First record of an Icacinaceae Miers fossil flower from Le Quesnoy (Ypresian, France) amber

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Flowers embedded in amber are rare. Only about 70 flowers or inflorescences have been described among which only one lamiid is known. Nevertheless, these fossils are important to our understanding of evolutionary process and past diversity due to the exceptional preservation of fragile structures not normally preserved. In this work, a new flower named Icacinanthium tainiaphorum sp. nov. from Le Quesnoy (Houdancourt, Oise, France) is described. Our phylogenetic analysis with extant species suggests that the affinity of this flower lies with the family Icacinaceae, close to Natsiatum or Hosiea. The fossil shows a combination of features unknown in extant Icacinaceae and we thus propose the description of a new fossil genus. It reveals a previously unknown diversity in the family and demonstrates the complementarity of different types of fossil preservation for a better understanding of past floral diversity.

Among the diverse organisms or parts of organisms embedded in amber, angiosperm flowers are exceedingly rare. Only ca. 70 flowers or inflorescences have been described to date, mostly from Cretaceous Burmese amber, Paleogene Baltic amber, Miocene Dominican amber and Late Oligocene-Early Miocene Mexican amber. In addition, we are noticing phylogenetic disparities. The rosid clade accounts for 39% of eudicot diversity but 44% of flowers embedded in amber. In contrast, the asterid clade, which represents half of the eudicot diversity, is represented in the fossil record by only 12 flowers (17%) in amber. Among these flowers, ca. 50% belong to Ericales and Cornales. Whilst five flowers belong to campanulids, only one represents the lamiid clade (in the order Gentianales), which corresponds to 26% of the extant eudicot diversity. Nevertheless, fossil flowers embedded in amber are generally important to understand evolutionary processes and past diversity because they are often exceptionally well preserved and provide insights into the morphology of fragile structures that are not normally preserved.

The locality at Le Quesnoy (Houdancourt, Oise, France), considered to be basal Eocene (Ypresian) was first studied in 1999. This first survey highlighted the abundance of insects and the presence of at least one flower of caesalpinoid legume in amber. The pollen included in the amber was studied using a new technique of extraction, but the diversity of the floral remains had to be studied extensively.

Here we study one flower from Le Quesnoy and assign it to the lamiid clade. This flower named Icacinanthium tainiaphorum sp. nov. is the first known fossil occurrence of a flower from order Icacinales. The affinity of this flower embedded in the resin of a tree might suggest that this species could have been a climber. This type of ecology is frequent in megathermal flora, which has developed in Europe during the Eocene global warming. This Icacinaceae flower in amber attests to the presence of an undocumented past diversity.

Results
Systematics.

Order Icacinales Tiegh.
Family Icacinaceae Miers.
Genus Icacinanthium Del Rio & De Franceschi, gen. nov.
Type species Icacinanthium tainiaphorum Del Rio & De Franceschi, sp. nov.

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Generic diagnosis: Flower small, actinomorphic, hypogynous and pentameric. Calyx cupular, petals lanceolate curved backwards, with a straight apex, fused at base in a short cup, tomentose on adaxial surface with long, simple flattened hairs with granular ornamentation, glabrous on abaxial surface. Stamens alternate to petals, free. Pollen small, triaperturate and echinate.

Etymology: “Icacinanthium” indicates the familial affinity to Icacinaceae (Icaci-) and that it is a flower (L = Anthos, flower).

Icacinanthium tainiaphorum Del Rio & De Franceschi, sp. nov. (Figs 1 and 2)

Holotype: Deposited in the collection of Palaeobotany of MNHN (MNHN.F.44051.)

Type Locality: Le Quesnoy, Oise, France

Stratigraphic age: Ypresian

Etymology: “tainiaphorum” refers to the flat “ribbon-like” (L = tainia, ribbon) hairs borne (L = phor, bearing) on the petals.

Specific diagnosis: As for the genus

Description: A single flower embedded in amber, almost completely preserved. Flower small, about 2.5 mm in diameter, at least unisexual male or hermaphrodite, actinomorphic pentameric and hypogynous (Fig. 1A,B).

