

RESEARCH ARTICLE

Revision of the Barremian fern *Coniopteris laciniata* from Las Hoyas and El Montsec (Spain): Highlighting its importance in the evolution of vegetation during the Early Cretaceous

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Abstract The species *Coniopteris laciniata* and *Sphenopteris wonnacottii* are heterophyllous ferns recovered from two Spanish Barremian localities, Las Hoyas and El Montsec respectively. The similarities between these species, observed in a study of a total of 66 hand specimens from both localities, indicate that they are conspecific. Following the rule of priority in botanical nomenclature, and because there are doubts about the assignment of this species to a higher taxonomic rank, the name *Coniopteris* is maintained. Characters of this fern and additional characters of other species of *Coniopteris* would support a diversification of polypod ferns during the Early Cretaceous. Metric architecture analyses suggest that the heterophylly of the plant was probably caused by the submersion of the apical part of fronds in water during their development, which would be consistent with the taphonomy of the remains in both localities.

Keywords Early Cretaceous; filiform frond; heterophylly; margin-dweller fern

■ INTRODUCTION

The laminated limestones of El Montsec (Barremian of Lleida, Spain) and Las Hoyas (Barremian of Cuenca, Spain) are rich in ferns of *Coniopteris*-like or *Sphenopteris*-like foliage types. Both taxa were erected as form genera used to describe fern foliage with different systematic assignments. *Coniopteris* Brongn. includes specimens from the Early Jurassic to the Early Cretaceous (Li & al., 2020) and this genus is generally included in Dicksoniaceae (Brongniart, 1849), but recently, some *Coniopteris* species have been grouped within Polypodiales (Li & al., 2020). *Sphenopteris* Brongn., on the other hand, includes specimens from localities that encompass Palaeozoic and Mesozoic concerning both ferns and pteridosperms (Taylor & al., 2009). As a result, both genera present widespread spatial and temporal distributions, and they have been recorded in many different habitats and environments (Van Konijnenburg-van Cittert, 2002; Taylor & al., 2009).

The remains assigned to *Coniopteris laciniata* Diéguez & N.Meléndez from Las Hoyas and to *Sphenopteris wonnacottii* Dilcher & C.R.Hill from El Montsec are morphologically quite similar showing heterophylly with lobed and filiform pinnules present in the same frond (Diéguez & Meléndez, 2000; Dilcher & Hill, 2003). Nonetheless, different interpretations of the heterophylly have been

addressed. Diéguez & Meléndez (2000) suggest that the reduction of the lamina of pinnules in *Coniopteris laciniata* is due to them bearing fertile organs, whereas Dilcher & Hill (2003) interpret the filiform pinnules in *Sphenopteris wonnacottii* as an adaptation to submersion in water, similarly to the extant *Ranunculus aquatilis* L. These authors interpret reniform pinnules at the apical area of the pinnae as fertile, although no sori were observed.

This contribution is a revision of the El Montsec and Las Hoyas *Coniopteris*-like and *Sphenopteris*-like foliage, in particular of those specimens which can be assigned either to *Coniopteris laciniata* or *Sphenopteris wonnacottii*. Revising the assignation of these ferns is relevant because it can prompt new evidence for the distribution of ferns and possibly the early distribution and diversification of Polypodiales. To such extent, 66 specimens from both localities have been studied to provide a precise description of the plant, and 24 specimens have been metrically characterised by means of the branching algorithms method (Campbell, 1996; Blanco-Moreno & al., 2019). Establishing the variability of the pinnules of these ferns and identifying the architectural factors that characterize lobed and filiform pinnules allow for a more precise determination and comprehension of the whole plant. The results of this comparative study have consequences on the interpretation of both the palaeoecology and distribution of

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these ferns. A discussion of the habit and habitat of the plants is also presented.

Geological context and taxonomic background. — El Montsec fossil site is located in the Serra del Montsec, in the province of Lleida (South Central Pyrenees, Organyà Rift Basin; Martín-Chivelet & al., 2019), and comprises two sites in the same area: La Pedrera de Meià, coordinates 46°55'N; 03°26'E, and La Cabrú, coordinates 46°55'N; 03°32'E (de Gibert & al., 2000), which are Barremian in age (Martín-Chivelet & al., 2019). The sites correspond to the same sequence of laminated limestones (Barale & al., 1984) that was interpreted as deposits generated in open lacustrine conditions (de Gibert & al., 2000).

Las Hoyas fossil site (coordinates 40°05'N; 01°53'W) is located in the Serranía de Cuenca (southwestern Iberian sector; Fregenal-Martínez & Meléndez, 2016), in the municipality of La Cierva, and has been proposed as the parastratotype of La Huérguina Formation. Las Hoyas consists of a set of laminated limestone lithosomes deposited during the Barremian, 126 to 129 Ma, based on charophytes and ostracods (Diéguez & al., 1995; Vicente & Martín-Closas, 2013) and this formation has been interpreted as a freshwater, regional, inland subtropical system of wetlands (Fregenal-Martínez & al., 2017).

In relation to the palaeobotanical content, Vidal (1902, 1915) was the first to identify *Coniopteris*-/*Sphenopteris*-like foliage at El Montsec and assigned it to *Sphenopteris* cf. *microclada* Saporta. In more modern revisions, Menéndez Amor (1951) assigned the *Sphenopteris*-like specimens to *Himnophyllites tenellinervis* Saporta, but Teixeira (1954) and Barale (1995) did not figure or discuss them. Later, Dilcher & Hill (2003) described a new species, *Sphenopteris wonnacottii* Dilcher & C.R.Hill, based on remains from El Montsec that are housed at the Natural History Museum, London.

At Las Hoyas, Diéguez & Meléndez (2000) were the first to identify two species of *Sphenopteris* (*S. fontanei* Seward, *S. fittonii* Seward), and two species of *Coniopteris* (*C. laciniata* Diéguez & N.Meléndez, *C. murrayana* Brongn.). The specimens identified as the genus *Sphenopteris* and the species *Coniopteris* cf. *murrayana* Brongn. by Diéguez & Meléndez (2000) were discussed as belonging to genera *Ruffordia* Seward or *Cladophlebis* Brongn., in the corresponding synthesis on the Las Hoyas floral association (Martín-Closas & al., 2016).

■ MATERIALS AND METHODS

The fern material presenting *Sphenopteris*-like or *Coniopteris*-like foliage from Las Hoyas, housed in the Museo de Paleontología de Castilla-La Mancha (Cuenca, Spain), and from El Montsec, housed in the Institut d'Estudis Ilerdençs (Lleida, Spain) and in the Muséum national d'Histoire naturelle (Paris, France), was thoroughly revised and described in detail to identify specimens that could be assigned either to *Coniopteris laciniata* or *Sphenopteris*

wonnacottii. Additionally, high-resolution pictures of the holotype of *Sphenopteris wonnacottii* (BMNH V.41257; Dilcher & Hill, 2003), housed at the Natural History Museum (London, U.K.) were studied (Fig. 1A,B). The remains of these two taxa mainly consist of penultimate and ultimate pinnules (Fig. 1). Additionally, two specimens preserving the rhizome and attached pinnules have been recovered: one from El Montsec presenting lobed pinnules, and another from Las Hoyas presenting filiform pinnules (Fig. 2). The remains were compared by a descriptive morphological study of each species.

