

Two new rarely collected species of Annonaceae from the Peruvian Amazon

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Abstract

While preparing a taxonomic revision of the Neotropical genus *Klarobelia* Chatrou (Annonaceae), two species new to science – *Klarobelia icoja* S.Lara & Chatrou, **sp. nov.**, and *Malmea abscondita* Chatrou & Gees, **sp. nov.** – were discovered. Both species are known from only two collections, made in Amazonian Peru.

We clarify their generic placement and taxonomic identity based on a comparison of morphological characters with previously described species and on molecular phylogenetic analysis of four plastid markers.

The conservation status of both species is assessed following IUCN criteria, and line drawings and distribution map are provided.

Key words: *Klarobelia*, *Malmea*, Neotropics, new species, taxonomy

Introduction

For the past three decades, considerable efforts have been made to describe the species diversity of Neotropical Annonaceae, resulting in many monographs, revisions, and ad hoc species descriptions (e.g., Murray 1993; Johnson and Murray 1995; Chatrou and He 1999; Maas et al. 2003, 2007, 2015; Erkens et al. 2017; Pombo et al. 2017; Pirie et al. 2018a; Lopes and Mello-Silva 2019; Bazante et al. 2024). Despite these recent comprehensive taxonomic studies and a global decline in efforts to collect tree species in the Neotropics (ter Steege et al. 2016; Sosef et al. 2017; Luján et al. 2024), new species continue to be discovered.

Klarobelia is a small Neotropical genus of Annonaceae that was described following the breakup of the polyphyletic genus *Malmea* (Chatrou 1998). Both genera still contain undescribed species due to the incompleteness of collected material. After the taxonomic revision in 1998, which recognized ten species, three additional species of *Klarobelia* were described – either in the framework of large floristic projects (Chatrou and Pirie 2003; Jørgensen et al. 2014) or to support local conservation efforts (Chatrou and Pirie 2005). As most species of *Klarobelia* are restricted to small areas, new collecting efforts in previously unexplored regions may reveal hitherto unknown species. The discovery of *Klarobelia rocioae* (Maas et al. 2019) – known only from a small



Academic editor: Thomas L.P. Couvreur

Received: 9 May 2025

Accepted: 30 June 2025

Published: 26 August 2025

Citation: Chatrou LW, Lara-Guerrero S, Gees L, Fonseca LHM (2025) Two new rarely collected species of Annonaceae from the Peruvian Amazon. *PhytoKeys* 262: 1–15. <https://doi.org/10.3897/phytokeys.262.158372>

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area in the Peruvian department of Pasco and first collected in 2003 during a community-based forest monitoring program (Vásquez M. et al. 2005; Kowler et al. 2020) – is a good case in point. Species of *Klarobelia* occur in western lowland Amazonia, Pacific South America, and Central America. The genus is characterized by a combination of the following features: a sunken midvein on the upper side of the leaves, axillary inflorescences, androdioecy, closed flower development, apocarpous fruits with single-seeded monocarps, a raphe that is a sunken, sinuous, or spiral groove on the seed surface, soft seeds with the consistency of cardboard, a striate seed surface, and lamellate ruminations. Species delimitation in *Klarobelia* is mainly based on leaf dimensions; pedicel length in flowering and fruiting stages; dimensions and indument of sepals and petals; dimensions and indument of the fruiting receptacle, monocarps, and stipes; and the shape of the raphe.

Whereas the distribution of *Klarobelia* is essentially centered in the lowland forests surrounding the Andes, *Malmea* has a broader range extending into the Guianas, Central Amazonia, and Brazil's Atlantic Forest. Like *Klarobelia*, however, all *Malmea* species have narrow, non-overlapping distribution ranges. After the division of *Malmea* into four genera (Chatrou 1998), the six remaining species were collectively represented by approximately 70 specimens, with three species known from only one or two collections. No additional species have been described since that revision. *Malmea* is characterized by the following features: a sunken midvein on the upper side of the leaves, terminal inflorescences, bisexual flowers, open flower development, apocarpous fruits with single-seeded monocarps, a slightly raised raphe, hard seeds with the consistency of glass, a pitted seed surface, and spiniform ruminations. Species delimitation in *Malmea* is mainly based on leaf dimensions; pedicel length in flowering and fruiting stages; dimensions and indument of the fruiting receptacle, stipes, and monocarps; and the shape of the raphe.

Due to their highly localized distributions, many species in these genera have been rarely collected. Several species of *Klarobelia* and *Malmea* are known from no more than four collections. Such infrequently encountered species with small ranges pose significant challenges to plant diversity research in the Neotropics. They are underrepresented in herbarium collections and inventory plot data, making them difficult for taxonomists to describe and for ecologists to include in diversity assessments (Pitman et al. 1999; ter Steege et al. 2013). In this paper, we describe two species of Annonaceae from the Peruvian Amazon that illustrate the challenges of studying this plant group. Both are known from only two specimens, and flowers are unknown for both species. Three of the four collections have been known for over 30 years; the fourth, previously misidentified and filed under *Klarobelia*, was discovered while preparing an update of the genus revision (Chatrou 1998). We feel compelled to describe these species, as undescribed taxa remain a barrier to unlocking baseline biodiversity data. Costello et al. (2013) list several strategies to increase taxonomic productivity, from coordinated field sampling in underrepresented habitats to enhanced interoperability among publications, databases, and scholarly platforms. Although their list is extensive, we suggest that describing new species despite incomplete morphological knowledge may also accelerate taxonomic progress.

Despite the paucity of specimens and the absence of flowers, the collections clearly represent distinct, new species of *Klarobelia* and *Malmea*. Like most

genera in tribe Malmeeae, these genera are defined by unique combinations of morphological characters (as outlined above), each of which individually displays high levels of homoplasy within the family. As these genera may be difficult for non-specialists to recognize, we supplement the species descriptions with phylogenetic analyses to demonstrate their placement within the monophyletic genera *Klarobelia* and *Malmea*, respectively.

Methods

Species descriptions are based on herbarium specimens from the Missouri Botanical Garden (MO), Field Museum of Natural History (F), and the herbarium of Utrecht University (U), now incorporated into the collection of Naturalis Biodiversity Center, Leiden, the Netherlands. The descriptions include only measurements taken from dried specimens. Line drawings were produced by SLG by digitizing specimens using Procreate version 5.3.7 on an iPad (9th generation) and then elaborating with ink on paper.

