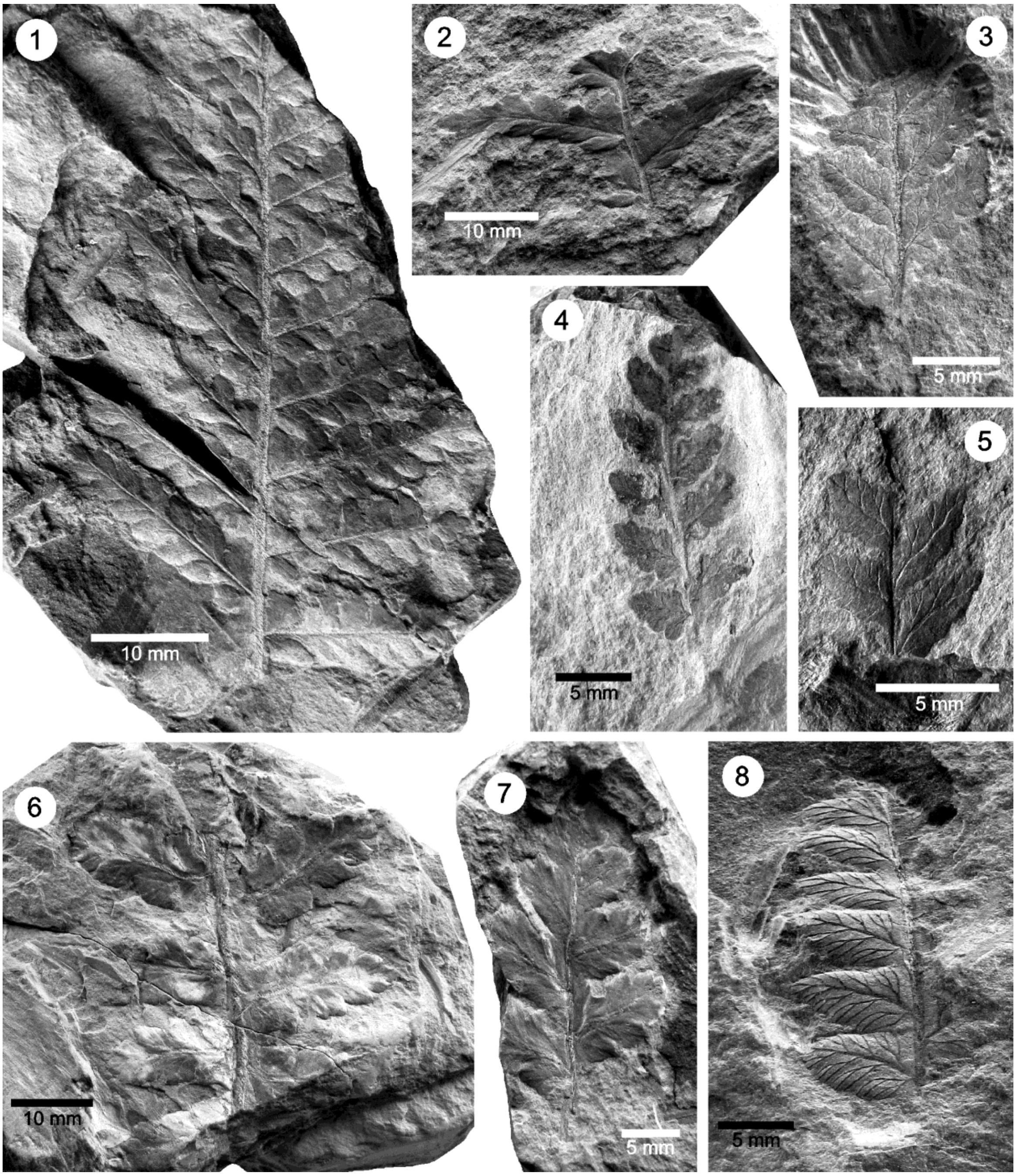


Plate VIII - Representative pteridopsids and pteridospermopsids in new lower Gzhelian outcrops of São Pedro da Cova, DCB, Portugal; 1, 2. *Sphenopteris tenuis* Schenk, 3–5. *Sphenopteris arberi* Kidston, 6, 7. *Sphenopteris fayoli* Zeiller, 8. *Oligocarpia leptophylla* (Bunbury) Grauvogel-Stamm & Doubinger.

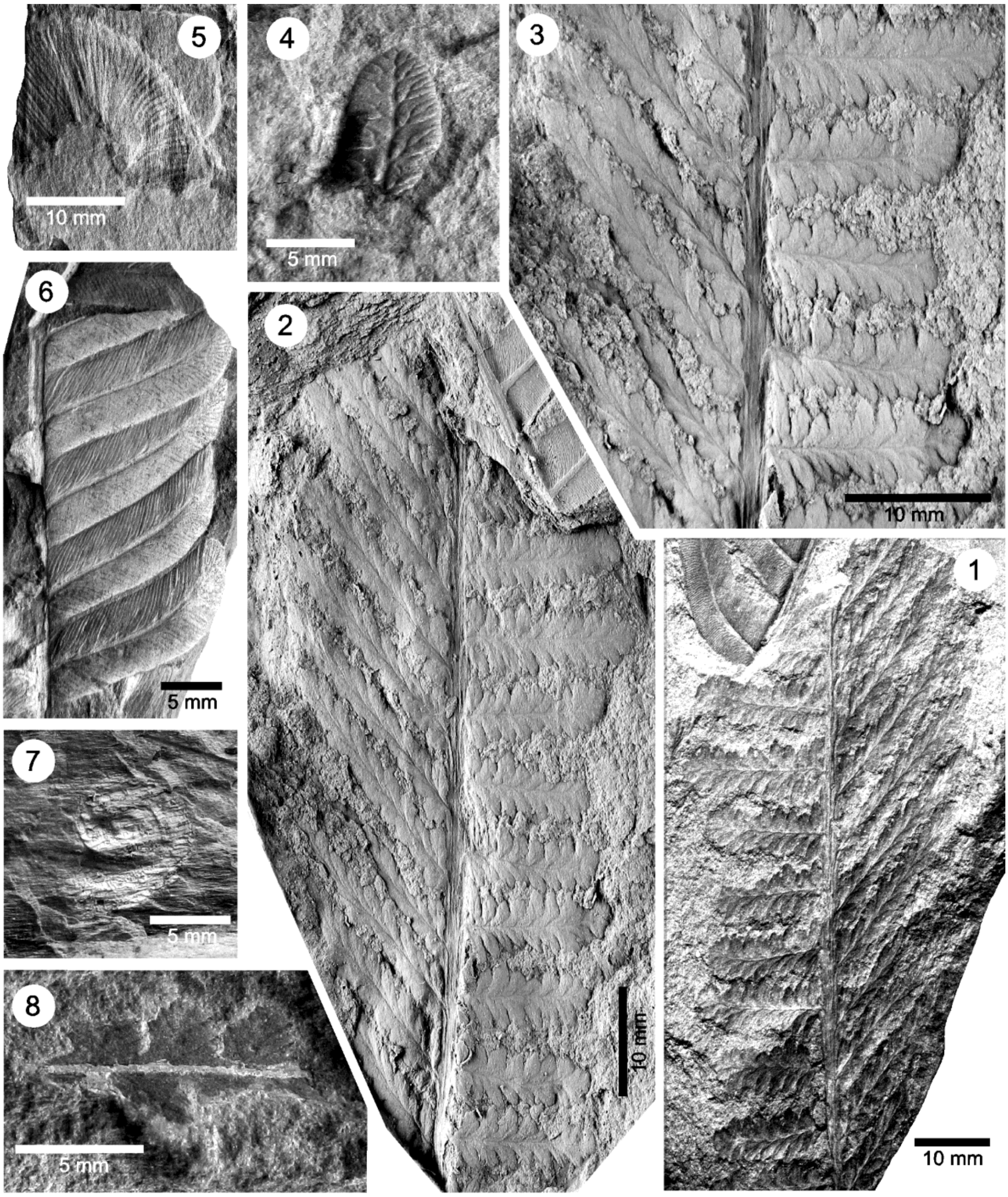


Plate IX - Additional pteridopsids and pteridospermopsids from the new lower Gzhelian outcrops of São Pedro da Cova, DCB, Portugal; 1–3. ***Alloiopteris teixeirai* sp. nov.** (1. Holotype UP-MHNFCP-154064a; 2, 3. Latex cast of paratype UP-MHNFCP-154064b), 4. *Lobatopteris viannae* (Teixeira) Wagner, 5. *Cyclopteris* sp., 6. *Callipteridium gigas* (von Gutbier) Weiss, 7. *Spiropteris* sp., 8. *Dicksoniites plukenetii* (von Schlotheim) Sterzel.

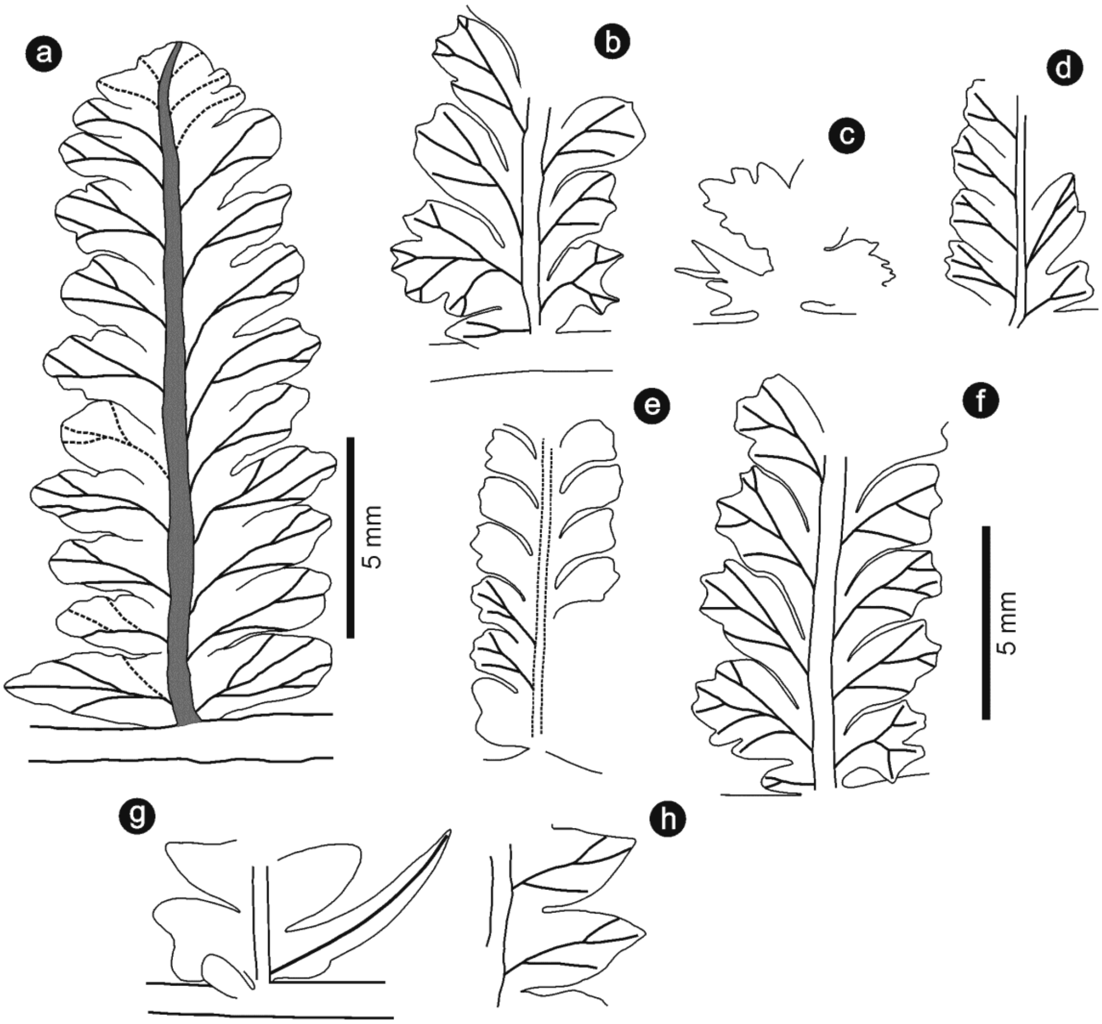


Fig. 20 - Schematic drawing of ***Alloiopteris teixeirai*** **sp. nov.** (drawn in camera lucida) and the most similar species (adapted from Brousmiche, 1983); (a) proximal/distal pinnule of ultimate pinna (holotype UP-MHNFCP-154064a) of *Alloiopteris teixeirai* sp. nov., (b–d) proximal and distal pinnules of ultimate pinna of *Alloiopteris erosa* (von Gutbier) White, (e) distal pinnule of ultimate pinna of *Alloiopteris erosa* (von Gutbier) White, (f) proximal? pinnule of ultimate pinna of *Alloiopteris erosa* (von Gutbier) White, (g) proximal pinnule of *Corynepteris similis* (Sternberg) Kidston, (h) teeth of a distal pinnule of *Corynepteris similis* (Sternberg) Kidston. Scale bar = 5 mm (b–f); no scale implied (g, h).

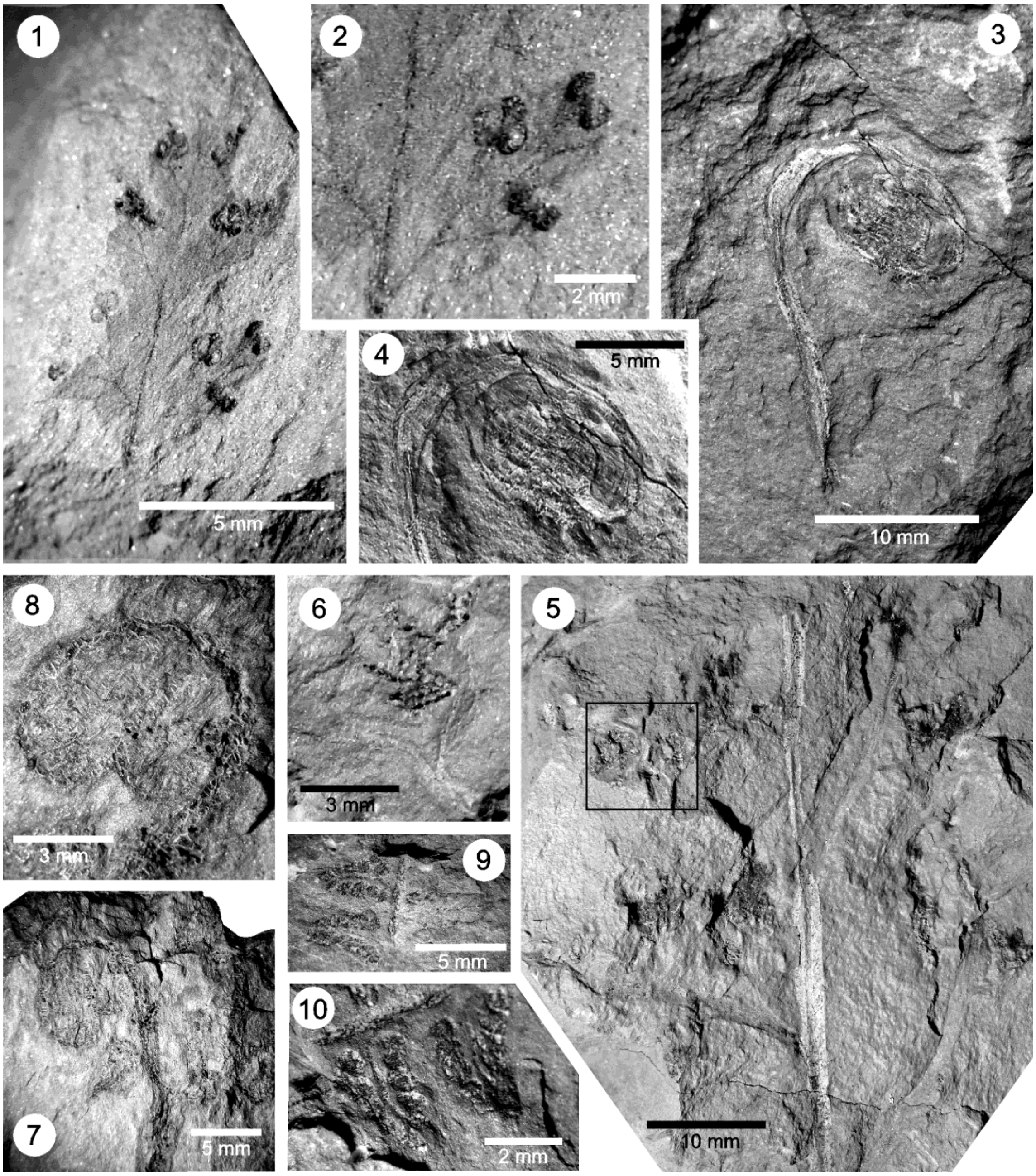


Plate X - Additional pteridopsids and pteridospermopsids from the new lower Gzhelian outcrops of São Pedro da Cova, DCB, Portugal; 1, 2. *Oligocarpia* sp. (fertile foliage), 3, 4. *Telangium* sp., 5, 6. *Stellatheca* sp., 7, 8. *Telangiopsis* sp., 9, 10. *Asterotheca* sp.

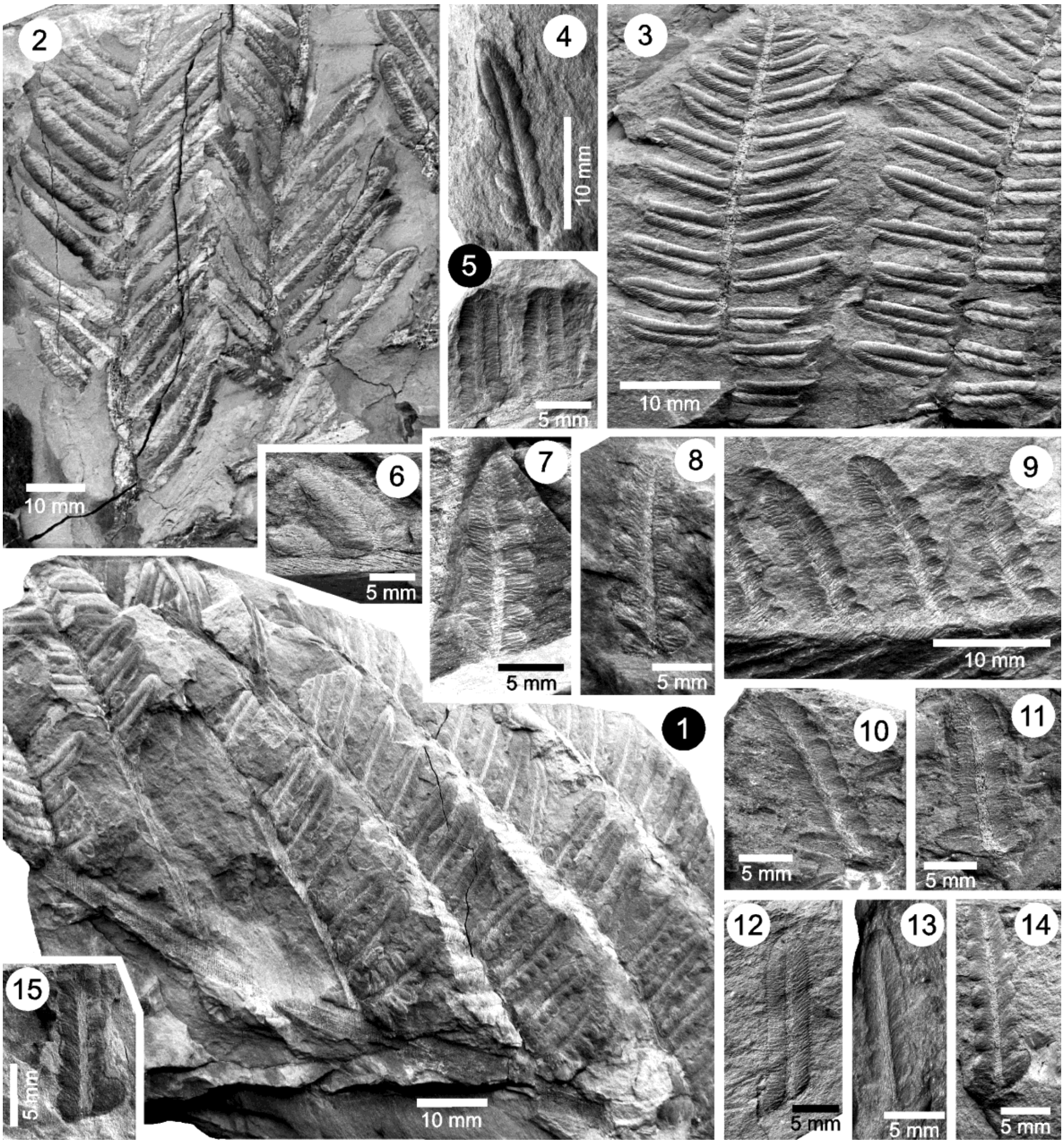


Plate XI - *Pecopteris alvarezii* sp. nov. São Pedro da Cova, DCB, Portugal; 1. Frond of penultimate pinnae showing very variable (lobate and non-lobate) pinnules (holotype UP-MHNFCP-154066), 2. Frond of penultimate pinnae showing lolate intermediate and proximal pinnules (Paratype UP-MHNFCP-154067), 3. Frond of penultimate pinnae showing non-lobate distal pinnules (Paratype UP-MHNFCP-154068), 4–15. Additional paratypes (4. UP-MHNFCP-154078; 5. UP-MHNFCP-154084; 6. UP-MHNFCP-154075; 7. UP-MHNFCP-154082; 8. UP-MHNFCP-154071; 9. UP-MHNFCP-154076; 10. UP-MHNFCP-154074; 11. UP-MHNFCP-154761; 12. UP-MHNFCP-154077; 13. UP-MHNFCP-154079; 14. UP-MHNFCP-154087; 15. UP-MHNFCP-154083).

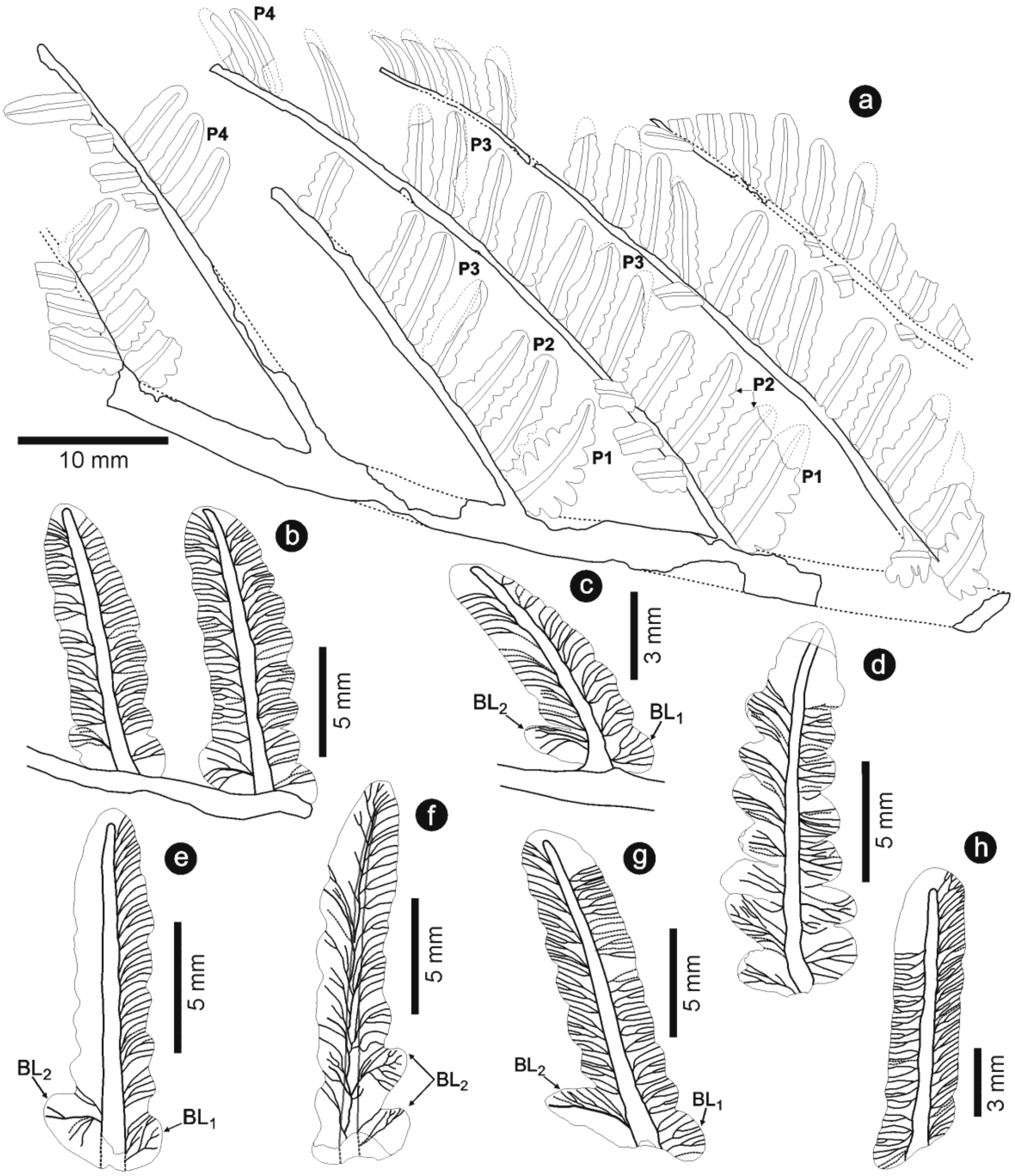


Fig. 21 - Camera lucida drawing holotype and variable pinnules of frond parts of the ***Pecopteris alvarezii* sp. nov.**; (a) Holotype UP-MHNFCP-154066 (see Plate XI, 1), (b, c, e–g) lobed intermediate pinnules (see Plate XI, 4, 6, 9, 10, 13), (d) lobed proximal pinnule (see Plate XI, 8), (h) non-lobed distal pinnule (see Plate XI, 12). Abbreviations: P1/P2, lobed to pinnately lobed proximal pinnules; P3, lobed intermediate pinnules; P4, non-lobed distal pinnules.

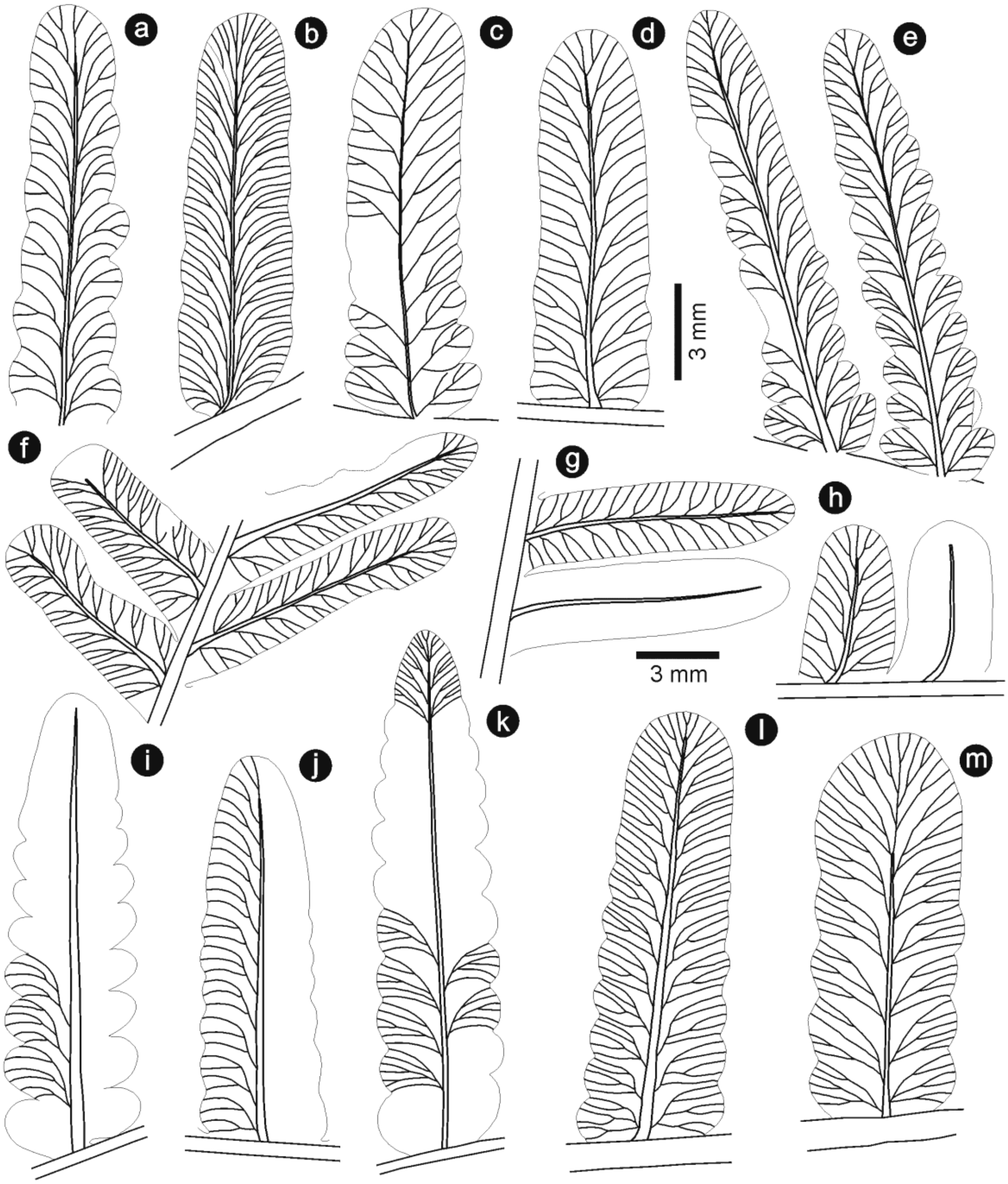


Fig. 22 - Comparative species of the *Pecopteris alvarezii* sp. nov. (adapted from Andrews *et al.*, 1970 (d, g–j, l); Langiaux, 1984 (c, e, f); Germer and Engel, 1986 (K, m); Barthel, 2009 (a, b)); (a, b) *Lobatopteris geinitzii* (von Gutbier) Wagner, (c, e) *Pecopteris saraefolia* var. *lobata* Corsin, (d) *Pecopteris saraefolia* ?var. *lobata* Corsin, (f, g) *Pecopteris saraefolia* Bertrand, (h–k) *Pecopteris miltonii* (Artis) Brongniart, (l, m) *Pecopteris volkmannii* Sauveur. No scale implied (a–c, e, f, h–m).

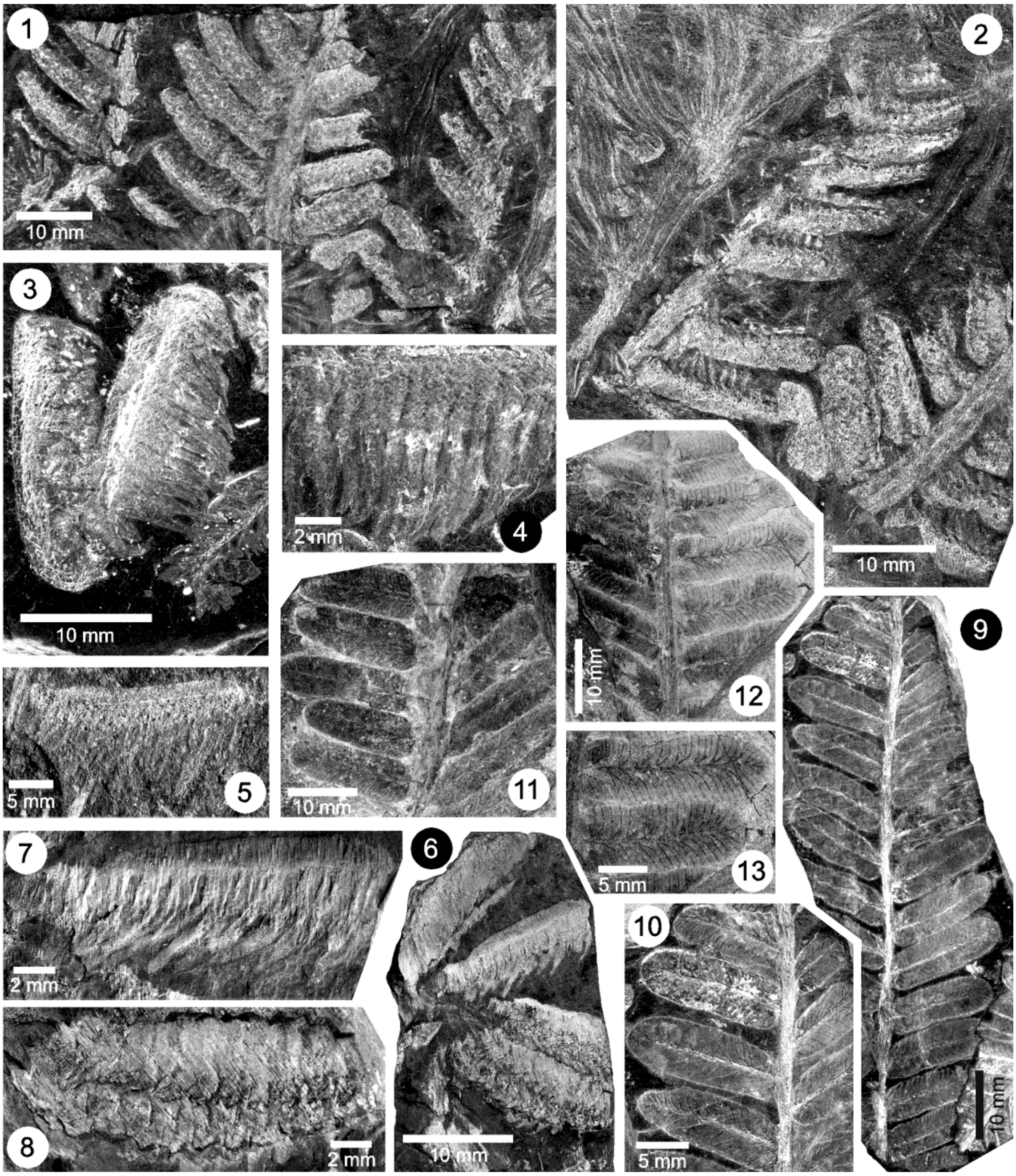


Plate XII - *Acitheca murphyi* sp. nov. Montes da Costa and São Pedro da Cova, DCB, Portugal; 1, 2. Frond of ultimate pinnae showing inserted fertile pinnules (1. Holotype UP-MHNFCP-130920a; 2. Paratype UP-MHNFCP-130920b; Montes da Costa), 3, 4. Isolated fertile pinnules showing very well-preserved sporangia (paratype UP-MHNFCP-130923; Montes da Costa), 5. Isolated fertile pinnule (paratype UP-MHNFCP-154758; Montes da Costa), 6–8. Isolated fertile pinnules showing synangia and sporangia (paratype UP-MHNFCP-130924; São Pedro da Cova), 9–13. Fronds of sterile ultimate pinnae (9, 10. Paratype UP-MHNFCP-130945; 11. Paratype UP-MHNFCP-130947; 12, 13. Paratype UP-MHNFCP-130948; Montes da Costa).