Material examined. — The material from Las Hoyas consists of 39 hand specimens with one fragment each, and the material from El Montsec consists of 27 fragments preserved in 13 hand specimens. Las Hoyas: MUPA-LH 371, 6337 a/b, 13576 a/b*, 14357 a/b*, 17262, 20016*, 20227 a/b, 20287 a/b, 20336, 20463 a/b, 21028 a/b, 21194*, 22448 a/b*, 23057 a/b, 23112, 23266 a/b*, 23459 a/b*, 26047*, 26375 a/b*, 28057, 28063 a/b, 28272 a/b, 28537*, 29498, 29729, 30368, 30451*, 30763*, 30836, 30837*, 30923, 31024 a/b*, 31028 a/b*, 31321 a/b, 31432 a/b*, 31433 a/b*, 33314, 35579 a/b, 39368*. El Montsec: BMNH V.41257*; G-421; LC-965-IEI*, 2901*; LP93-4043-IEI*, 4228; LP-491-IEI, 1593*, 4062; LP-1281-P; MNHN.F.17717, 17719, 17720 a/b. Hand specimens included in the metric analysis are marked by an asterisk.

Institutional abbreviations. — ADR-P, Armando Diaz Romeral collection, this abbreviation corresponds to the holotype of *Coniopteris laciniata* and the specimen is lost. BMNH V, Palaeobotany collection at the Natural History Museum, London, U.K.; G, Gomez collection, and LC-IEI, LP-IEI and LP-P El Montsec collection, all housed at the Institut d'Estudis Ilerdençs, Lleida, Spain; MUPA-LH, Las Hoyas Collection at the Museo de Las Ciencias de Castilla-La Mancha, Cuenca, Spain; MNHN.F, Palaeobotany collection at the Muséum national d'Histoire naturelle, Paris, France.

Taphonomic analysis. — Taphonomy, herein, explores two aspects: the preservation type, and fragment size. The preservation type includes four categories: charred compressions, impressions (imprints on the sediment), brownish compressions, and calcite infillings. Shiny black compressions are included within “brownish compressions”. The size of each fragment was recorded as the maximum length of the fragment. The proportion of each preservation type was revised for each locality, and the size distribution was graphed on a histogram. The significance of the difference in the distribution of fragment sizes per type of preservation was tested by Mann-Whitney non-parametric by pairs in SPSS Statistics v.27 software (IBM corporation).

Metric analysis. — A metric architecture analysis was implemented to observe differences between lobed and filiform pinnules, and to explore the variation within each type of pinnule. Nineteen fragments (18 specimens) from Las Hoyas were measured: 1 filiform ultimate pinna attached to the rhizome, 1 penultimate pinna, and 17 ultimate pinnules; 6 filiform, and 11 lobed. Also, 6 fragments (5 specimens) from El Montsec: 1 lobed ultimate pinna attached to the rhizome, and 5

isolated ultimate pinnae; 2 filiform, 3 lobed, and 1 showing the transformation from lobed to filiform. The method of branching algorithms adapted by Blanco-Moreno & al. (2019) was herein applied to test the variation of three variables along the pinna: (1) the insertion angle (from now on IA), measured as the smallest angle formed at the intersection between the pinna rachis and the pinnule petiolule; (2) distance between pinnae (from now on DBP), measured

as the length between the adaxial side of one petiolule to the next; and (3) first segment length (from now on FSL), measured as the length of the petiolule, up to the first lobe or branch of the pinnule (Fig. 3). When the FSL was not observable in completely fused lobed pinnules, pinnule length was used. All visible pinnules along the rachis were measured, and measurements from both the left and the right pinnules of each specimen were recorded and included in the analyses.

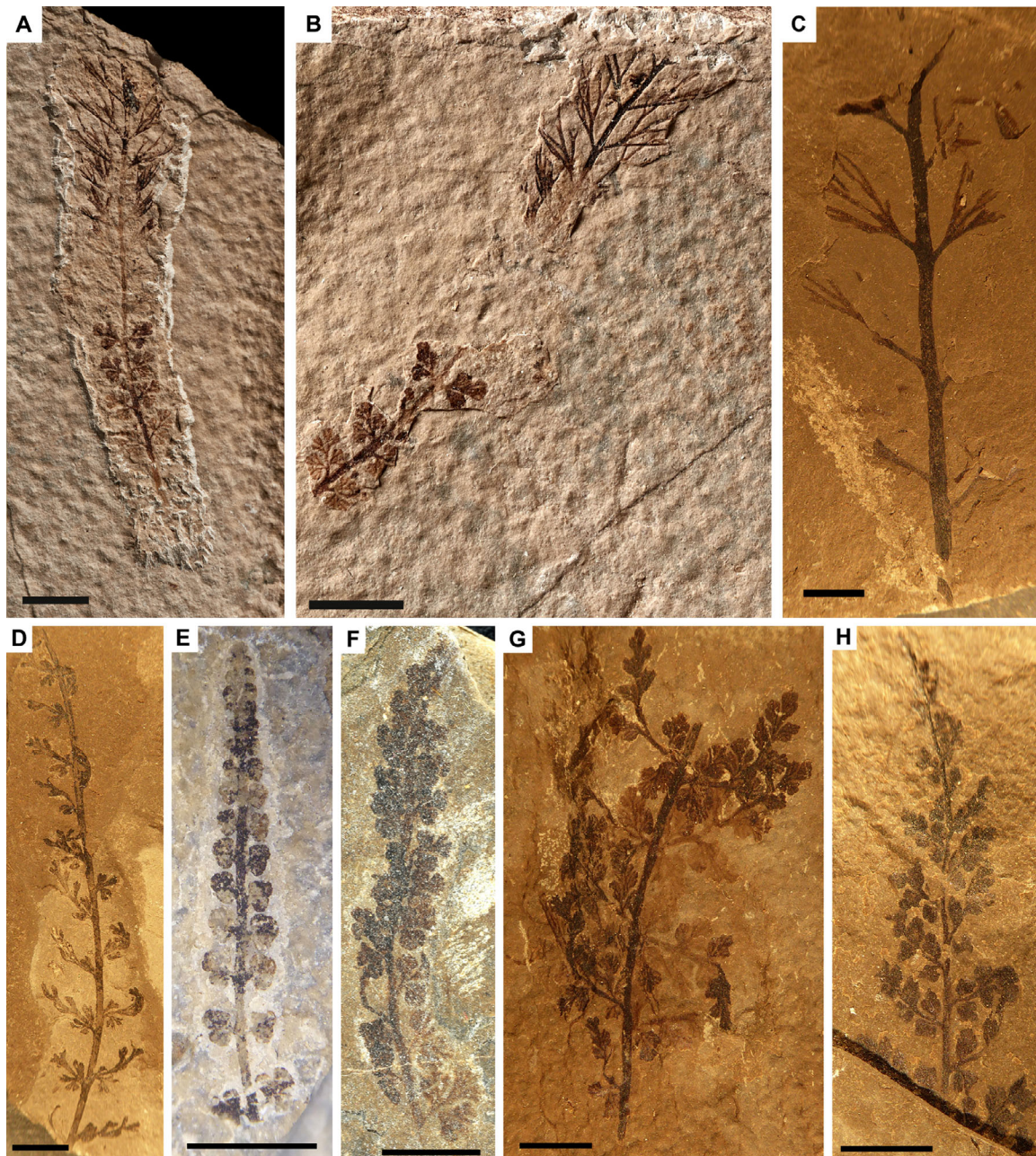


Fig. 1. *Coniopteris laciniata*. **A & B**, BMNH V.41257, part and counterpart of the holotype of *Sphenopteris wonnacottii*, preserving lobed and filiform pinnules (photographs provided by Trustees of the Natural History Museum, London): **A**, BMNH V.41257a; **B**, BMNH V.41257b. **C**, Ultimate pinna with filiform pinnules from Las Hoyas (MUPA-LH 31432). **D**, Ultimate pinna with long lobed pinnules from Las Hoyas (MUPA-LH 30836). **E**, Ultimate pinna preserving the transition from lobed to reniform pinnules from El Montsec (LP-491-IEI). **F**, Ultimate pinna with lobed pinnules from El Montsec (MNHN.F.17720). **G & H**, Penultimate pinna fragments from Las Hoyas: **G**, MUPA-LH 21028; **H**, MUPA-LH 20016. — Scale bars = 5 mm.