The distribution map was generated using QGIS 3.34.11, based on specimen data from F, U, and MO. Departmental borders in Perú were sourced from the Instituto Geográfico Nacional, as published on Plataforma Nacional de Datos Abiertos (<https://www.datosabiertos.gob.pe/dataset/limites-departamentales>). Coordinates for the paratype of the new *Malmea* species were georeferenced using the Georeferencing Calculator (Wieczorek and Wieczorek 2021), based on Zermoglio et al. (2020). Type specimens are referenced by their herbarium barcode numbers. The GeoCAT geospatial conservation assessment tool (Bachman et al. 2011) was used for the preliminary conservation assessment of the described species. The area of occupancy (AOO) was calculated using a cell size of 2 km, in accordance with Criterion B of the IUCN Red List (IUCN Standards and Petitions Committee 2024). As both species are known from only two specimens, a polygon encompassing these data points could not be drawn, and therefore the extent of occurrence (EOO) would be calculated as 0. Following the recommendation of the IUCN Standards and Petitions Committee (2024), EOO was set equal to AOO to maintain consistency with the definition of AOO as an area within EOO.

Molecular phylogenetic analyses

For the phylogenetic analysis, a supermatrix was compiled comprising 40 species of tribe Malmeeae (Chatrou et al. 2018; Nge et al. 2024; Helmstetter et al. 2025) and three outgroup species from subfamilies Ambavioideae and Annonoideae. Sequence data for plastid markers (*rbcL*, *trnLF*, *matK*, *psbA-trnH*) were included, most of which have been published previously (Pirie et al. 2005, 2006; Chatrou et al. 2012; Thomas et al. 2015). The new *Malmea* species described in this paper was included in earlier phylogenetic analyses as '*Malmea* sp. 0197' (Pirie et al. 2006, 2007; Chatrou et al. 2012; Pirie et al. 2018a, 2018b). For the new *Klarobelia* species, we sequenced *rbcL* (GenBank accession PV861990), *trnLF* (PV861992), and *matK* (PV861991), following methods described by Pirie et al. (2006), using DNA extracted from Mathias & Taylor 5036.

The four alignments – *rbcL* (1,376 positions), *trnLF* (937 positions), *matK* (831 positions), and *psbA-trnH* (531 positions) – were analyzed separately using

Bayesian phylogenetic inference performed with MrBayes 3.2.7 (Ronquist et al. 2012), available on the CIPRES portal in San Diego, CA, USA (<http://www.phylo.org/portal2>; Miller et al. 2010). For all analyses, DNA substitution models and phylogenetic parameters (e.g., topology, branch lengths) were estimated simultaneously using a reversible jump Markov chain Monte Carlo sampler (model-jumping; Huelsenbeck et al. 2004), allowing among-site rate heterogeneity (Γ). The MCMC chain was initially run for 25 million generations, with four simultaneous runs and four chains per run, using default settings for the acceptance rates and the temperature of the heated chains. Sampling occurred every 1,000 generations. Convergence diagnostics were assessed using the *sump* command in MrBayes and by examining ESS values in Tracer.

After confirming the absence of incongruence among the phylogenetic trees derived from the separate marker analyses, 55 indel characters derived from the *trnLF* alignment were added and scored using the simple indel coding method (Simmons and Ochoterena 2000). A concatenated analysis of the five data partitions was then performed using the same settings as above, with the addition of the binary model (Iset coding = variable; Lewis 2001) for the indel characters. After convergence was reached, maximum clade credibility trees were generated using LogCombiner and TreeAnnotator in BEAST (Drummond and Rambaut 2007).

Maximum likelihood bootstrap analyses, implementing the rapid heuristic bootstrap method described by Stamatakis et al. (2008), were conducted using RAxML v.8.2.12 (Stamatakis 2014).

Results and discussion

Molecular phylogenetic analyses

Bayesian phylogenetic inference of the four-marker dataset resulted in convergence of the two runs on equal posterior probability distributions, with sample sizes sufficient as indicated by the ESS values. The best tree from the RAxML analysis, that is, the tree with the highest likelihood value (best LH = -11766.962161), is shown in Fig. 1. Due to reduced species sampling, some support values were lower than those in previously published analyses based on the same data (e.g., Pirie et al. 2006). The principal result is the re-establishment of the well-supported monophyly of *Klarobelia* and *Malmea*, which justifies the inclusion of the new species in these genera.

Morphological characters

Despite the absence of flowers in both species, the presence of leaves, fruits, and seeds is sufficient to assign the two new species to *Klarobelia* and *Malmea*, respectively, and to distinguish them from their congeners. For *Klarobelia*, diagnostic features include general leaf morphology, the overall 'gestalt' of the fruit, and in particular the soft seeds with a sinuous groove-like raphe and lamellate ruminations. For *Malmea*, the key identifying features are general leaf morphology; terminal inflorescences, which are rare in Neotropical Annonaceae with apocarpous fruits; and seeds with a pitted surface and spiniform ruminations. Details on the characters that distinguish these species from their most similar congeners are provided in the diagnoses below.