The calyx is cupulate, filmy and very short. It is composed of 5 minute sepals, which are very difficult to distinguish. Scattered single-celled hairs are visible at the margin. Aestivation of the corolla is probably valvate according to the shape and position of the petals, which are fused at the base in a short cup. The petals are lanceolate, curved backwards in apical view (Figs 1A and 2) and with a straight apex (Fig. 1C), about 1.40 mm long and 0.7 mm broad. They are tomentose on the adaxial surface with long, simple flattened hairs with granular ornamentation, about 0.7 mm long and 0.025–0.036 mm broad; The stamens alternate with the petals and are erect but anthers were not preserved; Filaments are glabrous, about 0.15 mm in diameter, free from the petals and attached below the base of gynoecium. The globular gynoecium is free, possibly unilocular considering its shape, and glabrous. The ovary seems to be poorly developed or very small. The stigma is unknown, not preserved or not developed.

Figure 1. Icacinanthium tainiaphorum holotype, (A) flower in apical view with petals curved backwards, (B) same flower in basal view, (C) detail of petals in basal view (D) pollen grain showing echinate ornamentation (arrows) (E and F) other pollen grain showing pores (arrows). Scale: (A–C) = 1mm, (D–F) = 20μm.
The pollen is very small (about 20–25 µm in diameter), clearly echinate (Fig. 1D) and triporate (Fig. 1E,F). No colpus could be observed, but we cannot completely exclude the presence of faintly marked small colpi.

Phylogenetic analysis. The Bayesian analysis 50% majority-rule consensus tree is given in Fig. 3 (and Supplementary 1). We included 51 species whose 23 species represent 21 genera of Icacinaceae and 27 species represent all other groups of the asterid. We used a combined morphological and molecular data with 73 protein-coding genes for a total of 59132 bp and 22 morphological characters (see the material and method for more precisions). As expected, we found a topology similar to the previous phylogenetic study using the same DNA data for the species included here27. This fossil, when included in the analyses, is placed close to Natsiatum. However the node with Icacinanthium and Natsiatum have very low support (PPB < 0.95). In this sense, the position of Icacinanthium is considered as unresolved at the base of the group IV sensu Stull et al.27.

One hundred and ninety five (195) steps are necessary for the reconstruction of the history based on morphological characters by Mesquite's parsimony state reconstruction (0.34 CI and 0.47 RI). The position of Icacinanthium close to Natsiatum or Hosiea is supported by the same number of steps. This explains why only the nodes of the clades containing Natsiatum and Hosiea are over 0.95 PP. Of the 22 morphological characters, only the stamen position [16] and the symmetry of the flower [1] are non informative (Fig. 3; Supplementary 2). For the fossil flower, the main informative characters are the calyx shape [4], the petal and stamen fusion [10; 17] and all pollen characters [20; 21; 22]. Positioning uncertainties correspond to both characters for presence or absence of hair adaxially and abaxially on petals [13; 14].

Discussion

Only the presence of hairs on the outside of the petals seems to be synapomorphic for the Icacinaceae group (Fig. 3) according to our phylogenetic reconstruction. While Icacinanthium did not have hairs outside the petals, this state is also absent in four genera and some species of other genera within Icacinaceae, indicating a convergent loss of these hairs.

According to our ancestral state reconstruction, the Icacinaceae clade (excl. Cassinopsis) possesses small bisexual, pentamorous flowers with petal apex adaxially curved, stamen free from petals (this last state shared by all modern genera of Icacinaceae s.s, sensu Stull et al.25) and echinate pollen. Only the shape of the petal apex does

Figure 2. Drawing of Icacinanthium tainiaphorum gen. et sp. nov. in apical view; (ov) ovary; (s) stamens; (p) petals. Arrows and lines: position of section for pollen preparation. Scale bar = 1mm.
not match with this fossil flower; however, this feature also occurs in five extant genera of Icacinaceae and several species which also possess comparable straight apices.