Measurements were taken on photographs using the software ImageJ v.2 (Schneider & al., 2012).

The branching ratio (from now on BR), comparison between DBP and FSL, was observed by plotting these variables on an xy graph and linear regressions were calculated for each of the pinnule types. Additionally, a principal component analysis (from now on PCA) was performed, using a correlation matrix, and including IA, DBP and FSL. The results of the BR and PCA were graphed distinguishing between the types of pinnule and between localities. These analyses were performed using PAST v.4 software (Hammer & al., 2001).

■ RESULTS

Systematic Palaeontology

Order: Incertae sedis

Family: Incertae sedis

Genus: *Coniopteris* Brongn. in d'Orbigny, Dict. Univ. Hist. Nat. 13: 75. 1849.

Coniopteris laciniata Diéguez & N.Meléndez in Palaeontology 43: 1121. 2000 – **Lectotype (designated here):** [illustration in] Palaeontology 43: 1123, t. 2, fig. 1 & 2. 2000.

= *Sphenopteris wonnacottii* Dilcher & C.R.Hill in Courier Forschungsinst. Senckenberg 241: 112. 2003 – Holotype: BMNH V.41257 [pictured in Courier Forschungsinst. Senckenberg 241: 112, text-fig. 1; 117, t. 1, fig. 1 & 2].

Emended species diagnosis. – Creeping rhizome, bearing roots in an abaxial position that dichotomise at least once. Fronds once- or twice-pinnate, borne in an adaxial position, crowded in thick areas of the rhizome. Pinnae catadromically alternate bearing polymorphic, catadromically alternate or rarely subopposite, pinnules. Three types of pinnules are present: (1) deeply lobed pinnules, with up to 5 lobes; (2) filiform

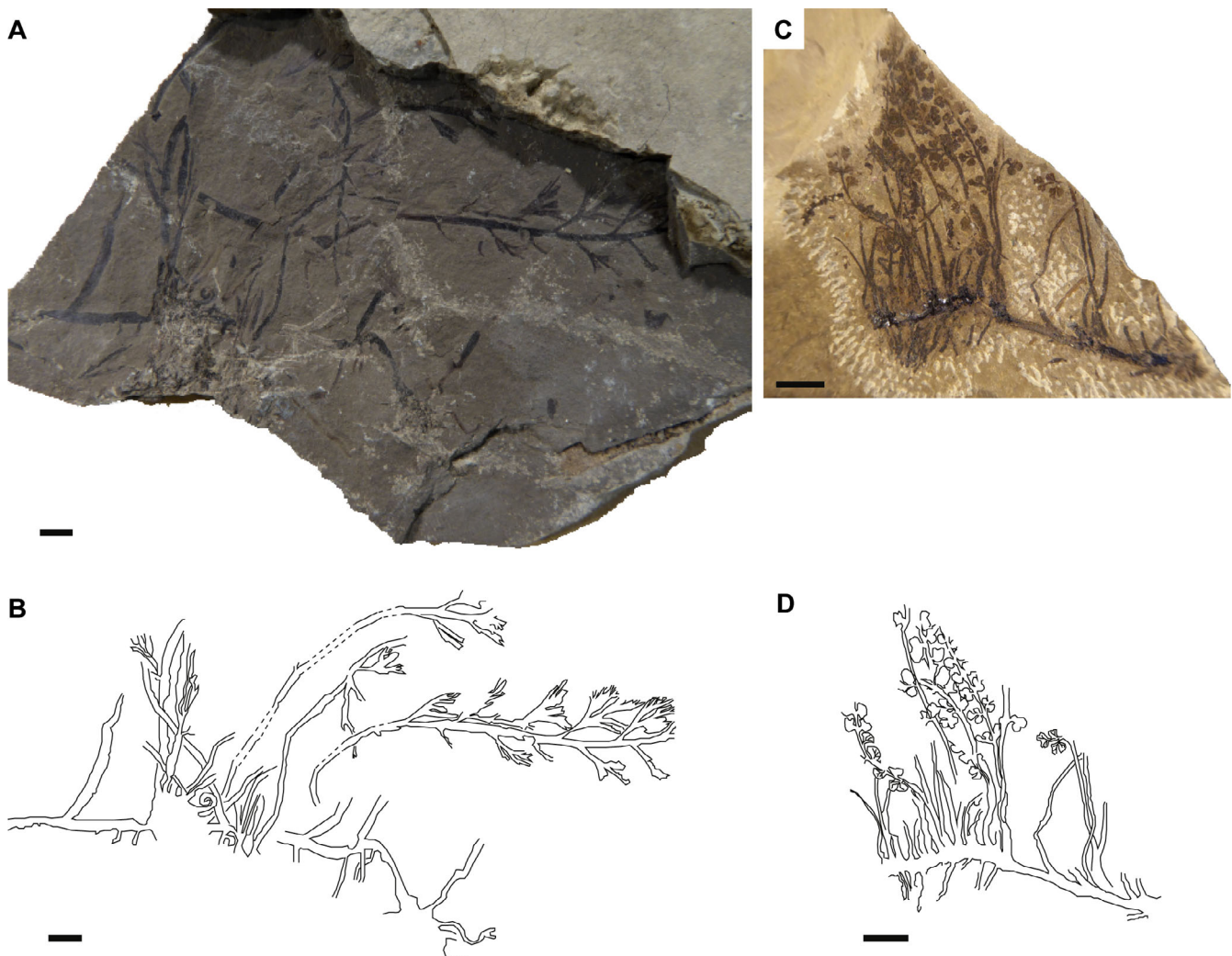


Fig. 2. Specimens and corresponding drawings of *Coniopteris laciniata* preserving the rhizome. **A & B**, Specimen MUPA-LH 31433 from Las Hoyas, presenting filiform pinnules; **C & D**, Specimen LC-965-IEI from El Montsec, presenting lobed pinnules. — Scale bars = 5 mm.

pinnules, larger in size, presenting very reduced lamina; (3) reniform pinnules. A continuum of forms connects all three types of pinnules.

Description. – Rhizome creeping, no clear branching is observed. Width homogeneous in areas where few or no fronds are borne, measuring up to 1.8 mm. Rhizome becomes more massive (up to 3 mm thick) and irregular where leaf and root insertions accumulate (Fig. 2). Roots arise from the abaxial part of the rhizome, measuring at least 8.5 mm long and 0.5 mm wide. Fronds twice-pinnate, emerging from the adaxial part of the rhizome at irregular intervals, tending to accumulate in certain areas. Leaves are born singly or in pairs. A crozier attached to the rhizome is observed (Fig. 2A,B), evidencing circinate vernation. Penultimate rachis flexuous, 0.2 to 1.5 mm wide. Ultimate pinnae are generally alternate and rarely subopposite, inserted at a wide angle (60° – 80°), and 1.9 to 6.8 mm apart from each other. Rachis width of the ultimate pinnae 0.2 to 1 mm, bearing polymorphic sphenopteroid pinnules inserted in catadromous disposition, subopposite to alternate, and attached to the rachis by a short petiolule or a very constricted base. Pinnules are generally inserted from 1 to 5 mm from each other, and at an angle of 50° to 70° , although basal most and apical most pinnules are

inserted at lower angles (35° – 45°). Three main types of pinnules are identified, although a continuum between each type is observed:

(1) Lobed pinnules (Figs. 1A,B,F–H, 2C,D). Basal pinnules are deeply lobed, consist of up to 5 catadromous lobes, and measure up to 5.7 mm long and 3.2 mm wide. Intermediate pinnules generally present 3 lobes and measure around 3 mm long and 3 mm wide. The smallest apical pinnules are 0.8 mm long and 0.9 mm wide and have 2 lobes. Venation is open dichotomous and generally catadromous. The main vein dichotomises into each of the lobes of the pinnule, and veins successively dichotomise inside the lobes, from one to three times. The number of successive dichotomies is related to the size of the pinnule.

