

## A new species of *Acithea* (Psaroniaceae, Marattiales) with exceptionally narrow and three-dimensionally preserved sporangia from the Buçaco Carboniferous Basin, western central Portugal

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### ARTICLE INFO

#### Keywords:

Adpressions  
Fossilised fern fructifications  
Sori  
In situ spores  
Marattiales  
Carboniferous of Portugal  
Western Iberia

### ABSTRACT

A new fern fossil-species *Acithea machadoi* sp. nov. is erected under the family Psaroniaceae (Marattiales), based on adpression fossil remains of fertile foliage from the Monsarros Formation (upper Stephanian C, upper Gzhelian) of the Buçaco Carboniferous Basin, in western central Portugal. *Acithea machadoi* comprises relatively narrow and long fertile pinnules bearing exceptionally and three-dimensionally preserved sporangia with in situ spores. These sporangia are elongate (fusiform) and one of the smallest documented for the genus, with a triangular pyramid-like shape in the upper part and rounded to hexagonal-like attachment base. Its occurrence within an assemblage dominated by mesophytes to hygrophytes, with fewer drought-tolerant forms, suggests a wetland environment with a seasonal climate, framed in the transition from humid to dry conditions in western Iberia during the Late Pennsylvanian–early Permian. This palaeobotanical finding provides new insights on the palaeoecology and species diversity of *Acithea*, whose currently known fossil record is certainly underestimated.

### 1. Introduction

The Marattiales are one of the best documented fern groups that have an essentially continuous fossil history from the Pennsylvanian (late Carboniferous) to the present day (Zodrow et al., 2006; Li et al., 2019). Their richness and diversity in the fossil record offer important opportunities to study large-scale evolutionary patterns over long geological intervals (e.g., Zodrow et al., 2006). Marattialeans had a global radiation during late Moscovian and Kasimovian times and are found in almost all Carboniferous/Permian terrestrial fossil localities throughout the world (DiMichele and Phillips, 2002; Li et al., 2019). The Palaeozoic marattialean members lived mainly in tropical environments, and their fossils comprise a variety of preservation states which unveil details of foliar morphology, reproductive structures, palynology, and cauline anatomy (Zodrow et al., 2006).

*Acithea* is one of the best-known distinct genera of Palaeozoic marattialean ferns. The name was erected by Schimper (1879) who described this fossil-genus based on sessile synangia composed by elongate sporangia with bristle-like apices (the type *A. polymorpha*;

Zodrow et al., 2006, fig. 9). Other species were later erected for the genus, presenting variations in the size of sporangia and their general shape, pinnule shape and variability, as well as, and the vein density and dividing. In general, the *Acithea* species show elongate sporangia, usually arranged in four per sorus (synangium), lingulate pinnules and pinnate venation (e.g., Zodrow et al., 2006; Cleal, 2015; Correia et al., 2018). Historically, the name *Acithea* was not accepted by most palaeobotanists at the time (e.g., Renault, 1883; Stur, 1883; Zeiller, 1888; Grand'Eury, 1890), but it eventually became widely recognised, following Kidston (1925) (Zodrow et al., 2006). It was subsequently used for adpression (compression-impression) specimens of pecopterid foliage (e.g., Stephani, 1901; Kidston, 1925; Langford, 1958; Janssen, 1965; Darrah, 1969; Mosbrugger, 1983; Zodrow et al., 2006). However, as noted by Corsin (1951), the assignment of such adpression specimens to genus *Acithea* without a detailed knowledge of their synangial morphology can be nomenclaturally questionable (Mapes and Schabliion, 1979; Cleal, 2015). Most Euramerican marattialeans adpressions from Pennsylvanian, including all *Acithea* species, belong to the Psaroniaceae family (Cleal, 2015; Li et al., 2019).

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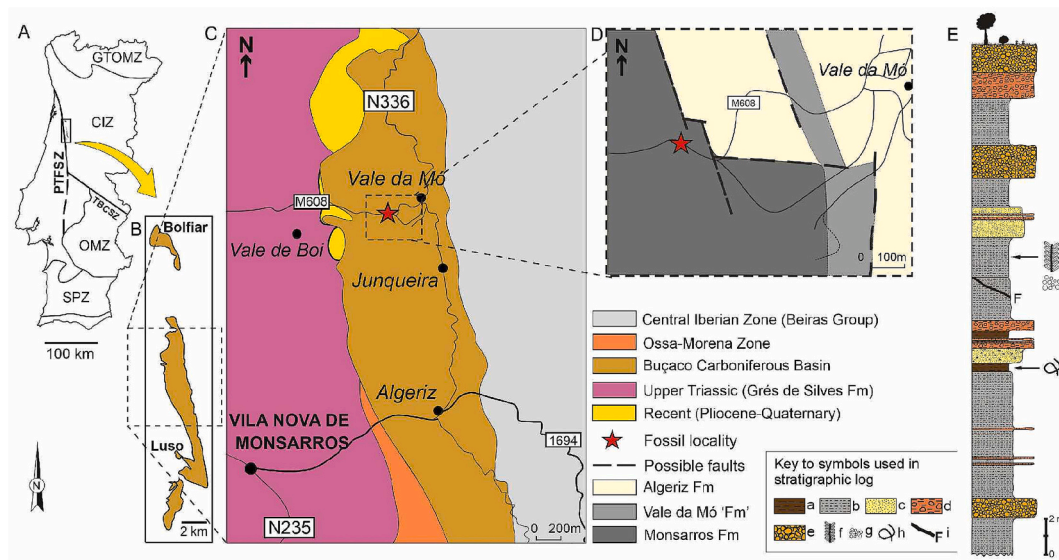
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<https://doi.org/10.1016/j.revpalbo.2024.105274>

Received 31 October 2024; Received in revised form 16 December 2024; Accepted 17 December 2024

Available online 22 December 2024

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**Fig. 1.** Regional geological setting of the Buçaco Carboniferous Basin (BCB; upper Stephanian C–lower Autunian, western central Portugal) and the studied locality. (A) Portugal tectonostructural units and the geographical setting of BCB. (B) Simplified sketch map of the BCB. (C) Geological sketch map of the Algeriz sector (adapted from Wagner et al., 1983, fig. 1a and Machado et al., 2018, fig. 1). (D) Simplified lithostratigraphic map of the studied Vale da Mó-Vale de Boi road section. (E) A schematic stratigraphic profile showing the different layers of rocks in which many plant fossil remains were deposited and preserved, including the new *Acitheca* species (Legend: a, shale; b, mudstone to siltstone; c, sandstone; d, matrix-supported conglomerate; e, clast-supported conglomerate; f, new *Acitheca* fossil; g, raindrop impressions; h, *Gordia* isp.; i, fault with  $\text{Fe}_2\text{O}_3$ ). Abbreviations: GTOMZ, Galiza-Trás-os-Montes Zone; CIZ, Central Iberian Zone; OMZ, Ossa-Morena Zone; SPZ, South Portuguese Zone; PTFSSZ, Porto-Tomar-Ferreira do Alentejo Shear Zone; TBCSZ, Tomar-Badajoz-Córdoba Shear Zone.

Here we describe a marattialean adpression specimen bearing exceptionally and three-dimensionally preserved sporangia with in situ spores from the Buçaco Carboniferous Basin (BCB; upper Stephanian C, upper Gzhelian), Portugal. It represents a new species of *Acitheca*, the first documented for the genus in the BCB, being the detailed morphology of its synangia and sporangia containing spores illustrated and its palaeoecological implications discussed.

