

A new Dominican amber fossil of the derived fern genus *Pleopeltis* confirms generic stasis in the epiphytic fern diversity of the West Indies

Harald Schneider · Alexander R. Schmidt ·
Paul C. Nascimbene · Jochen Heinrichs

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Abstract One of the grand objectives in the integration of fossils and phylogenetics is to obtain support for macroecological and macroevolutionary hypotheses. Here, we provide new evidence from Dominican amber fossils, which supports a likely stasis in the generic composition of epiphytic plant communities in the West Indies for at least 16 million years. The proposed hypothesis is based on the discovery of the first fossil of the Neotropical fern genus *Pleopeltis*. The relationships of this specimen to extant genera are studied using a dated phylogenetic framework to reconstruct the evolution of the characters preserved in the fossil, as well as by exploring the phylomorphospace of *Pleopeltis*. The fossil corroborates divergence time estimates obtained independently and also suggests the conservation of the generic composition of epiphytic communities. We discovered evidence for conserved morphotypes in the genus *Pleopeltis* occurring from the mid-Miocene to the present. The innovative use of phylomorphospace reconstruction provided crucial information about the affinities of the fossil. Rather than relying on reconstructing the evolution of single characters, this analysis integrates the evolution of all informative characters

observed to evaluate relationships of the fossilized morphotype to extant morphotypes.

Keywords Ancestral character evolution · Assignment of fossils · Epiphytic diversity · Diversification time estimates · Phylomorphospace · Stasis in ecological assemblages

Introduction

Dominican amber fossils have provided evidence for the conserved generic composition of epiphytic bryophyte communities in the West Indies since the Miocene (Grolle 1984; Gradstein 1993; Frahm and Newton 2005; Reiner-Drehwald et al. 2012; Heinrichs et al. 2013). In contrast, the paucity of ferns in this amber provides limited evidence of any similar taxic conservatism in these plants occurring in similar extant Caribbean habitats. Only two fern fossils have previously been described from these amber deposits (Gomez 1982; Lóriga et al. 2014). Each specimen represents the first fossil record of epiphytic fern genera and thus each provides critical information to our understanding of the assembly of the extant diversity of epiphytic vascular plants (Smith et al. 2006b; Zotz 2013). The recent report of a fossil *Elaphoglossum* (Lóriga et al. 2014) documented the presence of this widespread and species-rich genus since the Miocene, whereas the report of Gomez (1982) suggested the presence of the derived grammitid clade belonging to the species-rich family Polypodiaceae. The latter family contributes more than 50 % of the current epiphytic fern diversity in both Neotropical and Paleotropical forests (Zotz 2013). The putative grammitid fern reported by Gomez (1982) is the only known Neotropical fossil assigned to Polypodiaceae, whereas all other

H. Schneider (✉)
Department of Life Sciences, Natural History Museum, London, UK
e-mail: h.schneider@nhm.ac.uk

A. R. Schmidt
Department of Geobiology, Georg August University,
Göttingen, Germany

P. C. Nascimbene
Division of Invertebrate Zoology, American Museum of Natural
History, New York, NY, USA

J. Heinrichs
Systematic Botany and Mycology, Faculty of Biology, Ludwig
Maximilian University, Munich, Germany

Polypodiaceae fossils have been recovered from locations in the Asian (sub)tropics or temperate regions of Europe and North America (van Uffelen 1991; Collinson 2001; Kvacek 2001; Kvacek et al. 2004; Su et al. 2011; Wu et al. 2012; Jacques et al. 2013; Wen et al. 2013).