(2) Filiform pinnules (Figs. 1C,D, 2A,B). The widest rachises are associated to areas bearing filiform pinnules. These pinnules are inserted further apart than the other types of pinnules (up to 11 mm), and at a smaller angle (35° – 55°). They branch in catadromous, and rarely anadromous disposition, and measure up to 12.6 mm. No fertile organs are observed.

(3) Reniform pinnules (Fig. 1E). These pinnules are observed at the apical-most part of some pinnae bearing lobed pinnules exclusively, they have a reniform morphology, and venation is not observed. Size at Las Hoyas is from 1.4 to 2.2 mm long and 1.3 to 2 mm wide, the size at El Montsec is smaller, from 0.8 to 1.8 mm long and 0.9 to 1.8 mm wide. No fertile organs are observed.

Pinnae presenting a transition between types have been observed but are very rare (Fig. 1A,B,D,E herein and pl. 2 fig. 1 in Diéguez & Meléndez, 2000), and most specimens present either filiform or lobed pinnules exclusively (Figs. 1C,F–H, 2). Pinnae attached to the rhizome, bearing either lobed or filiform pinnules, have been observed (Fig. 2). These two pinnule morphologies are independent of their position within the pinna. Reniform pinnules have only been observed in a specific position, at the apex of pinnae bearing lobed pinnules and not filiform pinnules.

Holotype. – ADR-0119-P. Pictured in plates 2 and 3, and text-figure 4A,B in Diéguez & Meléndez (2000). Physical specimen lost.

Type localities. – Santa Maria de Meià (La Pedrera), Lleida (Spain), and Las Hoyas, Cuenca (Spain).

Stratigraphic occurrence. – La Pedrera de Rúbies Unit (de Gibert & al, 2000), and La Huérguina Formation (Fregenal-Martínez & al., 2017).

Age. – Barremian, Early Cretaceous.

Discussion. – The three types of pinnules herein observed correspond to the “frond forms” described for *Sphenopteris wonnacottii* (Dilcher & Hill, 2003). Based on the fragmentary condition of most of the specimens herein analysed, the continuum of pinnule forms observed in them, and the variability of their position in the frond, we prefer to note the heterophylly as a pinnule-level trait and use types of pinnules, rather than frond forms. Variability in ferns can be very high, where the form is controlled during its growth, and it is generally linked to the venation pattern during its development

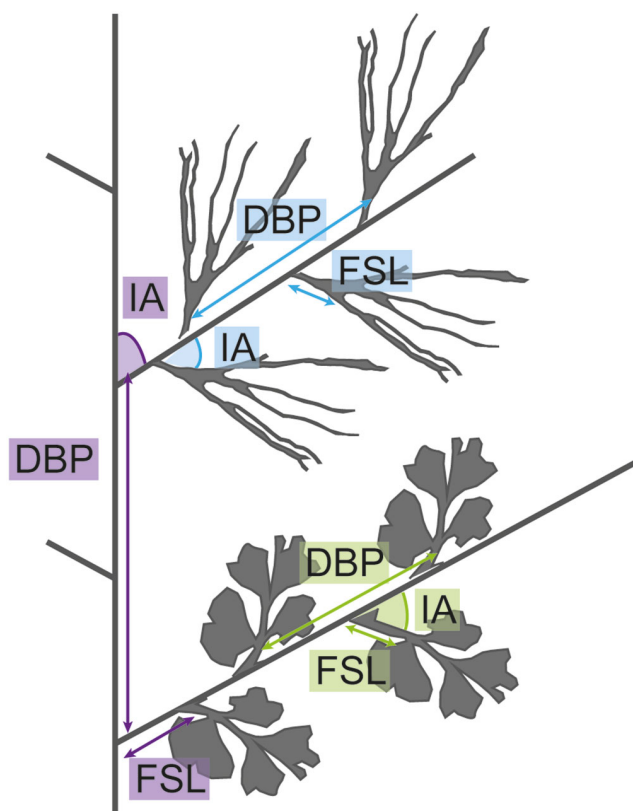


Fig. 3. Criteria used for the metric analysis represented on lobed (green) and filiform pinnules (blue), and twice-pinnate specimens (purple). IA, insertion angle; DBP, distance between pinnae; FSL, first segment length.

(Zurkowski & Gifford, 1988). Different types of pinnules could therefore be found in the same frond from a developmental point of view and would not necessarily be conserved along the same pinna or frond.

Our accurate study of all specimens analysed indicates that *Sphenopteris wonnacottii* is indistinguishable from *Coniopteris laciniata* (Diéguez & Meléndez, 2000), hence these two species should be considered conspecific. Following the rule of priority of the *International Code of Nomenclature for algae, fungi, and plants* (Turland & al., 2018), the name *Coniopteris laciniata* should be maintained and *Sphenopteris wonnacottii* become its heterotypic synonym. The holotype of *Coniopteris laciniata* (ADR-0119-P) designated by Diéguez & Meléndez (2000) cannot be found

in the institution referenced by the authors, and they did not designate paratypes, isotypes, or mention any other specimens that could be assigned to this species in their work. Therefore, an illustration of the holotype (ADR-0119-P) provided by Diéguez & Meléndez (2000) in protologue of the species has been designated as lectotype.

The filiform pinnules herein described are comparable to *Sphenopteris microclada* Saporta (Saporta, 1894). However, due to only filiform pinnules being described for this species, the name *Coniopteris laciniata* is tentatively maintained for the material herein presented, which shows three distinct pinule forms, until more material can be revised. The generic name *Coniopteris* is maintained here due to the impossibility to assign this species with certainty to either *Sphenopteris* or