## 2. Material and methods

### 2.1. Geological setting and palaeobotanical background

BCB (Fig. 1A, B), located in western central Portugal, corresponds to a narrow N-S syncline (maximum width 2 km), extending discontinuously for about 30 km, from Águeda (Aveiro) to Penacova (Coimbra). It is laterally limited by faults associated with the Porto-Tomar-Ferreira do Alentejo shear zone (PTFSZ; Fig. 1A, B). From north to south it is possible to distinguish three sectors, Águeda, Algeriz and Santa Cristina, apparently representing one single former synclinal structure, here called Algeriz-Santa Cristina Syncline (Fig. 1C). This syncline is strongly asymmetrical, with a long eastern limb and a vertical to inverted short western limb (Domingos et al., 1983; Gama Pereira et al., 2008). The position of this Pennsylvanian continental basin along the PTFSZ, between Ossa-Morena Zone and Central Iberian Zone, may have controlled the basin's sedimentation. Thus, a pull-apart model was previously proposed by Gama Pereira et al. (2008) and Flores et al. (2010), with the filling controlled by pulses of the PTFSZ and the palaeotopography. The formal stratigraphy of this basin was established by Wagner et al. (1983), who defined three formations: the basal Algeriz Formation, which consists of a 200 m thick sequence of breccia, succeeded by predominantly immature red conglomerates and sandstones; the Vale da Mó 'Formation', consisting of 40 m of fossil-rich grey siltstones and mudstones, interspersed with occasional layers of sandstone and coal shale; and the Monsarros Formation, a 600 m succession of coarse conglomerates, in a background of sandstones and organic-rich mudstones. Due to the frequent occurrence of grey siltstones and mudstones with coal shales in the Monsarros Formation, Machado (2010) suggested

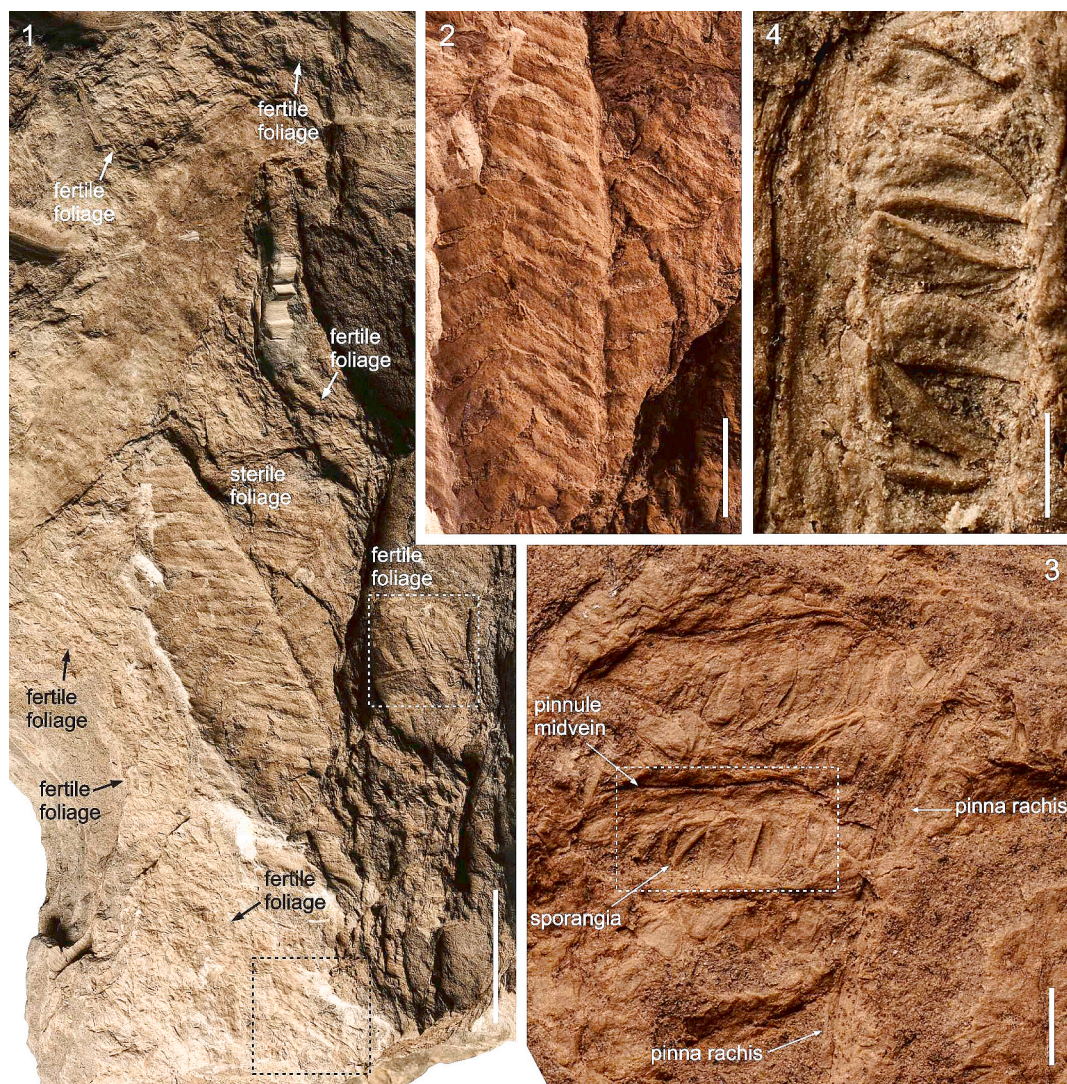
redefining the 'Vale da Mó Formation' of Wagner et al. (1983) as a member of the Monsarros Formation, informally calling the remaining overlying sequence of this unit the "Serradinho member".

The sedimentological and palaeontological data indicate a depositional environment in an alluvial regime for the basal part of the BCB, changing gradually to a fluvio-lacustrine infill, with fining-upward cycles of conglomerates, sandstones and organic-rich mudstones with occasional coal seams (Machado et al., 2018).

The age of the BCB has been a topic of much discussion (see Correia et al., 2023a, 2023b for further details). It has been assumed that deposition occurred in a relatively short time interval with all stratigraphic units being of similar age to the Rotliegend in Germany and Autunian in France (e.g., Lima, 1888/1892, 1894). Later authors (e.g., Teixeira, 1941, 1942a, 1942b, 1944; Courbouleix, 1974; Wagner, 1983; Wagner and Lemos de Sousa, 1983; Lemos de Sousa and Wagner, 1983; Wagner et al., 1983) suggested a late Stephanian C to early Autunian age interval and this is indicated by the diverse fossil flora including *Pseudomariopteris busquetii* (Zeiller) Danzé-Corsin, *Sphenophyllum thonii* von Mahr, *Sphenophyllum angustifolium* (Germar) Unger, *Taeniopteris multinervia* Weiss, *Dicksonites leptophylla* (Zeiller) Doubinger, and *Cyathocarpus cyatheus* (Schlotheim ex Brongniart) Mosbrugger (= *Scolecopteris cyathea* (Schlotheim ex Brongniart) Stur). More recently, Machado et al. (2018) described a palynological assemblage indicative of the *Potoneisporites novicus-bhardwajii-Cheiledonites major* (NBM) miospore biozone of Western Europe, corresponding to the end of the Stephanian (ca. global lower Gzhelian), with no evidence of the Autunian.