Recent phylogenetic studies have provided a framework to explore the generic composition of epiphytic diversity contributed by Polypodiaceae (Ranker et al. 2004; Schneider et al. 2004, 2010). These studies continue to improved the generic classification of Neotropical species diversity belonging to this family (e.g., Schneider et al. 2006; Smith et al. 2006a; Otto et al. 2009; Hirai et al. 2011; Kessler et al. 2011; Labiak 2011; Sundue et al. 2012; Sundue 2013) and have provided results on the assembly of the Neotropical fern diversity since the Eocene (e.g., Kreier and Schneider 2006; Janssen et al. 2007; Kreier et al. 2008; Schuettpelz and Pryer 2009; Labiak et al. 2010; Schneider et al. 2010; Rouhan et al. 2012; Sundue et al. 2014). However, these results were obtained using phylogenetic methods based exclusively on extant taxa and thus lack the confirmation obtained by discovery of fossil evidence.

Here, we infer the relationships of a newly discovered Dominican amber inclusion consisting of a fern leaf fragment assignable to the extant Neotropical Polypodiaceae genus *Pleopeltis*. The relationships of the fossil were explored by: (1) comparing morphological similarities with extant taxa; (2) identifying apomorphic character states by reconstructing the evolution of characters preserved in the fossil; and (3) analyses employing phylomorphospace reconstruction. To achieve this, we employed the phylogenetic framework provided by recent phylogenetic analyses that used plastid DNA sequence variation to infer relationships (Schneider et al. 2004; Otto et al. 2009). The phylomorphospace approach is used here for the first time to infer the relationships of a fossil to its extant relatives. Finally, we discuss the consistency of the new fossil with estimated divergence times of this genus that were calculated without incorporating the fossil as a calibration. Our approach provides a rather independent test for estimates of the divergence times of Neotropical Polypodiaceae and supports the assumed stasis of the generic composition of epiphytic communities since the Miocene.

Materials and methods

The investigated piece of amber belongs to the Dominican amber collection of the American Museum of Natural History, New York (AMNH-DR-ASHS-1). The age of the Dominican amber deposit has been recently constrained from the stratigraphic age estimation of Burdigalian (15.8–20.3 million years ago (Ma); Gradstein et al. 2004) to approximately 16 Ma (Iturralde-Vinent 2001). The 4.0×2.0×1.5-cm piece of amber containing the plant fragment was trimmed and

polished on all sides close to the inclusion using a series of emery papers with decreasing grit sizes on a Buehler Ecomet-3 variable speed flat lapidary wheel, with a fine stream of water. Stacks of digital images were taken with a Canon 60D digital camera and processed using Helicon Focus 5.0 to assemble a multifocus layer image.

The observed morphology of the amber inclusion was compared to that of extant ferns, especially *Pleopeltis* (Otto et al. 2009; Smith and Tejero-Diez 2014) and the *Pleopeltis polypodioides* complex (Sprunt et al. 2011). Observations of these ferns were directly obtained from specimens deposited in the herbaria of the Natural History Museum at London (BM). The relationships of the fossil were explored using a three-step approach. First, we inferred putative relationships based on morphological similarities to extant fern species. Then, the resulting hypothesis was investigated by reconstructing the evolution of the characters preserved in the fossil within the lineage to which the fossil belongs. Finally, we determined its location in the phylomorphospace of *Pleopeltis*.

The evolution of characters preserved in the fossil was studied using a consensus chronogram obtained with BEAST 1.7.5 (Drummond et al. 2012) and based on available plastid DNA sequence data (see Otto et al. 2009). The chronogram was calibrated by the age estimate of 39.2 Ma for the divergence of the clade comprising *Pecuma*, *Phlebodium*, *Pleopeltis* and *Polypodium* (Schuettpelz and Pryer 2009). Analyses were carried out using a relaxed lognormal clock model and assuming a Yule process (Drummond and Suchard 2010). The topology of the consensus chronogram was applied to reconstruct the evolution of morphological characters defined as discrete characters using both maximum parsimony and maximum likelihood reconstruction as implemented in Mesquite 2.75 (Maddison and Maddison 2012). The following characters and character states were selected based on the characters preserved in the fossil: (a) leaf dissection—undivided (0), pinnatifid (1) and pinnate to tripinnate (2); (b) pinnae length—1–3 cm (0) and >3 cm (1); (c) pinnae width—1 to 4 mm (0) and >4 mm (2); (d) pinnae base shape—straight (0), dilated (1) and constricted (2); (e) abaxial pinnae surface—naked (0), scales present but not overlapping (1) and scales present and overlapping (2); (f) adaxial pinnae surface—naked (0) and scales present (1); (g) margin of abaxial pinnae—fimbriate (0) and deeply divided (1); (h) length/width ratio of abaxial scales—1.0 to 1.5 (0) and >1.5 (1).