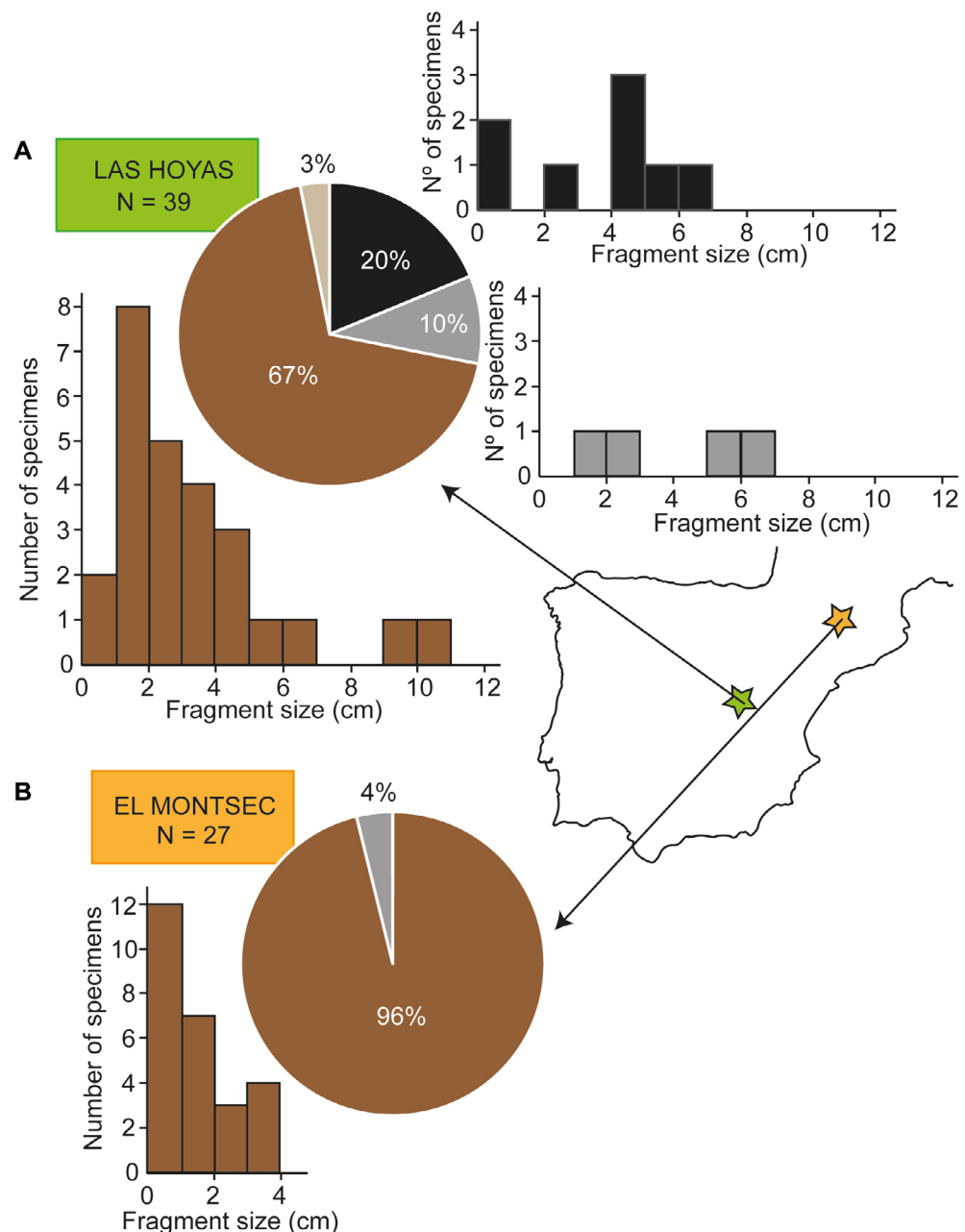


Fig. 4. Proportion of preservation types and size distribution per preservation type for the 66 *Coniopteris laciniata* fragments revised. **A**, Las Hoyas; **B**, El Montsec. — Black, charred compressions; grey, impressions; brown, brownish compressions; light brown, calcite infillings.

Coniopteris as no sori have been identified. *Coniopteris* frequently presents both sterile-fertile and basal-apical pinnule dimorphism, and finely dissected pinnules are frequent in the genus (Harris, 1961; Taylor & al., 2009). As far as we know, no fossil or extant fern with a comparable morphology and variability in pinnule form and position within the plant has been published to date.

Remarks. — This taxon was first discovered at Las Hoyas, by Diéguez & Meléndez (2000). However, the frond dimorphism was underestimated, and it was not until Dilcher & Hill (2003) described this same species as *Sphenopteris wonnacottii* based on material from El Montsec that the degree of reduction of the pinnule lamina was ascertained. After comparison with material from El Montsec, we have observed that the specimens assigned to *Sphenopteris fontanei* and *Coniopteris* cf. *murrayana* by Diéguez & Meléndez (2000) correspond to two different pinnae forms of *Coniopteris laciniata*: the fili-form pinnule area, and the form with typical lobed pinnules respectively.

Taphonomy. — Fossil fragments from El Montsec are all preserved as brownish compressions except for one impression (Fig. 4B). The mean size is 1.4 cm and the largest fragments have fili-form pinnules. At Las Hoyas, this species is most frequently found preserved as brownish compressions, consisting of 67% of the remains (Fig. 4A). Charred remains are the second most frequent preservation type, corresponding to 20% of the total sample. Four impressions have been recovered (that is 10% of the total remains), and only one specimen is preserved as a calcite infilling. The size distribution of the charred compressions, brownish compressions, and impressions (Fig. 4A) are significantly similar (Mann-Whitney tests by pairs Sig. > 0.05). At Las Hoyas, the mean size of the fragments is 3.16 cm, much larger than the material from El Montsec, and the size distribution is significantly different between the two localities (Mann-Whitney test Sig. = 0.001). Additionally, 53% of the specimens recovered from Las Hoyas are incomplete and therefore the fragment would be longer than observed (the hand specimen is broken, and the plant remain would have continued in the missing rock). Similarly to El Montsec, fronds with fili-form pinnules are all preserved as brownish compressions and are larger in mean size than the lobed remains (5.03 cm in mean).

Metric architecture analysis. — Both lobed and fili-form pinnules show metric differences (Figs. 5, 6). IA is smaller in fili-form pinnules, although they are very variable in both pinnule types, and there is no clear tendency along the pinna (Fig. 5A). DBP and FSL both diminish towards the apex in lobed pinnules. However, in the case of fili-form pinnules, FSL grows towards the apex, and the variation of DBP along the pinna does not follow a clear pattern (Fig. 5B,C).

The BR analysis clearly separates the pinnule types, and the general distributions of lobed and fili-form pinnules can be described by linear regressions (Fig. 6A; lobed: $y = 0.55x + 0.09$, $R^2 = 0.57$; fili-form: $y = 3.27x + 0.21$, $R^2 = 0.304$) with a general positive correlation between DBP

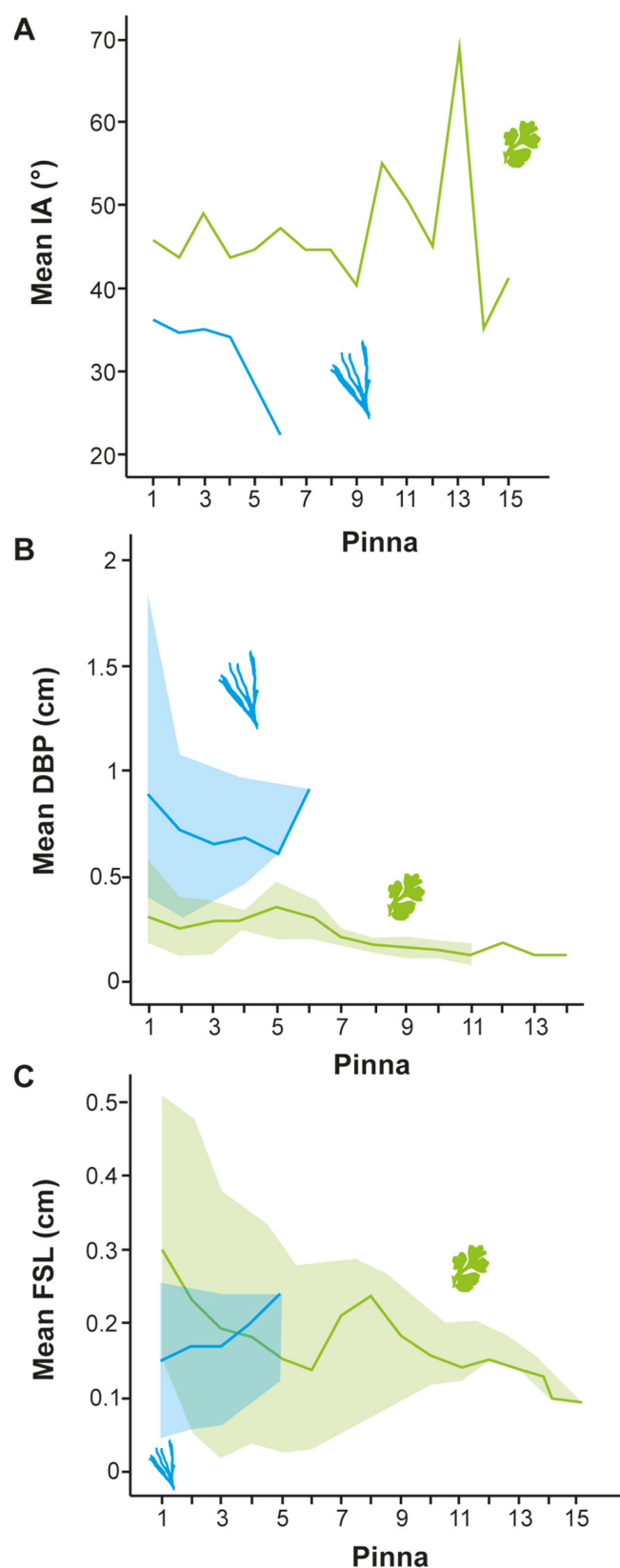


Fig. 5. Mean and standard deviation of the measurements along the pinnae performed on *Coniopteris laciniata* from Las Hoyas. **A**, Insertion angle (IA); **B**, Distance between pinnules (DBP); **C**, First segment length (FSL). — Green, lobed pinnules; blue, fili-form pinnules.

and FSL, although it is not very robust, especially for the fili-
form pinnules.