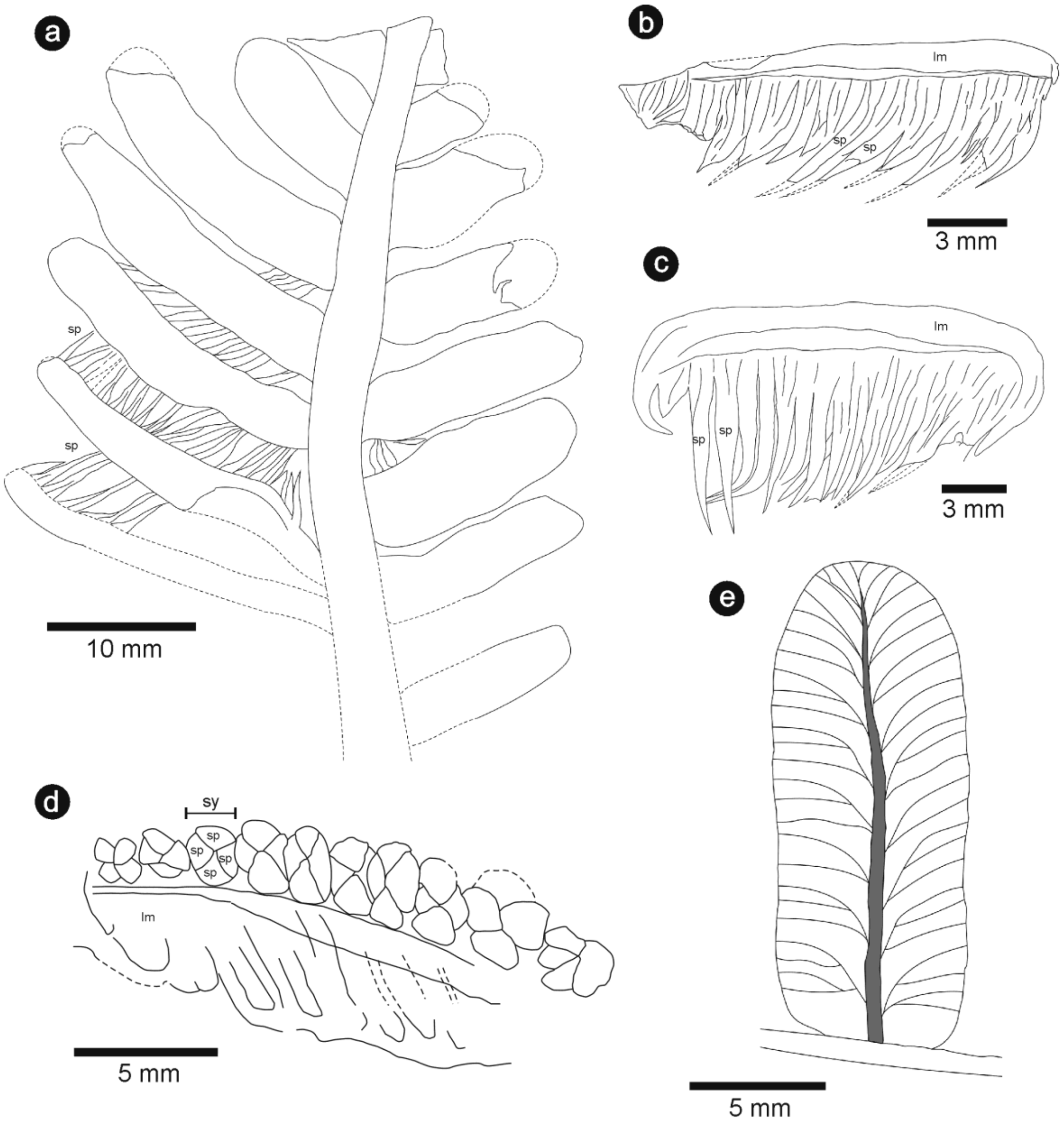


Fig. 23 - Schematic drawings of ***Acitheca murphyi*** **sp. nov.** in camera lucida; (a) fertile ultimate pinna (holotype; see Plate XII, 1), (b, c) reconstruction of fertile pinnules showing very long sporangia (see Plate XII, 3, 4, 7), (d) sporangia, synangia and lamina (see Plate XII, 8), (e) probably sterile pinnule assignable to *Acitheca murphyi* sp. nov. (see Plate XII, 12, 13). Abbreviations: sp, sporangium; sy, synangia; lm, lamina.

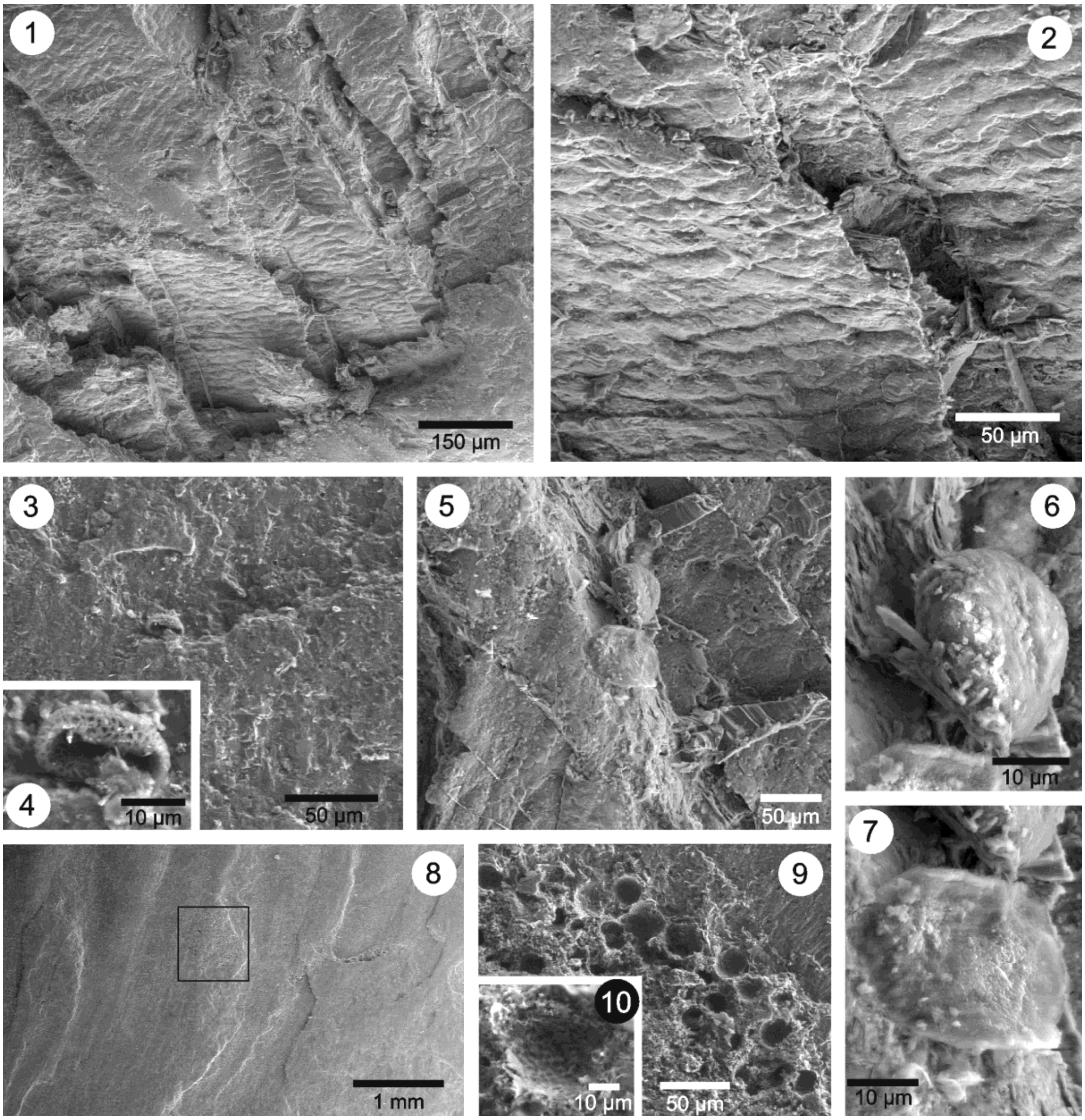
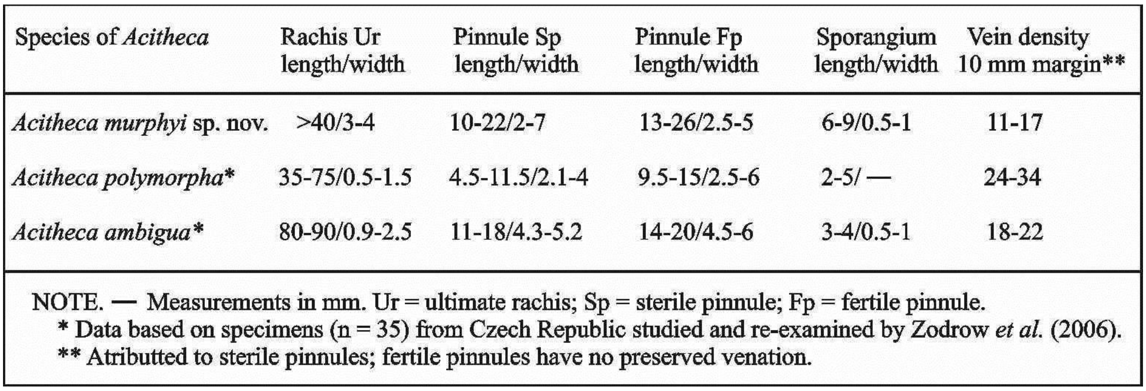


Plate XIII - *Acitheca murphyi* sp. nov. Montes da Costa and São Pedro da Cova, DCB, Portugal; 1, 2. Adaxial cuticles and elongate polygonal cells (paratype UP-MHNFCP-130924; São Pedro da Cova), 3, 4. Spore assigned to *Convolutispora*-like palynomorph (paratype UP-MHNFCP-130923; Montes da Costa), 5–7. Spores assigned to *Knoxisporites*-like palynomorph (paratype UP-MHNFCP-130924; São Pedro da Cova), 8–10. Probably taphonomic changes occurred on surface of the sporangia (paratype UP-MHNFCP-130923; Montes da Costa).

Table 3 - Comparative morphometric features among pinnules of ***Acitheca murphyi* sp. nov.**, *Acitheca polymorpha* (Brongniart) Schimper and *Acitheca ambigua* (Sternberg) Němejc.



Species of *Acitheca*	Rachis Ur length/width	Pinnule Sp length/width	Pinnule Fp length/width	Sporangium length/width	Vein density 10 mm margin**
Acitheca murphyi sp. nov.	>40/3-4	10-22/2-7	13-26/2.5-5	6-9/0.5-1	11-17
*Acitheca polymorpha**	35-75/0.5-1.5	4.5-11.5/2.1-4	9.5-15/2.5-6	2-5/ —	24-34
*Acitheca ambigua**	80-90/0.9-2.5	11-18/4.3-5.2	14-20/4.5-6	3-4/0.5-1	18-22

NOTE. — Measurements in mm. Ur = ultimate rachis; Sp = sterile pinnule; Fp = fertile pinnule.
* Data based on specimens (n = 35) from Czech Republic studied and re-examined by Zodrow *et al.* (2006).
** Atributted to sterile pinnules; fertile pinnules have no preserved venation.

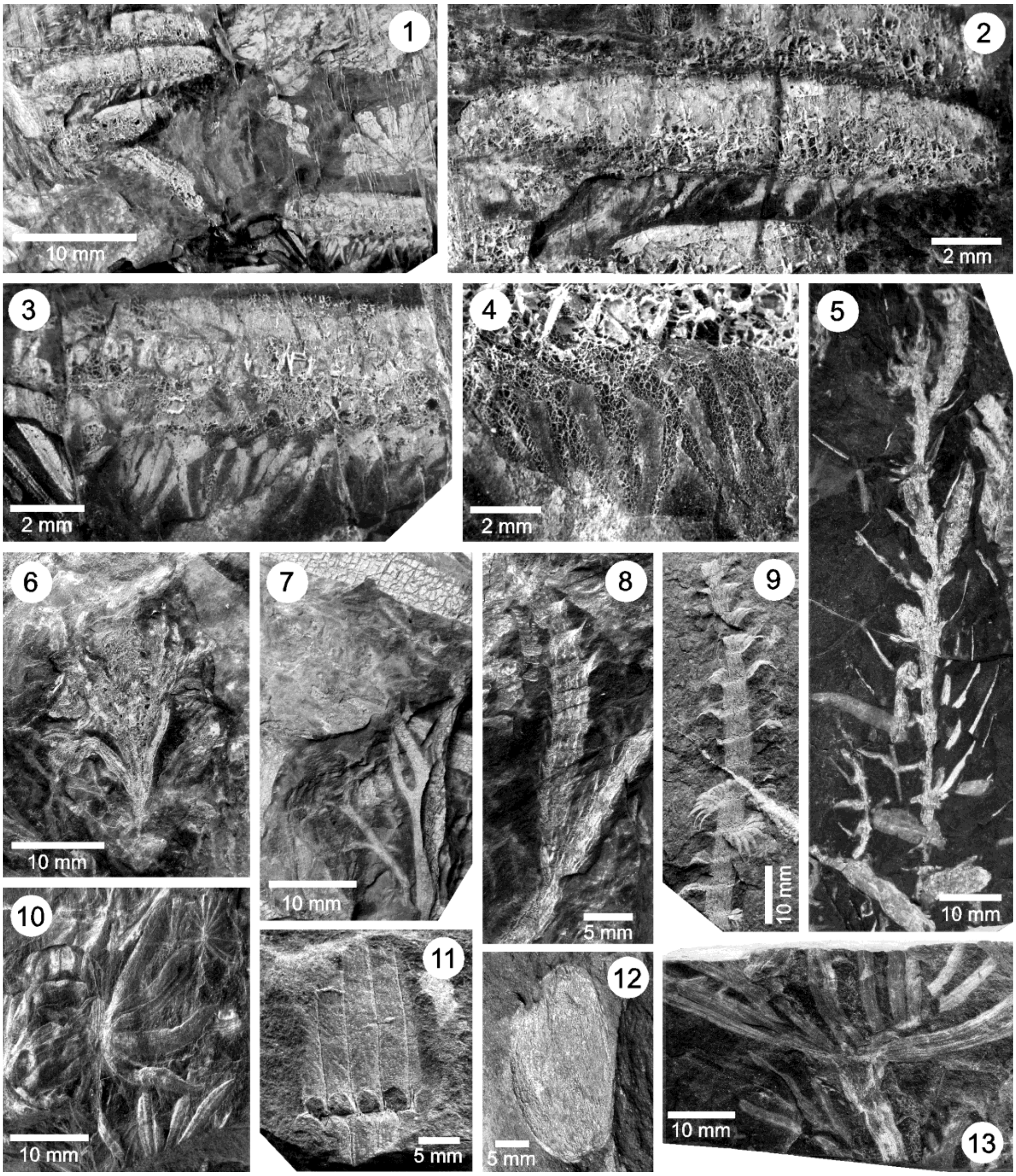


Plate XIV - Representative pteridopsids, pteridospermopsids and sphenopsids in new lower Gzhelian outcrops of Montes da Costa, DCB, Portugal; 1–4. *Acitheca* cf. *polymorpha* (Brongniart) Schimper (UP-MHNFCP-154762), 5. *Calamostachys calathifera* Sterzel, 6, *Telangiopsis* sp., 7. *Heterangium* sp., 8. *Calamostachys* sp., 9. *Calamostachys tuberculata* Sternberg, 10. *Stellotheca robusta* (Feistmantel) Surange & Prakash, 11. *Calamites suckowii* Brongniart, 12. Incertae sedis, 13. *Asterophyllites*? sp.

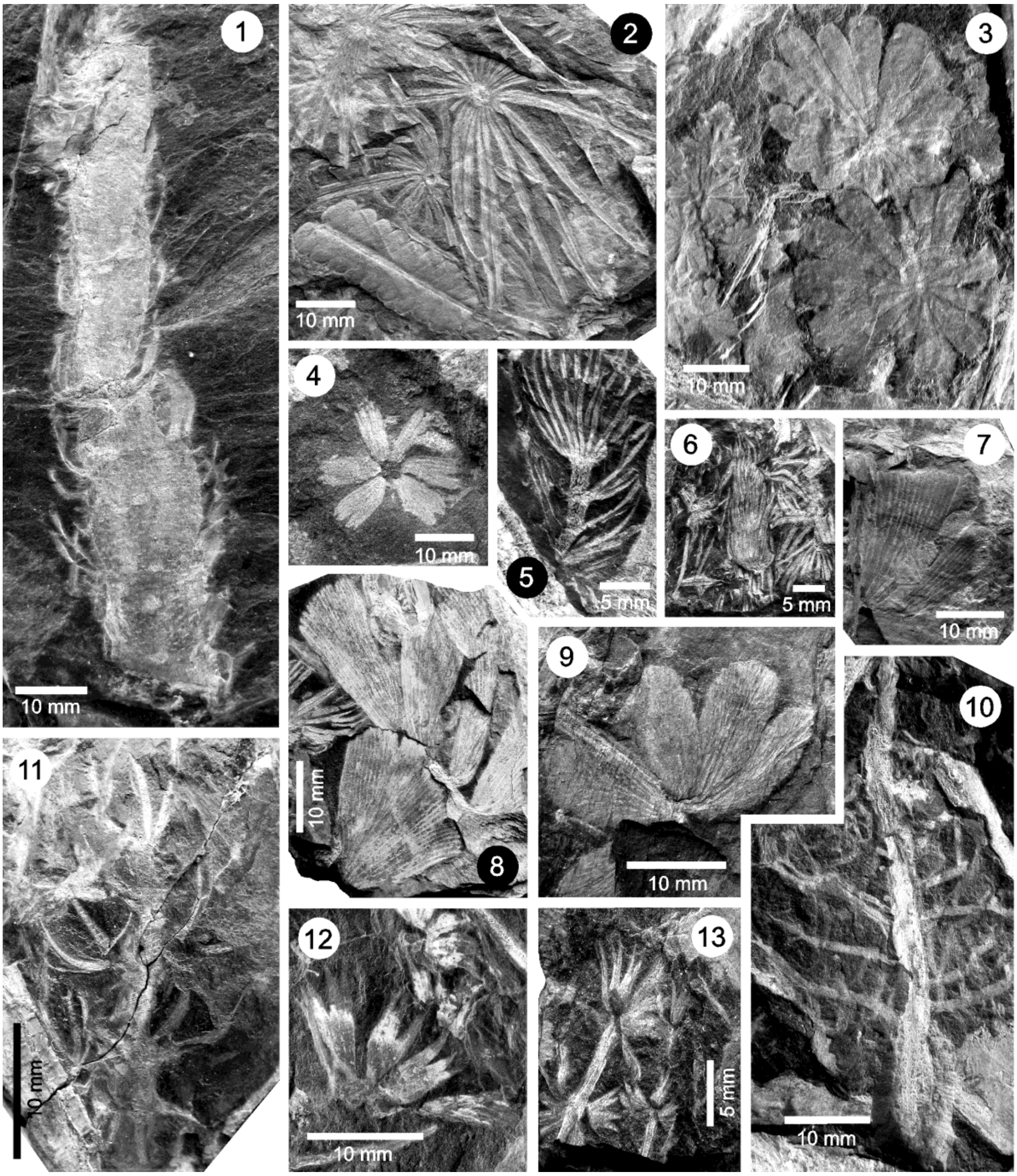


Plate XV - Representative sphenopsids in new lower Gzhelian outcrops of Montes da Costa, DCB, Portugal; 1, 10. Probably roots of sphenopsids, 2. *Annularia stellata* (von Schlotheim) Wood and *Pecopteris unita* Brongniart (=*Diplazites emarginatus* Göppert), 3. *Annularia carinata* von Gutbier (at the right) and *Annularia sphenophylloides* (Zenker) von Gutbier (at the left), 4. *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger, 5, 6. *Asterophyllites* sp., 7, 8. *Sphenophyllum costae* Sterzel (trizygioid leaves; see Bashforth and Zodrow, 2007), 9. *Lilpopia raciborskii* (Lilpop) Connor & Schaarschmidt, 11. *Annularia spicata* von Gutbier, 12. *Sphenophyllum costae* Sterzel (linear-laciniate leaves; see Bashforth and Zodrow, 2007), 13. *Sphenophyllum* cf. *costae* Sterzel.

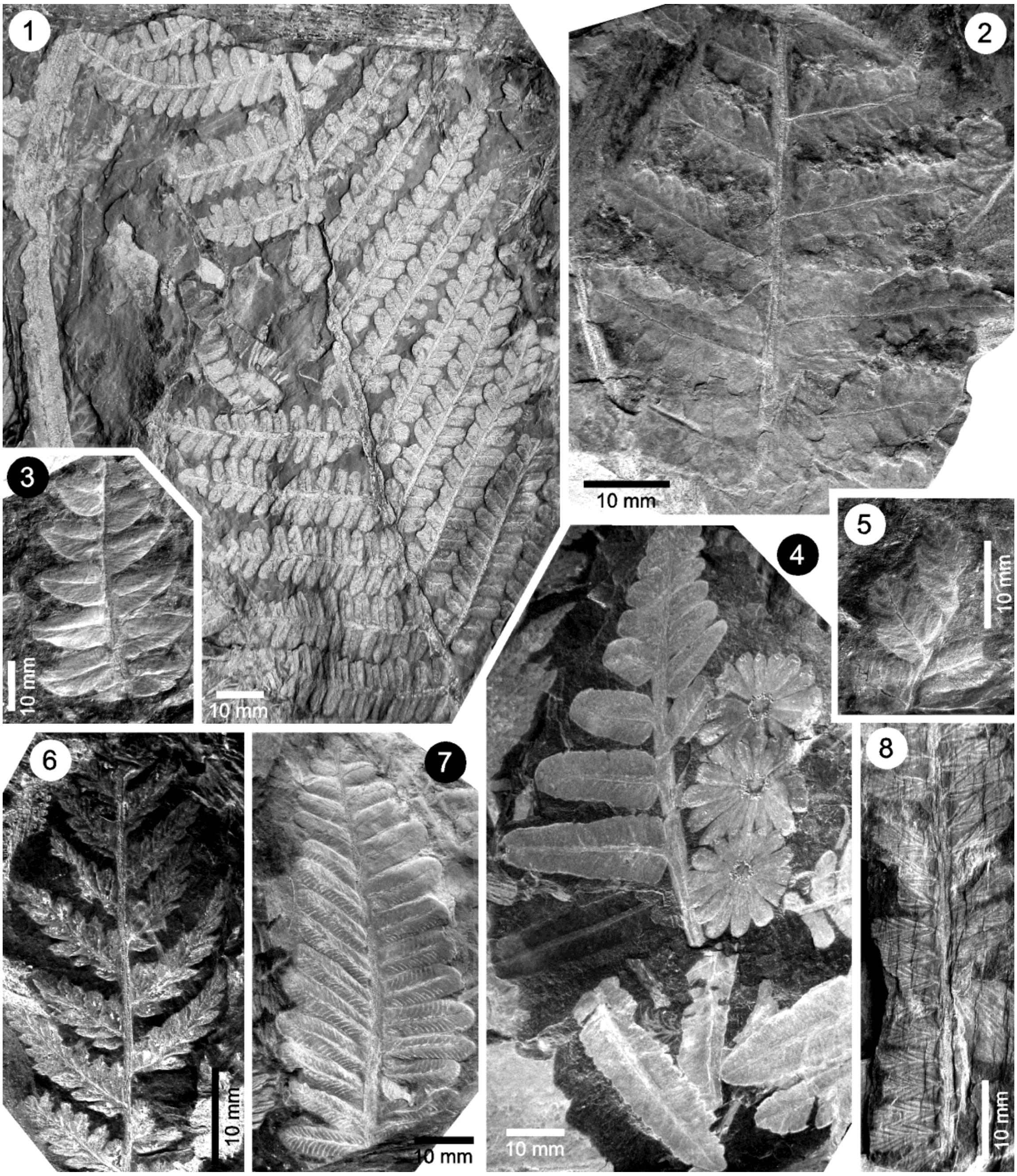


Plate XVI - Additional pteridopsids, pteridospermopsids and sphenopsids in new lower Gzhelian outcrops of Montes da Costa, DCB, Portugal; 1. *Pecopteris* cf. *candolleana* Brongniart and unidentified pteridopsid/pteridospermopsid axis showing *Aphlebia* inserted on both sides of the rachis (at the left side of image), 2. *Oligocarpia gutbieri* Göppert (sterile foliage), 3. *Pseudomariopteris cordato-ovata* (Weiss) Gillespie *et al.*, 4. *Pecopteris unita* Brongniart (=*Diplazites emarginatus* Göppert) and *Annularia sphenophylloides* (Zenker) von Gutbier, 5. *Oligocarpia leptophylla* (Bunbury) Grauvogel-Stamm & Doubinger (sterile foliage), 6. *Sphenopteris tenuis* Schenk, 7. *Pecopteris* sp., 8. *Nemejcopteris feminaeformis* (von Schlotheim) Barthel.

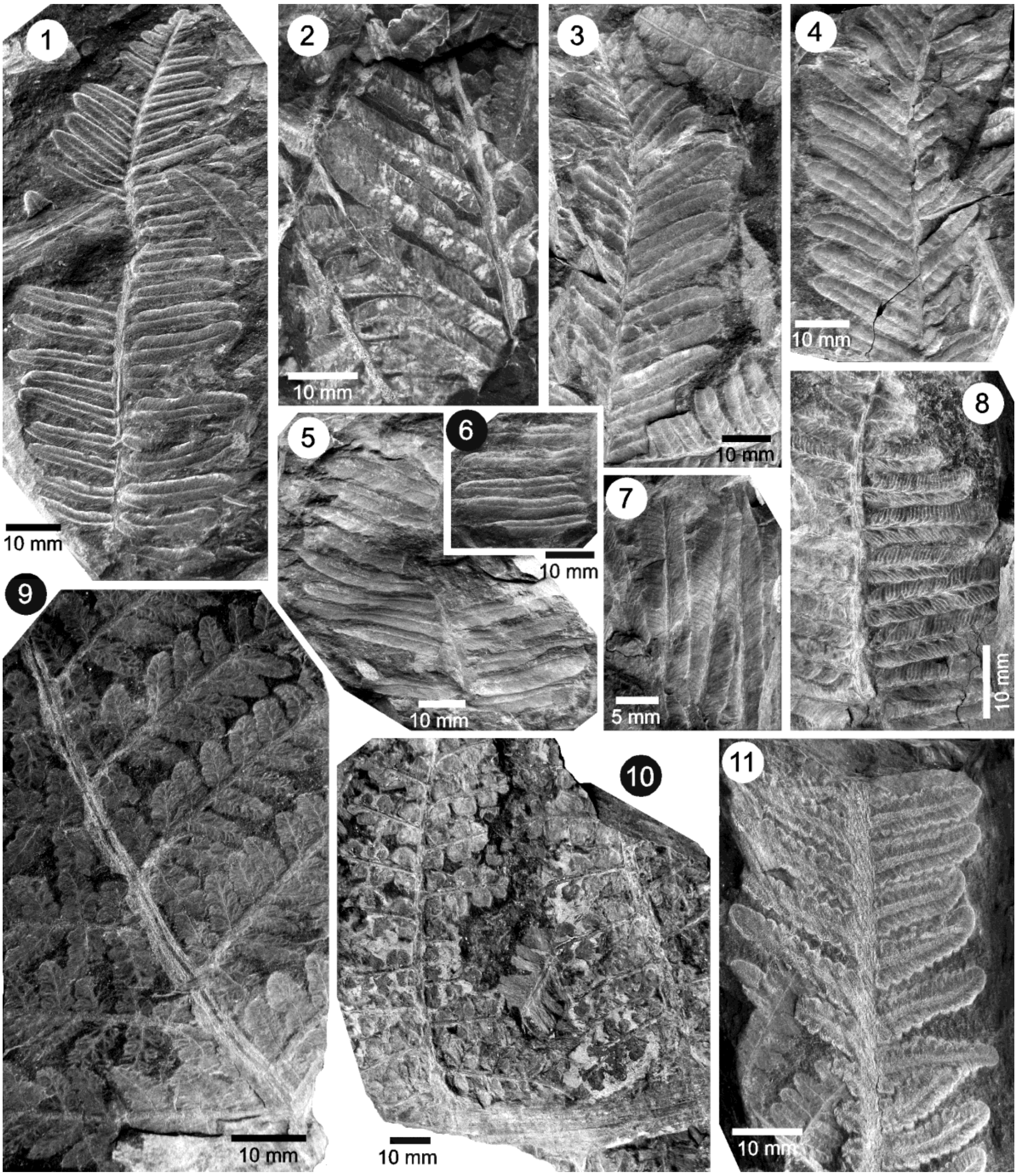


Plate XVII - Additional pteridopsids and pteridospermopsids in new lower Gzhelian outcrops of Montes da Costa, DCB, Portugal; 1. *Pecopteris* sp., 2–8. *Desmopteris* cf. *longifolia* Presl, 9. *Oligocarpia gutbieri* Göppert (sterile foliage), 10. *Eusphenopteris rotundiloba* (Němejc) Van Amerom, 11. *Pecopteris* cf. *miltonii* (Artis) Brongniart.

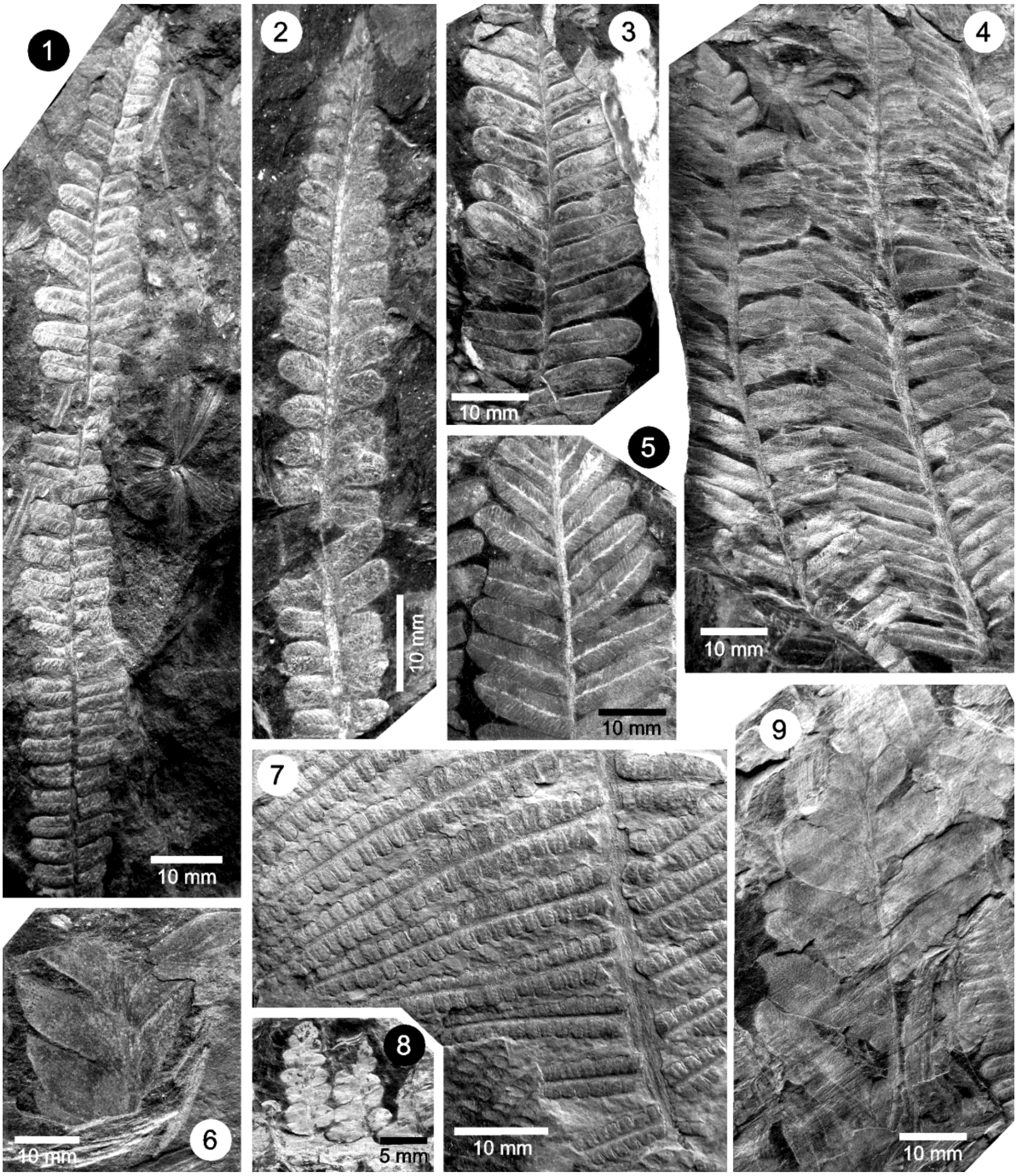


Plate XVIII - Additional pteridopsids and pteridospermopsids in new lower Gzhelian outcrops of Montes da Costa, DCB, Portugal; 1. *Pecopteris* cf. *monyi* Zeiller and *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger, 2. *Pecopteris* cf. *paleacea* Zeiller, 3–5. *Pecopteris* cf. *opulenta* Corsin, 6. *Odontopteris brardi* Brongniart, 7. *Pecopteris arborescens* (von Schlotheim) Brongniart, 8. *Sphenopteris* sp., 9. *Neuropteris ovata* ?var. *pseudovata* Gothan & Sze.