In contrast to the ancestral character state reconstruction of single characters, the phylomorphospace approach investigates the evolution of morphotypes. This method plots phylogenetic hypotheses on projections of morphological disparity obtained in principal coordinate analyses (Sidlauskas 2008). We used only characters preserved in the fossil and scored these for all included extant species. These analyses were carried out using PAST 3.0 (Hammer et al. 2001) to conduct the

principal coordinate analysis and the PDAP:PDTree package (Midford et al. 2011) in Mesquite. The fossil taxon was part of the principal coordinate analyses but not included in the phylogenetic analyses. To determine the phylogenetic relationships, we employed the consensus topology found in the BEAST analyses.

Results

Taxonomic account

Pleopeltis dominicensis H. Schneid., Heinrichs, A.R. Schmidt, sp. nov.

Type material. Holotype: AMNH-DR-ASHS-1 at the Dominican amber collection of the American Museum of Natural History, New York (Fig. 1).

Repository. All material is deposited in the American Museum of Natural History (AMNH).

Type locality. Burdigalian (early Miocene, ca. 15.8–20.3 Ma, Gradstein et al. 2004) amber bearing strata of Dominican Republic.

Etymology. The species epithet refers to the location of the mining site in the Dominican Republic.

Species diagnosis. Fern leaf fragment with pinnatifid dissection covered by overlapping peltate scales with fimbriate margins.

Description. The amber inclusion is composed of a single leaf fragment 3.5 cm in length (Fig. 1a). The leaf fragment has

a pinnatifid shape with a rachis diameter of 1.0 to 1.5 mm. The three entirely preserved pinnae are 2.2, 2.5 and 2.7 cm long with a width of 2.4 to 3.2 mm, and the dilated bases extended to 4.4 mm. The pinnae are curled, their bases are slightly dilated, and their apices likely obtuse. The abaxial surface of the pinnae and rachis is densely covered by overlapping peltate scales (Fig. 1b, c), whereas the adaxial surface is less densely covered by similar scales. At the lower surface, ovate spots of 0.6–0.7 × 1.0-mm size are not covered by these scales (Fig. 1a, arrowheads). They are arranged in rows on each side of the costa, and thus, they are likely exindusiate sori. The ovate-lanceolate scales are 0.35–0.64 mm long and 0.27–0.51 mm wide with a length/width ratio of 1.4–1.5 (Fig. 1b). The cell walls of the scales are sclerotic, especially those close to the centre. The scale margins are fimbriate (Fig. 1c).

Discussion

All preserved characters of the amber inclusion suggest close relationships to the genus *Pleopeltis* (Polypodiaceae). Polypodiaceae frequently displays a combination of pinnatifid leaves, ovate exindusiate sori and peltate scales attached to the either rhizome and/or leaves. Among Neotropical Polypodiaceae, the persistence of scales at the mature pinnae is a character unique to the genus *Pleopeltis* (Schneider et al. 2004; Otto et al. 2009; Smith and Tejero-Diez 2014), providing strong evidence for an affiliation of the amber inclusion to