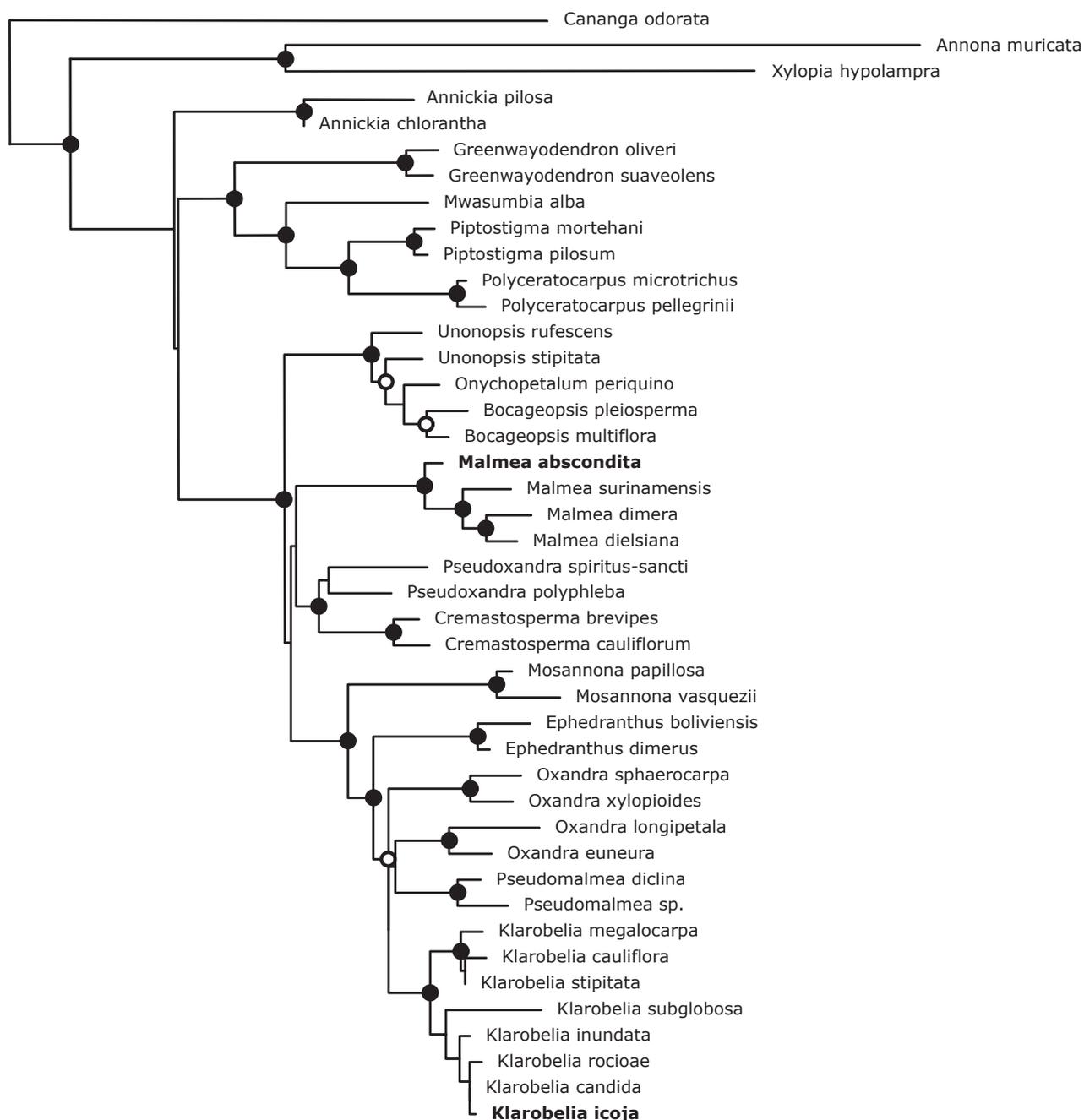


Figure 1. Phylogenetic position of *Malmea abscondita* and *Klarobelia icoja*. Best tree resulting from an RAxML analysis (best LH = -11766.962161) of a supermatrix of four plastid markers. Closed circles indicate Bayesian posterior probabilities ≥ 0.95 and RAxML bootstrap percentage $\geq 85\%$. Open circles indicate Bayesian posterior probabilities (≥ 0.95) only.

Taxonomic treatment

Klarobelia icoja S.Lara & Chatrou, sp. nov.

[urn:lsid:ipni.org:names:77368248-1](https://nomenclature.ipni.org/names/77368248-1)

Fig. 2

Type. PERU • [Dept. Ucayali: Province Padre Abad], vicinity of Aguaytía, [09°03'S, 075°30'W], 22 Jun 1961, *M.E. Mathias & D. Taylor 5390* (holotype: MO! [barcode MO-5509445]; isotype: F! [barcode V0205843F]).

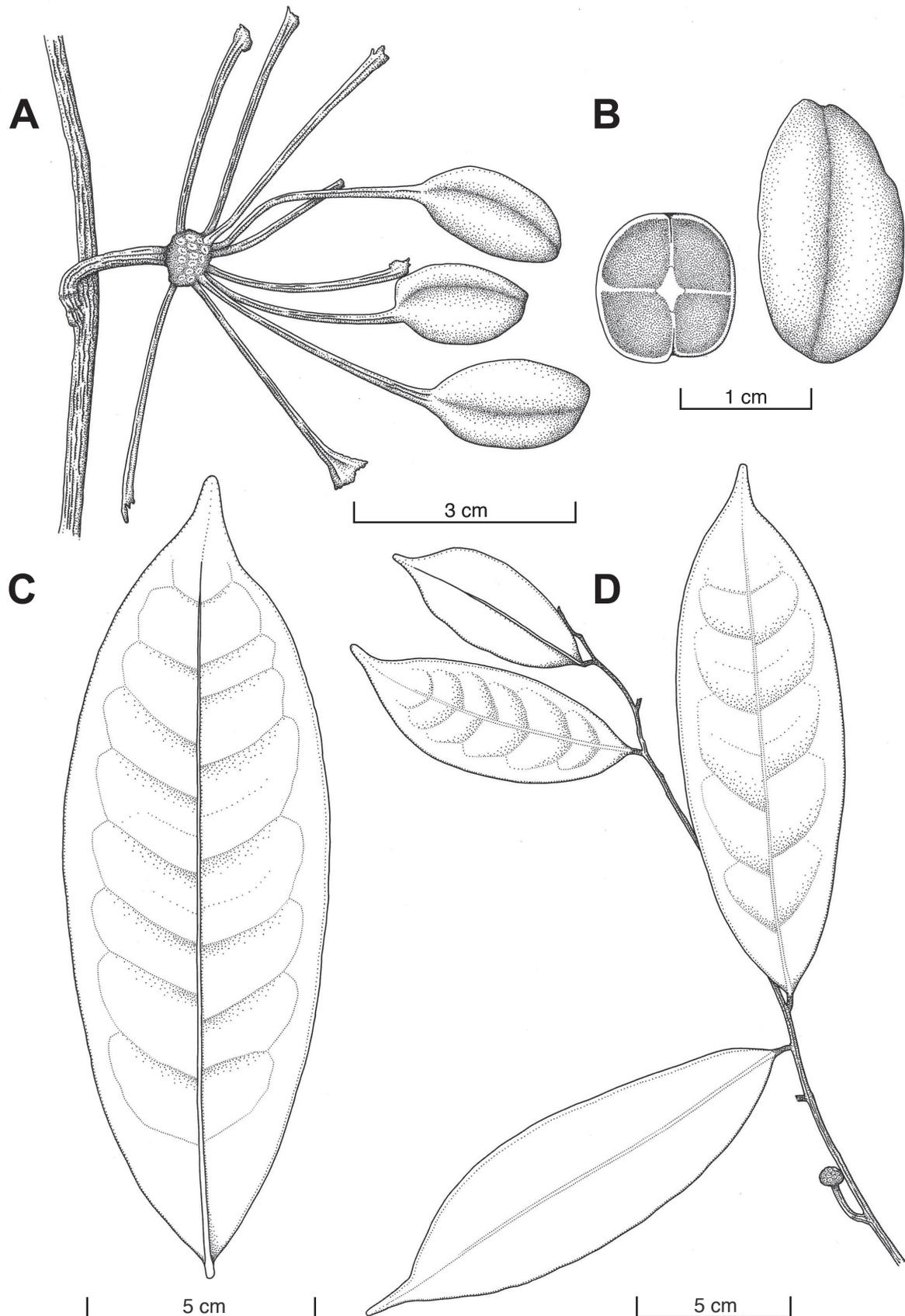


Figure 2. *Klarobelia icoja* S.Lara & Chatrou. **A.** Habit with fruit; **B.** Monocarp (right) and cross section of seed (left), showing the ruminations in four lamellate parts; **C;** Leaf; **D.** Habit with fruiting receptacle. (**A, C, D.** *Mathias & Taylor 5390*; **B.** *Mathias & Taylor 5036*).