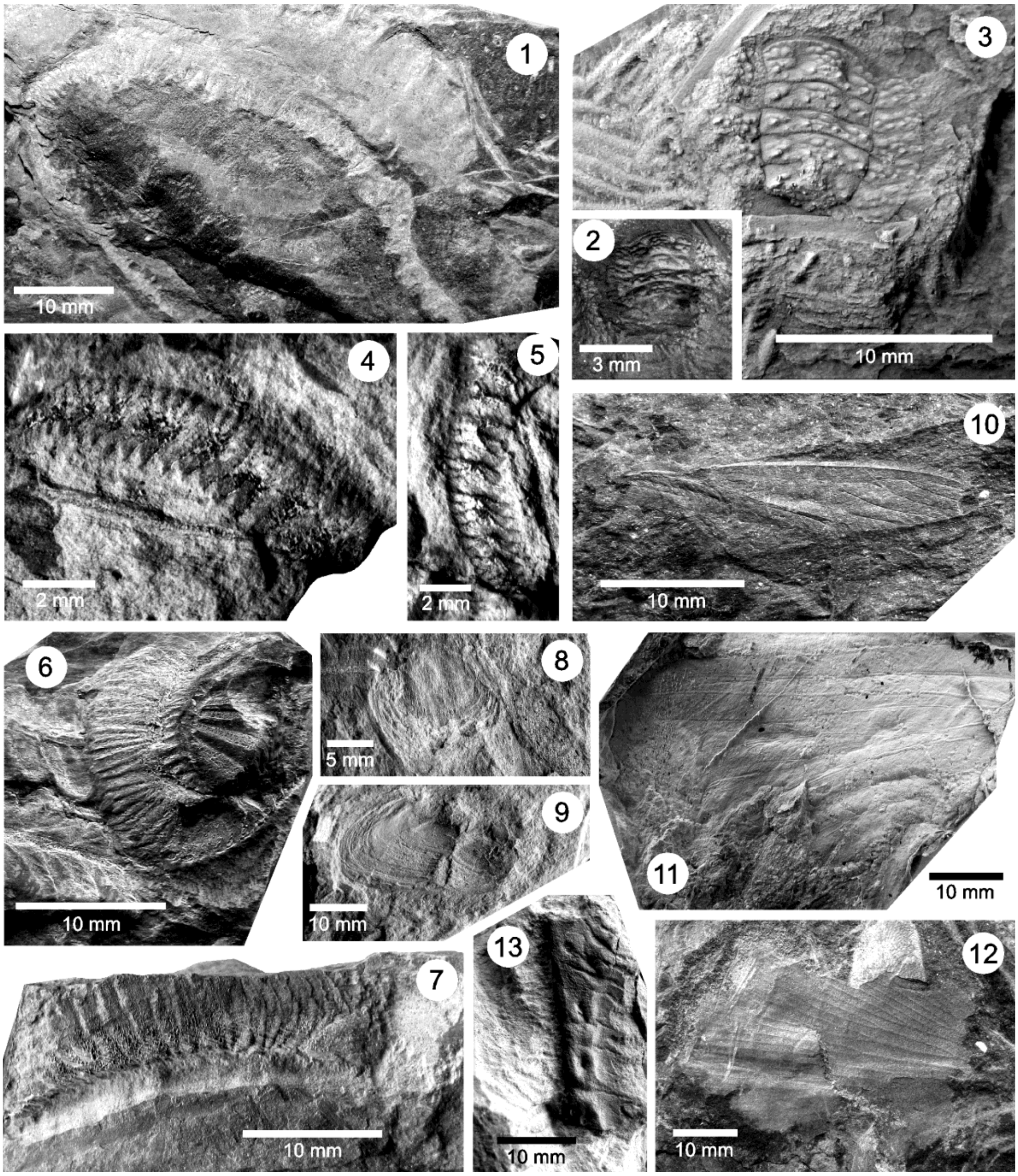


Plate XIX - Fossil faunal assemblages from the new lower Gzhelian outcrops of Montes da Costa and São Pedro da Cova, DCB, Portugal; 1. aff. *Pleurojulus biornatus* Fritsch (Montes da Costa), 2, 3. *Aphantomartus pustulatus* Scudder (3. Latex cast; São Pedro da Cova), 4–7. Unidentified myriapods (4, 5. São Pedro da Cova; 6. Montes da Costa; 7. Montes da Costa), 8, 9. *Anthraconaia* cf. *lusitanica* Teixeira (São Pedro da Cova), 10. *Lusitaneura covensis* Loureiro *et al.* (holotype specimen UP-MHNFCP-154771; São Pedro da Cova), 11. *Stenodictya*? *lusitanica* Correia *et al.* (latex cast of holotype specimen UP-MHNFCP-127180; São Pedro da Cova), 12. Unidentified palaeodictyopterid insect (Montes da Costa), 13. *Adelophthalmus* sp. (São Pedro da Cova).

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1.4. Revision of *Ilfeldia* and establishment of *Ovulepteris* gen. nov. from the Pennsylvanian of Europe, with a discussion on their concepts.

Adapted from Josef Pšenička, Pedro Correia, Zbyněk Šimůnek, Artur A. Sá, J. Brendan Murphy, Deolinda Flores

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Abstract

The present paper deals with taxonomic revision of fossil-genus *Ilfeldia* Remy and establishing a new fossil-genus *Ovulepteris* gen. nov. The fossil-genus *Ilfeldia* was established by Remy (1953) based on fertile material from Ilfeld Basin (Germany). Original paper not includes generic diagnose (only description). The concept of *Ilfeldia* in the paleobotanical literature is somewhat confused, and the systematic part of this paper therefore attempts to clarified diagnosis for this fossil-genus and original fossil-species *Ilfeldia jejunata* sensu Remy (1953) is renamed to *I. jejunataeformis* sp. nov. because species name *jejunata* (*Taeniopteris jejunata* Grand′Eury) is basionym for sterile taeniopterid leaves sensu Grand′Eury (1877). New fossil-species *Ilfeldia gregoriensis* sp. nov. is established from the São Pedro da Cova region in the Douro Carboniferous Basin (lower Gzhelian [lower Stephanian C], Upper Pennsylvanian, Portugal, Western Iberian Massif). The association of *I. gregoriensis* sp. nov. and large taenopterid leaves may reflect the dimorphism of fertile and sterile leaves of one parent plant, although such a relationship cannot be proven. A new fossil-genus *Ovulepteris* gen. nov. is established for leaves bearing ovule-type of reproductive organs. *Ovulepteris* gen. nov. has oblong leaves with partly reduced leaf lamina supporting ovule-type of reproductive organs situated on a leaf margin. The new fossil-genus *Ovulepteris* gen. nov. is established based on Obrhel´s (1957, 1965) material from Pennsylvanin of Czech Republic, which were originally described under names *Ilfeldia robusta* Obrhel and *I. lobecensis* Obrhel. Both species are replaced into new genus and established a new combinations *Ovulepteris robusta* (Obrhel) nov. comb. and *O. lobecensis* (Obrhel) nov. comb. Both genera *Ovulepteris* and *Ilfeldia* are associated with coriaceous taeniopterid leaves. Nevertheless, there is impossible to clarified if *Ilfeldia* represents synangia of true ferns or pollen organ of gymnosperms. Therefore, we applied concept of separation of two genera where one is represented ovule bearing leaves (*Ovulepteris*) and second synangia bearing leaves (*Ilfeldia*). We also retained the genus *Manebachia* Remy & Remy for synangia bearing taeniopterid leaves with strongly reduced and veinless leaf lamina. *Ovulepteris* gen. nov. probably represents some enigmatic group of pteridosperms which may be a dead evolutionary

line or can have some relationship in cycads evolution. Taxonomic affiliation of *Ilfeldia* and *Manebachia* is still unclear.

***Keywords*: *Ilfeldia*; *Taeniopteris*; *Ovulepteris*; *Manebachia*; fertile; Late Pennsylvanian; Portugal; Czech Republic.

1.4.1. Introduction

An enigmatic plant remains are time to time found in paleontological record. Many of them cannot be clearly classified in botanical system, because there is missing many important characters. Fossil-species of *Ilfelia*, established by Remy (1953), is typical example of this case. Only three species of *Ilfeldia* were established during paleobotanical histroy, *Ilfeldia jejunata* sensu Remy, 1953, *I. robusta* Obrhel and *I. lobecensis* Obrhel (Remy, 1953; Obrhel, 1957, 1965). Fossil-species of *Ilfeldia* has been generally characterized as plant with elongated leaves bearing reproductive organs on a leaf margin. Species of this genus are frequently associated with taeniopterid leaves (Remy, 1953; Obrhel, 1957; 1965; Barthel, 2006). Remy (1953) described fertile leaves of *Ilfeldia jejunata*, which come from Ilfeld locality, Ilfeld Basin, Germany, Gzhelian (late Stephanian) age, as conical or lanceolate leaves with a bluntly dentate margin and a thick midrib. The lateral veins arise acutely or are essentially parallel to the midrib, and thereafter arch strongly before extending to the lateral margin, which they reach at an angle of 80–90 degrees. The lateral veins typically dichotomize once close to the midrib, whereas a triple bifurcation of the lateral veins is very rare. Fertile leaves are up to 29 mm long and 7 mm wide, with approximately 25 synangia attached to both sides of the leaf margins. Cash-shaped synangia comprise six fused sporangia that are 350–420 µm long and contain oval, smooth monolete spores that are 34 µm in diameter (Remy, 1953). Nevertheless, Remy (1953) did not state if published generic and species descriptions were intended to be formal diagnose. Most problematic is the fact that Remy´s (1953) description of the fossil-genus includes many details that are rather species specific. It is thus not surprising that the generic description of *Ilfeldia* more or less corresponds to his description for the fossil-species *Ilfeldia jejunata*.

Remy (1953) also described leaves of *Taeniopteris jejunata* Grand′Eury from the same locality sterile, which he assumed to represent the sterile leaves of the same parent plant that produced fertile *Ilfeldia* leaves. Nevertheless, comparison of Remy′s (1953) fertile leaves with original *Taeniopetris jejunata* is complicated because Grand′Eury (1877) did not figure any specimen of this species. Grand′Eury (1877, p. 121) published only description. Later, Barthel (2006, p. 64) did not include Remy′s

(1953) sterile specimens in synonymy list of *T. jejunata* because he did not suppose that Remy′s (1953) specimens represented *Taeniopteris jejunata* sensu stricto. Using the species name *jejunata* is from nomenclatural point of view problematic, because *Taeniopteris jejunata* undoubtedly represent distinct fossil-species of uncertain affinity and still it in use as artificial species of primary sterile leaves. Due to this fact, we suggested the new species name *Ilfeldia jejunataeformis* sp. nov. (see systematic part of this paper). Remy (1953, fig. 5, pl. 7, fig. 7) also figured another specimen of leaves of ostensible *T. jejunata* that shows truncate/acute type basal part and attachment part of a leaf and its supporting rachis. Grand′Eury (1877) did not give description of the base of *T. jejunata*. Paradoxically, Sterzel (1893) stated that truncate/acute type of basal part is typical for *T. jejunata*. Regardless on this fact, Remy (1953) applied this pattern of trunctate/acute proximal part of leaves for fertile leaves and stated that *Ilfeldia jejunata* is probably fertile leaves of *Taeniopteris jejunata* with bipinnate frond organization.

Later Barthel *et al.* (1975) and Barthel (2006) described fertile and sterile leaves of *Taeniopteris* (*Ilfeldia*) *jejunata* from Rotliegen of Germany. Barthel *et al.* (1975, p. 477, fig. 1) illustrated leaves in which the distal part of the lamina is reduced in width and bears several small oval reproductive organs that are situated on the leaf margin and positioned over vein endings. Barthel *et al.* (1975) interpreted such reproductive organs as small ovules. Barthel (2006) also suggested that *Manebachia polysporangiata* Remy & Remy, which was originally established by Remy and Remy (1958) from the same area and strata like *Taeniopteris* (*Ilfeldia*) *jejunata*, having distally reduced lamina that lack secondary veins, represents the pollen organs of *Taeniopteris jejunata*. Nevertheless, this opinion is rather speculative, because the relationship is based on association only.

Two species of *Ilfeldia* have been established based on specimens from Kladno-Rakovník Basin (Czech Republic): *I. lobecensis* Obrhel (Obrhel, 1965) and *I. robusta* Obrhel (Obrhel, 1957). *Ilfeldia lobecensis* comes from Lobeč locality near Kralupy and Vltavou (Czech Republic). Strata of Lobeč locality belong to uppermost Moscovian (upper Asturian) according to Opluštil *et al.* (2005) and Bashforth *et al.* (2011). *Ilfeldia robusta* comes from Kvíček locality near Slaný. Strata of Kvíček locality belongs to upper Kasimovian (Stephanian B) according to Obrhel (1957). Both species are revised in this paper, because their affiliation to the fossil-genus *Ilfeldia* is questionable. *Ilfeldia lobecensis* shows leaves with reduced leaf lamina. Reproductive organs are absent and Obrhel (1965) described small impressions situated at the end of lateral veins that he assumed to represent the attachment point of reproductive organs. Unfortunately, these structures cannot be described in detail, becouse original Obrhel′s (1965) specimens are currently lost. *Ilfeldia robusta* shows reduced leaf lamina bearing reproductive organs which are attached on the end of lateral veins (Obrhel, 1957). The reproductive organs of *I. robusta* are described in detail in this paper. Based on revision of Obrhel (1965, 1957) specimens both fossil-species are placed into a new genus *Ovulepteris* gen. nov.

1.4.2. Affinity of taxa which can have relationship with studied *Ilfeldia* and *Ovulepteris* gen. nov.

Marginally/laterally arranged reproductive organs are known for several Paleozoic fossil-taxa, including ovule bearing taxa (often associated with *Taeniopteris*-like leaves), such as *Phasmatocycas* Mamay (Axsmith *et al.*, 2003), *Eophyllogonium* Mei *et al.* (Mei *et al.*, 1992), *Crossozamia* Pomel (Zhifeng and Thomas, 1989), *Archaeocycas* Mamay (Mamay, 1976) or *Sobernhheimia* Kerp (Kerp, 1983). Some of those genera are placed among cycads as *Crossozamia* or *Archaeocycas* (Zhifeng and Thomas, 1989; Mamay, 1976; Rozynek, 2008) and *Phasmatocycas* or *Sobernhheimia* are rather placed among pteridosperms (Kerp, 1983; Axmith *et al.*, 2003; Rozynek, 2008). Affinity of *Eophyllogonium* is still unclear.

Marginally arranged sporangia bearing taxa can be separated into two main groups. The first group represents a true ferns such as *Zeilleria* Kidston (Corsin, 1927; Thomas and Crampton, 1971), *Senftenbergia* Corda (Bek and Pšenička, 2001; Pšenička and Bek, 2003), *Boweria* Kidston (Frojdová *et al.*, in press) and *Acrangiophyllum* Mamay (Mamy, 1955). Remy (1953) compared the reproductive organs of *Ilfeldia jejunata* with *Zeilleria*-type reproductive organs or *Chorionopteris gleichenioides* (Corda) Kubart (= *Anachoropteris pulchra* Corda). According to Kubart (1917) *Chorionopteris gleichenioides* has sporangia organized into sorus placed between midvein and margin, non strictly marginal. Pšenička (2005) and Mamay (1955) mentioned that sporangia of *Zeilleria* and *Acrangiophyllum* may be special form of pollen organ (microsporangia) of pteridosperms. *Senftenbergia* or *Boweria* are clearly placed among leptosporangiuate ferns ((Bek and Pšenička, 2001; Pšenička and Bek, 2003, Frojdová *et al.*, in press). Nevertheless, both species have sphenopterid-type pinnules which are quite different to *Ilfeldia*.

The second group represents marginally arranged sporangia bearing taxa attached to taeniopterid leaves of uncertain affinity such as *Ilfeldia* Remy (Remy, 1953) or *Manebachia* Remy & Remy (Remy and Remy, 1958). There is not clear if sporangia of these fossil-genera represent pollen organs of gymnosperms or synangia of ferns. Remy (1953) described in situ spores of *Ilfeldia jejunata* sensu Remy (1953) with trilet mark that rather point to true ferns, but does not exclude gymnosperms. Some pollen of Palaeozoic gymnosperms have trilet or triletoid mark (Šimůnek *et al.*, 2009). However, information on some plants are for clear classification so far insufficient. Some species described under *Ilfeldia* and *Manebachia* bear ovule-like reproductive organs (e.g. *Ilfeldia robusta* Obrhel or *Taeniopteris* (*Ilfeldia*) *jejunata* sensu Barthel *et al.* (1975, p. 477, fig. 1) and some species bear synangia (e.g. *Ilfeldia jejunata* sensu Remy, 1953 or *Manebachia polysporangiata* Remy & Remy). This leads to an unclear view on members of both fossil genera. Based on these facts, the new proposal of classification of *Ilfeldia*, *Manebachia* and establishing of new genera *Ovulepteris* gen. nov. is done in this paper.

Two fossil-species (compression/impression) with sporangia affiliated to cycads were described from Cathaysian flora of Nord China such as *Cycadostrobus paleozoicus* Zhu and *Liulinia lacinulata* Wang (Zhu *et al.*, 1994; Wang, 1986). Both fossil-species show probably microsporohylle with microsporangia situated in proximal part of sporophylle. Microsporangia are attached to reduced leaf lamina. Both species are affiliated to true cycads (Zhu *et al.*, 1994; Wang, 1986) therefore there is not any direct evidence, except morphologically similarity, for this classification.

1.4.3. A new finding of *Ilfeldia* from Portugal

A new species of *Ilfeldia* is established in this paper which comes from Portugal. Intensive paleobotanical research of the paleoflora from the São Pedro da Cova region in the Douro Carboniferous Basin (lower Gzhelian [lower Stephanian C], Upper Pennsylvanian, Portugal, Western Iberian Massif) was organized through 2002 to 2015 by Pedro Correia (Institute of Earth Sciences, Pole of the Faculty of Sciences, University of Porto). Within the scope of this project, many plant fossils were excavated that represent several fossil-species. The most interesting discovery was a specimen that comprises fragments of small fertile and sterile leaves that are accompanied by large taeniopterid sterile leaves. The new finding of fossil remains from Portugal, represented by small fertile/sterile leaves, are comparable with fossil-genus *Ilfeldia*, which has not yet to be described from Portugal.

The large sterile leaves which accompanied small fertile/sterile leaves are placed among fossil-genus *Taeniopteris* Brongniart. *Taeniopteris* Brongniart (1828) was established for simple, linear leaves with parallel lateral margins, a strong midrib, and lateral veins that are unbranched or bifurcate near the midrib and run perpendicular to the leaf margin. As currently used, this artificial fossil-genus comprises a heterogeneous group of foliage that ranges from individual, strap-shaped leaves to pinnately organized fronds that comprise large and more or less petiolate leaves (e.g., Mamay, 1973, 1976; Remy and Remy, 1975; Taylor, 1981; Barthel, 2006; Taylor *et al.*, 2009). Leaves assigned to *Taeniopteris* have been found in strata that ranges from Carboniferous to Cretaceous in age (e.g., Blaschke and Grant-Mackie, 1976; Drinnan and Chambers, 1985; Howe and Cantrill, 2001; Pott *et al.*, 2007; Deng *et al.*, 2009; Taylor *et al.*, 2009; Bashforth *et al.*, in press). Given that *Taeniopteris* is an artificial fossil-taxon, specimens involve numerous systematic affinities, including true ferns, pteridosperms, cycads and bennettitaleans (the latter in Mesozoic rocks) (Cridland and Morris, 1960; Mamay, 1976; Barthel, 2006; Taylor *et al.*, 2009; Pott and Launis, 2015). The heterogeneous systematic affinities of material assigned to *Taeniopteris* have proved problematic in the identification of individual species.

Taeniopterids have previously been recorded in Carboniferous strata of Portugal. *Taeniopteris jejunata* and cf. *Taeniopteris multinervia* Weiss were described from the Douro Basin (lower Gzhelian [lower Stephanian C]) (Teixeira, 1940, 1944; Wagner, 1983), where Teixeira (1942) and Wagner and Lemos de Sousa (1983) recorded *T. jejunata* as common. Teixeira (1940) also established the new species *T. bertrandiana* Teixeira from the Douro Basin. *Taeniopteris jejunata* and *T. multinervis* also are known from the Buçaco Basin (lower Gzhelian [upper Stephanian C]) (Teixeira, 1942, 1944; Wagner, 1983).

1.4.4. Material and geological background

The specimens of *Ilfeldia gregoriensis* sp. nov. were collected in a new excavation (outcrop spc3) during fieldwork in 2006 in the Douro Carboniferous Basin (DCB) in the São Pedro da Cova region (NW Portugal; Figures 7, 24). Four specimens (UP-MHNFCP-154766–154769) preserved in laminated grey (Figure 24E, F) shale were selected for study, and are stored in the (NHMSUP). Specimen UP-MHNFCP-154766 was selected as holotype of *Ilfeldia gregoriensis* sp. nov. because contain as fertile so sterile leaves. Specimens were collected from lower Gzhelian (lower Stephanian C, Upper Pennsylvanian) strata. The fossils come from strata described as tectono-sedimentary unit D1 (UTS D1), near the top of the repeated stratigraphic sequence in the DCB (Figure 25). According to Pinto de Jesus (2001, p.148) UTS D1 comprises phytogenic and siliciclastic deposits of fluvial environment which are very fossiliferous, and they consist of alternating beds of coal, siltstone, mudstone and conglomerate (Figure 25). These strata may contain rare lenticular bodies of conglomerate or coarse sandstone (Pinto de Jesus, 2001; Figure 25).

Fig. 24 - New lower Gzhelian outcrops (spc3, TSU D1) of São Pedro da Cova (A–F). Excavation works during fieldwork in 2006. (image unpublished)

Specimens of *Ovulepteris robusta* nov. comb. (number E1303) is stored in the National Museum (Prague, Czech Republic). Holotype E1303 of *O. robusta* nov. comb. comes from abandoned quarry located near the village Kvíček, southwes of Slaný (Kladno-Rakovník Basin, Czech Republic). Specimen is preserved in grey/ocher laminated mudstone and comes probably from Hředle Member, Slaný Formation, Kasimovian (Stephanian B). Quarry is today closed and recultivated which unfortunately precludes verification of Obrhel (1957) description of the geological situation and a more precise sedimentological interpretation of the specimen section. Cf. *Ovulepteris lobecensis* nov. comb. (number E959) comes from Lobeč locality near Kralupy nad Vltavou (Kladno-Rakovník Basin, Czech Republic). The specimen was studied 2004 in the collection of National Museum in Prague. Actually this specimen is lost. Due to this fact is impossible to preclude verification of original description and to give more details of reproductive organs. We exluded this specimen to this study and we only figured photograph of this species. Specimen is preserved in ocher laminated mudstone and comes from upper part of Nýřany Formation, uppermost Moscovian (Asturian in the regional scale).

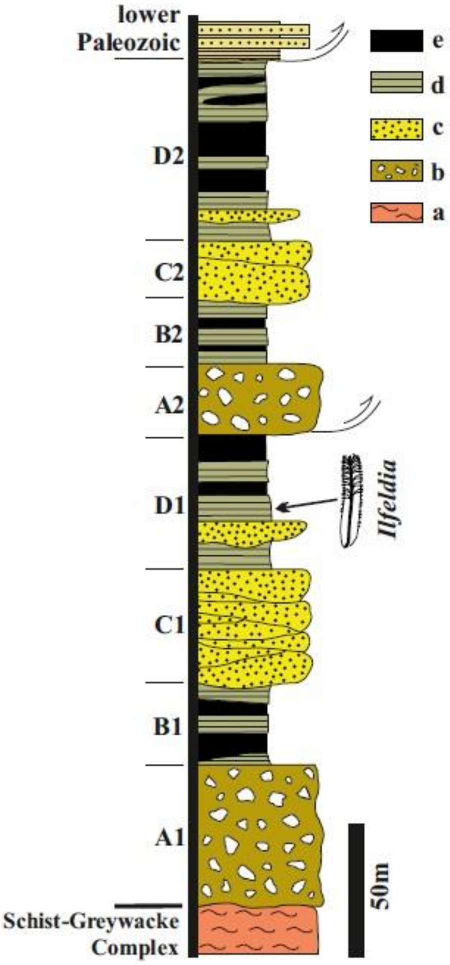

Fig. 25 - Stratigraphic and sedimentological column of DCB showing the different UTS (Adapted from Pinto de Jesus (2001). Geological materials illustrated in a, Schist-Greywacke Complex; b, breccias; c, conglomerates and sandstones; d, siltstones and shales; e, coal beds.

1.4.5. Descriptive part

1.4.5.1. *Ilfeldia gregoriensis* sp. nov. specimens from Portugal

1.4.5.1.1. Small fertile leaf form

Three incomplete fertile leaves (Plate XX, 1) and one nearly complete fertile leaf are preserved on specimen UP-MHNFCP-154766 (holotype, Plate XX, 4; Plate XXI, 1; see also Figure 26A). Leaf organization appears pinnatified (Plate XXI, 5; Figure 27), but the supporting rachis is not preserved. Leaves are oblong, 6 mm wide and at least 34 mm long (Plate XXI, 1, 5), but presumably were longer in life because leaf apices (possibly rounded or retuse/emarginated) are not preserved. Leaf bases are truncate and slightly narrowed. The leaf lamina is not reduced. Leaf margins are entire and essentially parallel, tapering very slightly towards the apex and base from the middle part of a leaf (Plate XX, 1). The midrib is strong, 0.8 mm thick, slightly longitudinally striated. Some leaves (Plate XXI, 1, 5; Figures 26A) show an arched midrib near the base, although it is not possible to determine if this is an original feature or the result of taphonomic processes. The midrib extends to the apex with the same thickness (Plate XXI, 1). Lateral veins are thinner than the midrib, arise at an acute angle (ca. 6°), dichotomize close to the midrib, and arch to reach the lateral margin at 78–80° (Plate XXI, 1). Veins are terminated by synangium that overlap the leaf margin (Plate XXI, 2; Plate XXII, 1). Some leaves show only impressions that probably represent the former position of sporangium attachment (Plate XXI, 5 arrows; Figure 26A, 27). The venation density is 12 veins per 10 mm on the leaf margin.

1.4.5.1.2. Reproductive organs

Reproductive organs are well preserved on one leaf on specimen UP-MHNFCP-154766 (holotype; Plate XXII, 1), where they are situated at the end of lateral veins and comprise synangia composed of two (rarely three) sporangia (Plate XXI, 3, 4; Plate XXII, 2, 3). Synangia are very small, being 0.6–0.7 mm long and 0.5 mm wide (Plate XXI, 3, 4; Plate XXII, 2, 3). Sporangia are attached to a short receptacle that is 70 µm long and 200 µm wide (Plate XXI, 3, 4; Plate XXII, 2, 3). Individual sporangia are reniform, tapering distally, 0.5–0.6 mm long and 210 µm wide (in widest part) (Plate XXI, 3, 4; Plate XXII, 2, 3). In situ spores could not be recovered because sporangia are preserved as impressions, sporadically covered by very oxidized and fragmented coaly matter. Accordingly, other details (e.g., cell structures, including presence of annulus) could not be defined.

1.4.5.1.3. Small sterile leaves

Sterile leaves are described based on plant remains from specimen UP-MHNFCP-154766 (holotype) (Plate XXI, 5), in addition to three small specimens with leaf fragments (Plate XXI, 6–8). A pinnate organization is assumed (Plate XXI, 5, 8). Leaves are oblong (Plate XXI, 6, 7) or spathulate (Plate XXI, 8), 6–11 mm wide and 25–34 mm long, although no leaves are complete and presumably were longer in life. Leaf margins are entire. Leaves have an obtusely rounded apex (Plate XXI, 8), and taper gradually towards the base starting at about 2/3 the leaf length (Plate XXI, 6, 8), eventually merging into the petiole (Plate XXI, 8). The midrib is strong, 0.7–0.8 mm thick, slightly longitudinally striated, arched near the base (Plate XXI, 5 arrow), and extend to the apex with the same thickness (Plate XXI, 6–8). Lateral veins are thin, arise at an acute angle (ca. 6°), and once- or twice-dichotomized. The first branch is near the midrib, whereas the second is irregularly distributed, sometimes occurring close to the midrib or about 1/2 of the distance to the lateral margin (Plate XXI, 7). Lateral veins reach the lateral margin at 80° (Plate XXI, 6–8). The venation density is 10–12 veins per 10 mm on the lateral margin.

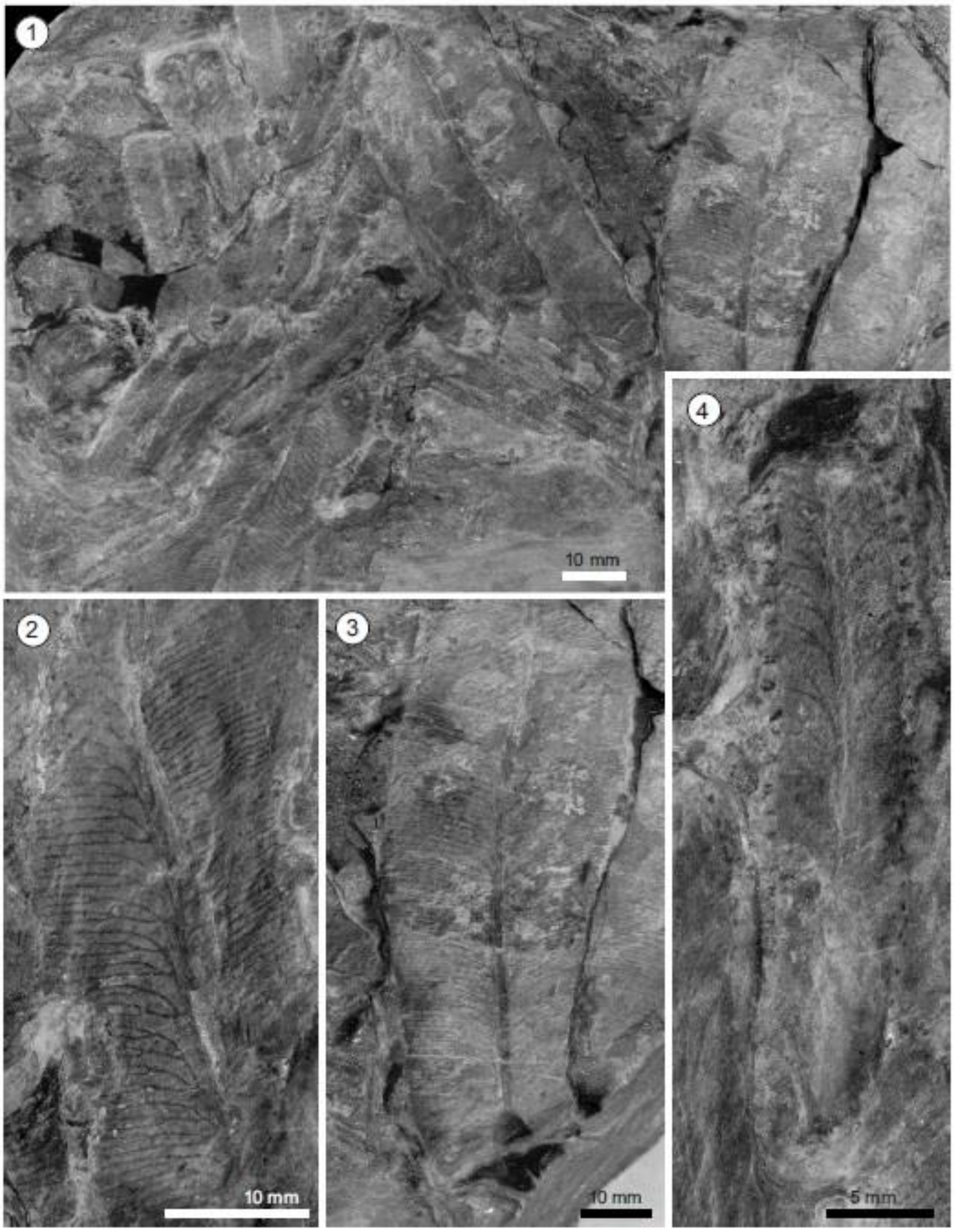

Plate XX – 1) Holotype specimen UP-MHNFCP-154766 showing fertile leaves of ***Ilfeldia gregoriensis*** **sp. nov.** associated with large *Taeniopteris*-like leaves. 2, 3) *Taeniopteris* cf. *carnoti*. 4) Nearly-complete fertile leaf of ***Ilfeldia gregoriensis*** **sp. nov.**

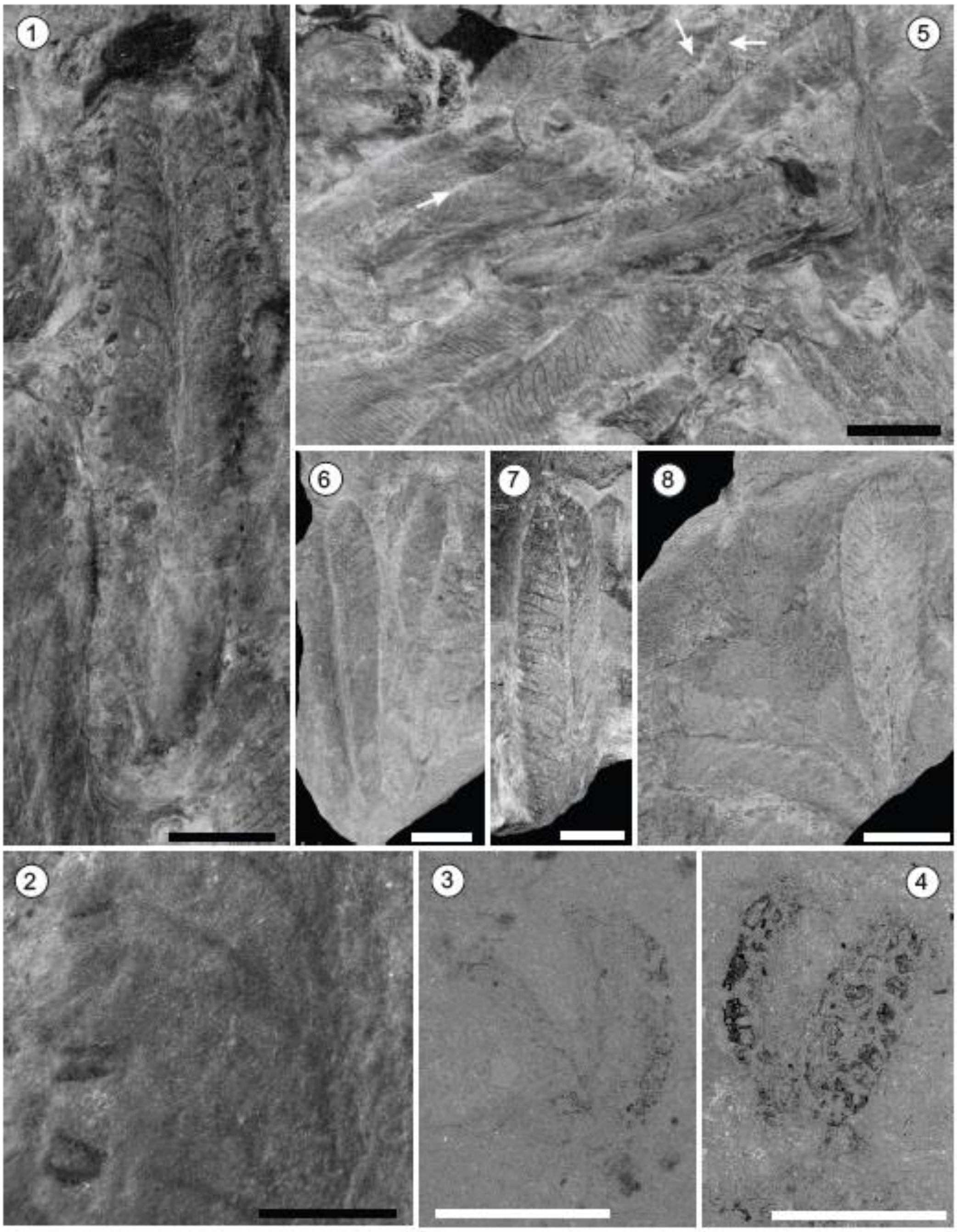

Plate XXI – All specimens ***Ilfeldia gregoriensis* sp. nov.**; 1) The best preserved and nearly-complete fertile leaf with synangia placed along the leaf margin; specimen No. UP-MHNFCP-154766; scale bar 5 mm. 2) Detail of leaf lamina with venation and synangia placed on the end of lateral veins; specimen No. UP-MHNFCP-154766; scale bar 2 mm. 3) Detail of synangium consists of two sporangia attached to very small pedice; specimen No UP-MHNFCP-154766; SEM; scale bar 500µm. 4) Detail of synangium consists of two sporangia attached to very small pedice (arrow). Black areas represent the remains of very-oxidized coal material; specimen No. UP-MHNFCP-154766; SEM; scale bar 500 µm. 5) Three fertile incomplete leaves (arrows) and one nearly complete fertile leaf preserved on specimen No UP-MHNFCP-154766; scale bar 10 mm. 6) Sterile leaves with well visible strong midrib; specimen No. UP-MHNFCP-154768; scale bar 5 mm. 7) Sterile leaf with well-preserved lateral veins; specimen No. UP-MHNFCP-154767; scale bar 5 mm. 8) Sterile leaves with tapering of leaf lamina toward base (pinnately organized frond?); specimen No. UP-MHNFCP-154769; scale bar 5 mm.