### 2.2. Fossil locality and material

The new marattialean fern fossil (Plates I, 1, 3, 4; Plates II–V) came from the Vale da Mó-Vale de Boi road (M608) section, a new locality of the Monsarros Formation (Fig. 1C, D; coordinates 40°26'28.1"N 8°22'41.4"W), about 500 m west of Vale da Mó (Anadia). The section is located in the eastern limb of the Algeriz-Santa Cristina Syncline, in the Algeriz sector, i.e., the northern part of the Buçaco Carboniferous Basin, western central Portugal (Fig. 1A). This section corresponds to the VMO (Vale de Mó) section of Machado (2010) and Machado et al. (2018), with



**Plate I.** *Acitheca machadoi* sp. nov. (holotype MGUTAD-1133), Vale da Mó-Vale de Boi road section, Monsarros Formation (upper Stephanian C–lower Autunian), Buçaco Carboniferous Basin, western central Portugal.

- 1 – General view of the holotype specimen showing the different remains of fertile foliage, including an associated frond fragment of sterile foliage. Scale bar 10 mm.
- 2 – Enlargement of rectangular box in in [Plate I](#), 1, showing a sterile frond fragment of an ultimate pinna (see more details in [Plate VI](#)). Scale bar 5 mm.
- 3 – Enlargement of rectangular box in [Plate I](#), 1, displaying an incomplete ultimate pinna bearing four fertile pinnules. Scale bar 1 mm.
- 4 – Enlargement of rectangular box in [Plate I](#), 3, showing three-dimensionally preserved (triangular pyramid-like shaped) dehiscid sporangia viewed on a lateral side, which are arranged on the pinnule lamina in sessile synangia (sori); note the striations that across longitudinally the surface of sporangia. Scale bar 0.5 mm.

the fossiliferous beds located at the top of VMO section 5 (see [Machado, 2010, fig. 4.4](#)). These correspond to an interval of less than 5 m of finely laminated, organic matter-rich mudstones, bounded by minor faults. We follow [Machado \(2010\)](#) who interpreted this sequence as part of the “Serradinho member” of the Monsarros Formation, which represents the top of one of the frequent cycles of this unit that begins with conglomerates that fine up to sandstones and are topped by mudstones. However, the possibility cannot be ruled out that the faults observed are more relevant and that these fossiliferous beds correspond to a portion of the ‘Vale da Mó Formation’ imbricated in the Monsarros Formation, as suggested by the simplified map of [Flores et al. \(2010, fig. 1A\)](#).

The holotype of the new marattialean species was found together with several adpression plant macroremains. Palaeoecological comments on this plant assemblage are provided in the Discussion section.

### 2.3. Sample preparation and repository

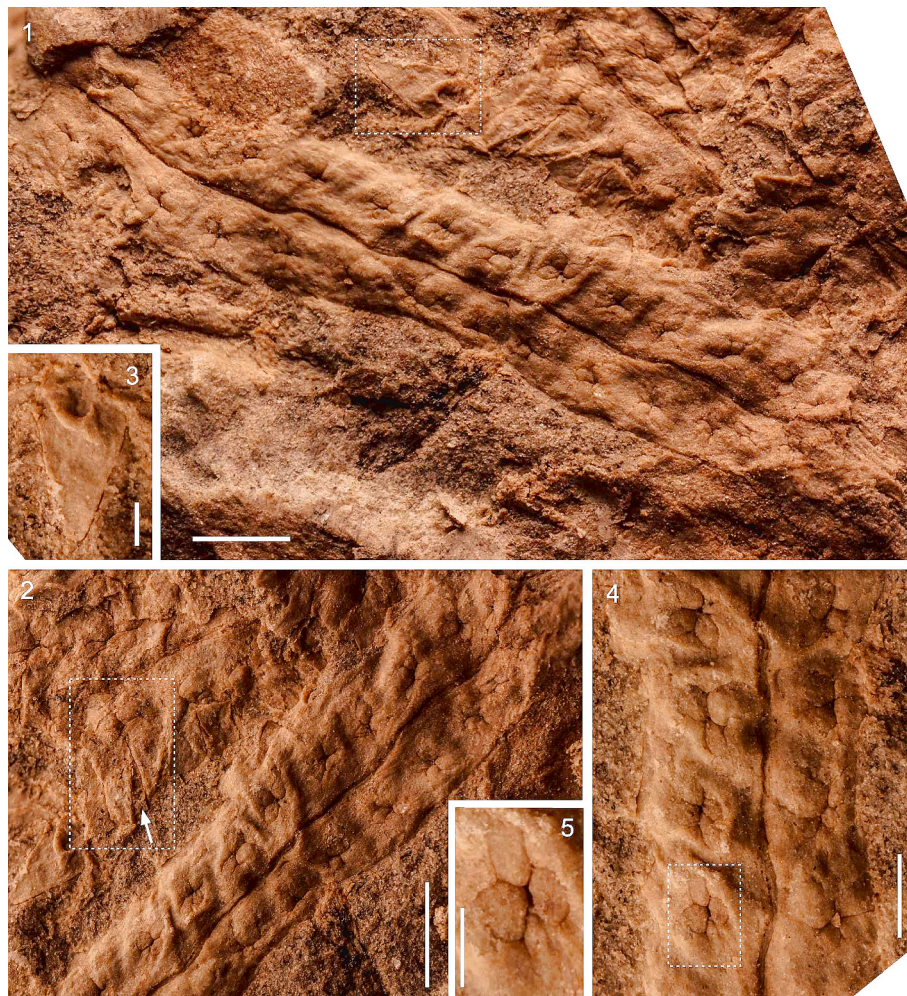
The studied fossil specimen was photographed using a Canon EOS

77D coupled with a Canon 100 mm f/2.8 L macro lens. A sample was processed for palynology studies and for testing the presence of in situ spores, at the National Laboratory for Energy and Geology (LNEG), using standard palynological laboratory procedures (e.g., [Riding and Warny, 2008](#)). The lab process involves the use of cold HCl (37%) and cold HF (48%) to remove carbonates and silicates, respectively. After acid procedures, all samples were sieved using a nylon sieve (11 µm mesh). The final residues were mounted on microscope slides using Entellan®, a commercial resin-based mounting medium and studied using a BX40 Olympus microscope. The slides are stored at the LNEG palynological collection. The type specimen is stored in the palaeontological collections of the Geological Museum Fernando Real of the University of Trás-os-Montes e Alto Douro (MGUTAD; Vila Real, Portugal).

### 3. Systematic palaeobotany

*Division:* Filicophyta.

*Class:* Polypodiopsida (ex-Marattiopsida) [Doweld, 2001](#).



**Plate II.** Details of the holotype (MGUTAD-1133) of *Acitheca machadoi* sp. nov.

1– An isolated fertile pinnule relatively narrow and long. Scale bar 1 mm.

2– Fertile pinnule viewed on a different angle associated with a fertile lamina fragment preserving a sessile synangium (sorus), showing two laterally preserved sporangia (highlighted in white rectangular box); white arrow indicates a longitudinal dehiscence from the distal part of sporangia. Scale bar 1 mm.

3 – Enlargement of rectangular box in [Plate II](#), 1, displaying an individual sclerified-like and robust sporangium. Scale bar 0.25 mm.

4 – Highlight of fertile pinnule showing bilaterally symmetrical and sessile synangia arranged on lamina in two rows flanking the midvein and near the pinnule margins. Scale bar 0.5 mm.