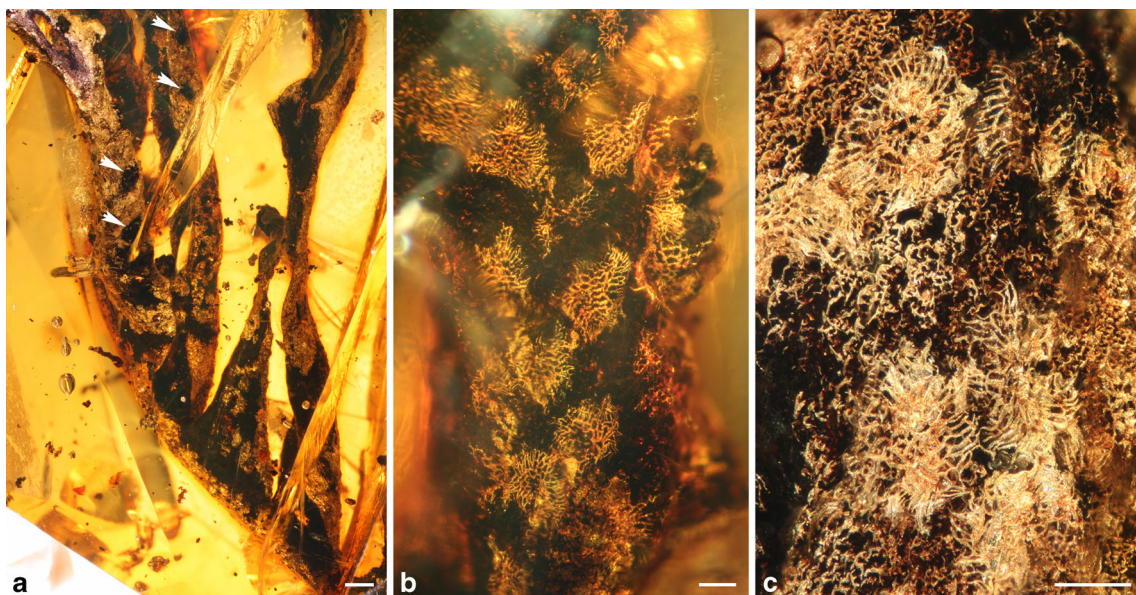


Fig. 1 Holotype of *Pleopeltis dominicensis* in Miocene Dominican amber (AMNH-DR-ASHS-1). **a** Pinnatifid leaf fragment including the petiole and several recurved pinnae. The surface of the pinnae is densely covered by overlapping scales. *Arrowheads* indicate ovate areas

without scales interpreted as sori. **b** Dense coverage of the abaxial pinnae surface by ovate-lanceolate, peltate scales. **c** Close-up of one of the pinnae scales showing the thickened cell walls especially at the centre and the fimbriate margins. *Scale bars*: 1 mm (**a**) and 200 μ m (**b**, **c**)

this genus. Phylogenetic analyses found scales persisting at mature leaves to be the apomorphy separating *Pleopeltis* from its closest relatives, such as *Pecluma*, *Phlebodium* and *Polypodium* (Schneider et al. 2004; Otto et al. 2009).

The curled pinnae resemble those found in the resurrection ferns of the *Pl. polypodioides* complex (Otto et al. 2009; Sprunt et al. 2011) but can also be found in other species. The abaxial surface of pinnae of these ferns is densely covered by overlapping scales consisting of ovate-lanceolate peltate pinnae with fimbriate margins and sclerotic centres (Sprunt et al. 2011), as observed in the fossil. The measures of the scales are within the range of scale measures reported for

abaxial pinnae scales of *Pl. polypodioides* (L.) E.G. Andrews & Windham subsp. *aciculare* (Weath.) and E.G. Andrews & Windham and related taxa (Sprunt et al. 2011), even though their scale length of 0.35 to 0.64 mm is a bit smaller than the minimum length reported for extant species (0.51 to 1.04 mm). In contrast, the width of 0.27 to 0.51 mm overlaps with the variation reported for extant taxa such as *Pl. polypodioides* subsp. *aciculare*. All characters observed in the fossil support a close relationship to these widespread extant ferns that occur throughout the Neotropics towards Eastern USA and South Africa. Today, a single member, *Pl. polypodioides* var. *polypodioides*, occurs in Jamaica, but this