1.4.5.2. Associated large *Taeniopteris*-like leaves

Specimen UP-MHNFCP-154766 (holotype) shows several large incomplete taeniopterid leaves (Plate XX, 2, 3) associated with smaller fertile leaves (Plate XX, 1). Leaves appear coriaceous and probably originally were spatulate, but neither apices nor bases are preserved (Plate XXIII, 1, 2). Lateral margins are entire and taper very gradually towards the base. Leaves are more than 90 mm long and 30 mm wide (in widest part of leaves). Midribs are rigid, longitudinally striated, and 3 mm wide (Plate XXIII, 3). Lateral veins are thin, arise at an acute angle (10°) (Plate XXIII, 1, 3; Figure 25C, D), sometime essentially parallel to midrib (often coincide with midrib), thereafter arch strongly before extending to leaf margin, and branch once or twice in close succession near the midrib. A third bifurcation occurs irregularly near the leaf margin (Plate XXIII, 1, 3; Figure 26C, D). The first bifurcation close to the midrib may be overlapped by the midrib. This would occur if the abaxial surface was exposed. Lateral veins reach the lateral margin at 70–80°. The venation density is 20–28 veins per 10 mm of leaf margin. The venation pattern may differ on either side of the midrib (e.g., density, frequency of branching, and angle of the veins) (Plate XXIII, 1).

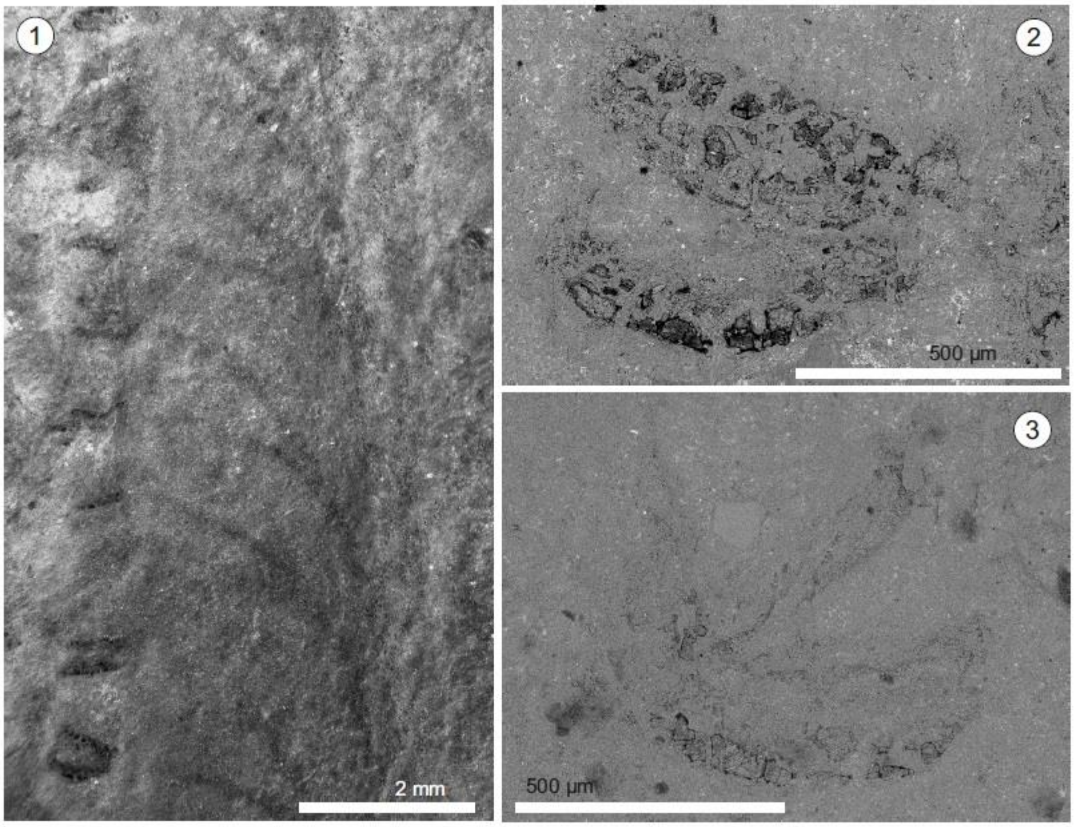

Plate XXII – Fertile leaf ***Ilfeldia gregoriensis* sp. nov.** from specimen No. UP-MHNFCP-154766. 1) Detail of venation and synangia placed on the end of lateral veins. 2, 3) SEM image of synangium composed of two sporangia.

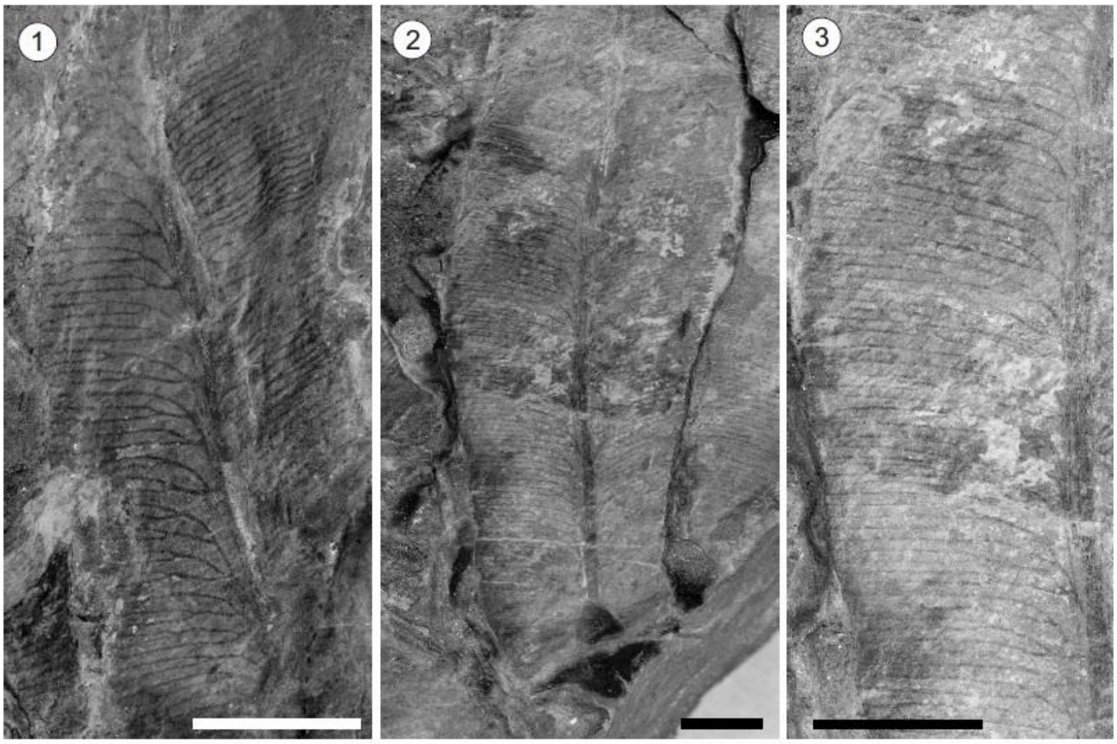

Plate XXIII – Large leaves of *Taeniopteris* cf. *carnoti*, all figures of specimen No. UP-MHNFCP-154766. 1) The venation on one left side of a leave is different from the venation on the right side of midrib; specimen; scale bar 10 mm. 2) The shape of leaf with strong midrib; specimen; scale bar 10 mm. 3) Detail of venation of leaf; specimen; scale bar 10 mm.

1.4.5.3. Description of holotype of *Ovulepteris robusta* nov. comb.

Holotype is represented by specimens E1303. Specimen is poor preserved. Coal material for is missing which does not allow us to get leaf or seed cuticle details. Fertile leaf is incomplete, more than 55 mm long and 12 mm wide. Leaf lamina is partly reduced, c. 1/4–1/3 whole pinnule lamina width on each side of midrib. Midrib is strong c. 2 mm broad, longitudinal striated, lateral veins arise at acute angle, twice dichotomized, arched, ending near the protruded leaf margin. The venation density is 5–6 veins per 10 mm of leaf margin. Ovules are placed on protruded marginal leaf segment. Protruded leaf margin partly covered ovules (c.1/3 of ovule) and they are closely invested by foliar lamina. They are probably attached to end of lateral veins, because vein is not visible on leaf margin which covered ovule from upper side and where is visible true margin. Ovules are represented by are small rounded or ellipsoid bodies, having 1.5–2 mm in diameter with granulated outer surface. These ovules are probably consist of a convex inner part and a more flattened outer part. The flattened outer part is not well visible but they are preserved by imprints surrounding these bodies oriented by micropyle toward midrib.

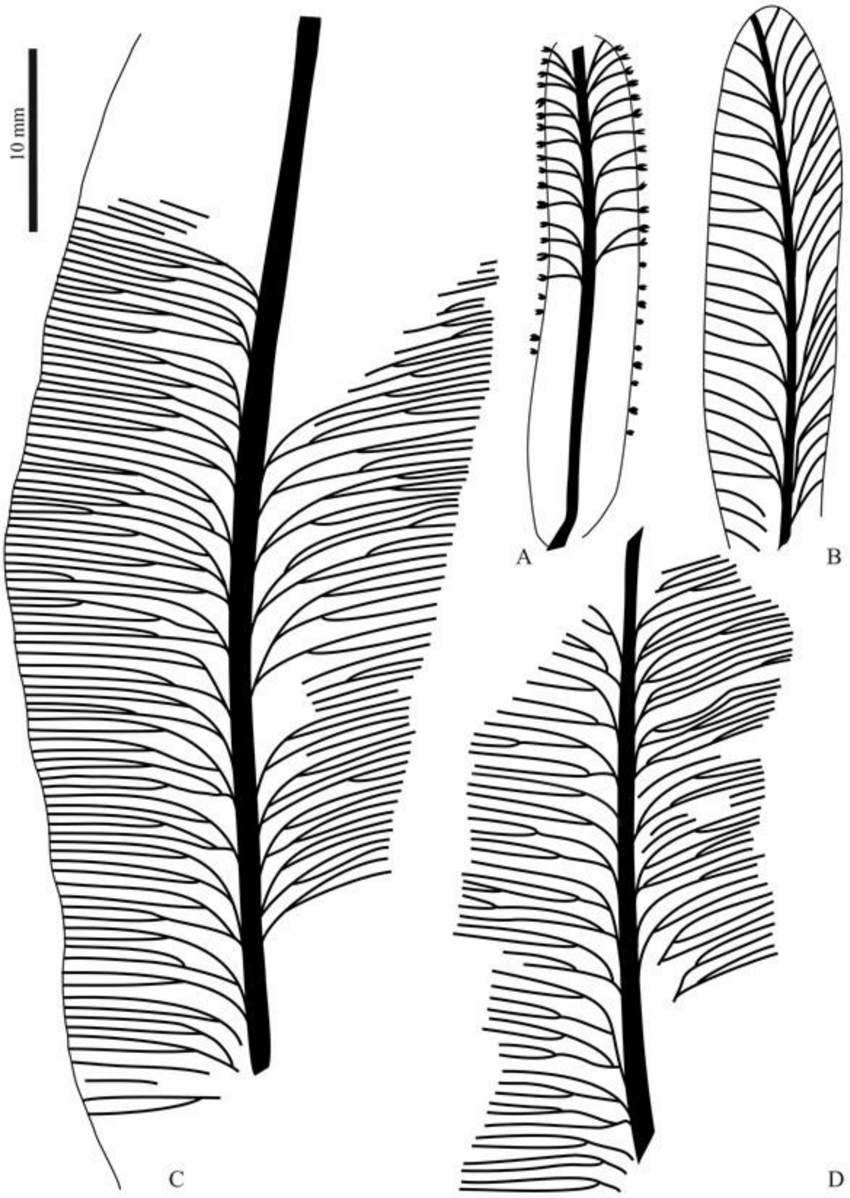

Fig. 26 – Venation diagrams of leaves remains of ***Ilfeldia gregoriensis* sp. nov.** (A, B) and *Taeniopteris* cf. *carnoti* (C, D). A) Fertile leaf from specimen No. UP-MHNFCP-154766. B) sterile specimens from specimen No. UP-MHNFCP-154767, C, D) Sterile leaves from specimen No. UP-MHNFCP-154766.

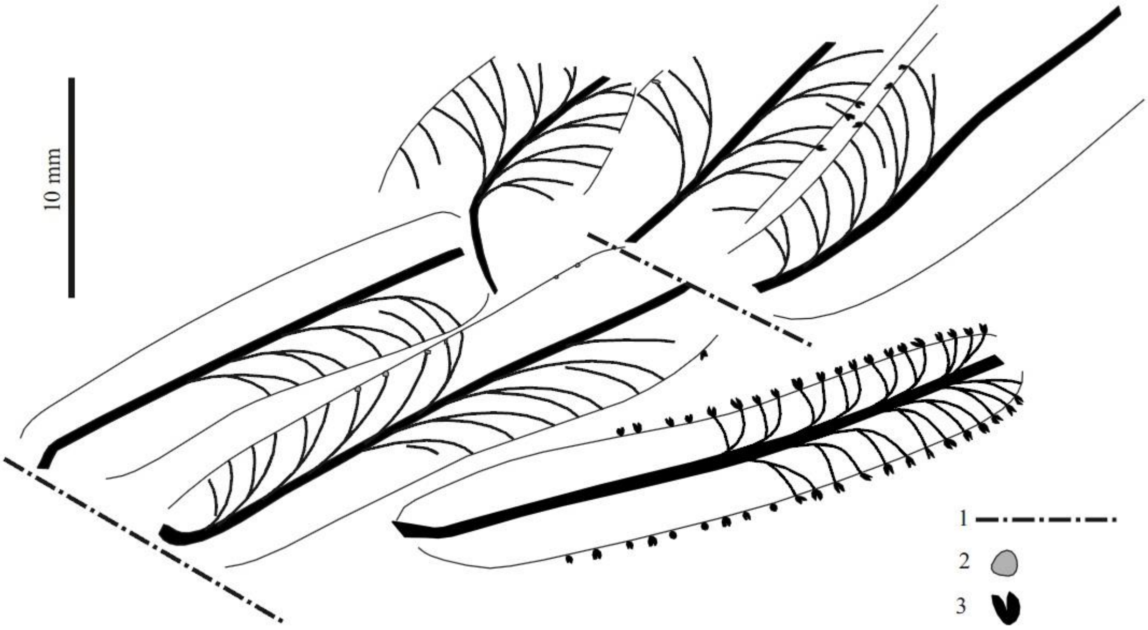

Fig. 27 – Fertile leaves of ***Ilfeldia gregoriensis* sp. nov.** in probable pinnately frond organization. 1) Probable location of rachis; 2, 3) Synangia.

1.4.6. Systematic part

Division: Incertae sedis
Order: Incertae sedis
Family: Incertae sedis
Genus: *Ilfeldia* Remy, 1953

Emended diagnosis: Leaves pinnately organized, oblong, taeniopterid type; leaf lamina not significantly reduced; each lateral vein terminated by synangium that extend beyond leaf margin; reproductive organs are synangia with free or fused sporangia.

Assigned species: *Ilfeldia jejunataeformis* sp. nov. and *Ilfeldia gregoriensis* sp. nov.

Type species: *Ilfeldia jejunataeformis* sp. nov.

Species: *Ilfeldia jejunataeformis* sp. nov.

1953 *Ilfeldia jejunata* Remy, p. 24, pl. 5, fig. 6, pl. 6, figs 1–10, pl. 7, figs 1–7.

Locality: Ilfeld locality, Ilfeld Basin, Germany

Horizon: Gzhelian (late Stephanian) age

Etymology: Species *jejunataeformis* is named based on similarity with sterile leaves of *Taeniopteris jejunata*.

Diagnose: Leaves conical or lanceolate fractionally reduced; leaf margins dentate, very tapered towards the apex and base from the middle part of leaf; midrib is strong, slightly longitudinally striated, extending to apex; lateral veins thin, arise at an acute angle, firstly parallel to the midrib and later flat arched, twice rarely thrice dichotomized and terminating at the edge at 80–90°; venation density is 10 veins per 10 mm on lateral margin; each vein terminated by cash-shaped synangium that situated in to tooth and extend beyond leaf margin; Synangia composed of six fused sporangia 0.35–0.42 mm long, which contain oval, smooth monolete spores, 32 µm in diameter.

Nomenclature remark: Remy′s (1953) specimens show similarity with sterile leaves of *Taeniopteris jejunata* and based on this fact Remy (1953) named his species *jejunata*. Nevertheless, there is no certainty that Remy´s (1953) fertile leaves and sterile leaves of *Taeniopteris jejunata* belong into the identical fossil-species. Due to this fact we suggest to use rather new species name *jejunataeformis* for fertile leaves which were described by Remy (1953) and species name *jejunata* can be fixed for sterile leaves of *Taeniopteris*.

Ilfeldia gregoriensis **sp. nov.**

Plate XX, 1, 4; Plates XXI, XXII; Figure 28B

Holotype: Specimen UP-MHNFCP-154766 (Plate XX, 1, 4; Plate XXI, 1–5) stored in the NHMSUP.

Paratypes: Specimens UP-MHNFCP-154767–154769 (Plate XXI, 6–8) stored in the NHMSUP.

Locality: Outcrop located in the São Pedro da Cova region, DCB, Portugal; Coordinates (WGS84): 41°09´44.60´´N, 08°30´23.10´´W.

Horizon: Laminated grey mudstone; UTS D1 established by Pinto de Jesus (2001, p. 148; Figure 25); lower Gzhelian (lower Stephanian C), Upper Pennsylvanian.

Etymology: "*gregoriensis*" is named in honour of the paleontologist Dra. Mena Schemm-Gregory (Geosciences Center of the University of Coimbra, Portugal), a world expert on fossil brachiopods, who tragically died in 2013 at age 36.

Diagnosis: Leaves oblong; leaf margins entire and essentially parallel, very slightly tapered towards the apex and base from the middle part of leaf; midrib is strong, slightly longitudinally striated, extending to apex; lateral veins thin, arise at an acute angle, once (rarely twice) dichotomized near the midrib, and arching to reach lateral margin at 78–80°; venation density is 12 veins per 10 mm on lateral margin; each vein terminated by synangium that extend beyond leaf margin; synangia composed of two (rarely three) sporangia, 0.6–0.7 mm long, and 0.5 mm wide; reniform sporangia tapering to distal end, 0.5–0.6 mm long and 210 µm wide, attached to short receptacle 70 µm long and 200 µm wide.

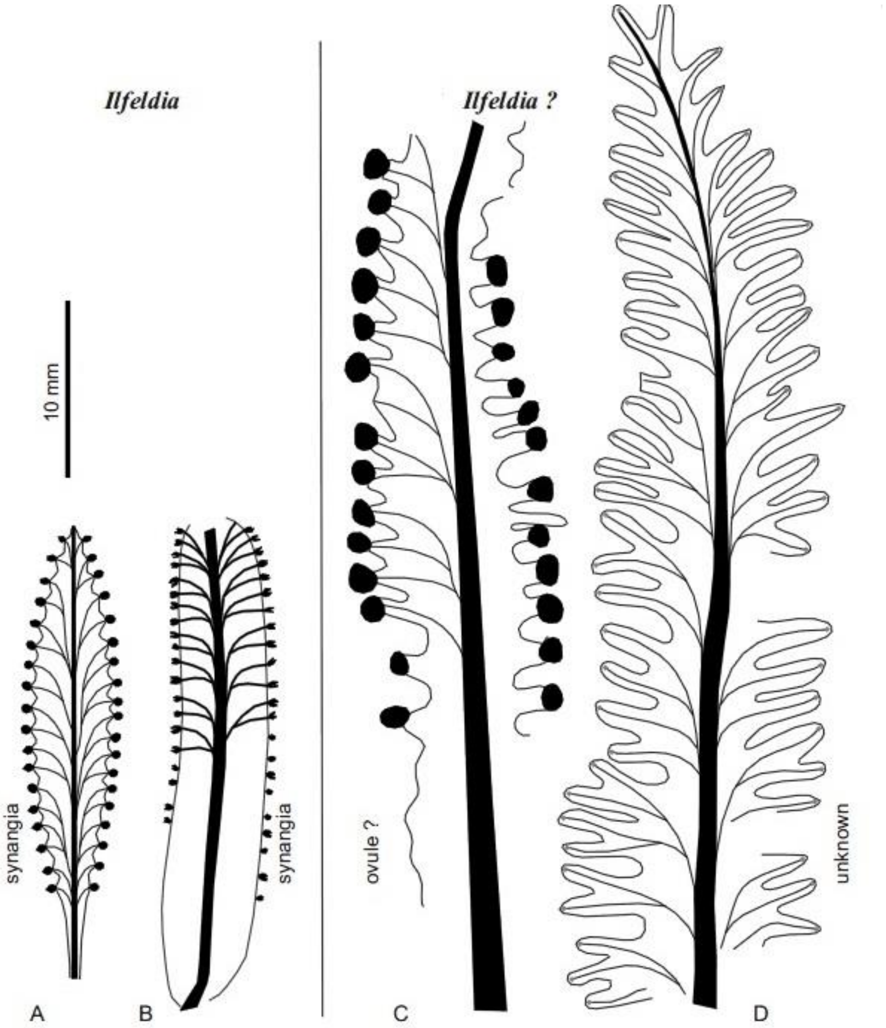

Fig. 28 – Comparison of known *Ilfeldia* specimens. A) *Ilfeldia jejunata* according to Remy (1953) bearing synangia, B) ***Ilfeldia gregoriensis*** **sp. nov.** bearing synangia, C) "*Ilfeldia*" *robusta* according to Obrhel (1975) bearing probably ovule and D) "*Ilfeldia*" *lobecensis* according to Obrhel (1965) where the type of reproductive organs is unknown.

Division: Pteridospermopsida?
Order: incertae sedis
Family: incertae sedis
Genus: *Ovulepteris* gen. nov.

Diagnose: Leaves oblong; midrib strong, taeniopterid type; leaf lamina partly reduced; each lateral vein terminated by ovule-like reproductive organ, placed on the end of protrusion leaf margin; proximal part of leaf lamina sterile.

Assigned species: *Ovulepteris robusta* (Obrhel) nov. comb., probably *O. lobecensis* (Obrhel) nov. comb. (see Figure 29).

Remarks: We included *O. lobecensis* to this new genus based on similarity of leaves. Nevertheless, the types of reproductive organs are unknown and due this fact affinity to this genus is still questionable.

Type species: *Ovulepteris robusta* (Obrhel) nov. comb.

Species *Ovulepteris robusta* (Obrhel, 1975) nov. comb.

Basionym - 1957 *Ilfeldia robusta* Obrhel p. 548, pl. 2, figs 1–3.

Holotype: Specimen E1303 stored in the National Museum, Prague, Czech Republic.

Locality: abandoned quarry located near the village Kvíček, southwes of Slaný, Kladno-Rakovník Basin, Czech Republic.

Horizon: grey/ocher laminated mudstone, Hředle member, Slaný Formation, Kasimovian (Stephanian B), Upper Pennsylvanian.

Diagnosis: Fertile leaf more than 55 mm long and 12 mm wide; leaf lamina partly reduced c. 1/4–1/3 whole pinnule lamina width on each side of midrib; midrib strong, longitudina striated; lateral veins arise at acute angle, twice dichotomized, arched, ending near the protruded leaf margin; venation density is 5–6 veins per 10 mm of leaf margin; ovule placed on protruded marginal leaf segment; protruded leaf margin partly covered ovules; ovules are small, rounded or ellipsoid, having 1.5–2 mm in diameter with granulated outer surface.

1.4.7. Discussion

1.4.7.1. Comparison of *Ilfeldia gregoriensis* sp. nov. with *Ilfeldia jejunataeformis* sp. nov.

The fossil-genus *Ilfeldia* was established by Remy (1953) based on fertile material from the Ilfeld locality, Ilfeld Basin, Germany. Remy (1953, p. 24) characterized the fossil-genus as rudimentary, conical or lanceolate leaves bearing synangia composed of six fused sporangia with a central cavity. The primary issue is that Remy (1953) assumed the sterile leaves associated with the fertile leaves belonged to *Taeniopteris jejunata* of Grand′Eury (1877), and despite the lack of organic connection or certainty of identity with *T. jejunata*, used the same specific epithet jejunata in erecting the type species of his new fossil-genus *Ilfeldia*. Remy (1953, p 29) described fertile leaves of *Ilfeldia jejunata* (*I. jejunataeformis* sp. nov. in this paper; see Figure 29) as: "*…conical or lanceolate leaves having a blunt dentate margin and a thick midrib. The lateral veins rise from a thick midrib, where lateral veins are parallel to the midrib and later flat arched and terminating at the edge at an angle of 80–90 degrees. Lateral veins are once dichotomized close to the midrib. Triple bifurcation of lateral veins is very rare. The fertile leaves are max. 29 mm long and 7 mm wide with c. 25 synangia attached to leaf margins on both sides of the leaf. Synangia are composed of six fused sporangia 0.35–0.42 mm long, which contain oval, smoohh monolete spores, 32 µm in diameter…*" (free translation from German). In comparison, *Ilfeldia gregoriensis* sp. nov. has oblong leaves that are ca. 34 mm long and 6 mm wide, with entire lateral margins, and a strong midrib that is slightly longitudinally striated and runs to the apex. Thin lateral veins arise at an acute angle, are once-dichtomized near the midrib, and arch before reaching the lateral margin at 78–80°. Each vein is terminated by synangium that overlap the leaf margin, and the leaf lamina is not reduced. Reproductive organs are represented by synangia composed of two (rarely three) reniform sporangia that taper distally and are 0.5–0.7 mm long and 0.21 mm wide. The size of leaves of *Ilfeldia jejunataeformis* sp. nov. and *Ilfeldia gregoriensis* sp. nov. are similar, but *Ilfeldia gregoriensis* sp. nov. has entire margins and *Ilfeldia jejunataeformis* sp. nov. has dentate margins. The reproductive organs of both species show significant differences. *Ilfeldia gregoriensis* sp. nov. has synangia with two (rarely three) free sporangia that are attached to pedicel, whereas *Ilfeldia jejunataeformis* sp. nov. has cash-shaped synangia that consist of six fused sporangia (Remy 1953).

Barthel *et al.* (1975) and Barthel (2006) published on fertile leaves assigned to *Taeniopteris* (*Ilfeldia*) *jejunata* from the Manebach Formation, Rotliegen, Germany. Barthel (2006, p. 65) figured on fig.152 specimen which exhibits ovulate reproductive organs that are marginally arranged on a partly reduced leaf lamina in the distal part of a leaf. The proximal part of the leaf is lacking reproductive organs, and instead has the typical development of a leaf lamina with taeniopterid venation. Nevertheless, in our opinion, the character of the reproductive organs does not correspond with Remy’s (1953) original concept of *Ilfeldia*, which he defined as having synangia that terminate lateral veins and occupy both margins from the distal to basal part of a leaf. Based on this fact, the specimen described by Barthel *et al.* (1975) and Barthel (2006) does not represent a species of *Ilfeldia* but rather a new genus *Ovulepteris* gen. nov.

1.4.7.2. Comparison of *Ilfeldia gregoriensis* nov. sp. with similar *Taeniopteris* species

Sterile leaves of *Ilfeldia gregoriensis* sp. nov. (Plate XXI, 6–8) closely resemble those of *Taeniopteris schlotheimi* Remy & Remy (Remy and Remy, 1975) both in venation pattern and leaf size (*T. schlotheimi* is 50 mm long and 7 mm wide, and *Ilfeldia gregoriensis* sp. nov. is ca. 34 mm long and 6 mm wide). However, these fossil-species differ in some morphological features. *Taeniopteris schlotheimi* bears leaves with an acute apex and cordate base (Remy and Remy, 1975, pl. 4, figs. 9–10; pl. 5, fig. 1; table 2; see also Hickey, 1977, appendix fig. 4), whereas leaves of *Ilfeldia gregoriensis* nov. sp. presumably have a rounded to retuse/emarginate apex and a truncate base (Plate XXI, 8), permitting differentiation. Barthel (2006, p. 64) synonimized *Taeniopteris schlothemii* with *T. jejunata*. Based on our opinion *Taeniopteris schlothemii* and *T. jejunata* species have different type of leaf bases and we suggest keeping separated both species. Nevertheless, it is worth querying whether or not the *T. schlotheimi*-leaf form (Remy and Remy 1975, p. 35, fig. 1) actually should be placed in the fossil-genus *Taeniopteris* sensu stricto, given its venation pattern where lateral veins are sparsely organized on leaf margin, arise at an acute angle and once- or twice-dichotomized, which is similar to venation of pinnules of the fossil-genus *Desmopteris* Stur [as mentioned by Remy and Remy (1975)] or some marattialean taxa such as *Pecopteris major* (Doubinger) Vetter or *Pecopteris ticleanue* Popa & Pšenička (Popa and Pšenička, 2010). Nevertheless, pinnules in the fossil-taxa *Desmopteris*, *Pecopteris major* and *P. ticleanui* are attached to the supporting rachis by their entire base, whereas leaves of *Taeniopteris schlotheimi* have a cordate or truncate base. But in many cases we have not preserved leaf base in taeniopterid specimens. These examples demonstrate the difficulty of working with the artificial fossil-genus *Taeniopteris*.

Leaves of *Ilfeldia gregoriensis* sp. nov. also are comparable to *Taeniopteris bertrandiana* Teixeira, especially in venation density, with both fossil-species having 12 veins per 10 mm of leaf margin. Teixeira (1940, p. 14, pl. 9, fig. 1) established *T. bertrandiana* based on distal fragments of sterile leaves from a different locality in the Douro Basin. Teixeira (1940, p. 14) described *T. bertrandiana* leaves as having perfectly rounded apices, straight and parallel lateral margins, and reaching about 30 mm wide. The midrib extends to the top of the leaf. Lateral veins arise from the midrib at an acute angle, branch twice near the base, resulting in four veins that reach the edge of the leaf at close to 90°. However, leaf figured by Teixeira (1940) on plate 9, figure 1 is oblanceolate with rather broadly acute apex and lateral margins which are tapered to base. Due to this fact several differences exist between *T. bertrandiana* and *Ilfeldia gregoriensis* sp. nov. *Taeniopteris bertrandiana* has leaves 70 mm long and 30 mm wide, whereas *Ilfeldia gregoriensis* sp. nov are 34 mm long and 6 mm wide. Pronounced oblanceolate leaf of *T. bertrandiana* is quite different to *Ilfeldia gregoriensis* sp. nov. which has oblong (Plate XXI, 6) or spathulate (Plate XXI, 8) leaves. Furthermore, *I. gregoriensis* sp. nov has thin lateral veins that arise at an acute angle, are once (rarely twice) dichtomized in close succession near the midrib, and terminate at the lateral margin at 78–80°, whereas *T. bertrandiana* has parralel lateral veins that branch twice in close succession near the midrib, yielding four veins that reach the edge of the leaf at angles close to 90°.