Diagnosis. *Klarobelia icoja* resembles *K. lucida* in the size of the monocarps and the thin fruit wall and *K. pumila* in the leaves, but it can be distinguished from *K. lucida* by the leaves with a length up to 19 cm (vs. 13 cm), narrower leaves with a length-width ratio of 3.3–3.5 (vs. 1.8–2.8), acute base (vs. obtuse to acute), and shorter pedicels of 12–17 mm long (vs. 17–68 mm long). *K. icoja* can be distinguished from *K. pumila* by the monocarps, which are longer (19–22 mm vs. 9–15 mm) and wider (10–11 mm vs. 6–8 mm), and by the longer stipes (28–37 mm vs. 12–20 mm).

Description. Tree up to 4 m tall. Young twigs and developing leaves sparsely covered with yellowish-brown, appressed hairs. Petiole 4–8 mm long, 1.0–1.5 mm wide, verrucose, glabrous. Lamina 11.3–19.0 cm long, 3.5–5.7 cm wide, length-width ratio 3.3–3.5, chartaceous, slightly bullate, elliptic, base acute, apex gradually acuminate, light olive green above and dark olive green below, glabrous above and below, primary vein impressed (to flat) above, 6–9 secondary veins per side, distance between secondary veins 11–22 mm, angles with primary vein 60–75°, loop-forming at right to obtuse angles, distance between loops and leaf margin 4–7 mm. Inflorescences ramiflorous, on the leafless part of the twig, single-flowered. Short shoot 2–3 mm long, 2.0–2.5 mm in diam. when fruiting. Bracts not observed. Pedicels 12–17 mm long, 1.5–2.0 mm in diam. (in fruit). Fruit of ca. 10 monocarps (scars suggest up to ca. 25 monocarps), orange-red in vivo, reddish brown to black in sicco, ellipsoid, 19–22 mm long, 10–11 mm in diam., glabrous, verrucose, raphe visible through fruit wall, stipes 28–37 mm long, 1 mm in diam., fruiting receptacle subglobose, 7–9 mm in diam., 4–6 mm high. Seed ellipsoid, 21 mm long, 10 mm in diam., brownish-orange, raphe a sinuous groove, ruminations in four lamellate parts.

Local names. Peru: Jicoja or Icoja, based on the holotype label.

Distribution and ecology. The species is known from the northern part of Ucayali, in the vicinity of Aguaytía, Perú (Fig. 3; only the locality of the type specimen is presented here, given the absence of latitude-longitude data of the second specimen). It grows in forests; information about its elevation range is unknown. The label of Mathias & Taylor 5036 mentions that the fruits are orange-red. Most monocarps in both collections have been removed while the stipe has remained on the fruit. In Annonaceae, monocarps that detach from fruit do so with the stipe attached to the monocarp, leaving scars of the stipe on the fruiting receptacle. The detachment of the monocarp only in this species is indicative of zoochory.

Preliminary conservation status. The label of the type specimen does not mention latitude and longitude. We took these from an earlier collection by the same collector on the same day (Mathias & Taylor 5368, *Miconia alternidomatia* Michelang.). To date, *Klarobelia icoja* is known only from two collections made over 50 years ago in two consecutive years in the vicinity of Aguaytía, with an AOO and EOO of 4 km². It falls under the IUCN category of data deficient (DD). A more detailed analysis of the population must be done to correctly assess its conservation status. Given the general geographical pattern of *Klarobelia*, characterized by small allopatric distributions, this is likely to be accomplished by more thorough inventories of the known area of occurrence.

Etymology. The specific epithet refers to the indigenous name of the species. “Icoja,” “hicoja,” or “jicoja,” however, is not unique to this species and refers to Annonaceae in general, as it has been reported for Peruvian species in the