5 – Enlargement of rectangular box in [Plate II](#), 4, showing a sessile synangium composed of four sporangia with hexagonal attachment base. Scale bar 0.25 mm.

**Order:** MARATTIALES [Prantl, 1874](#).

**Family:** PSARONIACEAE [Stenzel, 1906](#).

**Genus:** *Acitheca* [Schimper, 1879](#) emend. [Zodrow et al., 2006](#)

**Type species:** *Acitheca polymorpha* (Brongniart) [Schimper, 1879](#) (= *Pecopteris polymorpha* [Brongniart, 1834](#)) ([Clea, 2015](#), text-fig. 3D, F).

***Acitheca machadoi*** Correia, Pereira, Šimůnek, Sá and Pereira, sp. nov.

([Plates I](#), 1, 3, 4; [Plates II–V](#))

**Etymology:** Named after Gil Machado (Chronosurveys), a Portuguese geologist specialised in Palaeozoic Palynology who studied in detail the stratigraphy and palynological assemblages of the Buçaco Carboniferous Basin, including the section in which the new species was found.

**Diagnosis:** Relatively narrow and long fertile pinnules, bearing at least 13 synangia arranged on lamina in two rows flanking the midvein and near the pinnule margins. Bilaterally symmetrical and sessile synangia, composed of four elongate (fusiform type) and very small sporangia, with longitudinal striations. Longitudinally dehiscent, straight to slightly curved and sclerified-like sporangia, with a triangular pyramid-like shape in the upper part, becoming distally acute; sporangium attached to pinnule lamina by a rounded to hexagonal-like attachment base; spherical spores. Sterile pinnules lingulate with

prominent basiscopic lobe; simple to once bifurcate lateral veins; about 40 veins per cm at the pinnule margin.

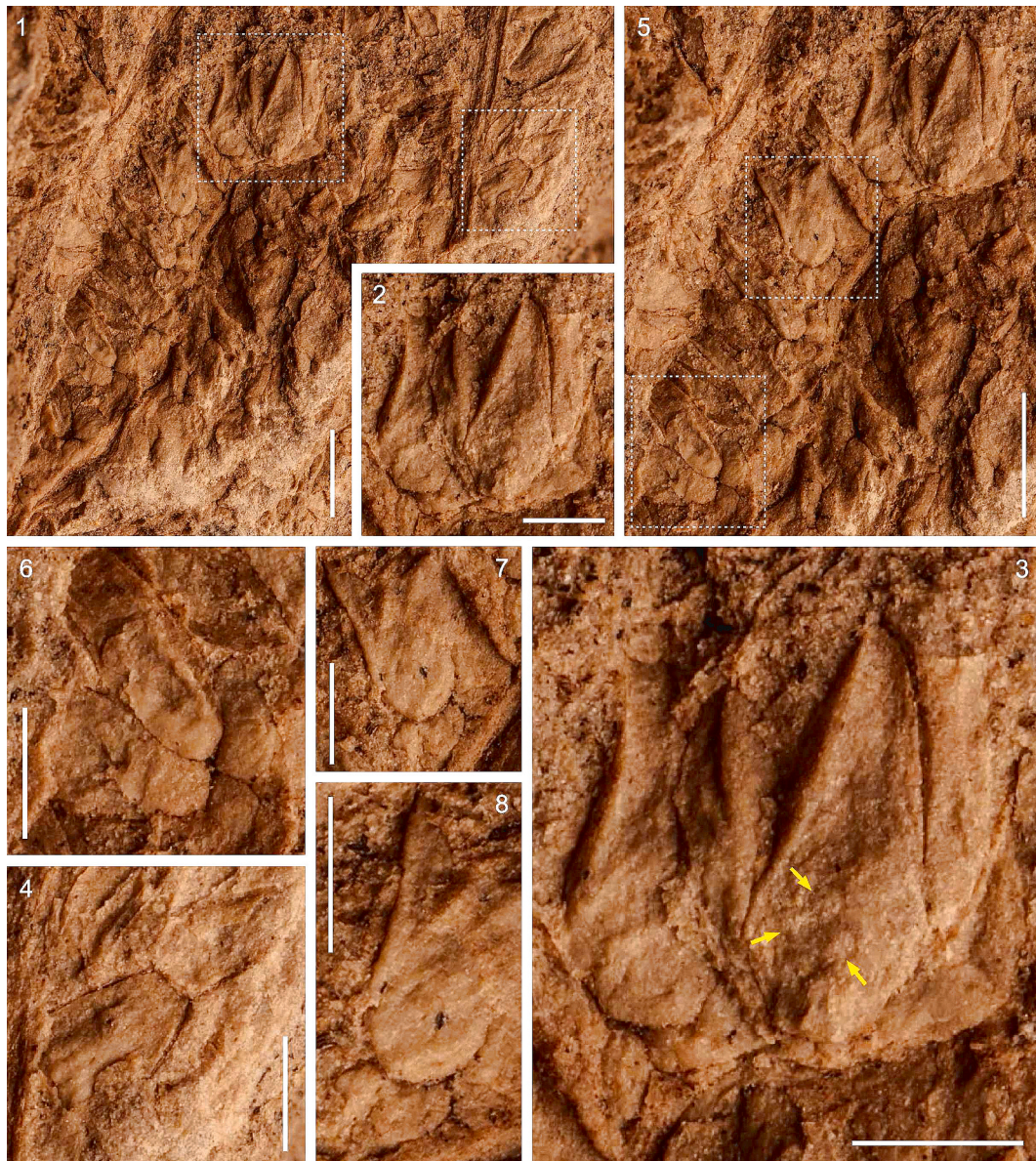
**Holotype:** Type specimen designated here on [Plate I](#), 1, with collection number “MGUTAD-1133”, is stored in the Geological Museum Fernando Real of the University of Trás-os-Montes e Alto Douro (MGUTAD).

**Type locality:** Road M608 (coordinates 40°26′28.1″N 8°22′41.4″W), from Vale da Mó to Vale de Boi, Anadia, Buçaco Carboniferous Basin, western central Portugal ([Fig. 1A–D](#)).

**Type horizon and age:** Grey laminated mudstones, lowermost part of the Monsarros Formation ([Fig. 1D, E](#)); late Stephanian C (late Gzhelian), Late Pennsylvanian.

**Description of the holotype:** The holotype specimen MGUTAD-1133 ([Plates I](#), 1, 3, 4; [Plates II–V](#)) comprises different fertile foliage remains, including putative sterile foliage, which compose the new species, consisting in ultimate pinnae and individual pinnules with synangia (sori) which show three-dimensionally preserved sporangia with in situ spores.

**Ultimate pinnae:** The type specimen contains a single ultimate pinna ([Plate I](#), 3, 4; [Plate IV](#)) with a preserved length of about 6.4 mm, showing four fertile pinnules.



**Plate III.** Details of the holotype (MGUTAD-1133) of *Acitheca machadoi* sp. nov.

1 – Highlight of synangia and sporangia with in situ spores. Scale bar 1 mm

2–3 – Enlargement of rectangular box in [Plate III](#), 1, showing three-dimensionally preserved synangium/sporangia. Yellow arrows indicate in situ spores. Scale bars 0.5 mm.

4 – Enlargement of rectangular box in [Plate III](#), 1, showing two-dimensionally preserved longitudinally dehisced sporangia. Scale bar 0.5 mm.

5 – Detail of [Plate III](#), 1. Scale bar 1 mm.