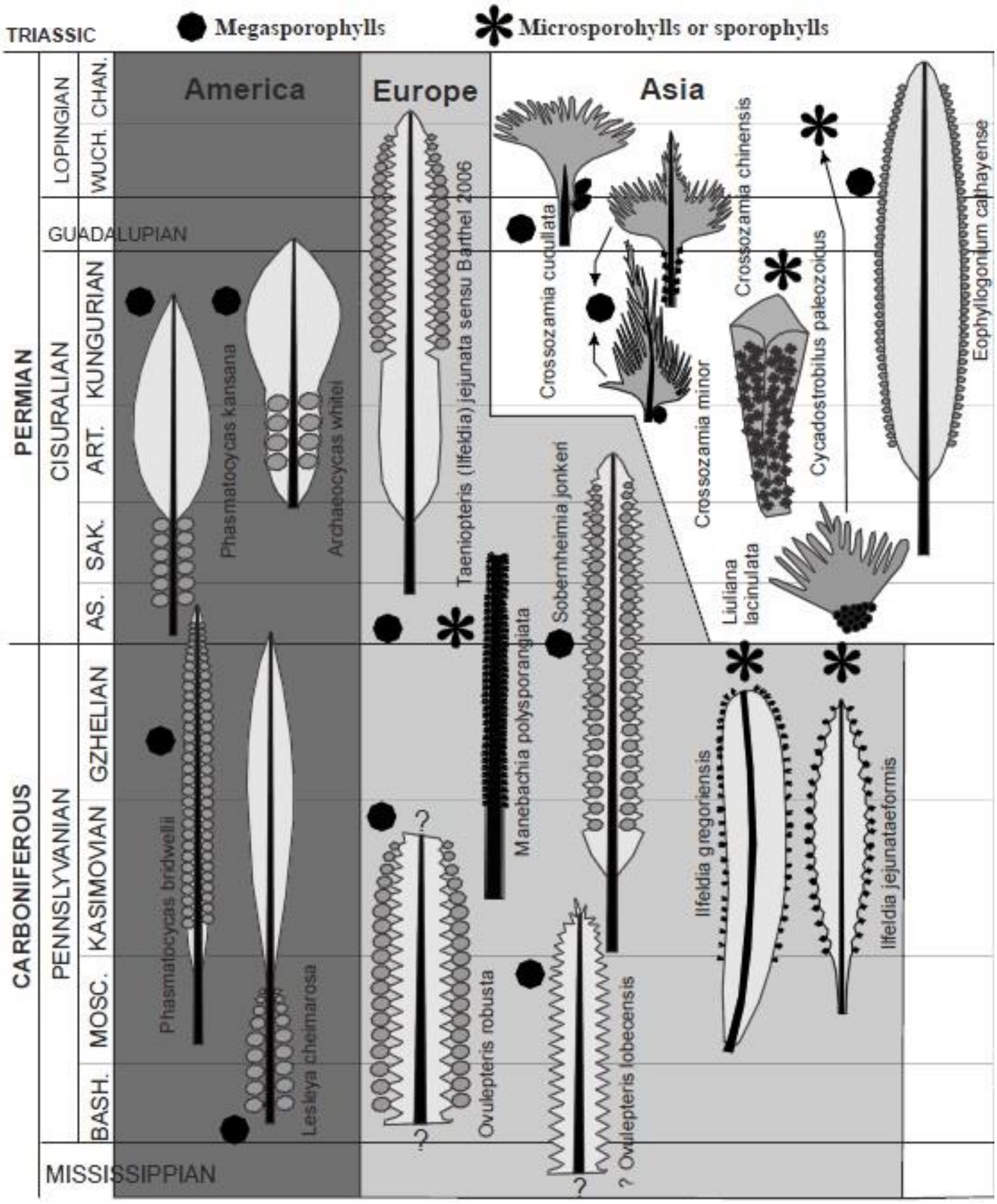

Fig. 29 – Idealized megasporophylls, microsporohylls or sporohylls of some cycad-like or pteridosperm plants in context with stratigraphicall and geographic occurrence (Pšenička *et al.*, in press).

1.4.7.3. Comparison of large *Taeniopteris* leaves which are associated of *Ilfeldia gregoriensis* sp. nov. with known fossil-species of *Taeniopteris*.

A clear concept of the diagnostic characters of the fossil-genus *Taeniopteris* remains elusive. Brongniart (1828) established *Taeniopteris* for simple, linear leaves with parallel lateral margins, a strong midrib, and lateral veins that are unbranched or bifurcate near the midrib before running perpendicular to the lateral margin. As currently employed, this artificial fossil-genus comprises a heterogeneous group of foliar forms, ranging from individual, strap-shaped leaves to pinnately organized fronds with large and more or less petiolate leaves. Tens of species have been established and described (e.g., Weiss, 1869; Halle, 1927; Zeiller, 1894; Remy and Remy, 1975; Mamay, 1973, 1976; Taylor, 1981; Barthel, 2006; Taylor *et al.*, 2009; and many others), but the quality of specimens and descriptions differs greatly among the erected fossil-species, making assignment to any given species challenging.

The venation density of studied specimens (Plate XXIII; Figure 26C, D) is 20–28 veins per 10 mm, which is comparable to several species, including *Taeniopteris abnormis* von Gutbier, *T. multinervia* Weiss, *T. acutangula* Kawasaki, *T. angelica* White, *T. angustifolia* Stockmans & Mathieu, *T. camptoneura* Jongmans, *T. carnoti* Renault & Zeiller, *T. doubingerii* Remy, *T. incrassata* Jongmans & Gothan, *T. integra* Stockmans & Mathieu, *T. mucronata* Kawasaki, *T. punctulata* Kawasaki, *T. serrata* Halle, *T. tenuis* Doubinger, *T. tingii* Halle, *T. tongshanensis* Stockmans & Mathieu, *T. yernauxi* Stockmans & Mathieu and *T. zeilleri* Bertrand. However, based on midrib thickness (3 mm) and leaf width (30 mm), the number of fossil-species comparable to the study material can be reduced to *T. acutangula*, *T. angelica* or *T. carnoti*.

Taeniopteris acutangula (Kawasaki, 1931, 1934), which is only known from South Korea, has leaves that reach 40 mm wide, a 4 mm thick midrib, and lateral veins that arise from the midrib at an angle near under 10º–20° which is comparable with Portugal specimen.

Taeniopteris angelica was described by White (1929, p. 93) as having leaves that are 45 mm wide, and a midrib that is 4 mm wide at the base and tapers to 1.2 mm wide at the distal end). White (1929) described the lateral veins as simple or once dichotomizing close to the midrib and running parallel to the margin. In the material at hand, a third bifurcation occurs irregularly near the leaf margin. White (1929) also characterized *T. angelica* as having very long, ribbon-like leaves that have nearly parallel lateral margins over much of their length, but that taper very gradually proximally and distally. In contrast, the study specimens have lateral margins that slowly taper towards the base (Plate XXIII, 2).

Taeniopteris carnoti was described by Renault and Zeiller (1888, p. 282) from the Commentry Basin of France, and is characterized by 25–30 mm wide leaves with a strong midrib (5–6 mm wide), longitudinally striuated, Lateral veins are simple or once dichotomizing close to the midrib under acute angle and running arched to the margin, 25–30 veins per centimetre of leaf margin. Renault and Zeiller (1888) figured specimen (holotype) on pl. 22, fig. 10. This specimen is represented by small fragment of middle part of leaf. There is engraving figures, not photographs, and we cannot be sure of identity with original specimen. Renault and Zeiller (1888) stated that lateral wins are simple or once dichotomizing close to the midrib, but specimen shows (Renault and Zeiller, 1888, pl. 22, fig. 10A) a third bifurcation occurs irregularly near the leaf margin which is comparable with material at hand. The problem is that is not well visible how lateral veins ongoing from midrib on specimen figured by (Renault and Zeiller, 1888, pl. 22, figs. 10, 10A). There is not visible any parallel lateral veins close to midrib. It may be due to fact that proximal part of lateral veins often coincide with midrib. This may indicates that the authors Renault and Zeiller (1888) included this part of the midrib in width midrib. The main difference of *T. carnoti* and Portugal specimen is in course of lateral veins from midrib to margin. Lateral veins of *T. carnoti* slowly arched to the margin [as shows specimens on pl. 22, figs. 10, 10A (Renault and Zeiller, 1888)], while lateral veins in material at hand arch strongly near midrib and going more or less parallel to the margin. Unfortunately, it is impossible to verify because original specimen figured by Renault and Zeiller (1888, pl. 22, fig. 10) is lost. However, the similarity of the two specimens is so great that Portuguese material can represent this species.

1.4.7.4. Discussion on the relationship of leaves of *Ilfeldia gregoriensis* sp. nov. and associated *Taeniopteris* leaves from Douro Basin

Specimen UP-MHNFCP-154766 (Plate XX) includes associated leaves of the fossil-species *Ilfeldia gregoriensis* sp. nov. and *Taeniopteris* cf. *carnoti*, respectively. The two forms may reflect leaf dimorphism, with *Ilfeldia gregoriensis* sp. nov. representing fertile leaves and *Taeniopteris* cf. *carnoti* (Plate XX, 2, 3; Plate XXIII) representing the large sterile leaves of a single parent plant. However, this hypothesis is not supported by the fact that small sterile (Plate XXI, 5–8) and fertile (Plate XXI, 1, 5) leaves assignable to *Ilfeldia gregoriensis* sp. nov., both approximately the same size and with a similar venation pattern, are occur together with large leaves of *Taeniopteris* sp. Plate XXI, 5 illustrates several small leaves (with a pinnatifid organization) with clearly attached synangia, leaves with marked impressions that probably represent detached synangia, and leaves with no sporangia. As such, the possibility that the sterile leaves represent leaves on which the sporangia had yet to develop cannot be ruled out. If such developmental stages are indeed represented, the implications are that it is not possible to strictly separate the fertile and sterile leaves, both of which belong to a smaller form assigned herein to *Ilfeldia gregoriensis* sp. nov. Furthermore, the possibility remains that *Ilfeldia gregoriensis* sp. nov. represents the fertile leaves and *Taeniopteris* sp. represents the sterile leaves of a single parent plant. Similar association fertile leaves and sterile taeniopterid leaves is possible observed in many fossil-species.

1.4.7.5. Comparison of *Ilfeldia* with fossil-taxa bearing marginal synangia

1.4.7.5.1. Comparison with *Manebachia* Remy & Remy

Ilfeldia resembles the fossil-genus *Manebachia*, which was established by Remy and Remy (1958) based on specimens from the Permian of Germany and is represented only by the fossil-species *Manebachia polysporangiata* Remy & Remy. Remy and Remy (1958, p. 10) published the following diagnosis for *Manebachia*: "...*Sporophylle fläching, mit rundlich gestellten, freien Sporangien. Sporangien ringlos...*", translating as "*Sporophyll flat, free sporangia attached to margin, sporangia ringless*". This brief diagnosis could be equally applied to Remy′s (1953) fossil-genus *Ilfeldia*. Nevertheless, *Manebachia* is characterized by flat, veinless, sporophylls that bear basally fused, small, free sporangia, arranged marginally on an extremely reduced leaf lamina or directly on the midrib. The sporophyll is 80–100 mm long and 11–12 mm wide, and is equipped with 18 to 20 sporangia per 10 mm of margin, which are grouped into synangia with two to four basally fused sporangia that are 3 mm long and 0.5 mm wide (Remy and Remy, 1958; Barthel, 2006). As such, *Manebachia* differs significantly from *Ilfeldia* in the following characters: leaf lamina of *M. polysporangiata* is distinctly reduced and veinless, whereas true *Ilfedia* species do not have a reduced (e.g., *I. gregoriensis* sp. nov.) or fractionally reduced (e.g., *I. jejunata*) leaf lamina and lateral veins are well developed. The reproductive organs of *Ilfeldia* are placed over the vein endings on the margin of leaf lamina, whereas the attachment of reproductive organs of *Manebachia* is not clearly understood (Remy and Remy, 1958; Barthel, 2009), either being attached to very reduced leaf lamina or directly to the midrib. According to Barthel (2006) *M. polysporangiata* represents the pollen organ of the plant that bore *Taeniopteris jejunata* leaves. This opinion is based on the fact that Barthel (2006) found the fossil-species *Taeniopteris jejunata*, *Ilfeldia jejunata* sensu Barthel (2006) and *Manebachia polysporangiata* at the same area and strata. However, we consider this opinion speculative.

1.4.7.5.2. Comparison with some true ferns with marginal synangia/sporangia

Marginally arranged reproductive organs are known from several true ferns, including *Zeilleria* Kidston, *Senftenbergia* Corda, *Boweria* Kidston or *Acrangiophyllum* Mamay. In all of these fossil-genera, sporangia are attached to sphenopteroid and pecopteroid pinnules unlike those of *Ilfeldia* leaves. Nonetheless, although some similarities are worthy of note.

Although *Zeilleria* has undergone detailed analysis (e.g., Corsin, 1927; Thomas and Crampton, 1971; Pšenička, 2005), the character of the reproductive organs remains indistinct. Pšenička (2005) presented the most detailed study of the reproductive organs of *Zeilleria zodrowii* Pšenička based on in situ material preserved in three dimensions in volcanic ash (Whetstone Horizon, Kladno Formation, Moscovian), in the Pilsen Basin, Czech Republic. According to Pšenička (2005), the synangia of *Z. zodrowii* are borne on sphenopteroid pinnules, with short and broad pedicels that extend from the end of lateral veins (3–5 synangia per pinnule). Synangia are oval, 0.6–0.8 mm long and 0.8–1.3 mm wide, and consist of five to eight (most commonly seven) exannulate sporangia and a unique inner-outer synangial sheat. Sporangia are placed between the inner-outer synangial sheat, attached to the inside tunic by a special inside column. The distal end of the outside tunic is divided into free ending segments, creating a relatively free lapel-like segment. Monolete spores are very small and of the *Laevigatosporites*-*Latosporites*-type. The reproductive organs of *Zeilleria zodrowii* are unique and unknown in any other plant group, and it is not clear if the affinity is with the true ferns or if the fossil-species is the pollen organ of a pteridosperm. Common features between *Zeilleria* and *Ilfeldia* include the fact that reproductive organs are represented by synangia that are marginally arranged on pinnules. Furthermore, according to Remy (1953), *Ilfeldia jejunataeformis* sp. nov. has fused sporangia filled with monolete spores, as found in *Z. zodrowii*. Remy (1953) also compared his material with *Zeilleria*. Nevertheless, the morphology of pinnules/pinnae differs considerably between the fossil-genera, although due to the great intrataxonomic variability in leaf form in some fern genera, a relationship between *Zeilleria* and *Ilfeldia* cannot be ruled out.

Acrangiophyllum was established by Mamay (1955) based on fertile material from Alabama, USA. Mamay (1955, p. 181) described the fossil-genus as fern with sphenopteroid pinnules that bear a single, marginal, eusporangiate, exannulate, sessile sporangia. It remains unclear if what was referred to as sporangia which represents a true sporangia of a cryptogam, or is the pollen organ of a seed plant. The organizations of the reproductive organs, which terminate on the lateral veins on each pinnule lobe on the margin, broadly resemble the organization of the reproductive organs in *Ilfeldia jejunata*. Nevertheless, Mamay (1955) recognized the reproductive organs of *Acrangiophyllum* as single eusporangiate and exannulate sporangia, whereas *Ilfeldia* has synangia that consist of two (rarely three) sporangia.

Worth noting is the comparison between the reproductive organs of *Ilfeldia* and some members of the true fern families Tedeleaceae, including *Senftenbergi plumosa* and *Tedelea glabra* (Baxter) Eggert & Taylor of late Paleozoic age (Bek and Pšenička, 2001; Pšenička and Bek, 2003), and Schizaeaceae of Jurassic age (Taylor *et al.*, 2009). All members of these families have marginally arranged reproductive organs attached to variably shaped pinnules. However, here the similarity between fossil-genera largely ends, as fossil-species of the Tedeleaceae and Schizaeaceae have individual or grouped (clustered) annulate sporangia with an apical annulus, whereas the reproductive organs of *Ilfeldia* are synangia that consist of exannulate sporangia.

Nonetheless, it is noteworthy that some fossil and extant members of the Schizaeaceae namely the genus *Lygodium* (climbing fern), exhibit pronounced leaf dimorphism (Manchester and Zavada, 1987), with fertile pinnae represented by cone-like structures (sorophores) that protrude from the edge of the pinnule lamina. Such dimorphism recalls the association of fertile *Ilfeldia* leaves with rather different sterile *Taeniopteris*-like leaves, which may represent elements one parent plant. The leaves of some extant *Lygodium*, such as *L. salicifolium* Zhang & Hanks (Zhang and Hanks, 2013), resemble the leaves of *Ilfeldia*. Ultimate pinnules of *Lygodium salicifolium* are 40–150 mm long and 5–20 mm wide, have a truncate to cordate base and acute and attenuate or sub-obtuse apex, and the lateral margins of sterile pinnules are finely crenate-serrate (Zhang and Hanks, 2013). Nevertheless, the reproductive organs of *L. salicifolium* are sorophores, which are not known in *Ilfeldia*. This comparison was provided to demonstrate the necessity of taking into account the possibility that *Ilfeldia* may be a representative of the true ferns.

Similarities with *Boweria* are only in the organization of fertile organs, which are situated on the end of lateral veins on the pinnule margin. Nevertheless, *Boweria* pinnules are strictly of the sphenopteroid type, comprising individual marginal sporangia (Frojdová *et al.*, in press).

The cask-shaped synangia of *Ilfeldia jejunata* also is known from the 'unita group' of marattialean ferns (Pšenička, 2005), such as *Diplazites* Göppert, *Ptychocarpus* Weiss or *Cyathotrachus* Watson [Millay (1977) transferred species from Cyathotrachus into the fossil-genera *Acaulangium* Millay and *Scolecopteris* Zenker]. Members of these fossil-genera have reproductive organs borne in two rows, one on each side of the pinnule midrib. Synangia are covered by a coating and comprise several sporangia, which is comparable with *I. jejunata* (but not with *I. gregoriensis* sp. nov.). Synangia of *Diplazites* or *Ptychocarpus* are attached to a receptacle and the sporangia are clavate with an obtuse distal end (Pšenička, 2005). Pinnule morphology only is well known for *Diplazites*, as this fossil-genus was described based on compression material.

Diplazites pinnules are tongue-shaped, and fused nearly to the bluntly rounded apex or barely united its basal parts, with a generally distinct venation pattern. Undivided lateral veins arise from the midrib at wide angles and arch upwards to reach the pinnule margin at a very sharp angle (Pšenička, 2005). Differences between *Ilfeldia* and members of the 'unita group' include the position of reproductive organs, being marginally arranged in *Ilfeldia* and situated between the margin and midvein in the 'unita group'. The pinnule morphologies and venation patterns also are significantly different, as ferns of the 'unita group' have pecopteroid pinnules with lateral veins that arise from the midvein at wide angles and arching upwards, whereas *Ilfeldia* has large leaves with lateral veins that arise from the midrib at an acute angle, arch downwards, and are once or twice dichotomized. Nevertheless, the character of the synangia of *Diplazites*, *Ptychocarpus* and *Cyathotrachus* are very similar to fossil-species of *Ilfeldi*a.

1.4.7.6. Comparison of *Ovulepteris* gen. nov. with the other ovule bearing taxa attached to taeniopterid leaves.

1.4.7.6.1. Comparison with *Eophyllogonium* Meit *et al.* and *Gigantonomia* Li & Yao

Ovulepteris gen. nov. can be compared with the fossil-genus *Eophyllogonium* Mei *et al.* and *Gigantonomia* Li & Yao, both from the Permian of China. Both genera are marginally seed-bearing leaves but in contrast of *Ovulepteris* they have gigantopterid-type of leaves. According to Mei *et al.* (1992, p. 99), *Eophyllogonium* is diagnosed as a lanceolate leaf that gradually narrows distally and has margins that bear regular symmetrical crenulations. Veins are pinnate in three orders, with tertiary veins anastomosing to form elongate, polygonal meshes. Seeds are elongate-oval to round-oval and borne abaxially along the leaf margins, inserted in the convex areas of crenulations. Some seeds bear a cone-like elongation that extends from the distal end. Fertile leaves of *Gigantonomia* is characterised by Li and Yao (1983) as linear with three orders of veins (anastomosing veins is indistinct), bearing seeds which are arranged in two rows at the end of secondary veins not extending to the leaf margin. The seeds are elliptical, covered by glandular dots (Li and Yao, 1983). The main differences of both genera and *Ovulepteris* are in type of leaves. *Eophyllogonium* and *Gigantonomia* have gigantopterid-type leaves with three orders of veins where tertiary veins order anastomosing (anastomosing in *Gigantonomia* questionable) while leaves of *Ovulepteris* have taeniopterid-type leaves with reduction of leaf lamina and only two orders of veins. Anastomosing in *Ovulepeteris* is not observed. Also stratigraphical distribution of *Eophyllogonium* and *Gigantonomia* is different – Permian age, while *Ovulepteris* comes from Pennsylvanian.

1.4.7.6.2. Comparison with *Phasmatocycas* Mamay and *Spermopteris* Cridland & Morris

Some similarities of *Ovulepteris* gen. nov. can be found in *Phasmatocycas* Mamay (Mamay, 1973; Gillespie and Pfefferkorn, 1986; Axsmith *et al.*, 2003) or *Spermopteris* Cridland & Morris (Cridland and Morris, 1960; Axsmith *et al.*, 2003). According to Cridlant and Morris (1960) and Mamay (1976), *Spermopteris* represents ovules of pteridosperms while ovules of *Phasmatocycas* represent ovule of primitive cycad megasporophylls. Later Axsmith *et al.* (2003) redescribed original material of *Spermopteris* and based on this new observation Axsmith *et al.* (2003) synonymized *Spermopteris* with *Phasmatocycas*. Axsmith *et al.* (2003) mentioned two species *Phasmatocycas bridwellii* Axsmith *et al.* and *P. kansana* Mamay. *P. bridwellii* comes from Gzhelian (uppermost Stephaian) and *P. kansana* comes from Permian age (Axsmith *et al.*, 2003). Generally *Phasmatocycas* can be characterised as ovule bearing taeniopterid leaves with narrow leaf lamina, lateral veins simple or once bifurcating. Ovules are attached their base to the lateral side of thick midrib and they are closely appressed to lamina producing persistent depression in abaxial side of the lamina (Axsmith *et al.*, 2003). Similarity can be found in fact that *Phasmatocycas*, as well as *Ovulepteris* gen. nov. bears ovules on taeniopterid leaves. Nevertheless, ovules of *Phasmatocycas* are attached directly to midrib and they are placed on abaxial side of leave while ovules of *Ovulepteris* gen. nov. are attached to end of lateral veins placed on leaf lamina margin. Mamy (1976, p. 7) published one poor preserved specimen assigned into *Spermatopteris* (*Spermatopteris* sp.) from Perry locality, Oklahoma, USA which comes from Permian age. Specimen represents a small taeniopterid leaf fragment with strong midrib and narrow leaf lamina placed on both side of midrib. The veins are closely spaced, occasionally dichotomized, and gently decurrent (Axsmith *et al.*, 2003). Reproductive organs are represented only some swellings, which are oblong or ovoid, 2.5 mm long and 1.5 mm wide (Axsmith *et al.*, 2003). Swellings are placed in two rows, each along the midrib. There is not clear if swellings represented true ovules. Mamay′s (1976) specimen is different to *Ovulepteris* gen. nov. *Ovulepteris* has distinctive leaf lamina which is only partly reduced, the midrib is not strong. Unfortunately clear character of reproductive organs of Mamay′s (1976) specimen cannot be done, due to this fact is impossible to make relevant comparison with *Ovulepteris* gen. nov.

1.4.7.6.3. Comparison with *Archaeocycas* Mamay

Archaeocycas was established by Mamay (1973) for primitive cycad megasporophylls from Permian age. Mamay (1973, 1976) characterised *Archaeocycas* as symmetrical megasporophyll with broad midrib bearing severap pairs of sessile, closely appressed ovules borne in two lateral rows on surface of reduced basal lamina close to midrib. Distal part of leave expanded as flattened sterile foliar blade (Mamay, 1973, 1976). Due to the fact that specimens of *Ovulepteris* gen. nov. are incomplete an distal and proximal parts of leaf (probably megasporophyll) are unknown, the comparison with *Archaeocycas* could be problematic. But holotype of *Ovulepteris robusta* nov. comb shows in upper part of leaf that marginal part to start tapering and there appears that in distal part is not any expanded flattened sterile foliar blade. *Ovulepteris* gen. nov. also has ovule-like organs placed on marginal part of leaf lamina in protruded segments.

1.4.7.6.4. Comparison with *Sobernheimia* Kerp

Sobernheimia was established by Kerp (1983) based on fertile material from Permian of Sobernheim, Nahe area, Germany. Kerp (1983, p. 175) characterised *Sobernheimia* as phylloid organ bearing two rows of ovoid ovule-like reproductive organs at margin of leaf lamina. The margin of leaf lamina is divided into lobes which are alternating with ovoid bodies (Kerp, 1983). The main difference of *Ovulepteris* gen. nov. and *Sobernheimia* is in placement of ovule-like reproductive organs. *Ovulepteris* gen. nov. has ovule-like organs placed on marginal part of leaf lamina in protruded segments while *Sobernheimia* has ovule-like organs placed among protruded segments/lobes. Kerp (1983) stated that attachment mode is not clear but there appears (Kerp, 1983, p. 176, pl. 1) that ovule-like organs are attached directly to strong midrib while ovule-like organs of *Ovulepteris* gen. nov. are probably attached to end of lateral veins.

1.4.7.6.5. Comparison with *Crossozamia* Pomel

Crossozamia was decribed by Pomel (1849) and later emended by Zhifeng and Thomas (1989). According to Zhifeng and Thomas (1989, p. 209), *Crossozamia* is characterized as megasporophyll with fan-shaped or palmate leaf lamina where distal margin is divided into tapering segments. Ovules are ovoidal to oblong attached laterally on each side of stalk with one or two ovules borne at proximal lateral margins of lamina (Zhifeng and Thomas, 1989). *Ovulepteris* gen. nov. differs from *Crossozamia* by the position of ovules on megasporophyll. *Crossozamia* has ovules attached to proximal lateral margins of lamina close to stalk while *Ovulepteris* gen. nov. has ovules attached probably to end of lateral veins on margin of leaf lamina. Distal end of *Ovulepteris* gen. nov. is unknow but marginal part in upper part of leaf to start tapering and there appears that in distal part is not any fan-shaped or palmate leaf lamina.

1.4.7.7. Discussion of the concept of separation of *Ilfeldia*, *Manebachia* and *Ovulepteris*

The genus *Ilfeldia* was long time (since Remy, 1953) considered as a monospecies genus with only one species *I. jejunata* (currently *I. jejunataeformis* sp. nov.) and comparable specimens never been described from any locality through the world. Later Remy and Remy (1958) established a new genus *Manebachia* which shows similarities to *Ilfeldia* (both genera bears synangia), but Remy and Remy (1958) decided to establish a new genus because *Manebachia* has significantly reduced and veinless leaf lamina. *Manebachia* is also a monospecies genus with only one species *M. polysporangiata*. Obrhel (1965) established another species *Ilfeldia robusta* (currently *Ovulopteris robusta* nov. comb.) and later Obrhel (1957) *Ilfeldia lobecensis* (currently cf. *Ovulepteris lobecensis* nov. comb.). Obrhel (1965) stated that reproductive organs of *Ilfeldia robusta* (currently *Ovulopteris robusta* nov. comb.) could represent seeds, but Obrhel (1965) had not been sure. From this time the genus *Ilfeldia* encompassed three species and contained synangia and seed bearing species. Barthel et al. (1975, p. 477, fig.1, pl. 1, figs 1, 2) and Barthel (2006, p. 65, fig. 152) placed fertile specimen bearing seeds from Breitenbach (Thüringen, Germany) to *Ilfeldia*, even to species *jejunata* [*Taeniopteris* (*Ilfeldia*) *jejunata*]. Barthel (2006) also virtually connected sterile leaves *Taeniopteris jejunata*, female *Taeniopteris* (*Ilfeldia*) *jejunata* and male *Manbebachia polysporangiata* into one nature plant. It means that Barthel (2006) excepted that these all fossil species belong to some gymnosperm plant. Due to the fact, that is impossible conclusively stated that synangia of *I. jejunata* (currently *I. jejunataeformis* sp. nov.), *I. gregoriensis* sp. nov. or *Manbebachia polysporangiata* represent pollen organs of some gymnosperms, cannot be unambiguously affiliated with ovule bearing species. Therefore, we suggest separated genus *Ilfeldia* for marginally synangia bearing leaves with not or little reduced leaf lamina and genera for seed bearing leaves. Based on a new observation and identification of type of reproductive organs from original species *Ilfeldia robusta*, in this paper we establish a new genus *Ovulepteris* gen. nov. The diagnose of this new genus is not identical with diagnoses of existing genera (see above) having leaves with ovules, therefore we establish a new genus. We also suggest to fix genus *Manbebachia* which is must be use for significantly reduced and veinless leaf lamina where synangia are attached to reduced lamina close to midrib. Based on our opinion, conservation of all three genera is logical and usable in future palaeobotanical researchs.

1.4.7.8. Evolutionary

The clear role of new genus *Ovulepteris* in evolution of plant is unclear. *Ovulepteris* has ovules attached to leaf lamina which is characteristic feature for pteridosperms according to Rozynek (2008). Nevertheless, long time already discussed the possibility that similar types of fertile leaves (e.g., *Phasmatocycas*, *Archeocycas*, *Lesleya*, *Sobernheimia* and others) may be placed among potential cycad ancestor or cycads (Mamay, 1969, 1976; Delevoryas, 1982; Axsmith *et al.*, 2003, Rozynek, 2008). Mamay (1969, 1976) supposed that cycads origin is in pteridosperms with entire taeniopterid leaves bearing ovules attached to leaf lamina. Delevoryas (1982) placed origin of cycads among medullosan pteridosperms with pinnately compound fossil-species as *Eremopteris zamioides* (Bertrand) Kidston or *Tinsleya texana* Mamay. Axsmith *et al.* (2003) deconstructed Mamay′s (1969, 1976) idea about phyletic shift of ovule position from laminar (pteridosperms) to the leaf midrib in real cycads based on fact that ovules were already attached to the midrib or stalk in some earliest taeniopterid fossils. Ovules attached by receptacle to proximal part of midrib (laminaless part of leaf) are known from *Lesleya* sp. sensu Leary (1990) from lowermost Bashkirian (Namurian B, C of the Southern Europe regional scale). Fertile leaves are associated with *Lesleya chaimarosa* Leary & Pfeffekorn. Leary (1990) was supposed that this fertile leaves with ovules probably represent a member of cycads but he did not bring some relevant data for this reason, except fact that ovules are attached to midrib in proximal part of leaf. It means that species of genera (e.g., *Ovulepteris* gen. nov.) with ovule attached to leaf lamina are known from Moscovian? respectively Kasimovian, (see Figure 28) while ovules attached to midrib is know from before age, Bashkirian. This fact endorses Axsmith *et al.*′s (2003) statement about the nesouhlas with phyletic shifting of ovule position from laminar (pteridosperms) to the leaf midrib of cycads. On the other hand, pteridosperms, as potential group of origin of cycads, are known from Mississippian (Galtier and Meyer-Berthaud, 2006). Therefore, the question about ancestors of cycads staying opened. Nobody has brought significant indicia (as anatomy information - e.g., girdling leaf traces) for clear affiliation of genera with potential relationship to cycads as *Phasmatocycas*, *Archeocycads* etc., to true cycads. These genera can represent some group of pteridosperms, like Axsmith *et al.* (2003) or Rozynek (2008) previously indicated. It seems that some pteridosperms can have ovules attached to midrib.

Figure 29 shows leaf forms some genera/species which are placed close to cycads. There is clear visible that ovule baring genera with taeniopterid leaves described from American localities [come from Bashkirian (Carboniferous) to Kungurian (Permian)] show ovules attached to midrib situated in proximal part of leaves and distal part of leaves are more or less sterile (excepting *Phasmatocycas bridwellii* where leaf lamina is sterile in proximal part of leaves). These genera/species point to megasporophyll of true cycads, but the significant features for affiliation to cycads like anatomy are still missing.

Ovule baring genera with taeniopterid leaves from European localities [come from uppermost Moscovian (Carboniferous) to Asselian (Permian)] show as genus (*Ovulepteris* gen. nov.) with ovules attached to leaf lamina so genus *Sobernheimia* with ovules probably attached to broad midrib or to leaf lamina near the midrib. *Ovulepteris* robusta nov. comb. shows great similarities with *Taeniopteris* (*Ilfeldia*) *jejunata* sensu Barthel (2006). Both species are separated around 16 million year gap without any significant morphology differentiation. Generally, genera/species with ovules attached to taneinopterid leaves from European localities are fixed to leaf lamina and in most of them are marginally arranged. Due to absence of detail information about ovules and anatomy of these species we can only speculated that all species represent some bizarre group of pteridosperms with unclear relationship to cycads. This opinion is supported by the fact that in contrast with cycads megasporophylls, sporophylls of this European ovule bearing species its sterile part is situated in proximal part of leaf, not in distal like in cycads. The form of ovule bearing leaves from this area is a part of Euramerican floral province but in comparison to American types European species show degree of uniformity through geological time (Figure 29). This fact supported opinion that these European species rather represent some enigmatic pteridosperm group and even they probably had not any evolutionary connection with true cycads.

Ovule baring genera with taeniopterid leaves from Asian localities come from late Permian [upper Kungurian and Wuchiapingian (Permian)] and show both type of ovule attachment. *Crossozamia* has ovules attached to stalk or proximal part of midrib and *Eophyllogonium* with ovules attached to margin of leaf lamina. These genera come from North China block and were a part of the Cathaysian floran province consisting of several different plant assemblages in comparison to Euramerican province. It means that several ecological barriers had to exist in this age. Based on this fact Zhifeng and Thomas (1989) stated that Nord China cycads evolved independently from a yet unknown ancestor. In this time, it is impossible to find some plausible ancestor, because there is unknown any similar fossils from lowermost Permian or Carboniferous.