In the PCA, the loadings of each variable in the two prin-
cipal components (from now on PCs) included in the graph
show that all of them contribute to the description of the frond
architecture separately (Table 1). The results show that in gen-
eral, filiform pinnules have a larger DBP, less variable and
generally smaller FSL, and much smaller IA, whereas lobed
pinnules have a larger range of FSL (Fig. 6B).

Notwithstanding, the specimen preserving the transition
between lobed and filiform pinnules (BMNH V.41257,
squares in Fig. 6A,B) shows very small pinnules and the three
variables do not follow the same distribution along the pinna
as the rest of the specimens studied. In this case, IA values
are constant along the pinna and FSL is longer in the filiform
pinnules. However, there is an increase in DBP towards the fi-
liform pinnules, similarly to what is observed in other speci-
mens. In both the BR and PCA analyses, the values of the
lobed pinnules in this specimen are grouped with the rhizome
bearing lobed pinnules (LC-965-IEI; green stars in Fig. 6A,B)
and the basal pinnae of the twice-pinnate specimen
(MUPA-LH 20016, purple dots in Fig. 6B). Interestingly,
the apical-most pinnae of twice-pinnate fronds, which are
fused into single pinnules (Fig. 1H), are grouped with the

lobed remains. The specimen preserving ultimate pinnae with
filiform pinnules attached to the rhizome (MUPA-LH 31433,
blue stars in Fig. 6B), shows a unique distribution in the PCA,
situated in between lobed and filiform remains.

DISCUSSION

All the remains herein studied belong to a single species,
with a continuum of pinnule variation and two extreme mor-
phologies that are architecturally distinct. These results allow
for discussions and interpretations of the plant’s habit and aut-
ecology, exploring the two hypotheses for the presence of the
filiform morphology, fertile vs amphibious, in depth.

Table 1. Principal component loadings for principal component
analysis.

	Component	
	1	2
Insertion angle (IA)	−0.641	0.289
Distance between pinnules (DBP)	0.637	−0.318
First segment length (FSL)	0.429	0.903

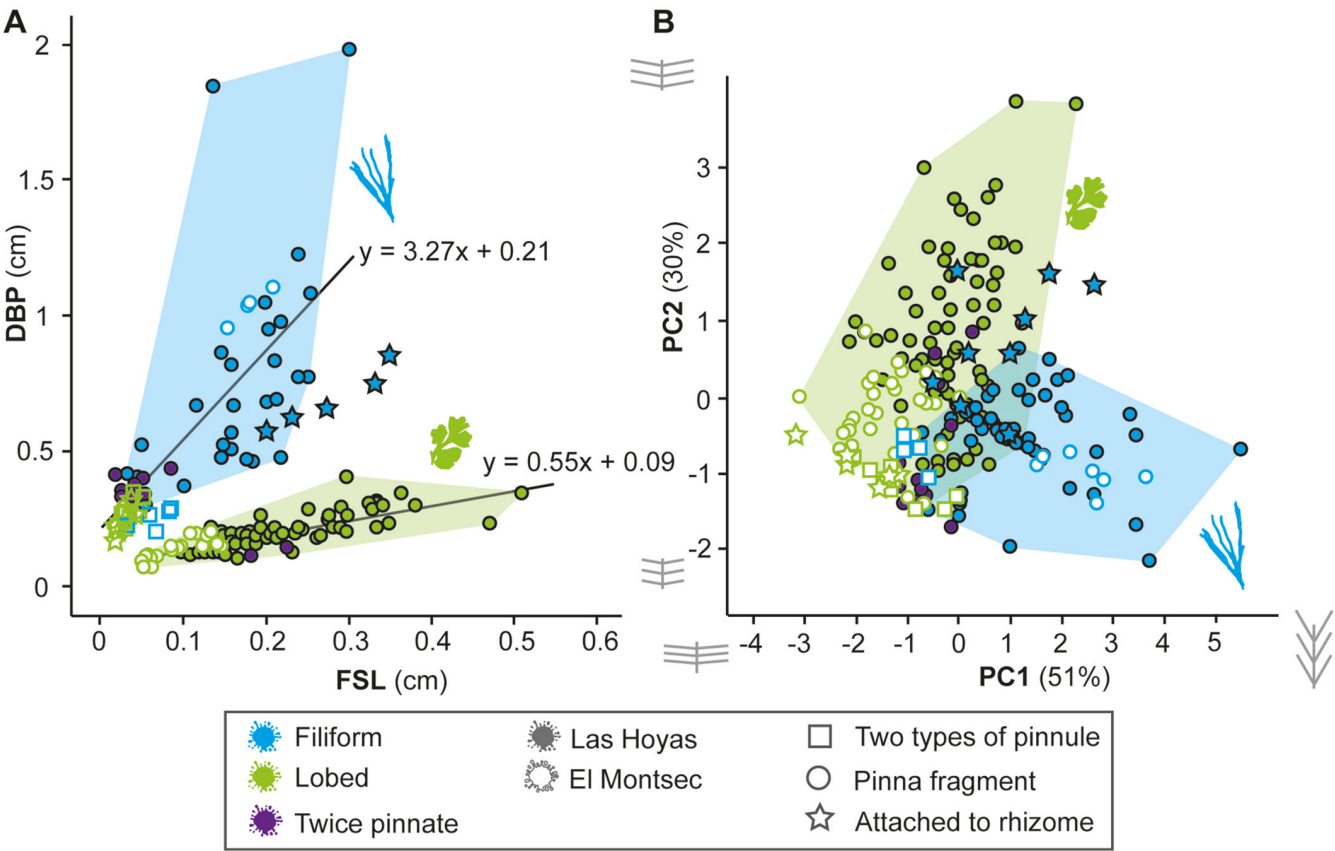


Fig. 6. Results of the metric analyses of specimens from Las Hoyas (filled-in shapes) and El Montsec (empty shapes). A, Branching ratio; B, PCA. — Green, lobed pinnules; blue, filiform pinnules; purple, twice pinnate (MUPA-LH 20016). Squares, specimen that shows pinnule type transition (BMNH V.41257); stars, pinnae attached to rhizome (MUPA-LH 31433, filled-in blue stars; LC-965-IEI, empty green stars).