The clade including both III and IV possesses unisexual flowers (except for Desmostachys), cupular calyx, petals fused at base and small and mainly porate pollen grains (synapomorphic). Moreover, petal apex orientation of Clade IV is unresolved with a preponderance of genera with straight apices, which would be a synapomorphic character for this clade, emphasizing affinities of I. tainiaphorum to this clade. We therefore hypothesize that this flower is a unisexual male flower, which would explain the poorly developed ovary and make a better fit with the phylogenetic position of the fossil (rather than a poor preservation of this organ during fossilisation).

Adaxial hairs of Emmotum nitens and Poraqueiba sericea have an irregularly moniliform shape, and thus clearly differ from the hairs seen in other species. In fact, all adaxial hairs of Icacinaceae s.s. considered here and Metteniusa petals are flattened and very simple, as what is found in Icacinanthium (Fig. 4). Icacinaceae hairs however are granular, more or less longitudinally extended while in Metteniusa we observe nodules surrounded by longitudinal furrows (Fig. 4F), very different from the Icacinaceae ornamentation. These observations corroborate the position of I. tainiaphorum within the family Icacinaceae. In this family, the external hairs are generally quite similar, with a tubular form, acute at the apex and with granular ornamentation (Fig. 4E). The hairs in the fossil appear to be homologous and the presence of these hairs is interpreted to be synapomorphic for Icacinaceae.

In any case this fossil shows a combination of characters unknown in extant Icacinaceae. Indeed, flowers of Natsiatum herpeticum, which have adaxial petal hairs, also have them abaxially. In contrast, Hosiea japonica flowers are glabrous, and there are also flowers with abaxially hairy petals, but not adaxially in four genera of clade IV. To our knowledge, only the flower of Merrilliodendron megacarpum, from clade II, has adaxial petal hairs only such as what we found in our fossil flower. In clade IV this character state is unknown and new, hence our proposal to treat it as an extinct genus.

The fossil record of Icacinaceae, predominantly from the Eocene of North America and Europe, is extensive. However no fossil flowers were until now attributed to this family. In fact, most of these fossils are endocarps, in particular from the modern genera Iodes, Phytocrene, and Pyrenacantha. Endocarp fossils of Natsiatum were described from the Middle Eocene of Tennessee (Natsiatum wilcoxiana) and Europe, fossils of Palaeohosiea, supposed to be close to the extant genus Hosiea, were described. However, no character supports affinity with Hosiea and no feature separates the fossils from the extant genus Iodes. The presence of Icacinaceae from Le Quesnoy was only mentioned briefly and was based on what appears to be a lignitic endocarp, but was attributed to the genus Iodes (personal observation). The link between these two types of fossils is questionable, thus indicating an unsuspected diversity for Eocene Icacinaceae.

Figure 3. Phylogenetic relationships among asterid species focused on the family Icacinaceae based on the combined 73-plastidial genes and 22 morphological characters. The 50% majority-rule consensus tree was constructed by Bayesian inference in MrBayes. Star indicates the placement of the fossil flower close to Natsiatum. Dotted lines indicate another possible position for the fossil, close to Hosiea. Mesquite orientation of pertinent characters is shown. (*) represent strong node (>95% PP).
Growth habits of extant Icacinaceae include lianas, shrubs or trees, distributed in tropical forests around the world. *Icacinanthium* is close to *Natsiatum* or *Hosiea*, both of which being Asian genera of climbing shrubs. *Icacinanthium* could testify for an Asian affinity of the Le Quesnoy Ypresian flora, as highlighted by studies on Menispermaceae and other comparable European sites. We thus hypothesize that *Icacinanthium* could be a climbing shrub, this type of ecology being frequent for megathermal flora that would have occurred in Europe during the early Eocene global warming phase.