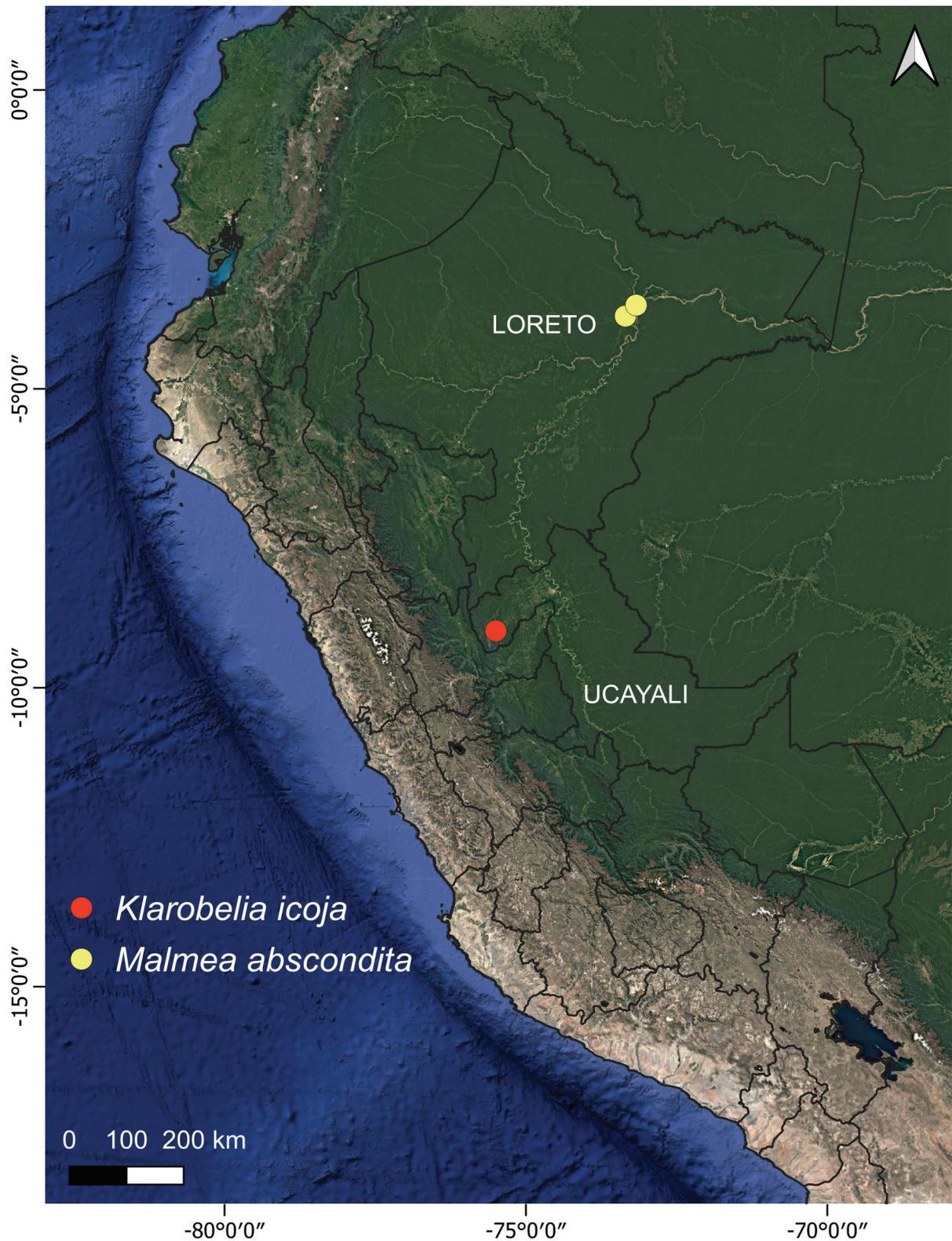


Figure 3. Distribution map of *Klarobelia icoja* S.Lara & Chatrou and *Malmea abscondita* Chatrou & Gees.

genera *Anaxagorea* (Maas and Westra 1984), *Bocageopsis* (Maas et al. 2007), *Crematosperma* (Pirie et al. 2018a), *Fusaea* (Chatrou and He 1999), *Guatteria* (Maas et al. 2015), and *Unonopsis* (Maas et al. 2007). The name *icoja* (pronunciation in International Phonetic Alphabet: i'koxa) is used by the indigenous

Quechua people (Sanz-Biset et al. 2009). This is suggesting the name may stem from Quechua or Runa simi, the indigenous language family that originated in central Peru, even though Sanz-Biset et al. (2009) indicate that indigenous Quechua plant names have been mixed with Spanish to varying degrees.

Additional specimen examined. PERU • [Ucayali: Province Padre Abad], vicinity of Aguaytía, high ground in forest southeast of house, don Diogenes del Aguila, east of Aguaytía, between Pucallpa road and Aguaytía river, 29 Jun 1960, M.E. Mathias & D. Taylor 5036 (MO!).

***Malmea abscondita* Chatrou & Gees, sp. nov.**

urn:lsid:ipni.org:names:77368249-1

Fig. 4

Type. PERU • Dept. Loreto: Río Nanay, San Pablo de Cuyana, Estación Biológica Miguel Alejandro, 03°47'S, 73°21'W, 9 Nov 1994, L.W. Chatrou, P.J.M. Maas, H. Rainer & F. Ayala 8 (holotype: USM! [specimen number USM-135298]; isotype: U! [barcode U-0089935, U-0089936]).

Diagnosis. *Malmea abscondita* is distinct from congeneric species by a combination of the following characters: narrowly elliptic leaves, few secondary veins, fewer monocarps, and longer stipes of the monocarps. The new species combines characters mostly found in *Malmea guianensis* R.E.Fr., *M. manausensis* Maas & J.M.S. Miralha, and *M. surinamensis* Chatrou. It differs from *Malmea guianensis* by the hairy inflorescences (vs. glabrous), the smaller number of monocarps (6–13 vs. 20), and shorter stipes (22–30 mm vs. 37–49 mm); from *M. manausensis* by the lower number of secondary veins (8–9 vs. 12–14 per side of the leaf), the longer and more slender stipes (22–30 mm long, 1 mm in diam. vs. 18–21 mm long, 2.5 mm in diam.); and from *M. surinamensis* by the lower number of secondary veins (8–9 vs. 10–13 per side of the leaf), the longer pedicels (43–57 mm vs. 40 mm), and the smaller number of monocarps (6–13 vs. 15–20).

Description. Small tree, 2.5–4 m tall, 2 cm in diam. Young twigs and lower side of petiole and basal part of midrib sparsely to rather densely covered with brown, appressed (to erecto-patent) hairs ca. 0.5 mm long (simply hairs hereafter). Petiole 4–6 mm long, 1.5–2 mm in diam., verrucose to rugulose. Lamina 19–30 cm long, 5–8 cm wide, length-width ratio (2.9–)3.3–4.2, chartaceous, narrowly elliptic or narrowly obovate, base cuneate to obtuse, apex gradually acuminate, olive green and shiny above, olive green (slightly darker than upper side) below, glabrous above, (sub-)glabrous below, secondary veins 8–9 per side, irregularly spaced with distance between secondary veins 14–35 mm, angles with primary vein 55–75°, loop-forming at right to obtuse angles, distance between loops and leaf margin 5–10 mm. Flowers unknown. Infructescences on leafy twigs, terminal or leaf-opposed, maximally 1 flower/fruit scar and 1 actual fruit on rhipidium, peduncles and pedicels sparsely to rather densely covered with short, yellowish-brown, appressed to erecto-patent hairs, bract densely covered with similar hairs. Peduncles 10 mm long, 1–2 mm in diam. Pedicels 43–57 mm long, 1 mm in diam. basally to 2.5 mm apically, sympodial rachis 3 mm long. Articulation 1 mm above axil of lower bract. Bracts 2.5 mm long, 2 mm wide, apex obtuse to rounded, semi-amplexant, lower bract near base of pedicel, upper bract halfway the pedicel. Fruit of 6–13 monocarps, blackish brown, ellipsoid, 13–16 mm long,