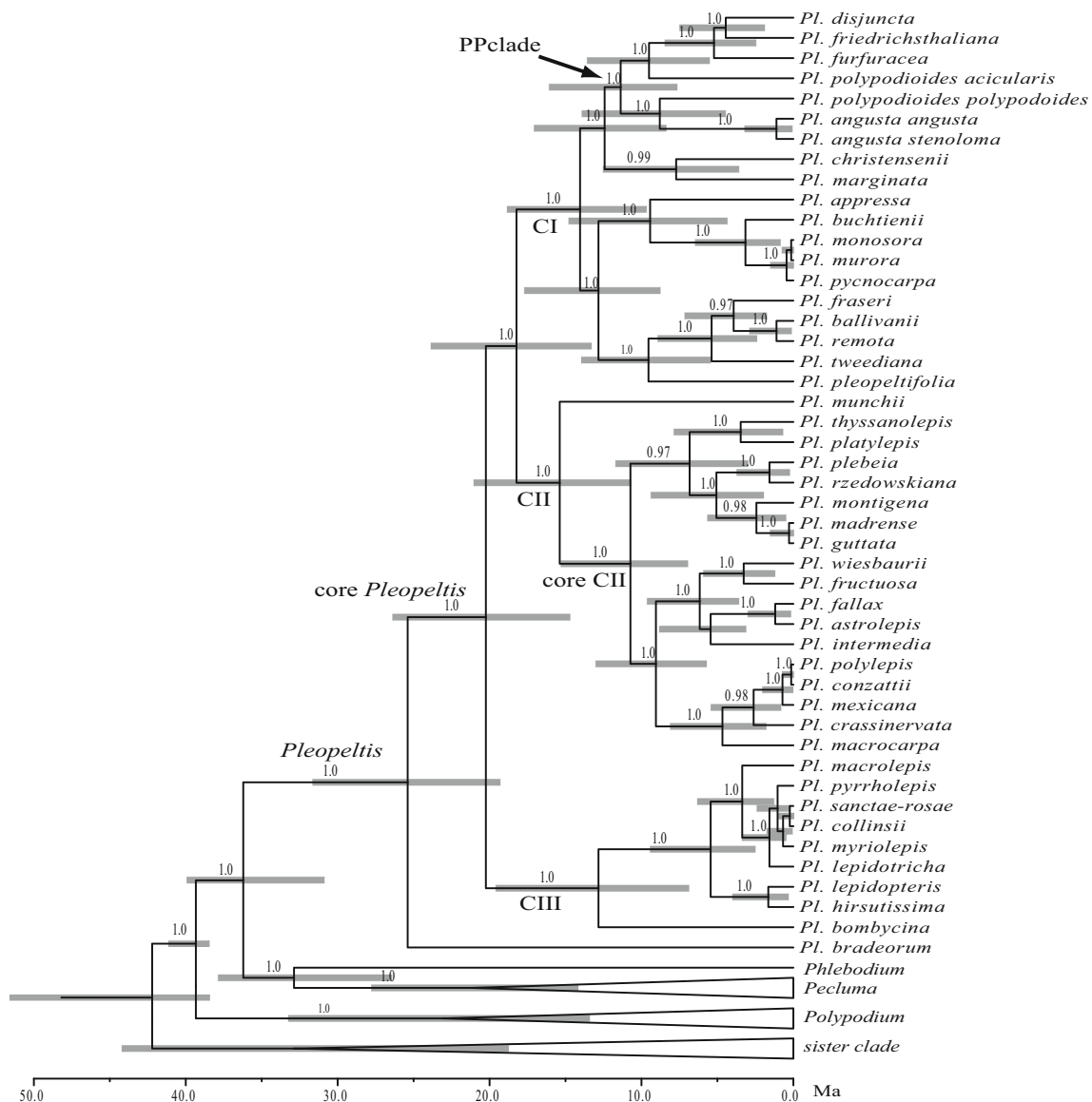


Fig. 2 Consensus chronogram obtained by BEAST analyses of a previously published plastid DNA dataset (Otto et al. 2009). Sister clades of *Pleopeltis* were collapsed. Time scale shown in million years to present (Ma). Posterior probabilities $p \geq 0.95$ were given above branches, whereas confidence age estimate intervals were shown as

grey vertical bars. The node position corresponded to the mean value. Within *Pleopeltis*, six nodes were marked: *Pleopeltis* node; core *Pleopeltis* node; the nodes of the main clades I, II and III; and the node of the *P. polypodioides* clade (PP clade)

taxon has slightly larger scales, measuring from 0.84 to 2.04×0.38 to 0.79 mm.

Ancestral character state reconstruction recovered all characters observed as putative plesiomorphic states in the core *Pleopeltis* clade. A pinnatifid leaf shape was found to be the ancestral leaf shape of *Pleopeltis* with a likelihood of 95 %. Both pinnae shape and scales showed homoplastic character states. The character states of the pinnae and scales shown by the fossil were found to be putative ancestral states of core *Pleopeltis*, main clade I and *Pl. polypodioides* clade (Fig. 2). For example, persistence of scales at the abaxial and adaxial surface of the pinnae was found to be the ancestral state of the core *Pleopeltis* clade with a likelihood of 65 and 73 %, respectively, and of main clade I with a likelihood of 69 and 70 %, respectively. Less ambiguous was the evolution of overlapping scales at the abaxial side of the pinnae. The character state shown by the fossils had less than a 50 % likelihood of being ancestral for either the core *Pleopeltis* clade (38 %) or main clade I (27 %) but showed a 57 % likelihood for the *Pl. polypodioides* clade. In summary, the ancestral character state reconstructions were consistent with the assignment of the fossil to *Pleopeltis* but failed to recover apomorphic character states allowing the unequivocal assignment to any clade within *Pleopeltis*.