The missing knowledge about male reproductive organs is another serious problem for classification of true Palaeozoic cycads. Anatomically preserved cycadalean male organ is represented by fossil-species *Lasiostrobus polysaccii* Taylor which comes from coal balls in the Upper Pennslyvanian of Illinois (USA). Nevertheless, Talyor (1970) mentioned that its affinity is controversial, and may be either a conifer or ginkgophyte. Mamay (1976, pl. 2. fig. 4) described small impression specimen which suggested to cycadalean male organ. This specimen comes from Lower Permian strata from Texas (USA). Due to conservation and the sample size, it is possible to doubt assignation to cycads. No other similar specimens of male reproductive organs are known from American localities from Paleozoic age.

Zhu *et al.* (1994) established *Cycadostrobilus paleozoicus* Zhu *et al.* for male (microstrobilus) organs probably from cycads from upper Permian (Kungurian) of China. Microsporophylls are helicaly organized on axis bearing small sessile synangia consist of 3–4 microsporangia, 0.5 mm long. *Cycadostrobilus paleozoicus* is associated with taeniopterid leaves *Taeniopteris norinii* Halle and with ovule bearing fossil-species *Crossozamia chinensis* (Zhuo & Du) Gao & Thomas. We can speculated that all three species *Cycadostrobilus paleozoicus* as male, *Crossozamia chinensis* as female and *Taeniopteris norinii* as vegetative parts which belong into one parent plant. Another male fossil-species is *Liulinia lacinulata* Wang established by Wang (1986) from upermost Permian. Microstrobilus consits of 10–15 helically arranged microsporophylls which are fimbriate distal part deeply dissected into many lacinules. Microsporangia are placed in proximal part of microsporophyll (Wang, 1986). *Liulinia lacinulata* is associated with taeniopterid leaves *Taeniopteris saiyuanensis* Halle. Nevertheless, affiliation both Chinese species to cycads is still unclear because we have not any anatomical or cuticular data.

Currently three species with sporangia and which are associated with taeniopterid leaves are known from Europe. Barthel (2006) believed (based on association) that sporangia bearing fossil-species *Manebachia polysporangiata* is a male reproductive organ of *Taeniopteris* (*Ilfeldia*) *jejunata* sensu Barthel (2006), female reproductive organ and vegetative *Taeniopteris jejunata* leaves. Nevertheless, earlier Remy (1953) connected *Ilfeldia jejunataeformis* sp. nov. with *Taeniopteris jejunata* leaves. *Ilfeldia jejunataeformis* sp. nov. and *Manebachia polysporangiata* are quite different fossil-species belonged into two different genera. This case shows that connection with associated vegetative leaves may leads to misinterpreting of taxa. The new species *Ilfeldia gregoriensis* sp. nov. is also associated with large taeniopterid leaves which can or not belong to the same parent plant. Generally, based on missing of important data, any of those fossil-species with sporagnia from Europe cannot be clearly affiliated into cycads. Theses fossil-species rather represent male organs of some group within pteridosperm. Nevertheless, we cannot exclude relationship to true ferns.

During paleobotany history many of mentioned genera/species in this paper were affiliated to cycads, but based on molecular sequence data of extant Cycadales (Bogler and Francisco-Ortega, 2004) assumed that true cycads lineage may have diverged from ancestor no later than Permian. It means that we can search of true cycads among known fossil-species known from uppermost Permian in Asia (Figure 29). This theory is supported by fact that well preserved cycad woods come from uppermost Permian of China (Wang *et al.*, 2011).

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1.5. Chronostratigrapic results from new paleobotanical occurrences of megafloral species in the Douro Carboniferous Basin (São Pedro da Cova – NW of Portugal)

Adapted from Pedro Correia, João Loureiro, Ary Pinto de Jesus
(Paleolusitana (2009), 1, 129-140)

Abstract

Present work deals with new evidences of palaeobotanical megafloristic species record in the sector of São Pedro da Cova of Douro Carboniferous Basin (BCD; NW of Portugal); for this study, we point out distinct Carboniferous ages which are highly suspected in the coal measures outcrops that are bounded by a reverse fault system.

Resumo: Assinalam-se e descrevem-se novas ocorrências de espécies megaflorísticas do Carbónico da Bacia Carbonífera do Douro (BCD; NW de Portugal), na região de São Pedro da Cova. As novas ocorrências paleobotânicas denunciam a existência de formações carboníferas com idades distintas, as quais, actualmente, se encontram conjuntamente incorporadas na BCD e datadas do Estefaniano C inferior, em afloramentos que se encontram tectonicamente escamizados por um sistema de falhas inversas.

Keywords**:** Stratigraphy; Carboniferous; Douro Carboniferous Basin; Megaflora.

1.5.1. Introduction

The new paleobotanical megafloral elements recently discovered in new outcrops located at the São Pedro da Cova region (outcrops spc1, spc2 and spc5; Figures 7, 30–32) are first described in the Douro Carboniferous Basin (DCB; NW Portugal). The description and classification of the new megafloral occurrences, as well as the respective integration in the flora list of DCB and subsequent revision, is prime importance for dating and to clarify several geological-structural problems in a geologically complex area such as the São Pedro da Cova. Thus, this work aims to contribute to scientific knowledge of the Carboniferous flora of Portugal, complementing the already excellently studied and published in a wide variety of works and investigations of several authors.

1.5.2. Geological setting

Please, see PART II (pag. 21).

1.5.3. Description of the new megafloral occurrences in DCB

***Lobatopteris corsini* Wagner, 1958** (Plate XXIV, A, C)

Stratigraphic distribution: upper Kasimovian–lower Gzhelian (Stephanian B and C of the Central/Western European regional scale)

1958 *Pecopteris corsini* Wagner; Wagner and Breimer (1958), 12, 14–19, pl. 5-10, fig. 6–11; pl. 11, figs. 28–28a.

1983 *Lobatopteris corsini* Wagner; Lemos de Sousa and Wagner (1985), 208–209, pl. 6, figs. 1-1a.

Description: This species is represented by two fronds of penultimate order. The ultimate pinnae show very small and lobed pinnules, and rounded at the apex pinnule. The base of the lateral margins does not reach the rachis. The midvein is not decurrent towards the pinnule apex and slightly winding. The lateral veins are strong and divided once to twice, which have running towards the upper part of limb. The lobed pinnules become a single pinnule at the most distal (apical) part of the frond.

Remarks: *Lobatopteris corsini* occurs in Buçaco Basin (lower Gzhelian [upper Stephanian C] to ?upper Gzhelian [Autunian in the regional scale]; e.g., Wagner, 1983).

***Oligocarpia gutbieri* Göppert, 1841** (Plate XXIV, B)

Stratigraphic distribution: middle Moscovian–lower Gzhelian (Asturian/Westphalian D to Stephanian C of the Central/Western European regional scale)

1836 *Oligocarpia gutbieri* Göppert; Göppert (1836), 41, pl. 4, fig. 1 e 2.

1983 *Oligocarpia gutbieri* Göppert; Lemos de Sousa and Wagner (1985), 203–204, pl. 1, fig. 2; pl. 3, figs. 1–1a.

Description: Frond of penultimate order; the pinnules (sterile) are grossly subtriangular and oval, with rounded apexes, and closely spaced between them. The midvein is slightly zigzag. The lateral veins are well-marked, only divided once and inclined, forming an angle of 60º with the midvein.

Remarks: *Oligocarpia gutbieri* is known in Carboniferous rocks of Spain (e.g., Wagner, 1983).

***Pecopteris arborescens* Schlotheim, 1804** (Plate XIV, D)

Stratigraphic distribution: upper Moscovian–lower Gzhelian (Stephanian A–?C of the Central/Western European regional scale)

1804 *Filicites arborescens* von Schlotheim; von Schlotheim (1804), 41, pl. VII, fig. 13.

1951 *Pecopteris arborescens* von Schlotheim; Corsin (1951), 326, pl. CLXX, CLXXI, CLXXII e CLXXIII.

Description: Terminal part of a triangular-shaped frond showing penultimate pinnae. The pinnules are very short (3–4 mm long and 1.5–2.0 mm wide), inserted perpendicularly to rachis in tapered shape, closely spaced between them, and showing a rounded apex. The midvein is quite pronounced and straight towards the pinnule base. The lateral veins are simple and slightly oblique, running towards the pinnule margins.

Remarks: *Pecopteris arborescens* occurs in Buçaco Basin (lower Gzhelian [upper Stephanian C] to ?upper Gzhelian [Autunian in the regional scale]; e.g., Wagner, 1983).

***Callipteridium* (*Praecallipteridium*) *jongmansi* Bertrand, 1932** (Plate XXIV, E, F)

Stratigraphic distribution: middle–upper Moscovian to lower Kasinovian (Asturian/Westphalian D to Cantabrian of the Central/Western European regional scale)

1932 *Pecopteridium jongmansi* Bertrand; Bertrand (1932), 100–102, pl. LX, figs. 1–3a.
1964 *Callipteridium* (*Praecallipteridium*) *jongmansi* Bertrand; Wagner (1966), 106–108, pl. 32, fig. 72.

Description: Frond of ultimate order showing subtriangular and large pinnules. The pinnules are attached to rachis cross whole width of pinnule base and are tenuously decurrent. The midvein is well pronounced and is not decurrent at the distal part of pinnule. The lateral veins are spaced (aprox. 45–47 veins per 10 mm of margin), oblique from the midvein and also emerging from the pinnule base.

Remarks: *Callipteridium gigas* is the most similar species that occurs commonly in Douro Basin (lower Stephanian C [lower Gzhelian]) (e.g., Wagner, 1983). *Callipteridium jongmansi* also has some similarities with *Callipteridium pseudogigas* Wagner from lower? Stephanian C (lower Gzhelian) strata of Spain (e.g., Wagner *et al.*, 1985, pl. 1, fig. 3). *Callipteridium jongmansi* occurs in Ervedosa Basin (upper Moscovian [upper Westphalian D/upper Asturian in the regional scale]; e.g., Wagner, 1983).

***Lobatopteris lamuriana* Heer, 1872** (Plate XXV, A)

Stratigraphic distribution: upper Moscovian–upper Kasimovian (Asturian/Westphalian D to Stephanian B of the Central/Western European regional scale)

1872 *Pecopteris lamuriana* Heer; Heer (1873), 13, fig. 12.

1983 *Lobatopteris lamuriana* Heer; Wagner (1985), 207–208, pl. 5, figs. 1–6.

Description: This species is represented by two frond fragments of ultimate pinnae. The pinnules are very elongate and narrow, with a lenght ranging between 20 to 25 mm cm and 3–4 mm in wide, and are inserted obliquely from the rachis. The pinnule margins are lobed in both sides and showing a rounded apex. The midvein is strong and decurrent at the pinnule base. The lateral veins are thin, running to pinnule margins.

Remarks: *Lobatopteris lamuriana* is described (*Lobatopteris* cf. *lamuriana*) in Santa Susana Basin (upper Moscovian [upper Westphalian D/upper Asturian in the regional scale]; e.g., Wagner, 1983).

***Annularia* cf. *radiata* (Brongniart, 1822) Sternberg, 1825** (Plate XXV, B, C)

Stratigraphic distribution: Serpukhovian–Gzhelian (Namurian–Autunian of the Central/Western European regional scale)

1822 *Asterophyllites radiata* Brongniart; Brongniart (1822), 8: 35, 89; pl. 2, figs. 7a–7b.

1949 *Annularia radiata* (Brongniart) Sternberg; Arnold (1949), 7 (9): 183–184, pl. 17, fig. 3.

Description: The leaves are very small size (5–8 mm long and 0.5–1.0 mm wide), lanceolate to linear, terminating distally in an acute mucro. The leaves are grouped in 7 to 8 leaves per whorl (verticil), ranging from 5 to 10 nodes. The midrib (central vein) of leaves is clearly visible and strong, reaching the terminal (distal) part.

Remarks: The Portuguese material shows closely similarities with Spanish material of *Annularia* (described as *Annularia* sp. nov.?) described by Castro (2005).

aff. *Rhodeopteridium subpetiolatum* Potonié, 1889 (Plate XXV, D)

Stratigraphic distribution: lower Bashkirian–lower Moscovian (upper Namurian to middle Westphalian of the Central/Western European regional scale)

Description: Pinnatifid frond of ultimate pinna showing (acicular) pinnules palmatopterid-type. The stem axis is strong with a lenght of 55 mm and 2 mm in width. The pinnules are inserted alternately around the stem axis, dividing (up 4th order of bifurcation) into small narrow branches of varying thickness (between 1.5 and 0.2 mm).

Remarks: The Portuguese material also shows similarities with *Rhodeites gutbieri* (Ettingshausen, 1852) Němejc, 1938 from the Moscovian B (Westphalian B) strata of Spain and Chech Republic (e.g., Pšenička and Schultka, 2009). *Rhodeopteridium subpetiolatum* is known in the lower Bashkirian (upper Namurian) to lower Moscovian (middle Westphalian) strata from Germany, Poland and Chech Republic (e.g., Pšenička and Schultka, 2009).

***Botryoconus* (*Cordaianthus*?) *femina* Grand'Eury, 1877** (Plate XXV, E)

Stratigraphic distribution: Pennsylvanian

1877 *Botryoconus femina* Grand'Eury; Grand'Eury (1877), 279–280, pl. XXXIII, figs. 1–1´.

Description: Well-developed strobili obliquely inserted in a large stem axis, on both sides. The strobili have globular shape and are sharp, 10–12 mm long and 5–8 mm wide, and are formed by numerous thin and finely ribbed scales, thereby protecting the embryo which is in state of latent life (seed).

Remarks: *Botryoconus* shows similarities with *Cordaianthus*, female reproductive organ of the genus *Cordaites*. *Cordaianthus* occurs in the Buçaco Basin (Gzhelian [upper Stephanian C to ?Autunian in the regional scale]; e.g., Wagner, 1983).

***Sphenophyllum angustifolium* (Germar, 1845) Göppert, 1848** (Plate XXV, F)

Stratigraphic distribution: Upper Pennsylvanian and lower Permian.

1845 *Sphenophyllites angustifolius* Germar; Germar (1845), 2–3: 18, pl. 7, figs. 4–7.

1958 *Shenophyllum angustifolium* (Germar) Göppert; Abbott (1958), 38 (174): 328–333, pl. 38, figs. 35, 40–41; pl. 44, fig. 65; pl. 49, fig. 90.

Description: The leaves are narrow reduced-size (5–8 mm and 1.5–2.0 mm wide) and grouped in 6 per whorl (verticil). They have wedge shape becoming forked doubly towards the distal (apical) part. At the first time, the leaves become bifid (bifurcated) ranging between 3 to 3.5 mm. A second bifurcation occurs near distal areas, becoming double forked, with a range between 1 and 1.5 mm.

Remarks: This species occurs in Buçaco Basin (Gzhelian [upper Stephanian C to ?Autunian in the regional scale]; e.g., Wagner, 1983).

***Poacordaites microstachys* (Goldenberg, 1869) Zeiller, 1878** (Plate XXV, G)

Stratigraphic distribution: lower Gzhelian (upper Stephanian of the Central/Western European regional scale)

1948 *Poacordaites microstachys* (Goldenberg) Zeiller; Closas (1958), pl. 6, fig. 8.

2007 *Poacordaites microstachys* (Goldenberg) Zeiller; Gómez-Alba (2007), pl. 14, figs. 1a–1b.

Description: Radially clustered leaves around of a branch or verticil. The leaf margins are parallel and consisting of thin and narrow veins, typical features described in the species *Poacordaites microstachys*.

Remarks: *Poacordaites microstachys* occurs in the Upper Pennsylvanin of Spain (e.g., Gómez-Alba, 2007).

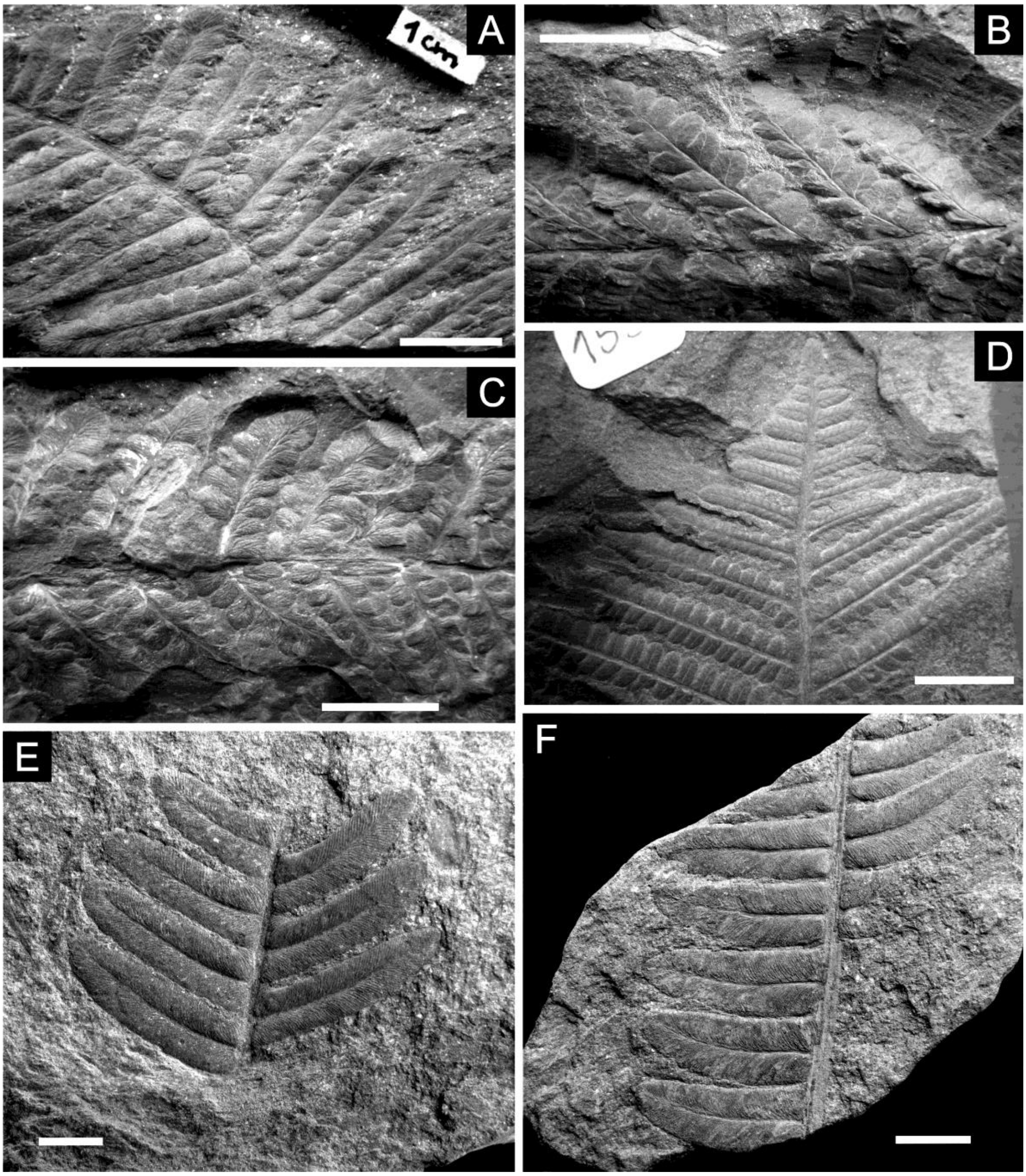

Plate XXIV. (unpublished)

A, C. ***Lobatopteris corsini*** **Wagner**

Locality— São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

B. ***Oligocarpia gutbieri*** **Göppert**

Locality—São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

D. ***Pecopteris arborescens*** **von Schlotheim**

Locality—São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

E, F. ***Callipteridium*** **(*****Praecallipteridium*****)** ***jongmansi*** **Bertrand**

Locality—São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

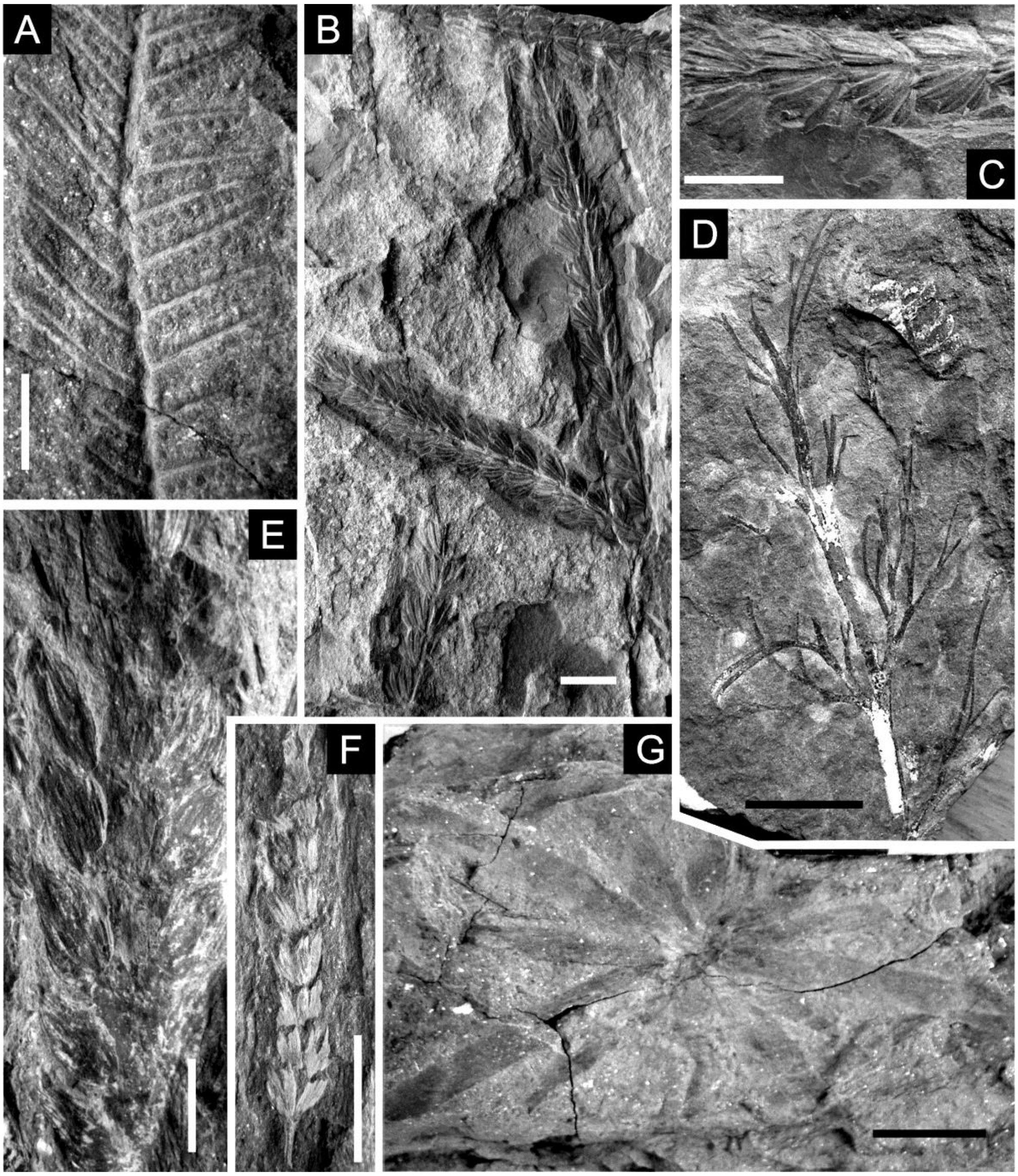

Plate XXV. (unpublished)

A. ***Lobatopteris lamuriana* Heer**

Locality— São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

B, C. ***Annularia* cf. *radiata* (Brongniart) Sternberg**

Locality—São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

D. **aff. *Rhodeopteridium subpetiolatum* Potonié**

Locality—São Pedro da Cova (outcrop spc5, TSU B2), DCB. Scale bar 10 mm.

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

Locality—São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

F. ***Sphenophyllum angustifolium* (Germar) Göppert**

Locality—São Pedro da Cova (outcrop spc2, TSU B1), DCB. Scale bar 10 mm.

G. ***Poacordaites microstachys* (Goldenberg) Zeiller**

Locality—São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

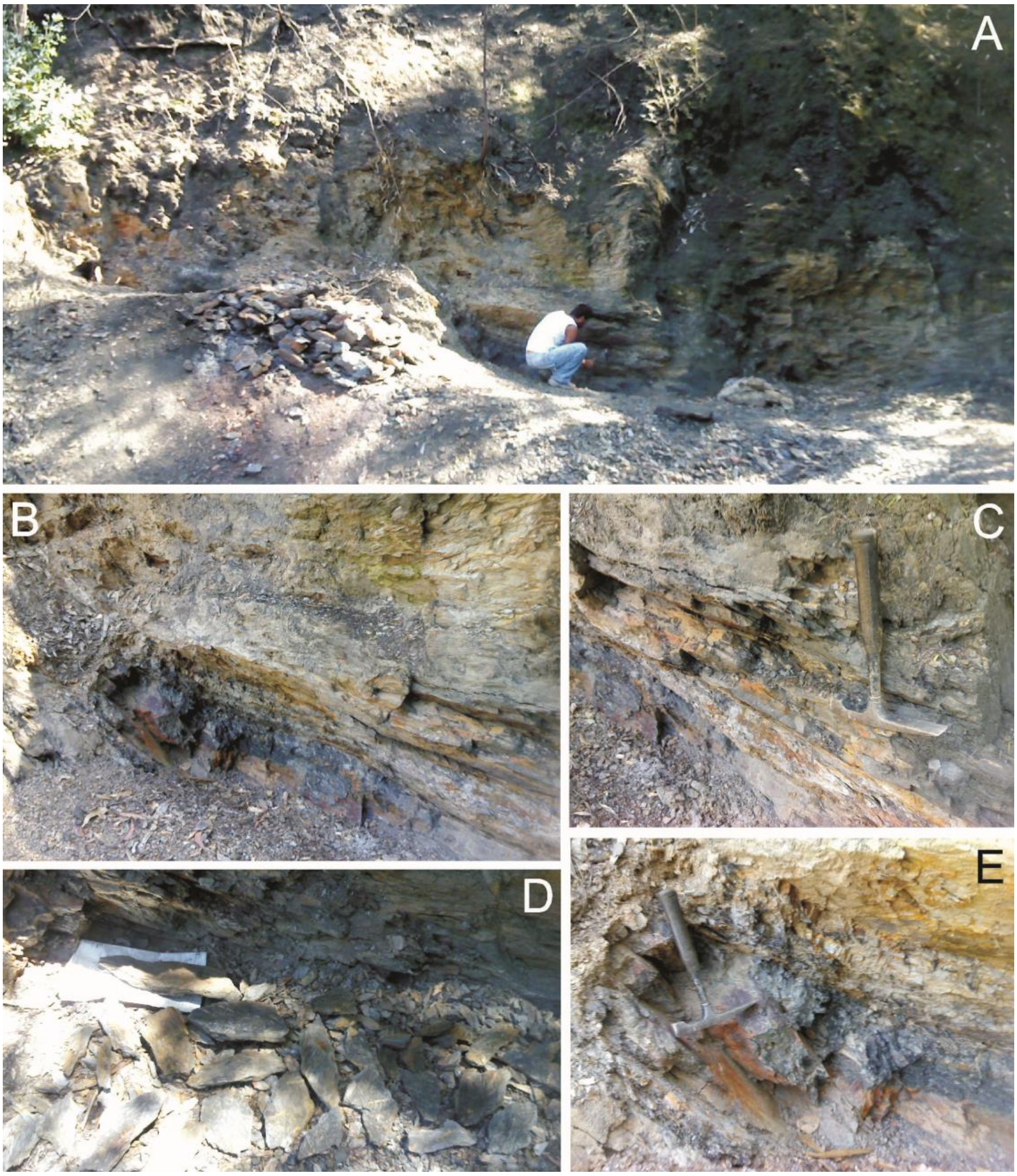

Fig. 30 - New outcrops (spc1, TSU B1) of São Pedro da Cova (A–E). Excavation works during fieldwork in 2004. (image unpublished)

Fig. 31 - New outcrops (spc2, TSU B1) of São Pedro da Cova. Excavation works during fieldwork in 2007. (image unpublished)

Fig. 32 - New outcrops (spc5, TSU B2) of São Pedro da Cova (João Paulo Loureiro as scale reference). Excavation works during fieldwork in 2007. (image unpublished)

1.5.4. Conclusions

The new paleobotanical occurrences seem to report various Carboniferous formations with different ages, bounded by a reverse fault system. These new occurrences include the biozone *Lobatopteris lamuriana* (Stephanian A) and typically upper Namurian and Westphalian/Cantabrian age species such as *Callipteridium jongmansi* and *Rhodeopteridium subpetiolatum*. The formations up to this study are jointly incorporated within DCB and considered as part of the same floral assemblages assigned to lower Stephanian C described to DCB. By studies conducted and presented herein, we consider that is very important to do a further study on the description, classification and characterization of the DCB floras, and the subsequent review of its flora list based on the integration of new fossil megafloral elements, with the aim the dating and clarification of various geological-structural problems within a geologically complex area such as São Pedro da Cova.

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1.6. Occurrence of new megafloristic elements in the Douro Basin (lower Stephanian C [lower Gzhelian], NW of Portugal)

Pedro Correia, João Loureiro, Ary Pinto de Jesus

(e-Terra (2010), 17 (10), 1-4)

Abstract

New megafloristic elements were found in the São Pedro da Cova region (Gondomar), Douro Basin (lower Stephanian C [lower Gzhelian]).

Resumo: Assinalam-se novos elementos megaflorísticos na Bacia Carbonífera do Douro (Estefaniano C inferior [Gzheliano inferior]), colectados na região de São Pedro da Cova (Gondomar).

1.6.1. Introduction

New paleobotanical elements recently discovered in new outcrops located at the São Pedro da Cova region are first described in the Douro Carboniferous Basin (DCB; lower Gzhelian [lower Stephanian C], NW Portugal). The description and classification of the new megafloral occurrences and their future integration into the DCB flora aims the updating thereof, complementing studies and researchs published in a wide variety of works, and thereby contributing to knowledge of the Carboniferous of Portugal.

1.6.2. Geological setting

Please, see PART II (pag. 21).

1.6.3. New megafloral elements in DCB

The study of the paleobotanical elements collected in DCB is result of determination of megafloral species and genera not yet recognized in the DCB, these species which list below:

Lepidostrobophyllum cf. *hastatum* (Lesquereux) Chaloner
Alloiopteris pecopteroides Gothan
Asterophyllites longifolius (Sternberg) Brongniart
Litostrobus (*Cordaianthus*?) *iowensis* Mamay
Pecopteris puertollanensis Wagner
Desmopteris sp. nov.

1.6.4. Description and taxonomic classification of specimens

***Alloiopteris pecopteroides* Gothan, 1913** (Plate XXVI, A)

Description: The pinnules are inserted perpendicularly to slightly inclined on stem axis. The pinnules show lobed to serreate margins and have similarities with genus *Aphlebia* Presl. The midvein is slightly winding and longitudinally striated. The pinnules display agglomerates of oval-shaped (seed-like) reproductive organs placed on almost all lamina.

Remarks: *Alloiopteris pecopteroides* occurs in the Serpukhovian–lower Bashkirian (Namurian of the Central/Western European regional scale) of Poland (Boureau and Doubinger, 1975).

***Asterophyllites longifolius* Sternberg (1825), Brongniart, 1828** (Plate XXVI, B)

Description: Articulated stem >110 mm long and 5 mm in width, showing long leaves and narrow, 50–60 mm in lenght. The internodes are short, not exceeding 10 mm in length.

Remarks: *Asterophyllites longifolius* is known in Buçaco Basin (Gzhelian [upper Stephanian C to ?Autunian in the regional scale], and it is first documented in the Douro Basin.

***Desmopteris* sp. nov.** (Plate XXVI, C)

Diagnosis and description: Near complete pinnule with 45 mm in lenght and 7 mm wide maximum, strongly lanceolate and narrow. The midvein is visible but very thin, and decurrent towards the end of apex. The lateral veins are very strong, few in number (5–6 veins per 10 mm of margin) and very spaced, running from the midvein forming angles very acute, and forked twice; they reach obliquely the pinnule margin asymmetricaly. Pinnule base not preserved.

Comparison: The Portuguese material (Figure 33) closely resembles *Desmopteris robustus* Doubinger and *Desmopteris longifolia* Presl based on the same pinnule-type and similar size (Figure 34). However, Portuguese sample clearly differs from *Desmopteris robustus* and *Desmopteris longifolia* based on the different venation pattern and vein density. *D. robustus* shows 12 veins per 10 mm of margin and *D. longifolia* displays about of 20 veins, whereas Portuguese specimen described here preserves only 5 to 6 veins.

Remarks: *D. robustus* occurs in upper Kasimovian/lower Gzhelian (Stephanian B and C in the regional scale) strata of the Europe, while *D. longifolia* is described in

Westphanian C from Bohemian Massif (e.g., Czech Republic; Boureau and Doubinger, 1975).

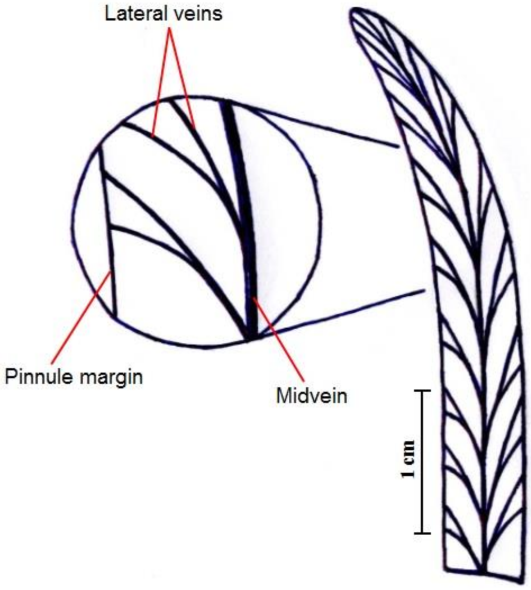

Fig. 33 - Interpretive drawing of ***Desmopteris* sp. nov.** (image unpublished)

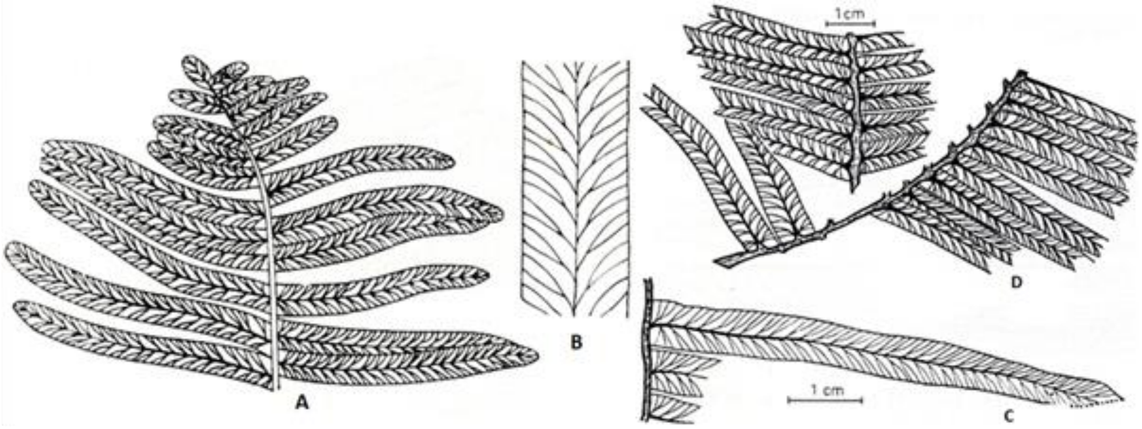

Fig. 34 - Compared species *Desmopteris longifolia* Presl (A, B) and *Desmopteris robustus* Doubinger (C, D), (schematic drawings from Boureau and Doubinger, 1975).