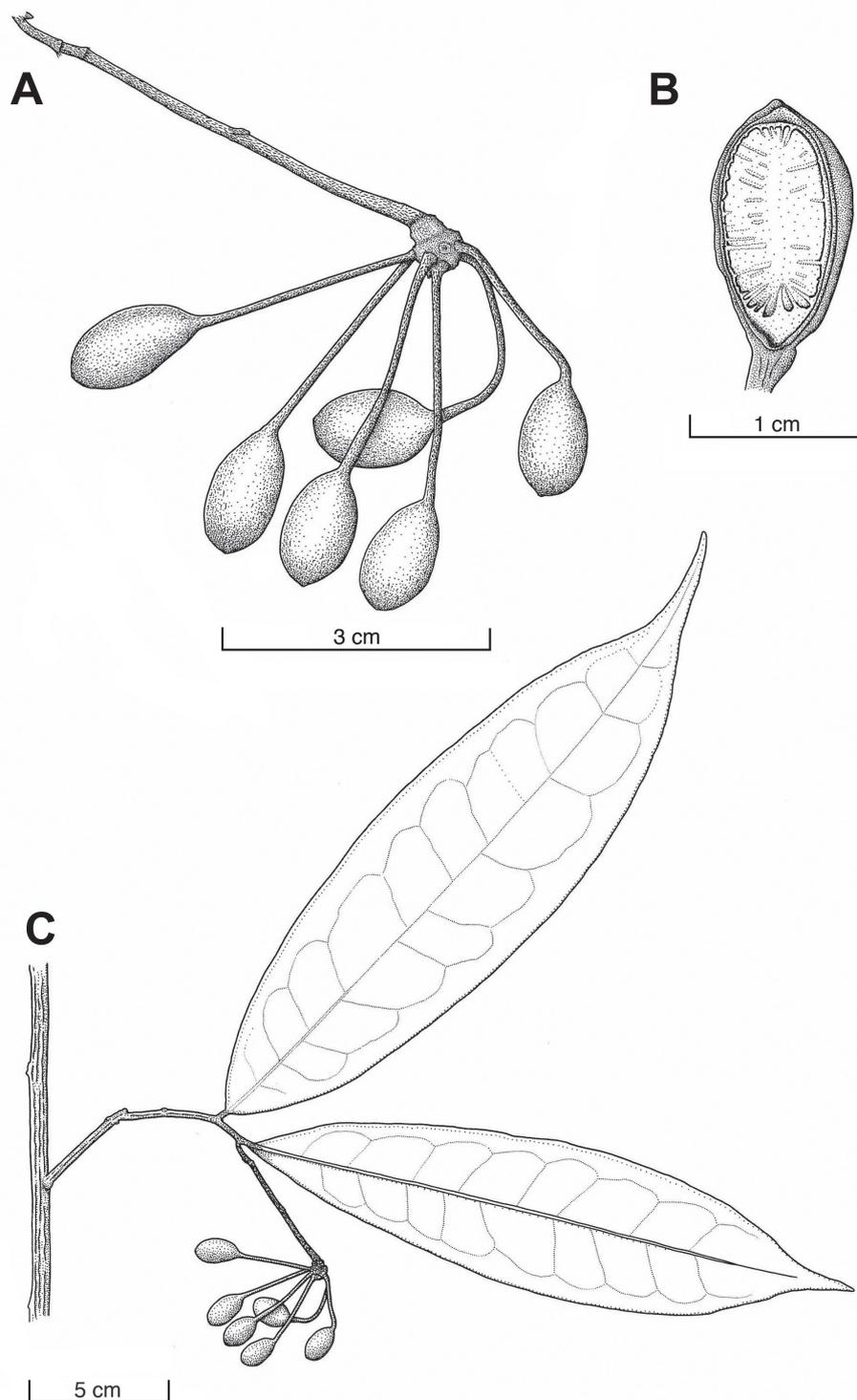


Figure 4. *Malmea abscondita* Chatrou & Gees. **A.** Fruit; **B.** Longitudinal section of monocarp, showing spiniform ruminations; **C.** Habit with fruit. (A–C. Chatrou et al. 8).

8–11 mm in diam., sparsely hairy except for densely hairy apex, verrucose; stipes blackish brown, 22–30 mm long, 1 mm in diam., sparsely to rather densely hairy; fruiting receptacle (sub)globose, 6–8 in diam., 6–9 mm high, (rather) densely hairy. Seeds ellipsoid, 12–15 mm long, 7–10 mm in diam., brown, surface pitted, raphe a slightly elevated rib, ruminations spiniform.

Distribution and habitat. The species is known from two localities near Río Nanay, west to northwest of Iquitos, in the Peruvian department of Loreto (Fig. 3). Both the occurrence in upland rainforest and periodically inundated rainforest have been reported.

Preliminary conservation status. To date, *Malmea abscondita* is known only from two collections made in the vicinity of Río Nanay, with an AOO and EOO of 8 km². The collection label of Rimachi 479 does not include latitude and longitude, and we estimated the collection locality to be just north of the mouth of Río Nanay, near the *carretera Nanay – Mazan*. The species falls under the IUCN category of data deficient (DD). A more detailed analysis of the population must be done to correctly assess its conservation status. Given the general geographical pattern of *Malmea*, characterized by small allopatric distributions, this is likely to be accomplished by more thorough inventories of the known area of occurrence.

Etymology. The specific epithet refers to the concealed, largely unnoticed existence of this species in the Amazonian forests of northern Peru, having been collected twice only in the past 52 years.

Additional specimen examined. PERU • [Loreto], Maynas, Trocha de la Astoria hasta Mazan, near mouth of Río Nanay, 2 Aug 1973, M. Rimachi Y. 479 (MO!).

Acknowledgments

The authors thank the curators of the Missouri Botanical Garden (MO), the Field Museum of Natural History (F), and the Naturalis Biodiversity Center (U) for the loan of specimens. The director and curators of the herbarium of Universidad Nacional Mayor de San Marcos (USM) are acknowledged for providing information on the type specimen of *Malmea abscondita*. We thank Roy Erkens and an anonymous reviewer for valuable comments that improved the manuscript. Dr. Diego Bogarín is thanked for his suggestions on the line drawings.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

This work was funded by Ghent University grant BOF.STG.2020.0017 to LWC.

Author contributions

Conceptualization: LWC. Data curation: LWC. Formal analysis: LHMF, LWC. Funding acquisition: LWC. Investigation: SLG, LG. Methodology: SLG, LWC. Supervision: LWC. Visualization: SLG. Writing – original draft: SLG, LWC. Writing – review and editing: LG, LHMF.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