Plant habit and autecology. — Specimens displaying both once-pinnate and twice-pinnate fronds are present in the sample. Although Diéguez & Meléndez (2000) describe the plant as tripinnate, no evidence of this has been observed in the specimens herein studied. The two specimens preserving the rhizome (LC-965-IEI, MUPA-LH 31433), bear fronds that seem to be once pinnate, although the connection of the pinnae and the rhizome is not always clear (Fig. 2). Other studied specimens show clearly bipinnate fronds (G-421; MUPA-LH 17262, 20016, 21028). The similarity in architecture observed between the penultimate pinnae and the once-pinnate pinnae with lobed pinnules borne on the

rhizome (LC-965-IEI), suggest that although the pinnae attached to the rhizome are once pinnate, the architecture is closer to twice-pinnate fronds than to the isolated once-pinnate ultimate pinnae. This could indicate that specimen LC-965-IEI corresponds to a young sporophyte, where fronds are once pinnate and would become twice pinnate during maturation. This condition can be observed in extant ferns such as *Angiopteris evecta* (G.Forst.) Hoffm. within the family Marattiaceae. The small size of this specimen also corroborates this hypothesis (Fig. 2). The unique architecture observed in the once-pinnate pinnae bearing filiform pinnules that are attached to the rhizome in this fern

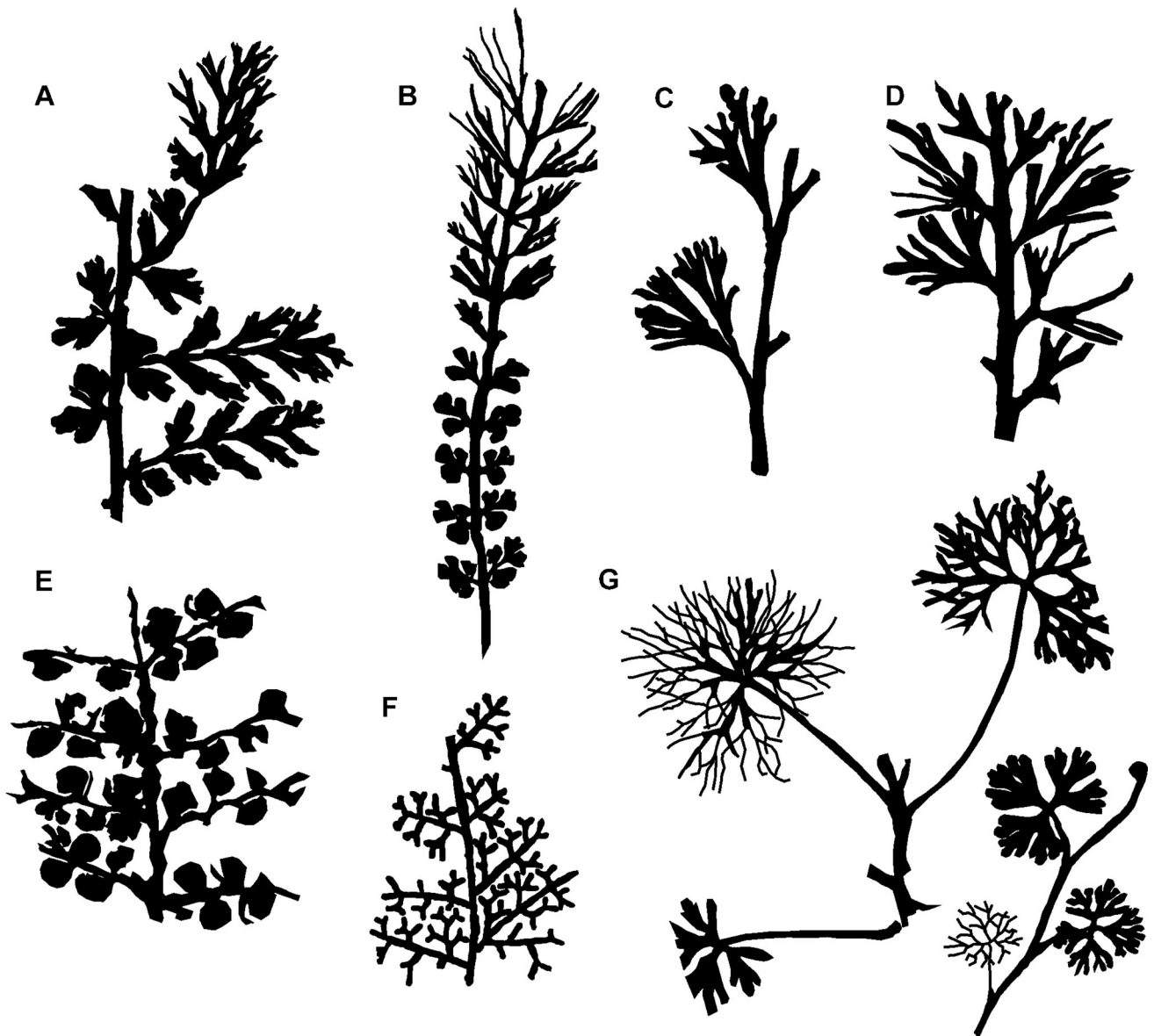


Fig. 7. Drawings representing the variability in the leaf morphology of specimens. **A–D**, *Coniopteris laciniata*: **A**, The missing holotype ADR-0119-P, figured by Diéguez & Meléndez (2000); **B**, BMNH V.41257; **C**, MUPA-LH 30451; **D**, MUPA-LH 21194. **E**, Fertile specimen (IRSNB b 7856, housed at the Royal Belgian Institute of Natural Sciences in Brussels, Belgium) of *Coniopteris* sp. from the Barremian-Aptian locality of Bernissart (Mons Basin, Belgium). **F**, Sterile specimen of *Coniopteris simplex* redrawn from Harris (1961). **G**, *Ranunculus flabellaris* Raf. based on specimens figured by Bostrack & Millington (1962).

(MUPA-LH 31433) could also indicate a young sporophyte, although it is larger in size than LC-965-IEI. As no bipinnate fronds with filiform pinnules have been observed in the current sample, this possibility cannot be ruled out.

The architectural differences identified between pinnae bearing lobed pinnules and pinnae bearing filiform pinnules in *Coniopteris laciniata* argue against the filiform pinnules being homologous to the fertile pinnae in some *Coniopteris* species. Other *Coniopteris* taxa with skeletonised areas that bear sori are clearly pinnate, and when the whole skeletonised area corresponds to a lower-order pinna, the rachises are straight (Fig. 7F). This is not the case for the filiform pinnules in *Coniopteris laciniata*, where the dichotomies follow the pattern of the venation of the lobed pinnules, which is not pinnate but dichotomous. Filiform pinnules themselves are significantly larger than lobed pinnules in *Coniopteris laciniata* and dichotomise many times (Fig. 7A–D). Skeletonised fertile pinnae of other *Coniopteris* species do not dichotomise more than once and are normally the same size as the pinnules preserving the lamina (see Fig. 7E,F and *Coniopteris* species discussed in Harris, 1961 for example). Additionally, no indusia comparable to those interpreted by Diéguez & Meléndez (2000) were identified on the filiform pinnules. On the other hand, the morphological diversity of the submerged leaves of the extant aquatic taxon *Ranunculus flabellaris* Raf. is more similar to that observed in *Coniopteris laciniata* (Fig. 7A–D,G) as already mentioned by Dilcher & Hill (2003). The pinnules in *Coniopteris laciniata* show a clear increase in the size and architectural complexity of the pinnules as they become filiform, similarly to what occurs in other submerged leaves (Fig. 7G).