***Litostrobus* (*Cordaianthus*?) *iowensis* Mamay, 1954** (Plate XXVI, D)

Description: Well-developed strobili obliquely inserted in a large stem axis, on both sides. The strobili are small and globular (oval) shape and have 2.0–2.5 mm in width; they are supported by sporophylls which are atached at the stem axis.

Remarks: *Litostrobus iowensis* is known in Pennsylvanian strata of United States (Boureau, 1964), and it is first reported in the Carboniferous of Portugal.

Pecopteris puertollanensis **Wagner, 1985** (Plate XXVI, E)

Description: Ultimate and penultimate pinnae showing small and well-individualized (entire) pinnules. The pinnules are subtriangular and have rounded apexes. The venation is strongly marked. The midvein is slightly zigzag and decurrent at the base. The lateral veins are strong, oblique and divided twice.

Remarks: *Pecopteris puertollanensis* shows similarities with *Pecopteris ameroni* Stockmans & Willière, *Pecopteris paleacea* Zeiller and *Pecopteris laxenervosa* Wagner & Lemos de Sousa. *Pecopteris puertollanensis* was identified and reported in lower Gzhelian (upper Stephanian of the Central/Western European regional scale) strata of Spain (Wagner, 1985).

Lepidostrobophyllum **cf.** ***hastatum*** **(Lesquereux, 1854) Chaloner, 1958** (Plate XXVI, F)

Description: Reproductive organ belonging to the genus *Lepidodendron* Sternberg. The sporophylls (aggregated into strobili) are grouped radially and are well developed, denoting a good state of maturation.

Remarks: *Lepidostrobophyllum hastatum* was recognized in Santa Susana Basin (upper Moscovian [upper Westphalian D/upper Asturian in the regional scale]; e.g., Wagner, 1983, 1985; Wagner and Talens, 1985).

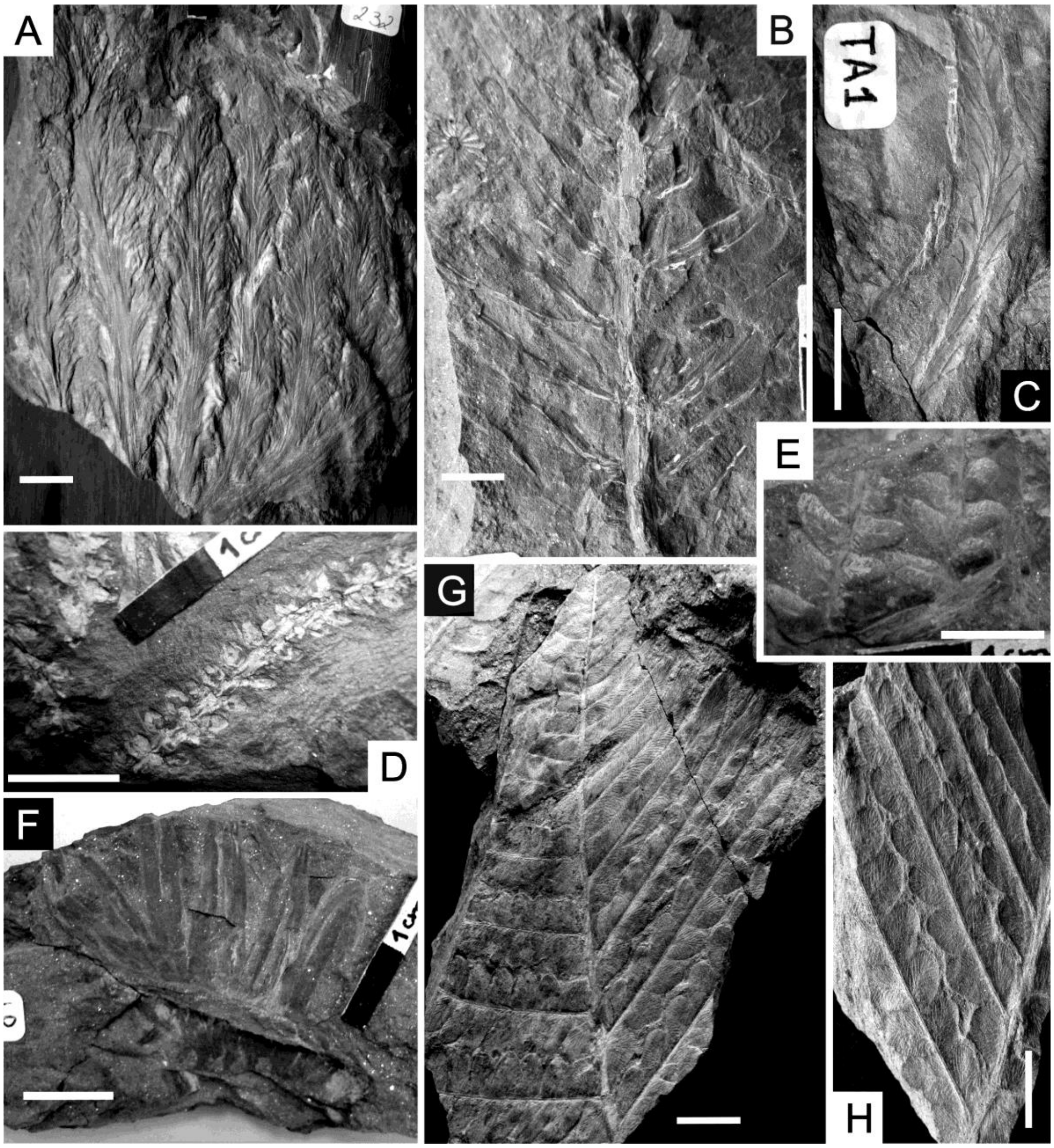

Plate XXVI. (unpublished)

A. ***Alloiopteris pecopteroides*** **Gothan**

Locality— São Pedro da Cova (outcrop spc3, TSU ?B1), DCB. Scale bar 10 mm.

B. ***Asterophyllites longifolius*** **(Sternberg) Brongniart**

Locality— São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

C. ***Desmopteris*** **sp. nov.**

Locality— São Pedro da Cova (outcrop spc3, TSU D1), DCB. Scale bar 10 mm.

D. ***Litostrobus*** **(*Cordaianthus*?)** ***iowensis*** **Mamay**

Locality— São Pedro da Cova (outcrop spc5, TSU B2), DCB. Scale bar 10 mm.

E. ***Pecopteris puertollanensis*** **Wagner**

Locality— São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

F. ***Lepidostrobophyllum*** **cf.** ***hastatum*** **(Lesquereux) Chaloner**

Locality— São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

G, H. ***Callipteridium*** **(*Praecallipteridium*)** ***zeilleri*** **Wagner** (previously described as *Odontopteris* [*Mixoneura*] *subcrenulata*; also figured in Plate XVII; see also description below)

Locality— São Pedro da Cova (outcrop spc4, TSU ?B1), DCB. Scale bar 10 mm.

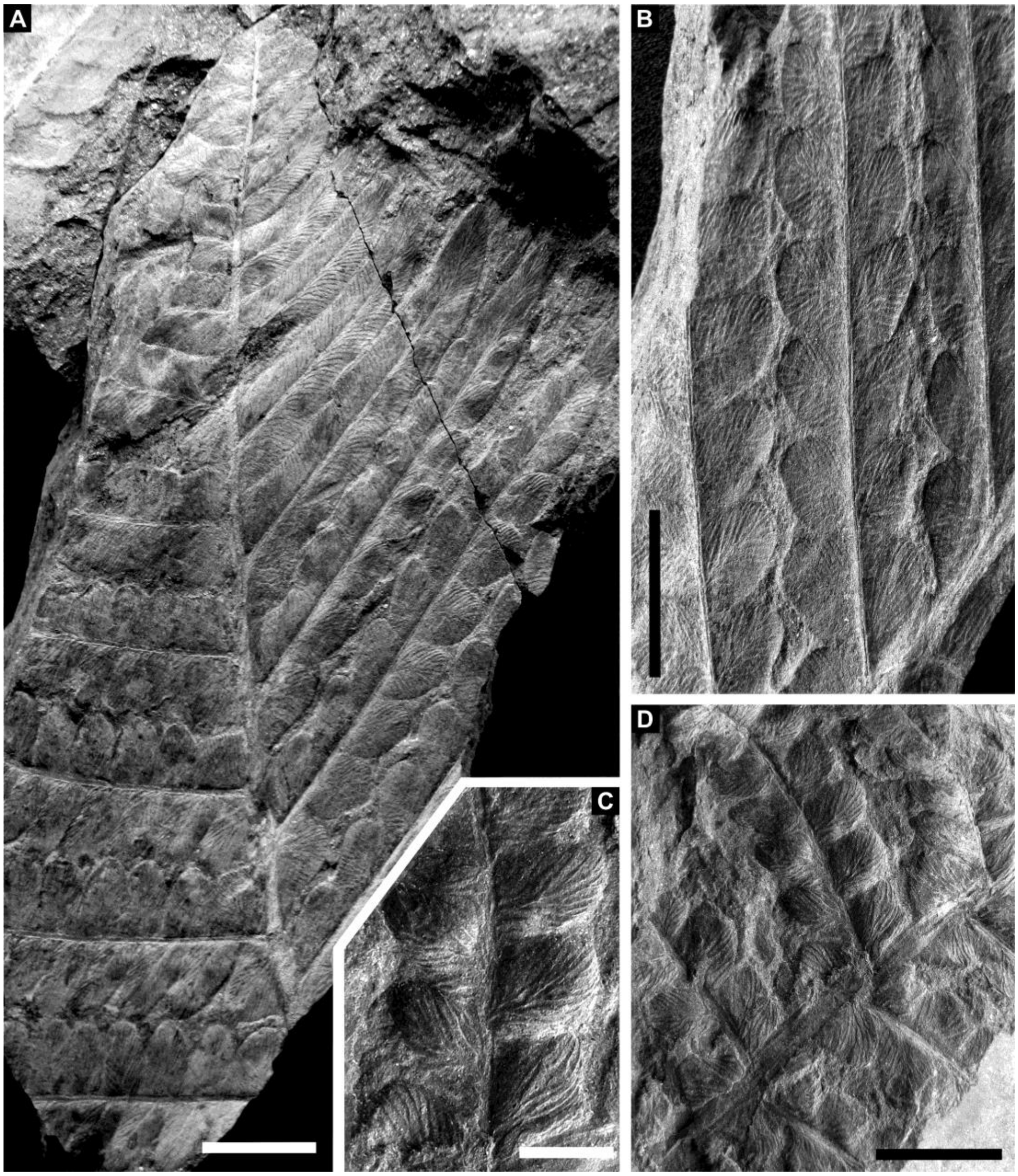

Plate XXVII - *Callipteridium* (*Praecallipteridium*) *zeilleri* Wagner. Scale bar 10 mm. (unpublished)

***Callipteridium* (*Praecallipteridium*) *zeilleri* Wagner, 1962**

Description of material: Ultimate and penultimate pinna fragments showing small, subtriangular and intercalary pinnules pecopterid-odontopterid type, with oval shape and slightly strangled at the base, acquiring the form of wedge in attachment to rachis. The lateral veins are well developed, coming directly from pinnule base and also of the midvein. The midvein is not well prominent or developed.

1.6.5. Final remarks

The continuing studies on the fossil flora from the DCB have led us to recognize a greater floral diversity which until now was known. The results presented here have aimed at the integration of new paleobotanical elements and the consequent updating of flora list of DCB, complementing previous works and researchs carried out by several authors, and thus contributing to increase of the scientific knowledge of its floral diversity.

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1.7. The autonomous life of the *Aphlebia* Presl, 1838: a newly recognized late Carboniferous group appeared during the climatic changes within Central Tropical Pangea

Adapted from Pedro Correia, Josef Pšenička, Zbyněk Šimůnek, Artur A. Sá, J. Brendan Murphy, Deolinda Flores

(Geological Society of America Abstracts with Programs, (2013). GSA's 125th Anniversary Annual Meeting & Exposition, Denver, USA)

1.7.1. Introduction

Aphlebia Presl, 1838 is described in the literature as a macroflora commonly found in paleobiological-paleoecological interaction with Carboniferous ferns. *Aphlebia* is normally connected along the main axis of the fern fronds and has a variety of irregular and pinnatifid leaves which display incomplete to poorly visible veins that are typically parallel. Its reproduction processes are unknown.

In this study, a new *Aphlebia* group and three new species were found in the DCB (lower Gzhelian, Upper Pennsylvanian; Portugal) with reproductive structures preserved and documented in compression-impression material.

1.7.2. Geological setting

Please, see PART II (pag. 21).

1.7.3. Material

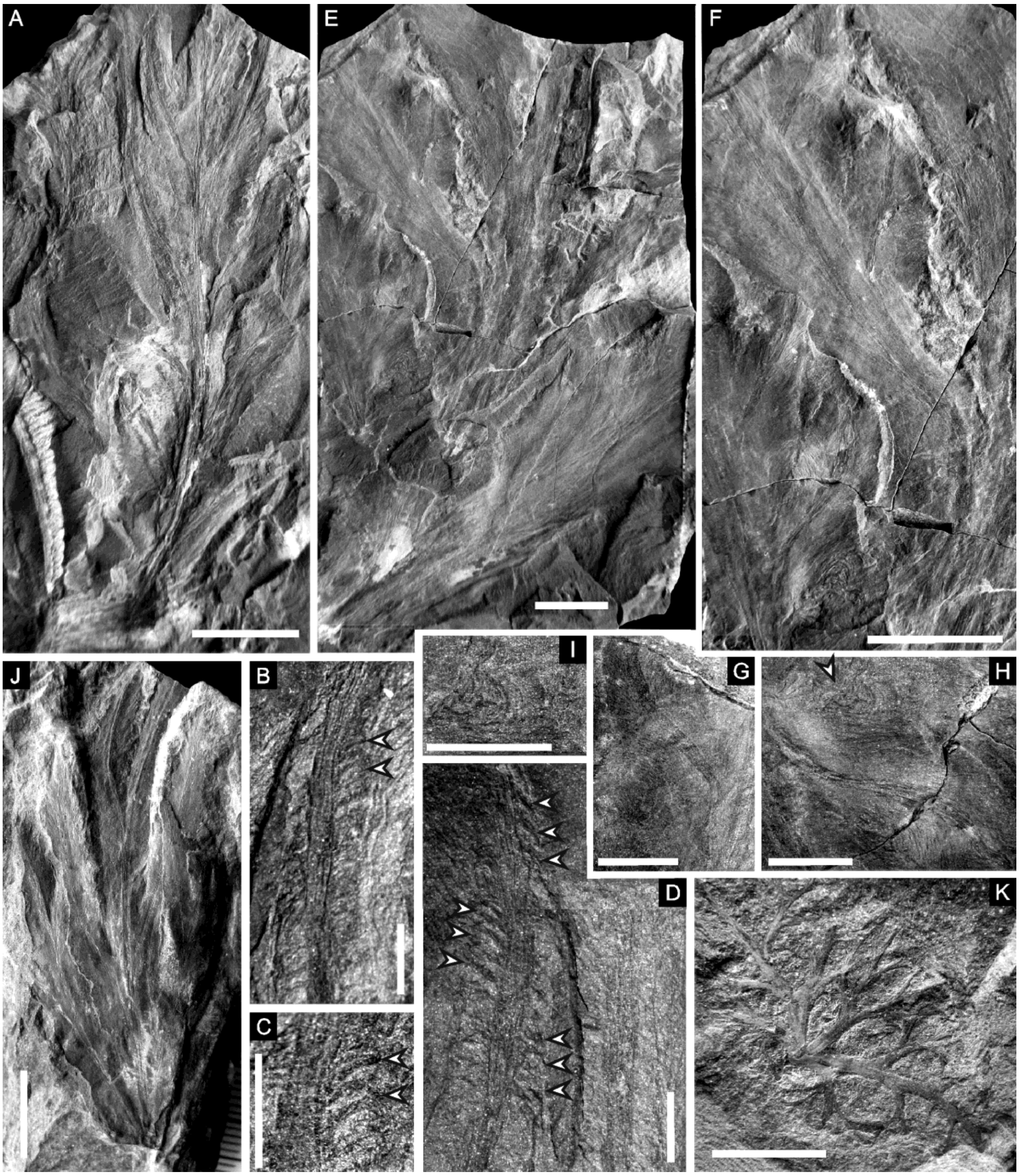

Plate XXVIII. (unpublished)

A–I. ***Aphlebia* sp. nov.**, pinnatifid fronds. A–D, fertile foliage (specimen 1; Figure 35A) showing probably sorus/sporangia (arrowed); E–I, sterile foliage (specimen 2; Figure 35B); G–I, pinnule-type foliage showing possibly fungal (fungi) terminations or trichomes.

Locality— São Pedro da Cova (outcrop spc5, TSU B2), DCB. Scale bar 10 mm. A, E, F: scale bar 10 mm; B–D/G–I: scale bar 5 mm.

J. ***Aphlebia* sp. nov.**, pinnatifid frond showing pinnule-type (sterile) foliage (specimen 3; Figure 35C).

Locality— São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

K. ***Aphlebia* sp. nov.** (specimen 4; Figure 35D).

Locality— São Pedro da Cova (outcrop spc1, TSU B1), DCB. Scale bar 10 mm.

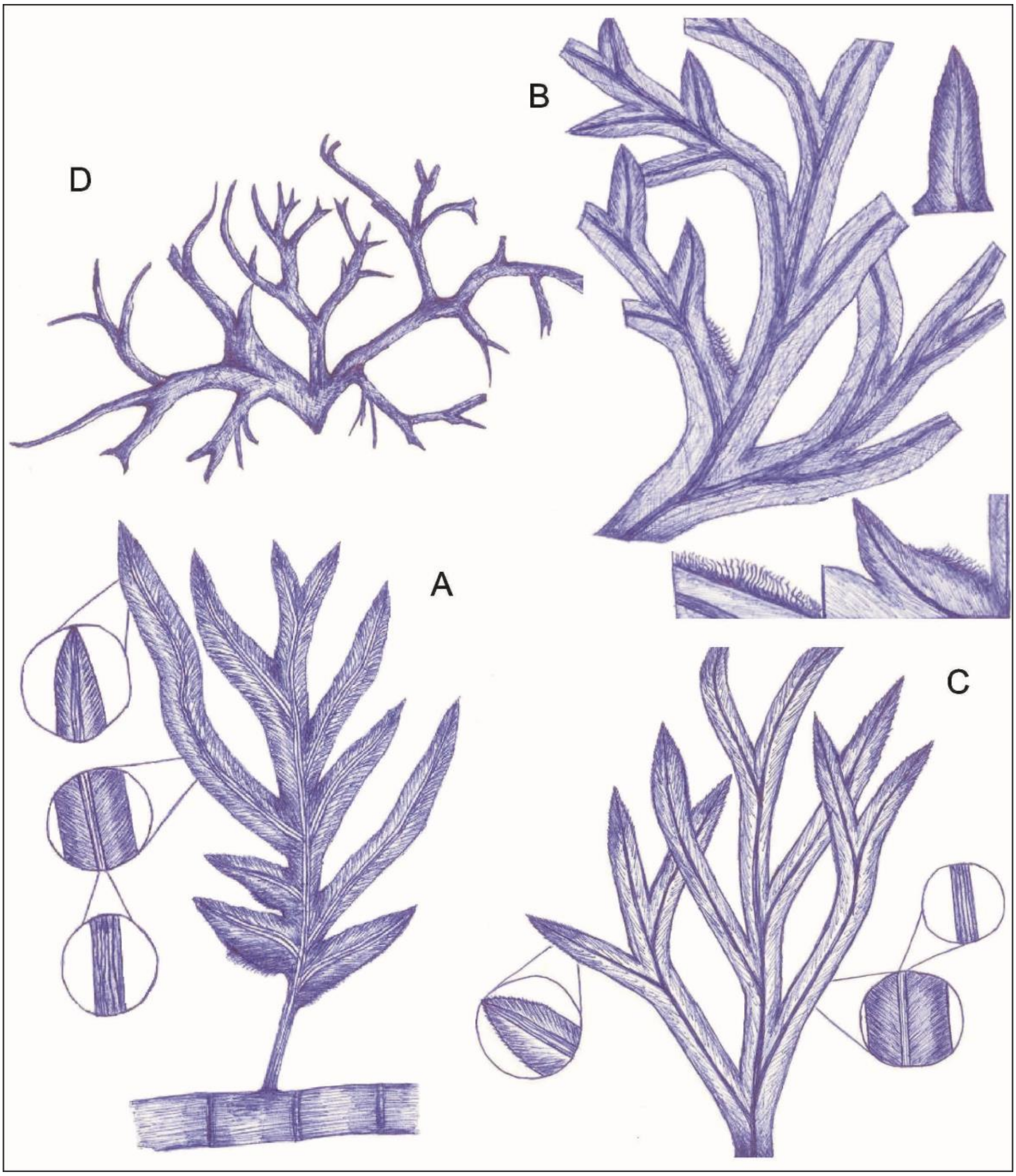

Fig. 35 – Interpretive drawings of the three new species of *Aphlebia* from the DCB. **A.** Specimen 1; **B.** Specimen 2; **C.** Specimen 3; **D.** Specimen 4. (image unpublished)

1.7.4. Discussion and conclusions of results

The reproduction structures of new material (Plate XXVIII, B–D) resemble sporangia which are typical of Carboniferous ferns. These new records indicate that late Carboniferous *Aphlebia* may have developed an autonomous life similar to the ferns that was probably driven by the climatic changes that occurred within Central Tropical Pangea during the Permian–Carboniferous.

2. FAUNA

2.1. *Lusitaneura covensis* n. gen., n. sp., first caloneurodea from the Carboniferous of Portugal (Insecta: Pterygota: Panorthoptera)

Adapted from João Paulo Loureiro, Pedro Correia, Andre Nel, Ary Pinto de Jesus *(Annales de la Société Entomologique de France (n.s.) (2010), 46 (1-2), 242-246)*

Abstract

Lusitaneura covensis n. gen., n. sp., from the late Carboniferous (lower Gzhelian [lower Stephanian C]) of the Douro Basin (NW of Portugal), is the first Portuguese representative of the Paleozoic insect order Caloneurodea.

Résumé: *Lusitaneura covensis* n. gen., n. sp., premier Caloneurodea du Carbonifère du Portugal (Insecta: Pterygota: Panorthoptera). *Lusitaneura covensis* n. gen., n. sp. est le premier représentant portugais de l'ordre d'insectes paléozoïques des Caloneurodea. Il provient du Carbonifère supérieur (Stéphanien C inférieur) du Bassin du Douro (NW du Portugal).

***Keywords*:** Insecta, Caloneurodea, late Carboniferous, Douro Basin, Portugal.

2.1.1. Introduction

Carlos Teixeira developed the study of the Carboniferous insects from Portugal in the years 1939–1950. He described alone or in collaboration with the French paleoentomologist Daniel Laurentiaux numerous fossils, mainly 'blattodean' taxa. In Teixeira (1946), is done the first description of fossil insects from the upper Stephanian outcrop of São Pedro da Cova (Douro Carboniferous Basin: São Pedro da Cova and Pejão coalfields), i.e., a *Palaeodictyoptera Homaloneura ribeiroi* Teixeira, a Blattinopsidae, and two 'blattodean' Phyloblattidae *Phyloblatta fonsecai* Teixeira and *P. carringtoni* Teixeira. The same author found numerous material in other Portuguese outcrops (brief summary in Laurentiaux and Teixeira, 1948, 1958), but no further fossil insect was found at São Pedro da Cova. Thanks to recent field researches, J. Loureiro and P. Correia discovered new fossil insects in São Pedro da Cova coalfield outcrops. These are a Palaeodictyoptera, several 'Blattodeans' and the first record of the order Caloneurodea from Portugal, currently described in the present work. This order is ranging stratigraphically from the Westphalian (late Carboniferous) to the Kazanian (late Permian) of North America, Europe, and Siberia. Its discovery in the Portuguese upper Stephanian is not surprising as this order is already well known from the French classical locality of Commentry similar in age as Douro Basin.

2.1.2. Geological setting

Please, see PART II (pag. 21).

2.1.3. Systematic paleontology

We follow the nomenclature of wing venation and classification of Béthoux *et al.* (2004).

Order: Caloneurodea Handlirsch, 1937
Family: uncertain

***Lusitaneura* n. gen.**

Type species: *Lusitaneura covensis* n. sp.
Etymology: Named after Lusitania and Caloneura.
Diagnosis: Wing characters only. ScP reaching costal margin in second third of wing length and subcostal area not very broad; three posterior branches of RP; MA with two branches with anterior branch not making a strong curve, and posterior branch with small secondary twigs emerging from it; no vein distally emerging from MP+CuA+CuPaα; no small branches of CuPaβ near posterior wing margin.

***Lusitaneura covensis* n. sp.**

Figure 36; Plate XIX, 10

Etymology: Named after São Pedro da Cova village.
Material: Holotype (No. collection: UP-MHNFCP-154771) stored in NHMSUP (a nearly complete wing, with cross-veins not well preserved except in anal area and between RA and RP). A plastic cast is stored at the Muséum national d'Histoire naturelle, Paris, France.
Age and outcrop: upper Carboniferous, lower Stephanian C, Douro Basin, São Pedro da Cova coalfield (outcrop spc2, TSU B1; Figures 3, 7), Portugal.
Horizon type: H6 horizon (Figure 37).
Description: A nearly complete wing, 21.7 mm long, 4.6 mm wide; ScP reaching anterior wing margin 15.1 mm distal of wing base; RA simple; first posterior branch of RP 10.0 mm of its origin; RP posteriorly pectinate with three branches, all simple; MA emerging from M+CuA+CuPaα just distal of the origin of RP; MA branched 1.2 mm distal of its origin; anterior branch of MA simple, posterior branch with three small posterior branches; MP+CuA+CuPaα simple, strongly convex; MP not emerging from

MP+CuA+CuPaα; CuPaβ and CuPb simple and strongly concave; AA1 simple, weakly convex; area between AA1 and AA2 with intercalary veins; cross-veins not well preserved except in anal area and between RA and RP, simple and straight.

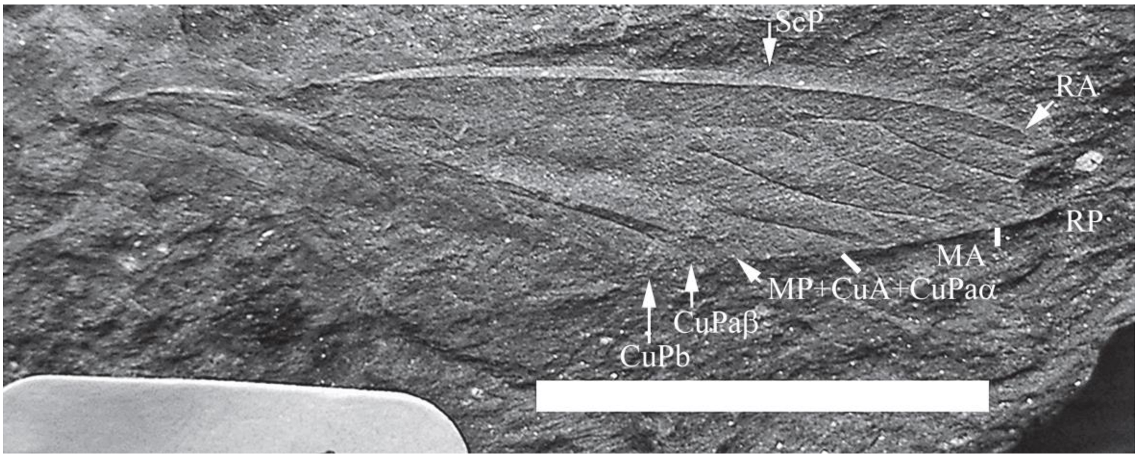

Fig. 36 - Photograph of wing of ***Lusitaneura covensis* n. gen., n. sp.** (holotype). Scale bar 10 mm.

2.1.4. Discussion

Lusitaneura n. gen. falls in the Caloneurodea Handlirsch because it has the diagnostic characters of this order: MA with two branches; a vein MP+CuA+CuPaα simple; fusion of CuPaα with MP+CuA; MP+CuA+CuPaα (convex) and CuPaβ (concave) close, parallel and straight; MP running fused with CuA+CuPaα at length; absence of anal fan. It has also the secondary character of the group, viz. RP posteriorly pectinated; marked convexity of crossveins (visible only in some of them, between RA and RP; absence of anterior branch of RA. The very short anterior branch CuPaα between MP+CuA and CuPa, typical of the Panorthoptera is hardly visible because this part of the wing is deteriorated.

For the weakness of the current familial classification within the Caloneurodea, we compare our fossil with the various genera currently attributed to this order (Béthoux et al. 2004).

Affinities with *Caloneura* Brongniart is unlikely because the apex of ScP is near the second third of wing length and subcostal area is not very broad. *Lusitaneura* n. gen. differs from *Gigagramma* Béthoux et al. in the absence of any vein distally emerging from CuA+CuPaα, and in the more basal position of apex of ScP. *Lusitaneura* n. gen. differs from *Sthenarocera* Brongniart in the presence of only three posterior branches of RP instead of 8–9. It differs from *Apsidoneura* Carpenter in the apex of ScP in a more basal position, anterior branch of MA not making a strong curve (also differences with *Homaloptila* Handlirsch), and RP with three branches, instead of two. *Lusitaneura* n. gen. differs from *Pleisiogramma* Carpenter in the MA with two branches, instead of being simple, and the apex of ScP in a more basal position. Differences with *Paleuthygramma* Martynov are the same plus the presence of a rather broad area of RP, instead of being strongly reduced in the latter. The same last difference concerns *Euthygramma* Martynov and *Anomalogramma* Carpenter, 1943 and *Nanogramma* Béthoux et al. The Gelasopteridae Carpenter (*Gelasopteron* Carpenter) are Neoptera of uncertain ordinal position, but possibly Caloneurodea. It differs also from *Lusitaneura* in the much reduced area of RP.

Caloneurella Carpenter shares with *Lusitaneura* the presence of three branches of RP, the posterior branch of MA with small secondary branches emerging from it but it diff ers in the longer ScP ending near apex of RA (Carpenter, 1934).

Pruvostiella Handlirsch is a caloneurodean genus based on a single species *P. lecomtei* Pruvost based on a rather incomplete wing with several structures missing. Nevertheless, it shares with *Lusitaneura* n. gen. the apex of ScP near second third of wing length, area of RP relatively broad with 2–3 branches; MA forked. *Lusitaneura* n. gen. differs from *Pruvostiella* in the absence of small branches of CuPaβ near posterior wing margin.

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2.2. First Paleozoic arachnid from Portugal and implications for Carboniferous paleobiogeography

Adapted from Pedro Correia, J. Brendan Murphy, Artur A. Sá, Rúben Domingos, Deolinda Flores
(Geological Journal (2013), 48, 101-107)

Abstract

The first occurrence of arachnids (*Aphantomartus pustulatus*) in the Carboniferous strata of Portugal is documented and its paleobiogeographic significance is assessed. The Aphantomartidae species are thought to be native to Central Europe where its oldest example is recorded in Middle–Upper Mississippian strata. Known occurrences are preserved along the flanks of mountains such as the Appalachian Mountains, the Cantabrian Mountains and the Valongo Anticline (Portugal, Iberian Massif) and provide clear evidence that the Aphantomartidae species probably lived in upland or mountainous environments. The Iberian Massif may have served as a 'link' between the migration routes of several terrestrial animals from North America and Eurasia, and this linkage constrains the paleogeographic and paleoenvironmental conditions in equatorial Pangaea during the Carboniferous and early Permian.

Keywords: Trigonotarbida; arachnid; *Aphantomartus*; paleobiogeography; Pangea; Laurasia; Iberian Massif; Carboniferous.

2.2.1. Introduction

The distribution of Paleozoic terrestrial faunas provides fundamental constraints for understanding the paleobiogeographic connections between continents (as first described by Wegener, 1912). The amalgamation of Laurasia and Gondwana in the late Paleozoic was one of the key events in the formation of Pangea and detailed paleontological data are required to provide a better understanding of its configuration and paleobiogeography. A key constraint is the co-occurrence of the same terrestrial animal species in Paleozoic strata with native (i.e., autochthonous) characteristics which allows the determination of migration routes between continental lands within Laurasia (i.e., North America and Eurasia). The trigonotarbid arachnids (Trigonotarbida) are among the earliest terrestrial animals and range in age from the late Silurian to the early Permian (e.g., Jeram *et al.*, 1990; Dunlop, 1995, 1996, 1997, 2010; Rössler, 1998; Dunlop *et al.*, 2008, 2009; Garwood *et al.*, 2009; Selden and Pillola, 2009; Garwood and Dunlop, 2010; Poschmann and Dunlop, 2010, 2011).