**Material and Method**

**Locality and fossil material.** The fossil resin remains were collected from 1997 to 2000 from the Le Quesnoy (Houdancourt, Oise, France) lignitic clay sediments which belong to the « argiles à lignites du Soissonais » Formation. These sediments are dated to the Ypresian (± 56 Ma) according to mammal biochronology (MP7) and palynological studies. This corresponds to the Sparnacian facies of the lower Ypresian (lower Eocene). Several fossil resin samples contain diverse organisms, principally arthropods (mainly insects), a few plant remains, mainly represented by pollen grains, but also a few flowers still to be studied. The fossils are...
kept in the collections of the Paris Muséum national d’histoire naturelle (MNHN). The specimen studied here is a flower embedded in this fossil resin here called amber, but produced by Detarioideae trees (Leguminosae)\(^\text{15, 41}\).

**Phylogenetic reconstructions.** Preliminary exploratory herbarium studies (P) focusing on small pentameric hypogynous flower with petals fused at the base and with stamens free from the petals lead to comparison of the flower in amber to those of the family Icacinaceae. We employed the most complete molecular data for the asterid clade focusing on the Icacinaceae\(^\text{42}\). Theses data were composed of 73 protein-coding genes for a total of 59132 bp. We retained 51 species among the 122 accessions available\(^\text{42}\) of which 23 species represent 21 genera of Icacinaceae. We included at least 2 species from other asterid orders, except for Meliaceae where we used 9 species as this order includes species which were formerly included in genera of Icacinaceae, which are morphologically close to Icacinaceae sensu stricto. All molecular characters are coded as missing for the flower in amber. In addition, we included 22 morphological floral characters corresponding to features potentially observable in the fossil flower (Supplementary 2). The final matrix contains 59135 characters.

Bayesian analyses were performed using MrBayes\(^\text{43}\) with a format type mixed with two partition: DNA type (with model by default, GTR + I + G) and Standard type (equal state frequencies with all topologies equally likely a priori with unconstrained branch lengths) for morphological data. Two independent but parallel analyses were performed using flat priors, starting from random trees and consisting of four chains each. The analysis was run for 5 million generations, sampling every 1000 generations and with 20% burn-in. Analysis of output parameter using Tracer v.1.6\(^\text{44}\) confirms the convergence of chains. A 50% majority-rule consensus tree was computed with posterior probability (PP) estimates for all nodes. We generally consider as non-supported nodes those with less than 0.95 PP.

**Morphological studies.** A morphology matrix was made using Xper\(^\text{37}\) containing 22 flower and pollen characters coded for 51 taxa including the Le Quesnoy flower (Supplementary 2).

The matrix was constructed from direct morphological observation of herbarium specimens (P, see Supplementary 3) and from bibliographic data for flowers\(^\text{28, 37, 48–57}\) and pollen\(^\text{58–63}\). We observed the flower embedded in amber using a light microscope (Nikon Eclipse80i). Numerous pollen grains were found around the flower and between hairs on the adaxial surface of the petals (Fig. 1D); the vicinity and abundance of grains of the same type indicate that they probably belong to the flower. The pollen was also extracted from the amber in order to obtain a better understanding of its type (Fig. 2) following a previously published protocol\(^\text{25}\) and observed using the same microscope. Before extraction we only observe the imprint left by the pollen in amber. After extraction, we show an exceptional preservation of grains with well-preserved exine wall and remains of cellular content. A darker zone could correspond to the rest of the nucleus (clearly visible on Fig. 1D). Due to the presence of echniae (spines), pollen grains could not be fully separated from resin and were observed still embedded inside a small resin block. All these features were mapped into the phylogeny using Mesquite software\(^\text{44}\) with a parsimony ancestral state reconstruction.

We conducted a qualitative study of adaxial petal hairs of Metteniusa, Poraqueiba, Nothapodytes, Mappia, Icacinia, Leretia, Mappianthus, Desmostachys and Natsiatum using SEM (Scanning Electron Microscopy) with a Jeol JCM6000 after the specimens were coated with gold-palladium.