6 – Enlargement of rectangular box in [Plate III](#), 5, displaying a bilaterally symmetrical synangium (sorus) composed of four elongate sporangia; note the sessile attachment (without pedicel) of synangium. Scale bar 0.5 mm.

7 – Enlargement of rectangular box in [Plate III](#), 5, displaying a synangium composed of sclerified-like sporangia with a rounded base. Scale bar 0.5 mm.

8 – Detail of sporangium shape of [Plate III](#), 7. Scale bar 0.5 mm.

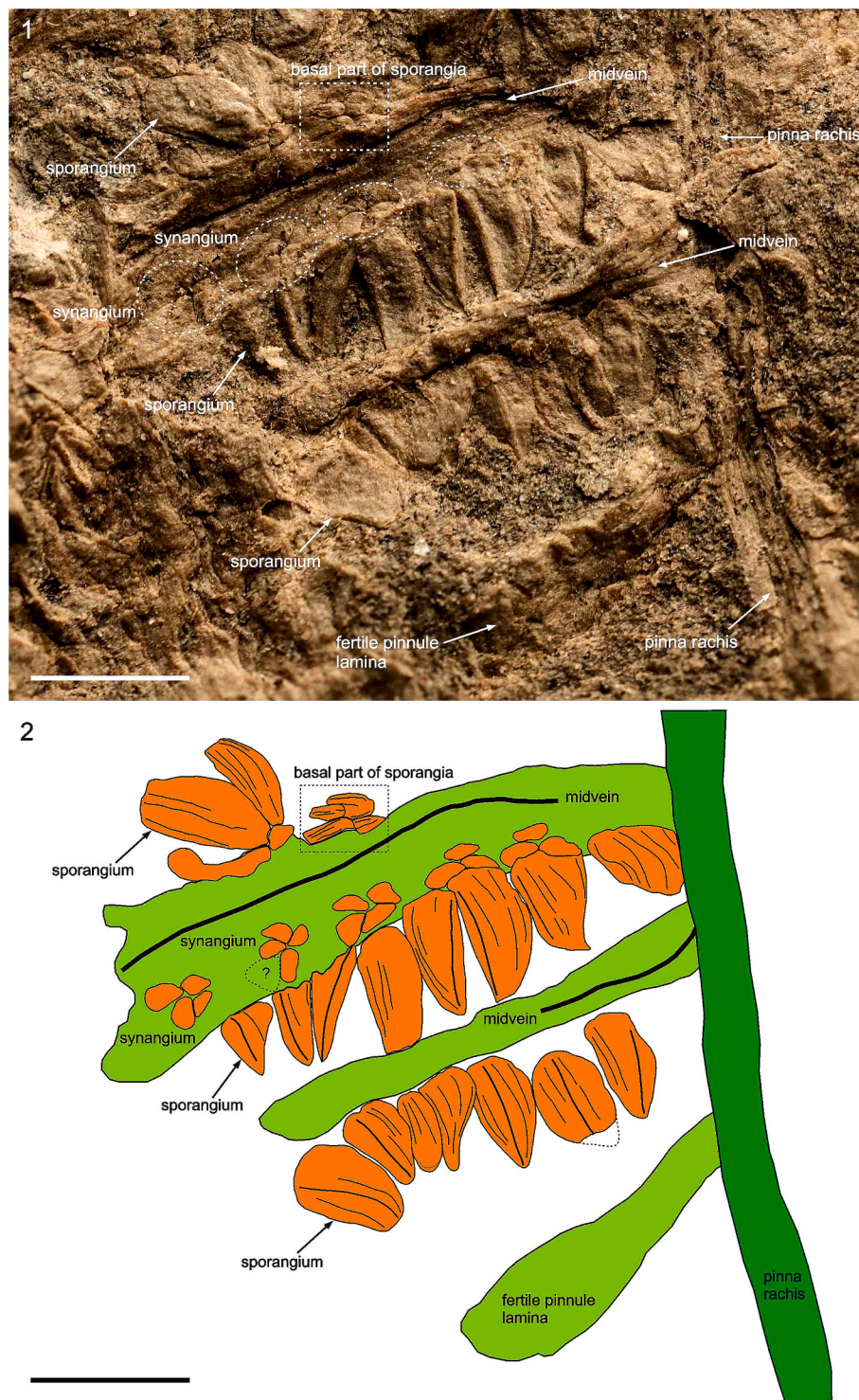
**Individual fertile pinnules:** The fertile pinnules ([Plate II](#), 1, 2, 4) are relatively narrow and long, up to 9.7 mm long by 1.0–1.6 mm wide, having a pectopterid form, and bearing at least 13 synangia arranged on lamina in two rows flanking the midvein and near the pinnule margins. The midvein is relatively strong ([Plate II](#), 1, 2, 4; [Plate IV](#)). The adaxial lamina surface is relatively folded on the margins ([Plate II](#)).

**Synangia:** The synangia ([Plate II](#), 4–5; [Plate III](#), 2–3, 6–8; [Plates IV, V](#)) are bilaterally symmetrical, averaging about 0.4–0.6 mm in diameter; they are composed of four elongate (fusiform type) and very small sporangia ([Plate I](#), 3–4; [Plate II](#), 2–3; [Plates III–V](#)), having a sessile attachment ([Plate I](#), 4; [Plate II](#), 4–5; [Plate III](#), 2–3, 6–8; [Plates IV, V](#)); for further information on soral attachment of different marattiacean ferns

see [Cleal, 2015](#), table 1; [Li et al., 2019](#), table 1).

**Sporangia:** The sporangia are elongate (fusiform) and very small, 0.5–1.2 mm long and 0.2–0.5 mm wide, longitudinally dehisced, straight to slightly curved and sclerified-like (rigid), displaying a triangular pyramid-like shape in the upper part, becoming distally acute ([Plate I](#), 4; [Plate III](#), 1–3, 5, 7,8; [Plates IV, V](#)); they are attached to pinnule lamina by a rounded to hexagonal-like attachment base ([Plate II](#), 4–5; [Plate III](#), 6–8), and show some longitudinal striations (see detail of longitudinal striations in [Plate I](#), 4; see also coloured restoration of synangia/sporangia in [Plate IV](#), 2).

**Spores:** The sporangia preserve in situ spores ([Plate III](#), 3; [Plate V](#)) which have a spherical-like shape and are about 89–115 µm in diameter.