Trigonotarbids were extinct spider-like animals that lacked silk-producing spinnerets, and their bodies were divided into a prosoma (i.e., cephalothorax) and opisthosoma (i.e., abdomen) a few centimetres in length. They are anatomically characterized by a box-shaped or triangular-subtriangular prosoma and by elliptical (oval) opisthosoma composed of 9 visible tergites (segments) divided into median and lateral plates (Petrunkevitch, 1913; Dunlop, 1995, 1996, 1997, 2010; Dunlop *et al.*, 2008, 2009; Garwood *et al.*, 2009; Poschmann and Dunlop, 2011; Garwood and Dunlop, 2010, 2011). The oldest trigonotarbid arachnids occur in the upper Silurian–Lower Devonian strata of Germany and Britain (e.g., Jeram *et al.*, 1990; Dunlop, 1996, 2010; Garwood and Dunlop, 2010; Poschmann and Dunlop, 2011). Several Early Devonian trigonotarbids occur in the Westerwald area of the Rhenish Slate Mountains in Germany (Poschmann and Dunlop, 2011). The youngest trigonotarbids are found in the early Permian 'Rotliegend' strata of Germany (e.g., Rössler, 1998; Rössler *et al.*, 2003; Dunlop, 2010; Garwood and Dunlop, 2010). Trigonotarbid arachnids are especially common in late Carboniferous strata 'Coal Measures' of Europe (e.g., Germany) and North America (e.g., Illinois and Ohio basins, USA; Pocock, 1911; Petrunkevitch, 1949; Dunlop, 1995, 2010; Easterday, 2003; Dunlop *et al.*, 2008; Garwood *et al.*, 2009).

A single occurrence of arachnids in Carboniferous strata of the Iberian Massif was reported by Selden and Romano (1983), who discovered a spider-like arachnid (the trigonotarbid species, *Aphantomartus areolatus* Pocock), in lower Kasimovian (Middle–Upper Pennsylvanian) strata of the Léon region (Cantabrian Mountains, NW Spain). Another species assigned to the genus *Aphantomartus* Pocock is *Aphantomartus pustulatus* Scudder. *Aphantomartus pustulatus* was a terrestrial arthropod and a very efficient predator (e.g., Rössler, 1998; Garwood and Dunlop, 2010). *Aphantomartus pustulatus* has a short body with strong and long legs and an armoured carapace which displays a dense dorsal tuberculation that protected it against attacks by potential predators (e.g., Rössler, 1998; Garwood *et al.*, 2009; Garwood and Dunlop, 2010). *Aphantomartus pustulatus* is one of the youngest trigonotarbids recorded in lower–upper Carboniferous strata. This species occurs in Middle Pennsylvanian strata of North America (e.g., Illinois and Ohio basins, USA; Maritimes basin, New Brunswick, Canada) (e.g., Rössler, 1998; Miller and Forbes, 2001; Easterday, 2003). Its oldest known occurrences are in Middle–Upper Mississippian strata of Poland and Germany (Rössler, 1998). *Aphantomartus pustulatus* and *A. areolatus* are two of the three species that comprise the family Aphantomartidae (see Selden and Romano, 1983; Rössler, 1998; Rössler *et al.*, 2003). Aphantomartidae species are very widespread and occur in North America and Europe (Britain, France, Belgium and the Czech

Republic) in strata that range from the Early to the Late Pennsylvanian in age (Rössler, 1998). They lived in environments that were dominated by fluvial depositional systems (Rössler, 1998). Within the habitat of Aphantomartidae individuals, a rich flora coexisted and included hydrophilic species, and terrestrial floral communities such as Lycophytales, Calamitales, Sphenophytales and Pteridospermaphytales (Rössler, 1998).

In this paper the first occurrence of a Paleozoic arachnid in Portugal is documented. The arachnid species described herein, *Aphantomartus pustulatus* was found in lower Gzhelian (Upper Pennsylvanian) strata of the São Pedro da Cova region (Douro Carboniferous Basin, NW Portugal, Iberian Massif). These new data have important implications for understanding the potential Late Paleozoic paleogeographic connection between North America and Eurasia during the amalgamation of Laurasia.

2.2.2. Geological setting

Please, see PART II (pag. 21).

2.2.3. First Paleozoic arachnid from the Carboniferous of Portugal

The trigonotarbid *Aphantomartus areolatus* from the lower Kasimovian (Middle–Upper Pennsylvanian) strata of the Léon region (Cantabrian Mountains, NW Spain, Iberian Massif) is currently the only documented record of an arachnid in the upper Paleozoic strata of the Iberian Massif (Selden and Romano, 1983). In this paper we document a second trigonotarbid occurrence (the first Paleozoic arachnid from Carboniferous of Portugal) in the lower Carboniferous strata of the Iberian Massif. The Portuguese arachnid, *Aphantomartus pustulatus*, was found in lower Gzhelian (Upper Pennsylvanian) strata of the São Pedro da Cova region (location outcrop (outcrop spc2, TSU B1; Figure 7): 41°09´44.65´´N; 08°30´25.73´´W; DCB). This specimen is preserved in light-to-dark gray shales (“insects level”: e.g., *Lusitaneura covensis* Loureiro *et al*.; Bed H6, Figures 37, 38). These shales are relatively compact, laminated and very fossiliferous with well-preserved plant fossils including: a rich terrestrial flora such as Pteridopsids and Pteridospermopsids (several genera are found: e.g., *Sphenopteris*, *Pecopteris*, *Lobatopteris*, *Callipteridium*, *Acitheca*, *Neuropteris*, *Cyclopteris*, *Oligocarpia* and *Diplotmema*); Calamitales (e.g., *Calamites*, *Asterophyllites*, *Annularia* and *Calamostachys*); Sphenophytales (e.g., *Sphenophyllum*); Cordaitales (e.g., *Cordaites*); and some Lycophytales (lycophytes uncertain). This flora is associated and/or interbedded with lacustrine deposits that are rich in fauna such as the non-marine bivalve *Anthraconaia* cf. *lusitanica* (Bed H6, Figures 37, 38).

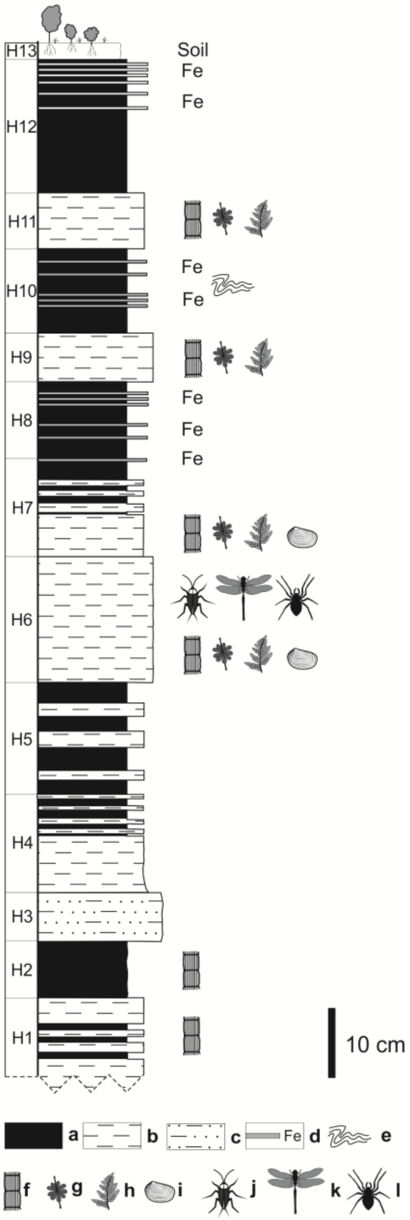

Fig. 37 - Stratigraphic log of the new lower Gzhelian outcrops of the Sao Pedro da Cova region; (a) coal levels, (b) shale levels, (c) siltitic levels, (d) clay with oxidized iron levels, (e) levels with tectonic deformation, (f) *Calamites* rich levels, (g) *Annularia* rich levels, (h) Filicopsids and Pteridospermopsids, (i) non-marine bivalves, (j) *Lusitaneura covensis* Loureiro *et al.*, (k) Palaeodictyoptera insects (e.g., *Stenodictya*? *lusitanica* Correia *et al.*), (l) *Aphantomartus pustulatus* Scudder. After Correia *et al.* (2013).

Fig. 38 - New lower Gzhelian outcrops (spc2, TSU B1) of the Sao Pedro da Cova (1–4): 1. Description of the different horizonts of the log; 2. Samples collection of the different horizonts; 3. H5 and H6 horizonts; 4. Shale levels containing trunks of *Calamites* interlayered with oxidized iron levels. Excavation works during fieldwork in 2010. (image unpublished)

2.2.4. Systematic paleontology

Subphylum: Chelicerata Heymons, 1901
Class: Arachnida Lamarck, 1801
Order: Trigonotarbida Petrunkevitch, 1949
Family: Aphantomartidae Petrunkevitch, 1945
(= Trigonomartidae Petrunkevitch, 1949)
Genus: *Aphantomartus* Pocock, 1911
Species: *Aphantomartus pustulatus* Scudder, 1884
Figure 39; Plate XIX, 2, 3)

Synonyms: See in Rössler (1998).

Holotype: No. 1752, collection at the U. S. Nat. Mus. (No. 37 984), Scudder (1890: pl. 40, figs. 5, 8), Mazon Creek, Illinois basin, USA, lower Allegheny (upper Moscovian, Middle Pennsylvanian).

Description: Material consists of a single specimen of the species *Aphantomartus pustulatus* found in lower Ghzelian (Upper Pennsylvanian) strata of São Pedro da Cova (DCB, NW Portugal, Figures 2, 7). This specimen is characterized by an opisthosoma and absence of the prosoma (= cephalothorax). The opisthosoma is elliptical and incomplete, and relatively well preserved; it is 10.5 mm in length and 9.5 mm in width. It displays two visible longitudinal sutures, and its median and lateral tergal plates are well differentiated; these tergites are covered by a dense and prominent dorsal tuberculation. Tergites 2–7 are visible, of which 2+3 are fused into a diplotergite, and the tergites 8 and 9 are lacking due to absence/destruction of the posteriormost portion/pygidium. The tubercles (0.3 mm to 0.9 mm in length) have an angular/triangular morphology, but some tubercles from the top of the opisthosoma (tergites 2+3) are rounded or sub-rounded. Some tubercles display underdeveloped small spines (characters only observable in latex cast). The connection area between the prosoma and opisthosoma is well marked and wide. Tergites 2 and 3 are merged or welded.

Material: Specimen and its latex cast are stored in the NHMSUP; Collection reference: UP-MHNFCP-094958.

Discussion and comparisons: The specimen of *Aphantomartus pustulatus* described herein closely resembles *Aphantomartus areolatus*: both species have elliptical opisthosomas (and triangular prosomas) which display several tergites covered by a dorsal tuberculation; and the same number of tergites (9, although this distinction is not observable owing to absence of the posterior most portion). However *A. pustulatus* differs from *A. areolatus* in that *A. pustulatus* has a more elliptical opisthosoma than that of *A. areolatus* (which has a more rounded morphology) and in comparison with this species, *A. pustulatus* displays a more prominent dorsal tuberculation. The tubercles from *A. areolatus* are slightly longer (0.5 to 1.0 mm in length) and more rounded, whereas those of *A. pustulatus* are angular and/or triangular and have underdeveloped small spines. All these characteristics allow us to assign taxonomically this specimen to the species *Aphantomartus pustulatus*.

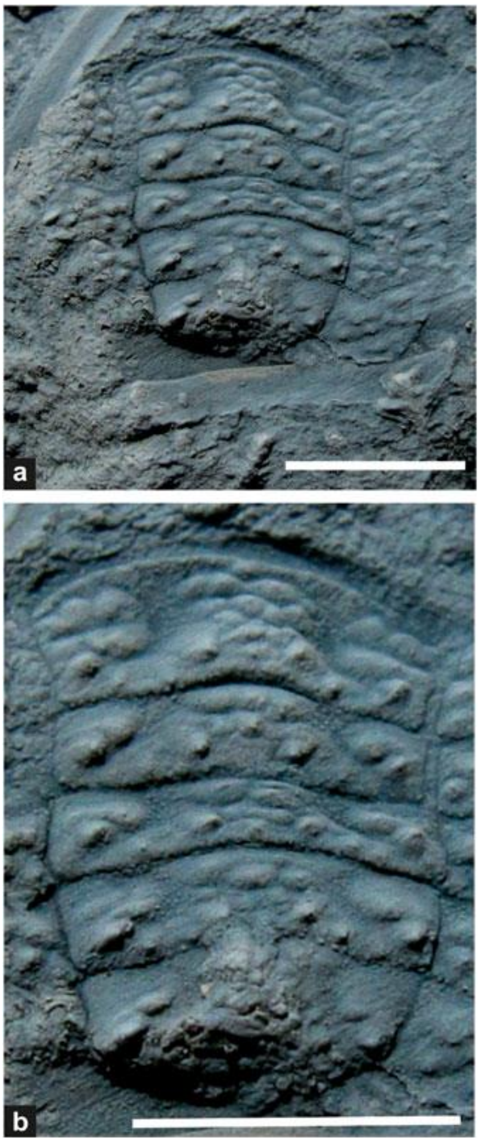

Fig. 39 - Trigonotarbid arachnid *Aphantomartus pustulatus* (a and b, dorsal view). Scale bar = 5 mm.

2.2.5. Discussion and conclusions

Aphantomartidae range in age from the middle Viséan (Middle Mississippian) to the lower Asselian (early Permian) (e.g., Rössler, 1998). Aphantomartidade species seem to have originated in Central Europe (e.g., Poland and Germany; European native species) where they occur commonly in Middle–Upper Mississippian strata (Figure 40). One of the oldest trigonotarbids (Early Devonian) occurs on mountain ranges (e.g., Rhenish Slate Mountains, Germany) (e.g., Poschmann and Dunlop, 2011). The youngest trigonotarbids (late Carboniferous) such as *Aphantomartus pustulatus* and *A. areolatus* lived in environments which were dominated by fluvial systems (Rössler, 1998). These fluvial systems are commonly associated with elevated areas such as uplands and mountains (e.g., Miall, 1996; Harvey, 1997). Furthermore, these animals resided in adjacent areas along the flanks of mountains such as the Appalachians (e.g., Illinois, Ohio and Maritimes basins) and the Cantabrians (Spain, Eastern Iberian Massif) (e.g., Selden and Romano, 1983; Rössler, 1998; Miller and Forbes, 2001; Easterday, 2003), as well as the Valongo Anticline (Portugal, Western Iberian Massif) (Figure 40). These paleoequatorial mountain ranges constitute a part of the Appalachian and Variscan orogens which were developed in the Late Devonian–early Permian during the amalgamation of Pangea (e.g., Fluteau *et al.*, 2001; Vai, 2003; Murphy and Nance, 2003). Therefore, these new data are clear evidence that the Aphantomartidae species probably lived in upland and/or mountainous areas, from where they were transported by fluvial systems and deposited in lowlands and intramontane basins, as was the case of the Aphantomartidae species in the DCB. This scenario implies probably the transport of their associated fauna and flora. The Iberian Massif, also, seems to have acted as a 'link' between migration routes of terrestrial animals (e.g., Aphantomartidade arachnids) of North America and Eurasia. The diachronous migration of these species (ranging from the middle Viséan to the lower Asselian) constrains the paleogeographic and paleoenvironmental conditions of North America and Eurasia, and suggests a proximal paleogeography during the Carboniferous and early Permian. These species represent, therefore, a potential paleobiogeographic marker that may be used to constrain continental reconstructions in the late Paleozoic.

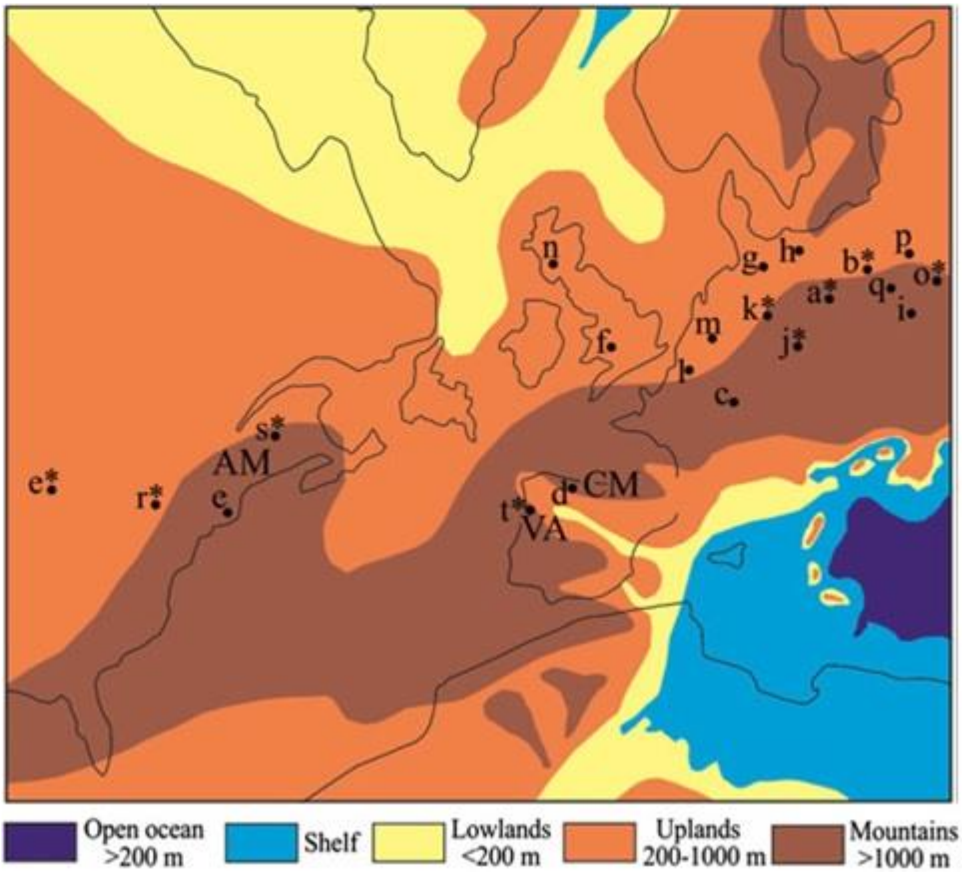

Fig. 40 - Paleogeographic map with the Aphantomartidae and *Aphantomartus pustulatus* (marked with an asterisk) distribution within the Pangea amalgamation during Carboniferous time. The paleoenvironments (lowlands, uplands and mountains) distribution is adapted from Kerp *et al.* (2006) and the paleogeographic maps from Colorado Plateau Geosystems, Inc (URL: http://www.cpgeosystems.com/). The map includes the documented occurrences by Rössler (1998; localities a to q), Miller and Forbes (2001; locality s – Maritimes Basin) and Easterday (2003; locality r – Ohio Basin). New locality t – DCB; VA - Valongo Anticline, CM – Cantabrian Mountains, AM – Appalachian Mountains.

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2.3. A new Palaeodictyoptera from the late Carboniferous of Portugal

Adapted from Pedro Correia, Andre Nel, Artur A. Sá, Rúben Domingos, André Carneiro, Deolinda Flores

(Annales de la Société Entomologique de France (N.S.) (2014), 49 (4), 398-401)

Abstract

A new species of winged insect (order Palaeodictyoptera), *Stenodictya*? *lusitanica* sp. nov., is recorded from the lower Gzhelian (Upper Pennsylvanian) of Douro basin, Portugal. It confirms the great diversity of the past entomofauna from this basin.

Résumé: Un nouveau Palaeodictyoptera du Carbonifère supérieur du Portugal. Un nouveau Palaeodictyoptera, *Stenodictya*? *lusitanica* sp. nov., est signalé du Gzhelien inférieur (Carbonifère supérieur) du Bassin du Douro, Portugal. Il confirme la grande diversité de l'ancienne entomofaune de ce bassin.

Keywords: *Stenodictya*; Insecta; fossils; Gzhelian; Douro Basin.

2.3.1. Introduction

The first studies on fossil insects of the Carboniferous of Portugal were described by Carlos Teixeira during 1930–1950 (1939, 1941, 1944, 1946) documented several Late Carboniferous insects, in particular in the Douro Basin (herein called DCB), with the description of new taxa reported in the São Pedro da Cova, Valdeão and Pejão coalfields. Nearly seven decades later, new studies (Loureiro *et al.*, 2010) were undertaken on the entomofauna of the DCB, with the description of the first Portuguese Caloneurodea, *Lusitaneura covensis* Loureiro *et al.* In the present study, a new Palaeodictyoptera is reported from the lower Gzhelian of the São Pedro da Cova region. This new insect differs from the palaeodictyopteran taxa already documented by Teixeira, and provides indications of a great diversity of insects during the Late Carboniferous in the DCB.

2.3.2. Geological setting

Please, see PART II (pag. 21).

2.3.3. New Palaeodictyoptera record

In this paper we document a new insect (Figure 41) of the order Palaeodictyoptera found in the lower Gzhelian (Upper Pennsylvanian) strata of São Pedro da Cova region location outcrop (outcrop spc2, TSU B1; Figures 3, 7): 41°09´44.65´´N, 08°30´25.73´´W; DCB, Portugal, Iberian Massif). The fossil material is preserved in light-to-dark gray shales ("insect level", with *Lusitaneura covensis* Loureiro *et al.*; Arachnida Trigonotarbida: *Aphantomartus pustulatus* Scudder, 1884 (Scudder, 1884; Correia *et al.*, 2013) and Eurypterida: cf. *Adelophthalmus* sp.). These shales are relatively compact, laminated and very fossiliferous with well-preserved plant fossils including a rich terrestrial flora-like Pteridopsids and Pteridospermopsids (several genera found: e.g., *Sphenopteris*, *Pecopteris*, *Lobatopteris*, *Callipteridium*, *Acitheca*, *Neuropteris*, *Cyclopteris*, *Oligocarpia* and *Diplotmema*); Calamitales (e.g., *Calamites*, *Asterophyllites*, *Annularia* and *Calamostachys*); Sphenophytales (e.g., *Sphenophyllum*); Cordaitales (e.g., *Cordaites*); and some Lycophytales (lycophytes uncertain). This flora is associated and/or interbedded with lacustrine deposits that are rich in fauna such as the non-marine bivalve *Anthraconaia* cf. *lusitanica* Teixeira.

2.3.4. Systematic paleontology

Class: Insecta
Order: Palaeodictyoptera Goldenberg, 1877
Family: ?Dictyoneuridae Handlirsch, 1906
Genus: *Stenodictya* Brongniart, 1893

***Stenodictya*? *lusitanica* sp. nov.**
Figure 41 (see also Plate XIX, 11)

Etymology: Named after the ancient name Lusitania for Portugal.
Material: Holotype specimen UP-MHNFCP-127180, stored in the collection of the NHMSUP.
Diagnosis: The three anterior branches of MP are regularly emerging from the stem of MP; part of RP basal of first fork of this vein very long.
Horizon type: H6 horizon (Figures 37, 38).
Description: This fossil is a fragment of the median part of a wing, 59.0 mm long, 29.5 mm wide; crossveins are not clearly preserved but some very faint ones are visible, especially in costal area; are between costa and ScP 3.8 mm wide, with numerous simple crossveins between them; ScP and RA parallel with no clear crossveins in a 2.3 mm wide area between them; a long stem of RP between its base on radius and first distal branch, 33 mm long, only one posterior branch of RP preserved; median vein anteriorly pectinate with four preserved branches, namely a simple MA and a three-

branched MP; CuA simple, weakly curved; CuP with two or three branches; anal area not preserved.

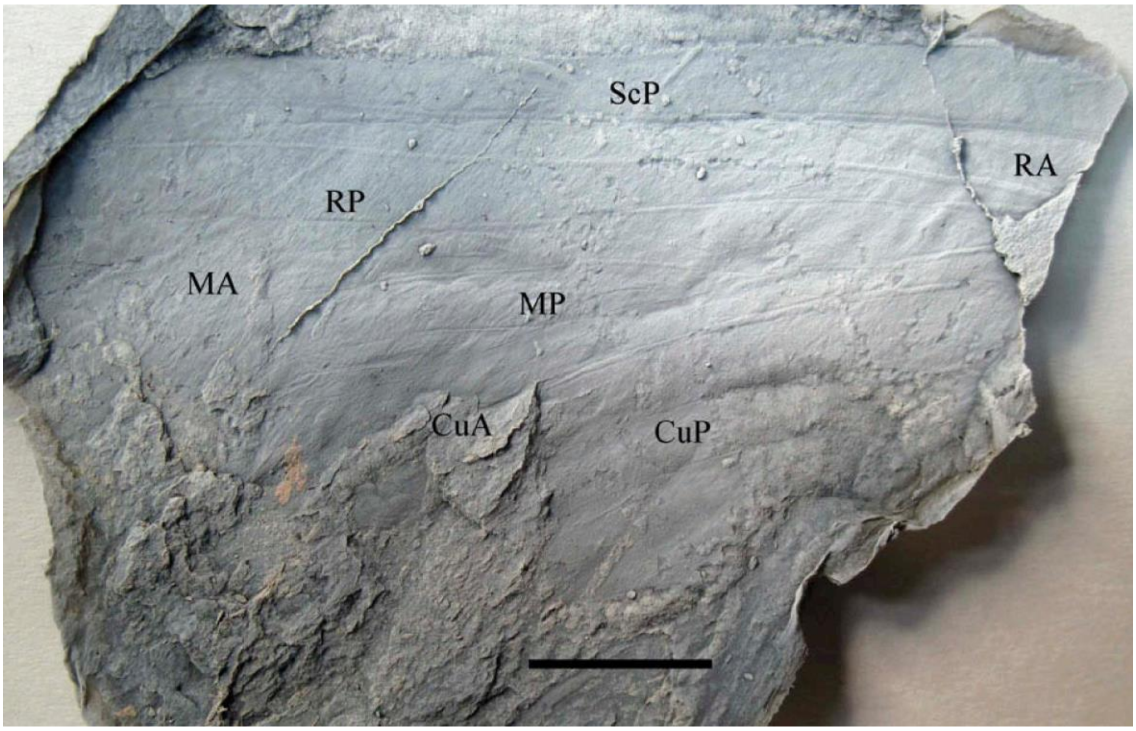

Fig. 41 - *Stenodictya*? *lusitanica* sp. nov., photograph of wing (latex cast). Scale bar represents 10 mm.

2.3.5. Discussion

This fossil is clearly that of a palaeodictyoptera wing for the long parallel ScP and radial stem, absence of braces between main veins, shape of median and cubital veins, etc., but it is too incomplete for an accurate family attribution although it greatly resembles a Dictyoneuridae, especially in the CuA simple and the shape of median vein with a simple MA and a anteriorly pectinate MP (very similar to that of *Microdictya* Brongniart for instance). Nevertheless, similar patterns of venation are also present in some other families, the Breyeriidae *Breyeria* Borre for instance (see Carpenter, 1992). This fossil clearly belongs to a species different from the Eugereonidae *Valdeania medeirosi* Teixeira, 1941 and the Spilapteridae *Homaloneura ribeiroi* Teixeira, 1946 from the same outcrop in the median vein anteriorly pectinate instead of being forked two times and in the CuA simple. We provisionally attribute it to a new species of the genus *Stenodictya* but with some uncertainly.

This new fossil confirms that the insects of the DCB were certainly more diverse than what the current discoveries would suggest. Further studies will certainly lead to the discoveries of better-preserved specimens of great interest.

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PART V – GENERAL CONCLUSIONS AND FINAL REMARKS

1. Revision of the DCB flora and fauna and new elements

The new megafloral and faunal elements described in the present work are first reported in the DCB, and implies a significant revision of the list of flora previously published by several authors. Some of the new elements are first documented not only in the DCB, but also in the Portuguese Carboniferous. These new occurrences comprise floral 42 species (cited below), including 11 new species, of 34 different genera. In addition, an associated fauna is also first documented in the DCB with description of two new taxa.

FLORA

Pteridospermopsida:
  Trigonocarpales (Medullosales):
    Callipteridium jongmansi Bertrand
    Cyclopteris sp.
    Neuropteris crenulata Brongniart
    Odontopteris schlotheimii Brongniart
  Callistophytales:
    Telangiopsis sp.
    Telangium sp.
?Pteridospermopsida:
  Order uncertain:
    aff. *Rhodeopteridium subpetiolatum* Potonié
Cycadopsida (?Pteridospermopsida):
    Lesleya iberiensis sp. nov.
Pteridopsida (Polypodiopsida):
  Marattiales:
    Acitheca murphyi sp. nov.
    Lobatopteris lamuriana Heer
    Lobatopteris corsini Wagner
    Pecopteris alvarezii sp. nov.
    Pecopteris arborescens von Schlotheim
    Pecopteris cf. *miltonii* (Artis) Brongniart
    Pecopteris cf. *opulenta* Corsin
    Pecopteris puertollanensis Wagner
  Coenopteridales:
    Alloiopteris teixeirai sp. nov.
    Alloiopteris pecopteroides Gothan

Desmopteris sp. nov.
Desmopteris cf. *longifolia* Presl
Filicales:
Oligocarpia gutbieri Göppert
Order uncertain:
Stellatheca sp.
Fern crozier:
Spiropteris sp.
Sphenopsida:
Sphenophyllales:
Sphenophyllum angustifolium Germar
Sphenophyllostachys sp.
Equisetales:
Annularia noronhai sp. nov.
Annularia carinata von Gutbier
Annularia spicata von Gutbier
Annularia cf. *radiata* Brongniart
Asterophyllites longifolius (Sternberg) Brongniart
Calamites insignis Sauveur
Calamostachys grandis Zeiller (Jongmans)
Calamostachys calathifera Weiss
Phyllotheca (*Calamariophyllum*?) *wegeneri* sp. nov.
Stellotheca robusta (Feistmantel) Surange & Prakash
Cordaitopsida:
Cordaitales:
Botryoconus (*Cordaianthus*?) *femina* Grand′Eury
Cordaites foliolatus Grand′Eury
Litostrobus (*Cordaianthus*?) *iowensis* Mamay
Poacordaites microstachys Goldenberg
Lycopsida:
Lepidostrobophyllum cf. *hastatum* (Lesquereux) Chaloner
Incertae sedis:
Ilfeldia gregoriensis sp. nov.
Sphenopteris arberi Kidston
Sphenopteris fayoli Zeiller
Sphenopteris tenuis Schenk
Taeniopteris cf. *carnoti* Renault & Zeiller

Pteridophylla:

Aphlebia sp. nov. (three new species)

FAUNA

Insecta:

Lusitaneura covensis gen. nov., sp. nov.

Stenodictya? *lusitanica* sp. nov.

Arachnida:

Aphantomartus pustulatus Scudder

Eurypterida:

Adelophthalmus sp.

Myriapoda:

aff. *Pleurojulus biornatus* Fritsch

Myriapods indet.

Bivalvia:

Anthraconaia? sp.

These new occurrences were collected and sampled (particularly fossil flora specimens) in new fossil sites (outcrops) located in São Pedro da Cova and Montes da Costa (Ermesinde) regions. The new megafloral elements indicate that a high diversity of paleoflora lived and evolved in the DCB. Future studies of these new fossil sites are needed and are of paramount importance to enhance our understanding of the paleontological diversity of the DCB.

2. New perspectives in future studies: stratigraphic, paleoenvironmental, paleoclimatic, paleoecologic and paleogeographic implications

2.1. Stratigraphic implications

The identification of these new paleobotanical elements have controversial chronostratigraphic implications for the DCB. The new megafloral elements comprise mostly early Gzhelian (late Stephanian)-age species, but probable elements of different stratigraphic (ages) ranges have been documented in the new studied outcrops. They include species occurring in lower Bashkirian (upper Namurian), Moscovian (middle–upper Westphanian) and Kasimovian (lower–middle Stephanian) sequences such as aff. *Rhodeopteridium subpetiolatum* Potonié, *Lobatopteris lamuriana* Heer, *Pecopteris* cf. *miltonii* (Artis) Brongniart and *Callipteridium jongmansi* Bertrand (see the different stratigraphic ranges of macrofloral species for the Iberian Massif according to Wagner, 1966, 1983, 1984; Figure 6). However, further studies will be needed concerning the description and classification of additional fossils from the new outcrops, and consequently, to clarify the age of the different formations and explanation of various geological and structural problems still not well understood in the DCB, particularly in São Pedro da Cova and Montes da Costa regions. Thus, based on the new paleobotanical data, the late Carboniferous outcrops studied and considered indiscriminately as belonging to the lower Gzhelian (lower Stephanian C), suggest the existence of units with different ages, probably resulting from different depositional times.

2.2. Paleoenvironmental, paleoecologic, paleoclimatic and paleogeographic implications

The new fossil occurrences described herein include first records in Iberian Massif such as enigmatic dryland flora *Lesleya* and the arachnid *Aphantomartus pustulatus*, and they represent significant floral and faunal affinities and paleogeographic, paleoenvironmental and paleoclimatic constraints between Laurentia and Iberian Massif during the final amalgamation of the Pangea in the Late Pennsylvanian. The co-occurrence of these fossil megafloral and faunal elements in the DCB also provide new insights for their paleoenvironment and paleoecology, as well as deduction of the paleoclimatic conditions in which they are located, within the Iberian Massif. Their fossil deposits indicate that most of floral and faunal assemblages lived in riparian environments within mountainous (intramontane) regions from the Variscan orogen during the Late Pennsylvanian.

In conclusion, the discovery of above mentioned new taxa described in the studied outcrops located within a small area such as DCB, provide clear evidence that this basin preserved a diverse fossil megaflora, including many floral species native/endemic to region, and a specific climatic, environmental (dryland intramontane environment) and ecological conditions, which are largely determinated by location of the region and surrounding topography dominated by adjacent mountainous areas such as Valongo Anticline.

3. Protection and preservation of the new outcrops of São Pedro da Cova and Montes da Costa localities

The obtained results presented in this work allowed the execution of an assessment focused on the protection and conservation (Geoconservation) of the new fossiliferous outcrops reported in the São Pedro da Cova and Montes da Costa regions. The paleontological records in conjunction with peculiar stratigraphic, geological and structural features described in both regions are of scientific, educational, and possibly economic and touristic importance. These are enough reasons that the studied formations can be considered geological sites justifying their protection, identifying threats to its integrity and providing management solutions.

Thus, based on present results, one of the goals of this work will be to promote the necessary actions to consider as geosites the different outcrops that preserve exceptional paleontological, geological and structural features, with great scientific and didactic interest. Such potential geosites contain singular and rare fossils of megafloral and faunal elements, which are fundamental to scientific knowledge and its dissemination, and for these reasons, they should be considered as an integral part of the geological heritage of Portugal and protected by the Geoconservation legislation, to ensure among others that future generation of scientists can continue to investigate them.