The fossil taxon was placed close to representatives of the *Pl. polypodioides* clade in the phylomorphospace analysis (Fig. 3). This analysis does not reconstruct the evolution of single characters but instead reflects the integration of these characters into morphotypes. By employing this method, we are able to address the integration of characters during the assembly of morphological disparity during the diversification of this genus. Therefore, we were able to explore previously

undetected information. With the exception of *Pleopeltis angusta* Humb. & Bonpl. ex Willd., all species of the *Pl. polypodioides* clade occupied a small range of the morphospace exploited by *Pleopeltis*. The fossil taxon was placed within this range supporting the assignment to this clade.

In conclusion, the exploration of the amber fossil utilizing the phylogenetic framework did not reject its assignment to *Pl. polypodioides* as suggested by morphological similarities. However, some ambiguity was seen concerning the evolution of these similarities. Evidence for homoplasy was found for all characters, and the states preserved in the fossil were found to most likely be the ancestral character states for three putative calibration nodes: core *Pleopeltis*, main clade I and *Pl. polypodioides* clade. The absence of apomorphic character states prevented an unequivocal assignment of the fossil to any node represented within the *Pleopeltis* tree. In contrast, the phylomorphospace analysis enabled to identify assignments by considering the combination of character states of the fossil that are unique to the *Pl. polypodioides* clade. The phylomorphospace approaches, therefore, addressed successfully the problem of circumscribing extant *Pl. polypodioides* caused by a lack of accumulation of diagnostic features due to the conservation of ancestral character states (Otto et al. 2009; Sprunt et al. 2011). Taking into account the unresolved species taxonomy of the extant members of this clade (Sprunt et al. 2011), the obtained data are insufficient to assign this fossil unequivocally to any extant species, and thus, the fossil is treated here as a new species.