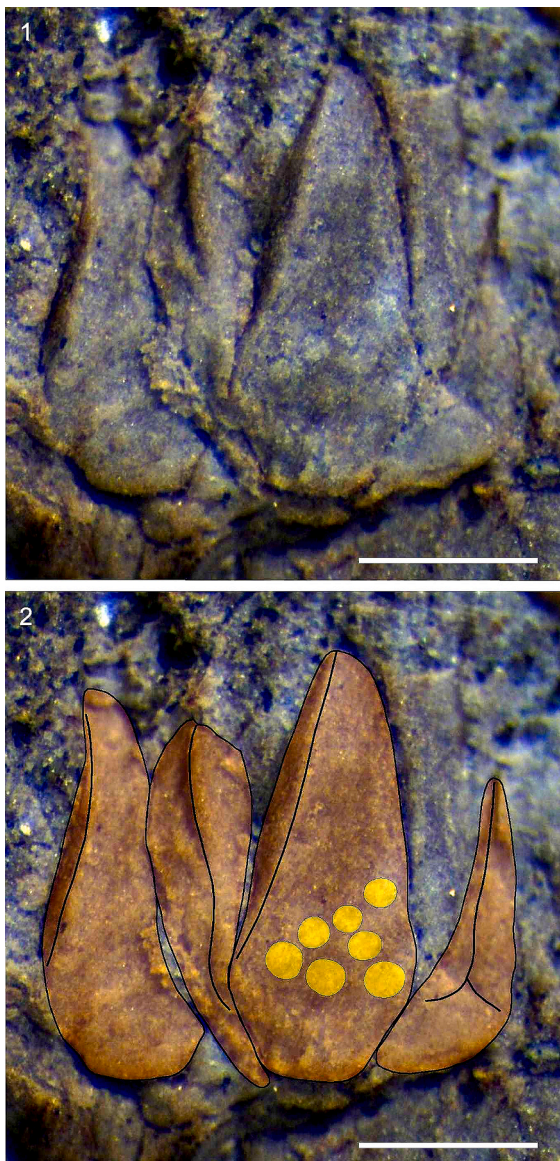


**Plate IV.** Details of the holotype (MGUTAD-1133) of *Acitheca machadoi* sp. nov.  
 1 – Highlight of a fertile ultimate pinna showing arrangement of the synangia and sporangia on the pinnule lamina and other details of pinna.  
 2 – Coloured restoration of fertile ultimate pinna. Scale bars 1 mm.

The spores have undergone permineralisation/silicification making it impossible to accurately classify them taxonomically using acid palynological processing.

**Sterile foliage:** A single fragment of sterile foliage of about 25 mm long is associated with fertile foliage (Plate I, 2; Plate VI). The sterile pinnules are of pecopterid form, having a length of about 6.6–7.0 mm and 1.4–1.6 mm in width. The pinnules have lingulate shape with prominent basiscopic lobe. Their margins are slightly convex with relatively blunt

apex. They are attached to the rachis with the whole base. The midvein is prominent from the base near the pinnule apex. The venation is poorly preserved, but veins are visible in parts. Lateral veins are curved and reach the pinnule margin at angles 70° to neatly perpendicular. It seems that some veins are divided once just near the midvein and other veins are simple (see Fig. 2). The venation density is estimated to 40 veins per cm at the pinnule margin.



**Plate V.** Details of the holotype (MGUTAD-1133) of *Acitheca machadoi* sp. nov. 1 – Highlight of a synangium showing three-dimensionally preserved (triangular pyramid-like shaped) dehiscent sporangia with in situ spores. 2 – Coloured restoration of synangium (in situ spores highlighted in yellow spherical shaped structures). Scale bars 0.5 mm.

## 4. Discussion

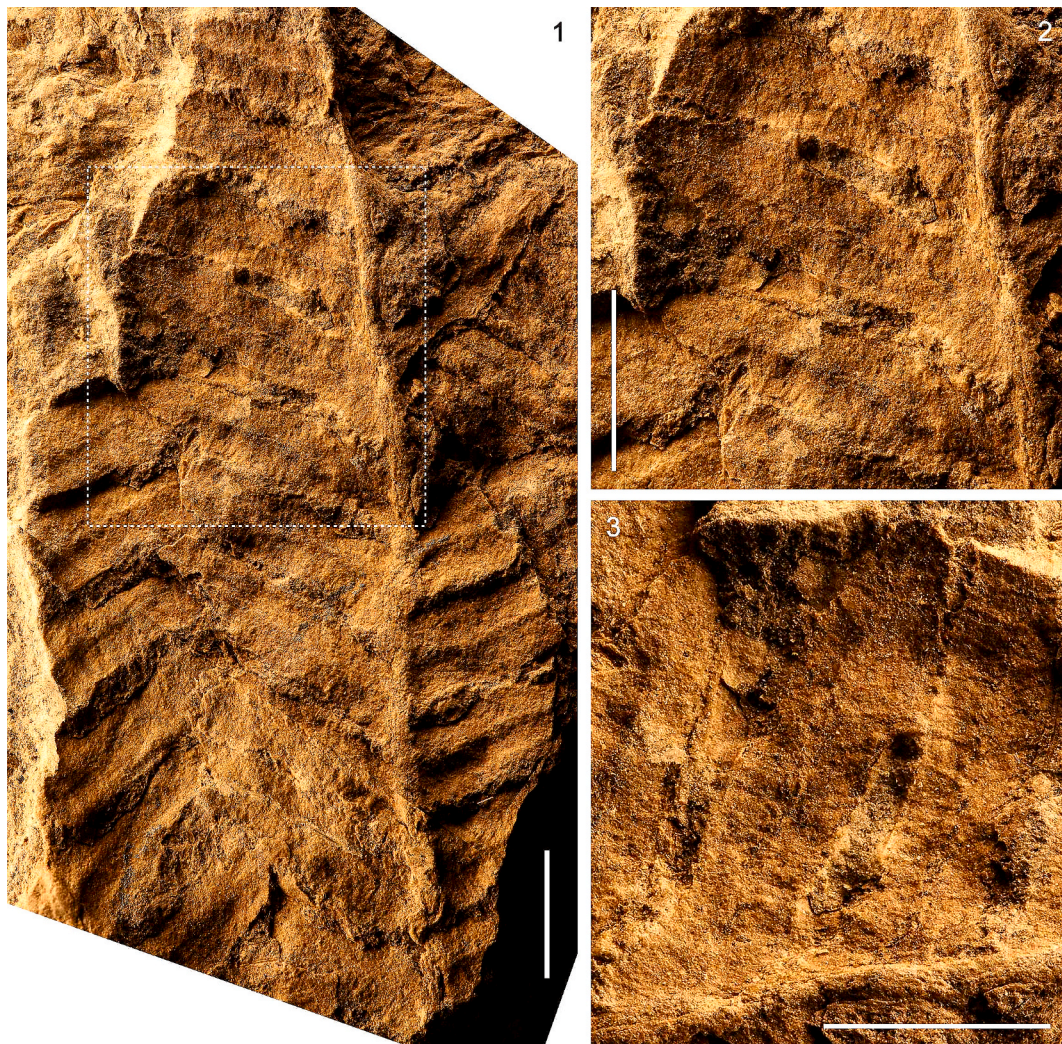
### 4.1. Generic assignment and comparisons

*Acitheca machadoi* sp. nov. erected herein (Plates I, 1, 3, 4; Plates II–V) is assigned to genus *Acitheca* because it shares the common diagnostic characters of genus – sessile synangia, elongate (fusiform) sporangia and similar number (four) of sporangia per sorus (synangium). Some characters like sessile soral attachment and similar number of sporangia are shared by other marattialean ferns, such as *Asterotheca* Presl ex Corda, 1845 emend. Cleal, 2015. However, *Asterotheca* differs from *Acitheca* by having large, squat and bulbous (rounded) sporangia (for further information on the soral attachment of the different marattialean ferns see Cleal, 2015, table 1; Li et al., 2019, table 1). In comparison with other related marattialean genera, *Scolecoperis* Zenker emend. Millay, 1979 also shares with *Acitheca* a similar number of sporangia per sorus and elongate sporangia. However, *Scolecoperis*

differs from *Acitheca* by having pedicellate synangia (e.g., Andrews et al., 1970, fig. 170A; Mapes and Schabillion, 1979; Li et al., 2019, figs. 8, 13D, 14C; for summary of the comparative characters of the reproductive organ genera in Marattiales, see Li et al., 2019, table 1). Additionally, the marattialean genus *Cyathocarpus* described by Weiss (1869) shows a superficial resemblance to *Acitheca* by the (pedicellate?) sori composed of 4–5 small ovoid to?elongate and longitudinally dehiscent sporangia (see Cleal, 2015; Sun et al., 2017). *Cyathocarpus* has been considered by some authors a younger synonym of *Scolecoperis* (e.g., Andrews et al., 1970; Millay, 1979; Barthel, 1980, 2005a, 2005b). Recently, Cleal (2015) proposed *Cyathocarpus* and *Scolecoperis* as two nomenclaturally distinct fossil-genera based on the different modes of preservation of their types, an adpression genus (*Cyathocarpus*) and an anatomically preserved genus (*Scolecoperis*). For more detailed information on adpression and permineralised marattialean genera mentioned above, see Table 1.