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**References**

1. Cruickshank, R. D. & Ko, K. Geology of an amber locality in the Hukawng Valley, northern Myanmar. *J. Asian Earth Sci.* 21, 441–455 (2003).
2. Poinar, G. Jr., Chambers, K. L. & Buckley, R. *Eocene psiloxylon burmensis* gen. and sp. nov., an Early Cretaceous eudicot flower (Angiospermae) in Burmese amber. *J. Bot. Res. Inst. Tex.* 1, 91–96 (2007).
3. Poinar, G. Jr. & Chambers, K. L. *Palaeoanithella huangi* gen. and sp. nov., an early Cretaceous flower (Angiospermae) in Burmese amber. *SIDA Contrib.* 21, 2087–2092 (2005).
4. Poinar, G. O. Jr. *Programinis burmitis* gen. et sp. nov., and *P. laminatus* sp. nov., an Early Cretaceous grass-like monocots in Burmese amber. *Aust. Syst. Bot.* 17, 497–504 (2004).
5. Göppert, J. H. R., Menge, A. & Conwentz, H. W. *Die Flora des Bernsteins*, und ihre Beziehungen zur Flora der Tertiärformation und der Gegenwart (Engelmann, Leipzig, 1886).
6. Weitschat, W. & Wichard, W. *Atlas der Pflanzen und Tiere im baltischen Bernstein* (F. Pfeil, München, 1998).
7. Iurrulde- Vincent, M. A. & MacPhee, R. D. E. Age and paleogeographical origin of Dominican amber. *Science* 273, 1850 (1996).
8. Chambers, K. L., Poinar, G. O. Jr. & Chanderbali, A. S. *Treptostemon* (Lauraceae), a new genus of fossil flower from Mid-Tertiary Dominican amber. *J. Bot. Res. Inst. Tex.* 6, 551–556 (2012).
9. Chambers, K. L., Poinar, G. O. Jr. & Brown, A. E. Two fossil flowers of *Trichilia* (Meliaeaceae) in Dominican amber. *J. Bot. Res. Inst. Tex.* 5, 463–468 (2011).
10. Chambers, K. L., Poinar, G. O. Jr. & Brown, A. E. A fossil flower of *Persea* (Lauraceae) in Tertiary Dominican amber. *J. Bot. Res. Inst. Tex.* 5, 457–462 (2011).
11. Chambers, K. L. & Poinar, G. O. Jr. *Ticodonella palacios* sp. nov. (Ticodendraceae), a Mid-Tertiary Fossil Flower in Dominican Amber. *J. Bot. Res. Inst. Tex.* 8, 559–564 (2014).
12. Poinar, G. Fossil palm flowers in Dominican and Baltic amber. *Bot. J. Linn. Soc.* 139, 361–367 (2002).
13. Poinar, G. Fossil palm flowers in Dominican and Mexican amber. *Bot. J. Linn. Soc.* 138, 57–61 (2002).
14. Poinar, G. & Columbus, J. T. *Alaria styliformis* gen. et sp. nov. (Pooideae: Bambusoideae) in Dominican amber. *Hist. Biol.* 25, 691–696 (2013).
15. Poinar, G. Jr. & Judziewicz, E. J. *Pharus primocinclus* (Poaceae: Pharoideae: Phareae) from Dominican amber. *SIDA Contrib.* 21, 2095–2103 (2005).
16. Poinar, G. Jr. & Steeves, R. *Virola dominicana* sp. nov. (Myristicaceae) from Dominican amber. *Botany* 91, 530–534 (2013).
17. Poinar, G. O. Jr. *Hymenea protera* sp. n. (Leguminosae, Caesalpinioideae) from Dominican amber has African affinities. *Experientia* 47, 1075–1082 (1991).
18. Poinar, G. O. Jr., Chambers, K. L. & Brown, A. E. *Trochanthera lepidota* gen. and sp. nov., a fossil angiosperm inflorescence in Dominican amber. *J. Bot. Res. Inst. Tex.* 2, 1167–1173 (2008).
19. Calvillo-Canadell, L., Cevallos-Ferriz, S. R. S. & Rico-Arce, L. *Miocene Hymeneeae* flowers preserved in amber from Simojovel de Allende, Chiapas, Mexico. *Rev. Palaeobot. Palynol.* 160, 126–134 (2010).