The resulting inference has consequences for the interpretation of the fossil in the context of the divergence time hypothesis (Fig. 2). The initial assignment based on similarity

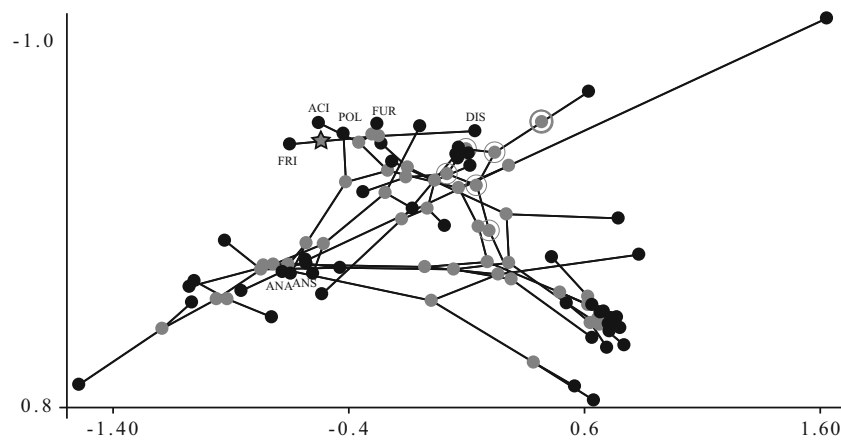


Fig. 3 Phylomorphospace of *Pleopeltis*. Phylogenetic relationships (as shown in Fig. 2) plotted onto the projection of the morphological disparity of *Pleopeltis* obtained using principal coordinate analyses of a matrix including only characters preserved in the fossil. Black dots correspond to extant species and grey dots to nodes in the phylogenetic tree, lines correspond to branches, and the star indicates the position of the fossil taxon. Grey dots with a grey ring indicate the basal node of

Pleopeltis; the core *Pleopeltis* clade; and the basal nodes of main clades I, II, III. Abbreviations correspond to extant species of the *Pl. polypodioides* clade: ACI *Pl. polypodioides* var. *aciculare*, ANA *Pl. angusta* var. *angusta*, ANS *Pl. angusta* var. *stenoloma*, DIS *Pl. disjuncta*, FRI *Pl. friedrichsthaliana*, FUR *Pl. furfuracea*, POL *Pl. polypodioides* var. *polypodioides*

traced the fossil to the node of the *Pl. polypodioides* clade. This node was estimated to be as old as 17.0 to 8.4 Ma and thus younger than expected under the similarity-based assignment of ~16 Ma (Iturralde-Vinent 2001). However, ancestral character state reconstruction did not reject alternative assignments to main clade I (estimated age 9.7–18.8 Ma), core *Pleopeltis* clade (estimated age 14.7 to 26.3 Ma) and the *Pleopeltis* clade (estimated age 19.3 to 31.6 Ma). The phylomorphospace analyses provided further evidence for close relationships of this fossil to extant species of the *Pl. polypodioides* clade. Given the available evidence, it may be either a representative of the crown group (estimated age 17.0 to 8.4 Ma) or the stem group (estimated age of 18.8 to 9.7 Ma) of this clade. If this interpretation is considered, the older estimates of the confidence interval overlap with the assumed age of the fossil (~16 Ma), whereas the younger estimates are rejected.

The newly discovered fossil supports the assumption that the genera contributing to the extant epiphytic Neotropical diversity were already present in the early Miocene. This is consistent with the hypothesis of the accumulation of epiphytic fern diversity at least since the early Cenozoic and rapid accumulation of generic diversity of these ferns in the late Oligocene and Miocene (Schneider et al. 2010). In combination with the reports on liverworts and mosses, the fossil also provides new evidence suggesting stasis of morphotypic and generic diversity, but not necessarily stasis of species diversity in Caribbean forests.

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