About 14 species have been previously assigned to genus *Acitheca*: the type (*A. polymorpha* Schimper (Schimper, 1879 emend. Zoderow et al., 2006)), *Acitheca bucklandii* (Brongniart) Schimper (Schimper, 1879), *A. fertilis* (Grand'Eury) Schimper (Schimper, 1879), *A. pteroides* (Brongniart) Schimper (Schimper, 1879), *A. isomorpha* De Stefani (De Stefani, 1901), *A. ambigua* (Sternberg) Nĕmejĭc (Nĕmejĭc, 1934), *A. salviniaefolia* Stockmans and Mathieu (Stockmans and Mathieu, 1939), *A. longifolia* (Brongniart) Corsin (Corsin, 1955), *A. cupressioides* Li et al. (Li et al., 1974), *A. adaensis* Mapes and Schabillion (Mapes and Schabillion, 1979), *A. unifurcata* Yang and Chen (in Hou et al., 1979), *A. hemitelioides* Popa (Popa, 2001), *A. allii* Zoderow et al. (Zoderow et al., 2006), and *A. murphyi* Correia et al. (Correia et al., 2018) (see Zoderow et al., 2006; Cleal, 2015; Correia et al., 2018). Among them, *A. pteroides*, *A. fertilis*, *A. cupressioides*, *A. isomorpha*, and *A. salviniaefolia* have been revised and considered either junior taxonomic synonyms of *A. polymorpha* or representatives of other genera (e.g., Stur, 1883; Feistmantel, 1885; Zoderow et al., 2006). The name “*A. hemitelioides*” should also be considered as synonym of *Cyathocarpus hemitelioides* (according Mosbrugger, 1983), previously assigned to the fossil-genus *Pecopteris* and later *Scolecoperis*. The specimens figured by Popa (2001, text-fig. 1 and pl. I, 1) show undivided (simple) veins, which are characteristic of the pinnule venation of *Cyathocarpus*, whereas *Acitheca* has usually divided lateral veins of polymorphopterid type (Mapes and Schabillion, 1979; Zoderow et al., 2006, fig. 2; Cleal, 2015, text-fig. 2; Guo et al., 2024; see Table 1). However, it must be noted that the simple veins of “*A. hemitelioides*” are strongly inclined and slightly curved at the specimen figured by Popa (2001, pl. I, fig. 1), whereas typical “*Pecopteris* (*Cyathocarpus*) *hemitelioides*” has more or less straight veins. The text-fig. 3 illustrated on Popa (2001) shows three sporangia per sorus. *Acitheca* has usually four sporangia (*Asterotheca*, *Scolecoperis* and *Cyathocarpus* have more or less five sporangia per sorus). If there are only three sporangia per sorus, they must have been very wide in comparison to their length (as it is shown in text-figs. 3 and 4 of Popa, 2001). The sporangia are too short for *Acitheca* and lack the typical terminal bristles or hooks (see e.g., Zoderow et al., 2006; Correia et al., 2018). Unfortunately, these features are not possible to check in greater detail on Popa (2001) photographs. We believe that the Popa’s species may belong to a different genus than *Acitheca*, potentially representing a new genus within the Psaroniaceae family.

In comparison with the most similar species, *Acitheca machadoi* sp. nov. resembles *Acitheca adaensis* from the Middle Pennsylvanian (Desmoinesian/upper Moscovian) Wewoka Formation of Oklahoma (USA) in the sporangium size and shape and number of sporangia per synangium. Nevertheless, *A. machadoi* sp. nov. clearly differs from *A. adaensis* by having more robust and curved sporangia and by the hexagonal attachment base of its sporangia (see Plate II, 4–5). Moreover, *A. machadoi* sp. nov. is distinguishable from *A. adaensis* by the smaller width of synangia (Plate I, 4; Plate II, 1, 2, 4, 5; Plate III, 6–8; Plate IV). For further species comparisons, see Table 2.



**Plate VI.** Putative sterile foliage of *Acitheca machadoi* sp. nov. (see [Plate I](#), 2).

1 – A sterile frond segment of ultimate pinna. Scale bar 3 mm.

2 – Enlargement of rectangular box in [Plate VI](#), 1, showing details of the shape, venation and base attachment of pinnules. Scale bar 3 mm.

3 – Highlight of pinnules attached to rachis showing its shape, base attachment and venation pattern. Scale bar 3 mm.

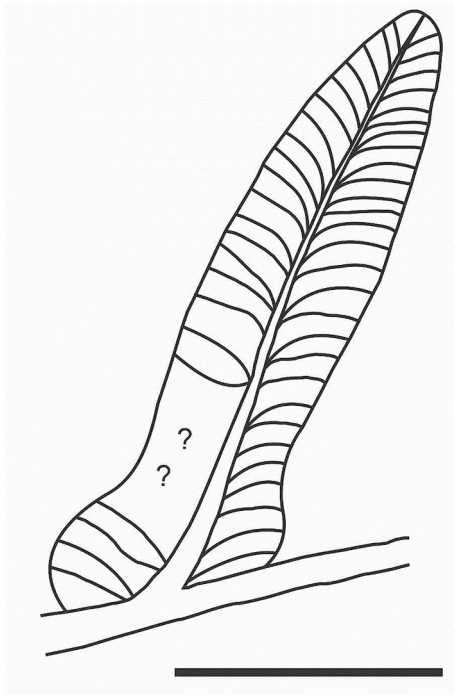


Fig. 2. Line drawing of venation pattern of the sterile foliage, illustrated in Plate VI, 3. Scale bar 3 mm.

#### 4.2. Associated sterile foliage

A sterile frond segment is affiliated to *Acitheca machadoi* sp. nov. (preserved on the same slab; Plate I, 2; Plate VI). The sterile pinnules of pectopterid form are slightly smaller (6.6–7.0 mm long) than the fertile pinnules (up to 9.7 mm long).

The high venation density (ca. 40 veins per cm at the pinnule margin) is comparable to *Acitheca polymorpha* that has 31–38 veins per cm according to Zодrow et al. (2006). On the other hand, the pattern of lateral veins of the sterile pinnules (Fig. 2) is similar to pinnule venation of *Cyathocarpus*, *Scolecopteris* and *Asterotheca*, which are characterised by having simple/once bifurcate veins (e.g., Zодrow et al., 2006; Cleal, 2015; Guo et al., 2024; see the main characteristics of the Palaeozoic marattialean genera in Table 1). Sterile pinnules of *Acitheca* generally display a lateral-venation of polymorphopterid type which is characterised by two to three times divided lateral veins (e.g., Mapes and Schabillion, 1979; Zодrow et al., 2006, fig. 2; Cleal, 2015, text-fig. 2; Guo et al., 2024). For all that, the affinity of this pinna with the fertile pinna is not excluded, because fertile pinnules have also undivided lateral veins.