20. Castañeda-Pozadas, C. & Cevallos-Ferriz, S. R. Swietenia (Meliaceae) flower in Late Oligocene–Early Miocene amber from Simojovel de Allende, Chiapas, Mexico. Am. J. Bot. 94, 1821–1827 (2007).
21. Chambers, K. L., Poinar, G. O. Jr. & Brown, A. E. A new fossil species of Colophonitis (Arecaceae) from Mid-Tertiary Mexican amber. J. Bot. Res. Inst. Tex. 6, 557–560 (2012).
22. Magallon, S., Crane, P. R. & Herendeen, P. S. Phylogenetic pattern, diversity, and diversification of eudicots. Ann. Mo. Bot. Gard. 86, 397–372 (1999).
23. Poinar, G. O. & Poinar, R. The amber forest: a reconstruction of a vanished world (Princeton University Press, 1999).
24. Nel, A. et al. Un gisement spars crénacien exceptionnel à plantes, arthropodes et vertébrés (Éocène basalt, MP7): Le Quesnoy (Oise, France). Comptes Rendus de l'Académie des Sci.-Ser. IIA - Earth Planet. Sci. 329, 65–72 (1999).
25. De Franceschi, D., Dejax, J. & De Ploëg, G. Extraction du pollen inclus dans l'ambre [Sparsacien du Quesnoy (Oise), bassin de Paris]; vers une nouvelle spécialité de la paléo-palynologie. Comptes Rendus de l'Académie des Sci.-Ser. IIA - Earth Planet. Sci. 330, 227–233 (2000).
26. Dejax, J., De Franceschi, D., Lugardon, B., De Ploëg, G. & Arnold, V. Le contenu cellulaire du pollen fossilisé dans l'ambre, préservé à l'état organique. Comptes Rendus de l'Académie des Sci.-Ser. IIA - Earth Planet. Sci. 332, 339–344 (2001).
27. Stull, G. W., Duno de Stefano, R., Solits, D. E. & Solits, P. S. Resolving basal lamid palynology and the circumscription of Icacinaceae with a plastome-scale data set. Am. J. Bot. 102, 1794–1813 (2015).
28. Endress, P. K. & Rapini, A. Floral structure of Emmotum (Icacinaceae sensu stricto or Emmotaceae), a phylogenetically isolated genus of lamids with a unique pseudotrimerous gynoeceum, bitegmic ovules and monosporangiate thecae. Ann. Bot. 114, 945–959 (2014).
29. Knolbloch, E. & Mai, D. H. Monographie der Früchte und Samen in der Kreide von Mitteleuropa (Vydal Ustrediin ustav geologicky, Praha, 1986).
30. Manchester, S. R. Fruits and seeds of the Middle Eocene nut beds flora, Clarno Formation, Oregon (Paleontological Research Institution, New York, 1994).
31. Reid, E. M. & Chandler, M. E. The London Clay flora (The British Museum of Natural History, London, 1933).
32. Collinson, M. E., Manchester, S. R. & Wilde, V. Fossil fruit and seeds of the Middle Eocene Messel biota, Germany (Abh. Senckenb. Ges. Naturforsch., Stuttgart, 2012).
33. Stull, G. W., Herrera, F., Manchester, S. R., Jaramillo, C. & Tiffney, B. H. Fruits of an ‘Old World’ tribe (Phytocreneae; Icacinaceae) from the Paleogene of North and South America. Syst. Bot. 37, 784–794 (2012).
34. Stull, G. W., Moore, B. R. & Manchester, S. R. Fruits of Icacinaceae from the Eocene of Southern North America and their biogeographic implications. Int. J. Plant Sci. 172, 935–947 (2011).
35. Kvacik, Z. & Bužek, C. Endocarps and foliage of the flowering plant family Icacinaceae from the Tertiary of Europe. Tert. Res. 15, 121–138 (1993).