There are clear differences between the architecture observed in the specimen described by Dilcher & Hill (2003), BMNH V.41257, which presents both lobed and filiform pinnules, and the general architecture of the rest of the specimens. Lobed and filiform pinnules in this specimen are grouped with intermediate forms, but the general tendency of the pinnule

architecture along the pinna is reversed due to the increase in FSL and also large IA observed for the filiform pinnules. The anomaly in the FSL trend, however, agrees with the general tendency in pinnae bearing filiform pinnules, which shows an increase towards de apex. IA is much conserved in this specimen, with values in the lobed-pinnule range. As pinnule insertion angle is established before the pinna unfurls, the large insertion angle in the range of lobed pinnules would suggest this pinna initially developed out of water and was submerged at a later stage of its development. Extant amphibious plants that present heterophylly respond to different environmental factors that are related to underwater conditions during their development. For example, the fern *Marsilea* L. grows aerial-type leaves, which are broader and less dissected, in presence of blue light and high levels of CO₂ (Lin & Yang, 1999). Additionally, the small size of the pinna fragment and its pinnules, together with similarity of the lobed pinnule segment of the specimen preserving both types of pinnules (BMNH V.41257) with the architecture of the pinnae attached to the rhizome from El Montsec (LC-965-IEI) could suggest this specimen is also juvenile. In this case, differences in architecture could also be due to the immaturity of the specimen.

Plant habitat. — The taphonomic analyses show that there is a small proportion of charred remains of this species, indicating that it would not have been frequently affected by fires, and that most of the material of this fern preserved at Las Hoyas and El Montsec was produced by other agents. Fire is a very frequent agent in the production of other fern species in these localities, for example *Weichselia reticulata* (Stokes & Webb) Fontaine (Martín-Closas & al., 2016). Also, the remains of *Coniopteris laciniata* at Las Hoyas show differences in size and abundance in relation to other ferns from the locality, the mean fragment size is significantly larger for this species, and its remains are comparably not very abundant (see Blanco-Moreno & al., 2018 for data on *Weichselia reticulata* as a

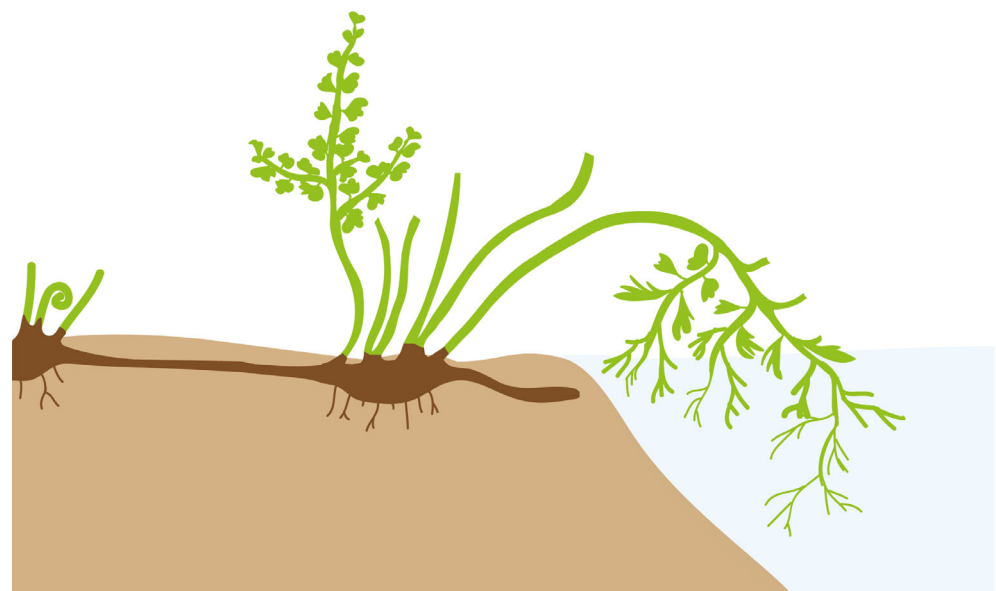


Fig. 8. Whole plant schematic reconstruction showing general habit and pinnule morphological diversity.

comparison). This could be interpreted as evidence that the plants lived at a larger distance from the depositional site, due to the low abundance of remains, and the possibility to be transported during a longer period of time, as larger fragments take more time to waterlog (Nichols & al., 2000). However, low abundances of plant species can also occur due to a preservation bias by selective decay, where taxa that are locally abundant and live near the depositional environment are more readily degraded by detritivores, and hence more rarely preserved (Spicer, 1991). In addition, the preservation of the rhizome of the plant also suggests para-autochthony, and rhizomes are very rare remains in both localities. Moreover, if the remains were produced in lentic environments such as pools and lakes, the size selection would be mainly influenced by the architecture of the plant and necrobiotic agents instead of transport in water (Blanco-Moreno & al., 2022), which in the case of *Coniopteris laciniata* might be different from the other fern species from Las Hoyas, producing larger fragments (Blanco-Moreno, 2020).

Plant reconstruction. — The results of the analyses herein performed would indicate that *Coniopteris laciniata* was a small fern with tufts of leaves arising at intervals from thin, creeping rhizomes (Fig. 8). Fronds were twice pinnate in maturity and once pinnate in young specimens. Pinnae bore filiform pinnules when they developed underwater, and lobed pinnules when they developed subaerially. The habitat of this plant was probably alkaline soils at the margin of the pools and ponds of Las Hoyas and El Montsec where the remains were deposited, or on the margin of streams and creeks that flowed into those water bodies.

Systematic importance. — The ferns of the families Matoniaceae, Gleicheniaceae, Dicksoniaceae, and Osmundaceae were relatively abundant during the Early Cretaceous (Vakhrameev, 1991; Coiffard & al., 2007). At the mid Early Cretaceous the proportion of Osmundaceae and Matoniaceae decreased, whereas the proportion of Dicksoniaceae and Polypodiales rose towards the Albian. This replacement has been associated with the radiation of angiosperms and niches becoming available for opportunistic fern taxa (Schneider & al., 2004; Coiffard & al., 2007). The absence of fertile material in both El Montsec and Las Hoyas makes the assignment of this fern to either group impossible. Dilcher & Hill (2003), place this species close to *Ceratopteris* Brongn. or *Eriosorus* Fée, both in Pteridaceae, and they also mention similarities with Marsileaceae and Salviniaceae. Both El Montsec and Las Hoyas have a fern taxa assemblage, which, in general, presents a typical Jurassic to earliest Cretaceous structure. However, the presence of *Coniopteris laciniata*, if related to Polypodiales as it has been recently suggested for other *Coniopteris* species preserving fertile structures (Li & al., 2020), could indicate a more modern fern assemblage in these localities, where early angiosperms have also been recovered, i.e., *Montsechia vidalii* (Zeilner) C.Teixeira (Gomez & al., 2015), *Ranunculus ferrerii* (C.Teixeira) Blanc-Louvel (Barale & al., 1984), and *Iterophyllum lobatum* Barral & al. at Las Hoyas (Barral & al., 2013). This would support the diversification of Polypodiales during

the Late Cretaceous, related to the diversification of angiosperms as suggested by Schneider & al. (2004).

■ CONCLUSION

The conspecificity of *Coniopteris laciniata* and *Sphenopteris wonnacottii* increases the range of distribution of the taxon, and links it to depositional environments with alkaline soils and presence of calm waters. The reconstruction of this plant is made possible with the aid of the metric analyses performed in this work, which permit a better understanding of the architecture and habit of the plant. Additionally, they allow for comparison with the architecture of other plants with lobed and filiform pinnules. The unique morphology and variability of the pinnules of *Coniopteris laciniata* sets it aside from other species of this genus as a very well-defined species. Future studies must be conducted to better understand the autecology of *Coniopteris laciniata* as well as to corroborate the putative assignment of this species to Polypodiales and its implications in the evolution of the vegetation in the Early Cretaceous.

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■ AUTHOR CONTRIBUTIONS

CB-M designed and performed the research, collected the data, performed the analyses, and wrote the initial draft of the manuscript. ÁDB collaborated in the design of the research, the interpretation, and writing of the subsequent manuscript drafts. — CB-M, <https://orcid.org/0000-0001-6614-286X>; ÁDB, <https://orcid.org/0000-0003-1598-7963>

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