**Table 1**  
Major characteristics of the compared Palaeozoic marattialean genera.

Major characteristics of the compared Palaeozoic marattialean genera.						
Genus	Typical pinnule venation	Synangial attachment	Sporangium general form	Sporangia per synangium	Spore dimension	Reference
<i>Acitheca</i> Schimper emend. Zодrow et al.	Polymorphopterid	Sessile	Elongate	3–5 (usually 4)	34–116 µm	Zодrow et al., 2006
<i>Asterotheca</i> Presl ex Corda emend. Cleal	Simple/once bifurcate to? polymorphopterid	Sessile	Large, squat and bulbous (rounded)	4–6	64–120 µm/ 17–28 µm	Balme, 1995; Cleal, 2015
<i>Scolecopteris</i> Zenker emend. Millay	Polymorphopterid	Pedicellate	Elongate	4–10	11–66 µm	Millay, 1979; Li et al., 2019; Sun et al., 2025
<i>Cyathocarpus</i> Weiss emend. Cleal	Simple/once bifurcate	Pedicellate?	Ovoid to?elongate	4 or 5	14–61 µm	Cleal, 2015; Sun et al., 2017; Guo et al., 2024

#### 4.3. Palaeoecological considerations

The type-locality and horizon of *Acitheca machadoi* sp. nov. comprises a relatively diverse fossil flora, composed of many adpression (compression-impression) plant macroremains of pteridopsid species (ferns), mainly marattialeans (e.g., *Asterotheca*, *Acitheca* and *Cyathocarpus/Pecopteris*-like sp.) and filicaleans (e.g., *Oligocarpia*), gigantic cordaitaleans (*Cordaites*), pteridosperms (e.g., *Odontopteris* and *Pseudomariopteris*), and some sphenopsids (e.g., *Annularia*, *Calamites* and *Asterophyllites*?). The floral assemblage also includes some cordaitalean (*Cardiocarpus* and *Carpolites*) and medullosalean (*Trigonocarpus/Pachytesta*) seeds, as well as, various indeterminate fern/pteridosperm stems.

The predominance of fossils of pteridopsids and pteridosperms indicates that the resident flora was essentially composed of mesophytes to hygrophytes, which prevailed in clastic wetland settings (fragmented in small and scattered wetland refugia?) in the Vale da Mó-Vale de Boi area within BCB during intervals of moist sub-humid climate. However, the co-occurrence of drought-tolerant floras, such as *Cordaites*, suggests a relatively seasonal climate (tendentially dry sub-humid) for the habitats where these plants, including *A. machadoi* sp. nov., lived (see Bashforth et al., 2021, table 1, the segregation of habitats, floral types, and main plant groups that existed in tropical Euramerican Pangaea during the Pennsylvanian, according to seasonality of precipitation and climate). This mixture of wetland and drought-tolerant taxa is in accordance with the change in climatic conditions in the region where these floras were deposited and preserved, in intramontane environments during a transition interval from wet to dry climate in the Late Pennsylvanian–early Permian (ca. 300–299 Ma) (e.g., Correia et al., 2023c).

#### 5. Conclusions

This paper describes a new species of marattialean fern, *Acitheca machadoi* sp. nov., based on an adpression fossil from the Monsarros Formation (upper Stephanian C, upper Gzhelian) of the Buçaco Carboniferous Basin, in western central Portugal.

*Acitheca machadoi* is mainly characterised by having relatively narrow and long fertile pinnules bearing elongate (fusiform) and very small sporangia, with a triangular pyramid-like shape in the upper part and rounded to hexagonal-like attachment base, distinguishing it from other species of the genus. This new species has some of the smallest sporangia recorded for the genus *Acitheca* and sheds light on the genus's palaeoecology and diversity, with its fossil record likely underrepresented. Found within an assemblage dominated by mesophytes to hygrophytes and rarer drought-tolerant floras like *Cordaites*, this species would inhabit wetland environments of the western Iberia under a seasonal climate during the late Pennsylvanian-early Permian transition.

*Acitheca machadoi* is the first record of this genus in the Buçaco Carboniferous Basin and the third representative of the genus (including the type species *Acitheca polymorpha*) documented in the Portuguese Carboniferous, after Correia et al. (2018) have recently described *Acitheca murphyi* in the Douro Carboniferous Basin, north-western Portugal.

**Table 2**  
 Summary of the comparative morphological and morphometric characters between *Acitheca machadoidi* sp. nov. and the most similar species, *A. adaeensis* (Mapes and Schablikon, 1979), *A. ambigua* (Sternberg) Némecj, 1934, *A. allii* Zdrorow et al., 2006, and *A. polymorpha* (Brongniart) Schimper, 1879 (emend. Zdrorow et al., 2006). Data compiled from descriptions and figures according to authors cited (including data from Pšenička, 2005).  
 (1) Fertile and sterile pinnules. (2) Putative fertile foliage.

Parent plants	Sporangium length (mm)	General form of sporangium	Sporangium apex	Syngonium symmetry	Fertile pinnule length (mm)	Sterile pinnule length (mm)	General form of pinnule <sup>(1)</sup>	Vein density (per cm on margin)	Lateral-venation pattern	Diameter of spore (µm)
<i>Acitheca adaeensis</i>	ca. 0.6?	Elongate (pyriform)	acute	Radially symmetrical	6–13	No data	“Pecopterid form” with incurved and deeply incised margins	14 veins	Paired unbranched veins	65
<i>Acitheca ambigua</i>	3–4	Elongate	Pointed	No data	14–20	Up to 17	Elongate-linguaeform, apically round	18–22 veins	Thin veins, once to twice forked	50–110
<i>Acitheca allii</i>	1.3–2.2	Elongate-clavate	acute	Radially symmetrical	6–12	6–12	Elongate-suboval with obtuse apex	28 veins	Veins divided twice or three times	58–89
<i>Acitheca polymorpha</i>	2.3–5.0	elongate	Bristle to hook-shaped	no data	no data	10–13	Subtriangular, linguaeform and pinnatifid	31–38 veins	Thin veins, once to thrice forked	44–108
<i>Acitheca machadoidi</i> sp. nov.	0.5–1.2	elongate, triangular pyramid-shaped	acute	bilaterally symmetrical	up to 9.7	6.6–7.0 <sup>(2)</sup>	Narrow and long fertile pinnule; lingulate sterile pinnule With basiscopic lobe	40 veins	simple to once bifurcate lateral veins	89–115

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2024.105274>.

## Funding

This study was supported by Portuguese funds by Fundação para a Ciência e a Tecnologia, I.P. (Portugal) in the frame of the UIDB/00073/2020 (DOI [10.54499/UIDB/00073/2020](https://doi.org/10.54499/UIDB/00073/2020); <https://doi.org/10.54499/UIDB/00073/2020>), UIDP/00073/2020 project of the I&D unit Geosciences Center (CGeo). Grant Agency of the Czech Republic – grant project GA CR 22-11661K. This research is a contribution of the UNESCO Chair on “Geoparks, Sustainable Regional Development and Healthy Lifestyles” of the University of Trás-os-Montes e Alto Douro, Portugal.

## Declaration of competing interest

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

## Data availability

No data was used for the research described in the article.

## Acknowledgements

We thank Prof. M. Popa (Bucharest) and an anonymous reviewer for their constructive comments that helped improve the submitted manuscript.

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