36. Stull, G. W., Adams, N. F., Manchester, S. R., Sykes, D. & Collinson, M. E. Revision of Icacinaceae from the Eocene London Clay flora based on X-ray micro-CT. Botany 94, 713–745 (2016).
37. Peng, H. & Howard, R. A. In Flora of China 11 (ed. Wu, Z. Y., Raven, P. H., Hong) 505–513 (Sc. Press. Beijing- Missouri Botanical Garden, St. Louis, 2008).
38. Jacques, F. M. B. & De Franceschi, D. Endocarps of Menispermaceae from Le Quesnoy outcrop (Sparnacian facies, Lower Eocene, Pas-de-Calais, Pas de Calais). Rev. Palaeobot. Palynol. 135, 61–70 (2005).
39. Cleal, C. J., Thomas, B. A., Batten, D. J. & Collinson, M. E. Mesozoic and Tertiary palaeobotany of Great Britain (Geological conservation review series, Peterborough, 2001).
40. Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. Trends, rhythms, and aberrations in global climate 64 Ma to present. Science 292, 686–693 (2001).
41. Zachos, J. C. et al. Extreme warming of mid-latitude coastal ocean during the Paleocene–Eocene Thermal Maximum: inferences from TEX86 and isotope data. Geology 34, 737–740 (2006).
42. Cavagnetto, C. La palynoflore d’un gisement d’ambre de l’Éocène basal du Bassin Parisien (Le Quesnoy, France). Palaeontogr. Abt. B 255, 147–171 (2000).
43. De Franceschi, D. & De Ploëg, G. Origine de l’ambre des faciès sparsiens (Éocène inférieur) du Bassin de Paris: le bois de l’ambre producteur. Geodiversitas 25, 633–647 (2003).
44. Jossang, J., Bel-Kassaoui, H., Jossang, A., Seuleiman, M. & Nel, A. Quesnoin, a novel pentacyclic ent-diterpene from 55 million years old Oise amber. Ann. Mo. Bot. Gard. 90, 179–199 (2003).
45. Bridson, D. M. A Revision of the family Vahliaceae. Kew Bull. 47, 737–740 (1992).
46. Rambaut, A., Suchard, M. A., Xie, D. & Drummond, A. J. Tracer v1. 6 (2014).
47. Ung, V., Dubus, G., Zaragauta-Bagils, R. & Vignes-Lebbe, R. Xp2r: introducing e-taxonomy. Bioinformatics 26, 703–704 (2010).
48. Bridson, D. M. A. Revision of the family Vahliaeae. Kew Bull. 30, 163–182 (1975).
49. Dahling, G. V. Systematics and evolution of Garrya. Contrib. Gray Herb. Harv. Univ. 209, 1–104 (1978).
50. Davenport, L. J. A monograph of Hydrolea (Hydrophyllaceae). Rhodora 169–208 (1988).
51. De La Bâthie, P. In: Flore du Cameroun et des Comores (ed. A. Aubréville et J-F. Leroy) 90–99 (Museum National d'Histoire Naturelle, Paris, 1973).
52. Gonzalez, F. A. & Rudall, P. J. Flower and fruit characters in the early-divergent lamid family Metteniusiaceae, with particular reference to the evolution of pseudomonomy. Am. J. Bot. 97, 191–206 (2010).
53. Howard, R. A. Study of the Icacinaceae IV. Considerations of the new world genera. Contrib. Gray Herb. Harvard Univ. 142, 3–60 (1942).
54. Morat, P. & Veillon, J. M. In: Flore de la Nouvelle-Calédonie et Dépendances 15 (ed. A. Aubréville et J-F. Leroy) 90–99 (1949).
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Author Contributions
C.D.R. and D.D.F. performed the morphological and phylogenetic analysis; C.D.R. and D.D.F. prepared the figures, D.D.F. drew Fig. 2; D.D.F. and T.H. designed the program; C.D.R. and D.D.F. prepared the manuscript.

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