- Bachman S, Moat J, Hill AW, de la Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: Geospatial conservation assessment tool. *ZooKeys* 150: 117–126. <https://doi.org/10.3897/zookeys.150.2109>
- Bazante ML, Maas PJM, Siqueira GS, Lima JG, Udulutsch RG, Barbosa MRdV (2024) *Duguetia rolimii* (Annonaceae), a new large tree species from the Atlantic Forest of Espírito Santo, Brazil. *Acta Botanica Brasílica* 38: e20230231. <https://doi.org/10.1590/1677-941x-abb-2023-0231>
- Chatrou LW (1998) Changing Genera. Systematic Studies in Neotropical and West African Annonaceae. PhD dissertation, Utrecht University, Utrecht, 224 pp.
- Chatrou LW, He P (1999) Studies in Annonaceae XXXIII. A revision of *Fusaea* (Baill.) Saff. *Brittonia* 52: 181–203. <https://doi.org/10.2307/2666627>
- Chatrou LW, Pirie MD (2003) Two new species of Annonaceae from Bolivia. *Revista de la Sociedad Boliviana de Botánica* 4: 25–30.
- Chatrou LW, Pirie MD (2005) Three new rarely collected and endangered species of Annonaceae from Venezuela. *Blumea* 50: 33–40. <https://doi.org/10.3767/000651905X623265>
- Chatrou LW, Pirie MD, Erkens RHJ, Couvreur TLP, Neubig KM, Abbott JR, Mols JB, Maas JW, Saunders RMK, Chase MW (2012) A new subfamilial and tribal classification of the pantropical flowering plant family Annonaceae informed by molecular phylogenetics. *Botanical Journal of the Linnean Society* 169: 5–40. <https://doi.org/10.1111/j.1095-8339.2012.01235.x>
- Chatrou LW, Turner IM, Klitgaard BB, Maas PJM, Utteridge TMA (2018) A linear sequence to facilitate curation of herbarium specimens of Annonaceae. *Kew Bulletin* 73: 39. <https://doi.org/10.1007/s12225-018-9764-3>
- Costello MJ, May RM, Stork NE (2013) Can we name Earth's species before they go extinct? *Science* 339: 413–416. <https://doi.org/10.1126/science.1230318>
- Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 214. <https://doi.org/10.1186/1471-2148-7-214>
- Erkens R, Oosterhof J, Westra LYT, Maas PJM (2017) Revisions of *Ruizodendron* and *Pseudephedranthus* (Annonaceae) including a new species and an overview of most up-to-date revisions of Neotropical Annonaceae genera. *PhytoKeys* 86: 75–96. <https://doi.org/10.3897/phytokeys.86.13773>
- Helmstetter AJ, Ezedin Z, Lírio EJd, Oliveira SMd, Chatrou LW, Erkens RHJ, Larridon I, Leempoel K, Maurin O, Roy S, Zuntini AR, Baker WJ, Couvreur TLP, Forest F, Sauquet H (2025) Towards a phylogenomic classification of Magnoliidae. *American Journal of Botany* 112: e16451. <https://doi.org/10.1002/ajb2.16451>
- Huelsenbeck JP, Larget B, Alfaro ME (2004) Bayesian phylogenetic model selection using reversible jump Markov Chain Monte Carlo. *Molecular Biology and Evolution* 21: 1123–1133. <https://doi.org/10.1093/molbev/msh123>

- IUCN Standards and Petitions Committee (2024) Guidelines for Using the IUCN Red List Categories and Criteria: Version 16. Gland, Switzerland: International Union for Conservation of Nature.
- Johnson DM, Murray NA (1995) Synopsis of the tribe Bocageae (Annonaceae), with revisions of *Cardiopetalum*, *Froesiodendron*, *Trigynaea*, *Bocagea*, and *Hornschuchia*. *Brittonia* 47: 248–319. <https://doi.org/10.2307/2807118>
- Jørgensen PM, Nee MH, Beck SG (2014) Catálogo de las plantas vasculares de Bolivia. Missouri Botanical Garden, St. Louis.
- Kowler LF, Kumar Pratihast A, Pérez Ojeda del Arco A, Larson AM, Braun C, Herold M (2020) Aiming for sustainability and scalability: Community engagement in forest payment schemes. *Forests* 11: 444. <https://doi.org/10.3390/f11040444>
- Lewis PO (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology* 50: 913–925. <https://doi.org/10.1080/106351501753462876>
- Lopes JC, Mello-Silva R (2019) Revision and morphological phylogeny of *Ephedranthus*, a Neotropical genus of Annonaceae. *Annals of the Missouri Botanical Garden* 104: 244–261. <https://doi.org/10.3417/2019305>
- Luján M, Lemos RM, Lucas E, Michelangeli FA, Prance GT, Pennington TD, Rzedowski J, Santamaría-Aguilar D, Serpell E, Sothers CA, Zuntini AR (2024) Trials and tribulations of Neotropical plant taxonomy: Pace of tree species description. *Plants, People, Planet* 6: 515–527. <https://doi.org/10.1002/ppp3.10469>
- Maas PJM, Westra LYT (1984) Studies in Annonaceae. II. A monograph of the genus *Anaxagorea* A.St.Hil., part 1. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 105: 73–134.
- Maas PJM, Westra LYT, Chatrou LW (2003) *Duguetia*. *Flora Neotropica Monograph* 88. The New York Botanical Garden, New York.
- Maas PJM, Westra LYT, Vermeer M (2007) Revision of the Neotropical genera *Bocageopsis*, *Onychopetalum*, and *Unonopsis* (Annonaceae). *Blumea* 52: 413–554. <https://doi.org/10.3767/000651907X608909>
- Maas PJM, Westra LYT, Arias Guerrero S, Lobão AQ, Scharf U, Zamora NA, Erkens RHJ (2015) Confronting a morphological nightmare: Revision of the Neotropical genus *Guatteria* (Annonaceae). *Blumea* 60: 1–219. <https://doi.org/10.3767/000651915X690341>
- Maas PJM, Westra LYT, Chatrou LW, Verspagen N, Rainer H, Zamora NA, Erkens RHJ (2019) Twelve new and exciting Annonaceae from the Neotropics. *PhytoKeys* 126: 25–69. <https://doi.org/10.3897/phytokeys.126.33913>
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*. IEEE, New Orleans, 1–8. <https://doi.org/10.1109/GCE.2010.5676129>
- Murray NA (1993) Revision of *Cymbopetalum* and *Porcelia*. *Systematic Botany Monographs* 40: 1–121. <https://doi.org/10.2307/25027830>
- Nge FJ, Chaowasku T, Damthongdee A, Wiya C, Soulé VRC, Rodrigues-Vaz C, Bruy D, Mariac C, Chatrou LW, Chen J, Choo LM, Dagallier L-PMJ, Erkens RHJ, Johnson DM, Leeratiwong C, Lobão AQ, Lopes JC, Martínez-Velarde MF, Munzinger J, Murray NA, Neo WL, Rakotoarinivo M, Ortiz-Rodriguez AE, Sonké B, Thomas DC, Wieringa JJ, Couvreur TLP (2024) Complete genus-level phylogenomics and new subtribal classification of the pantropical plant family Annonaceae. *Taxon* 73: 1341–1369. <https://doi.org/10.1002/tax.13260>

- Pirie MD, Chatrou LW, Erkens RHJ, Maas JW, van der Niet T, Mols JB, Richardson JE (2005) Phylogeny reconstruction and molecular dating in four Neotropical genera of Annonaceae: the effect of taxon sampling in age estimation. In: Bakker FT, Chatrou LW, Gravendeel B, Pelser PB (Eds) Plant species-level systematics: new perspectives on pattern and process. A.R.G. Gantner Verlag, Ruggell, Liechtenstein, 149–174.
- Pirie MD, Chatrou LW, Mols JB, Erkens RHJ, Oosterhof J (2006) 'Andean-centred' genera in the short-branch clade of Annonaceae: Testing biogeographical hypotheses using phylogeny reconstruction and molecular dating. *Journal of Biogeography* 33: 31–46. <https://doi.org/10.1111/j.1365-2699.2005.01388.x>
- Pirie MD, Balcazar Vargas MP, Botermans M, Bakker FT, Chatrou LW (2007) Ancient paralogy in the cpDNA *trnL-F* region in Annonaceae: Implications for plant molecular systematics. *American Journal of Botany* 94: 1003–1016. <https://doi.org/10.3732/ajb.94.6.1003>
- Pirie MD, Chatrou LW, Maas PJM (2018a) A taxonomic revision of the Neotropical genus *Crematosperma* (Annonaceae), including five new species. *PhytoKeys* 112: 1–141. <https://doi.org/10.3897/phytokeys.112.24897.figure15>
- Pirie MD, Maas PJM, Wilschut RA, Melchers-Sharrott H, Chatrou LW (2018b) Parallel diversifications of *Crematosperma* and *Mosannona* (Annonaceae), tropical rainforest trees tracking Neogene upheaval of South America. *Royal Society Open Science* 5: 171561. <https://doi.org/10.1098/rsos.171561>
- Pitman NCA, Terborgh J, Silman MR, Nuñez VP (1999) Tree species distributions in an upper Amazonian forest. *Ecology* 80: 2651–2661. [https://doi.org/10.1890/0012-9658\(1999\)080\[2651:TSDIAU\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2651:TSDIAU]2.0.CO;2)
- Pombo MM, Johnson DM, Chatrou LW, Zartman CE (2017) *Xylopia annoniflora* (Annonaceae): A new species from central Amazonia. *Phytotaxa* 317: 130–136. <https://doi.org/10.11646/phytotaxa.317.2.5>
- Ronquist F, Teslenko M, Van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Sanz-Biset J, Campos-de-la-Cruz J, Epiquién-Rivera MA, Cañigueral S (2009) A first survey on the medicinal plants of the Chazuta valley (Peruvian Amazon). *Journal of Ethnopharmacology* 122: 333–362. <https://doi.org/10.1016/j.jep.2008.12.009>
- Simmons MP, Ochoterena H (2000) Gaps as characters in sequence-based phylogenetic analysis. *Systematic Biology* 49: 369–381. <https://doi.org/10.1093/sysbio/49.2.369>
- Sosef MSM, Dauby G, Blach-Overgaard A, van der Burgt X, Catarino L, Damen T, Deblauwe V, Dessein S, Dransfield J, Droissart V, Duarte MC, Engledow H, Fadeur G, Figueira R, Gereau RE, Hardy OJ, Harris DJ, de Heij J, Janssens S, Klomberg Y, Ley AC, Mackinder BA, Meerts P, van de Poel JL, Sonké B, Stévant T, Stoffelen P, Svenning J-C, Sepulchre P, Zaiss R, Wieringa JJ, Couvreur TLP (2017) Exploring the floristic diversity of tropical Africa. *BMC Biology* 15: 15. <https://doi.org/10.1186/s12915-017-0356-8>
- Stamatakis A (2014) RAXML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics (Oxford, England)* 30: 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAXML web servers. *Systematic Biology* 57: 758–771. <https://doi.org/10.1080/10635150802429642>
- ter Steege H, Pitman NCA, Sabatier D, Baraloto C, Salomão RP, Guevara JE, Phillips OL, Castilho CV, Magnusson WE, Molino J-F, Monteagudo A, Núñez Vargas P, Montero JC, Feldpausch TR, Coronado ENH, Killeen TJ, Mostacedo B, Vasquez R, Assis RL,

- Terborgh J, Wittmann F, Andrade A, Laurance WF, Laurance SGW, Marimon BS, Marimon B-H, Guimarães Vieira IC, Amaral IL, Brienens R, Castellanos H, Cárdenas López D, Duivenvoorden JF, Mogollón HF, Matos FDA, Dávila N, García-Villacorta R, Stevenson Diaz PR, Costa F, Emilio T, Levis C, Schiatti J, Souza P, Alonso A, Dallmeier F, Montoya AJD, Fernandez Piedade MT, Araujo-Murakami A, Arroyo L, Gribel R, Fine PVA, Peres CA, Toledo M, Aymard CGA, Baker TR, Cerón C, Engel J, Henkel TW, Maas PJM, Petronelli P, Stropp J, Zartman CE, Daly D, Neill D, Silveira M, Paredes MR, Chave J, Lima Filho DA, Jørgensen PM, Fuentes A, Schöngart J, Cornejo Valverde F, Di Fiore A, Jimenez EM, Peñuela Mora MC, Phillips JF, Rivas G, van Andel TR, von Hildebrand P, Hoffman B, Zent EL, Malhi Y, Prieto A, Rudas A, Ruschell AR, Silva N, Vos V, Zent S, Oliveira AA, Schutz AC, Gonzales T, Trindade Nascimento M, Ramirez-Angulo H, Sierra R, Tirado M, Umaña Medina MN, van der Heijden G, Vela CIA, Vilanova Torre E, Vriesendorp C, Wang O, Young KR, Baider C, Balslev H, Ferreira C, Mesones I, Torres-Lezama A, Urrego Giraldo LE, Zagt R, Alexiades MN, Hernandez L, Huamantupa-Chuquimaco I, Milliken W, Palacios Cuenca W, Pauletto D, Valderrama Sandoval E, Valenzuela Gamarra L, Dexter KG, Feeley K, Lopez-Gonzalez G, Silman MR (2013) Hyperdominance in the Amazonian tree flora. *Science* 342: 1243092. <https://doi.org/10.1126/science.1243092>
- ter Steege H, Vaessen RW, Cárdenas-López D, Sabatier D, Antonelli A, de Oliveira SM, Pitman NCA, Jørgensen PM, Salomão RP (2016) The discovery of the Amazonian tree flora with an updated checklist of all known tree taxa. *Scientific Reports* 6: 29549. <https://doi.org/10.1038/srep29549>
- Thomas DC, Chatrou LW, Stull GW, Johnson DM, Harris DJ, Thongpaiboj U, Saunders RMK (2015) The historical origins of palaeotropical intercontinental disjunctions in the pantropical flowering plant family Annonaceae. *Perspectives in Plant Ecology, Evolution and Systematics* 17: 1–16. <https://doi.org/10.1016/j.ppees.2014.11.001>
- Vásquez MR, Rojas GR, Monteagudo MA, Meza VK, Van der Werff H, Ortiz-Gentry R, Catchpole D (2005) Flora vascular de la selva central del Perú: Una aproximación de la composición florística de tres áreas naturales protegidas. *Arnaldoa* 12: 112–125.
- Wieczorek C, Wieczorek J (2021) Georeferencing Calculator. <http://georeferencing.org/georefcalculator/gc.html>
- Zermoglio PF, Chapman AD, Wieczorek JR, Luna MC, Bloom DA (2020) Georeferencing Quick Reference Guide. GBIF Secretariat, Copenhagen. <https://doi.org/10.35035/e09p-h128>