RESEARCH ARTICLE

Edaphic isolation as a driver of divergence in a new Amazonian species of *Diclinanona* (Annonaceae)

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Abstract For many years a mysterious collection made during an expedition to Venezuelan Amazonia in 1992 was in a folder at the former Utrecht Herbarium as "unidentified Annonaceae". Several different genera were suggested for identification but since flowers were lacking it was unclear where this taxon should be placed. One of the suggestions based on seed morphology was the little-known Annonaceae genus *Diclinanona.* However, the texture and venation of the leaves were very different from the other three species of that genus. In this study, based on a phylogenomic analysis it is shown that this taxon indeed forms a monophyletic clade with the other three species of *Diclinanona*, to which it is sister. It is therefore described as a new species, *Diclinanona coriacea.* Principal component analysis and linear discriminant analysis reveal that soil variables are particularly important for the spatial separation of the species, supporting the hypothesis that soils are important drivers of speciation and ecological differentiation for this group in the Amazon region.

Keywords climatic variables; ecology; herbarium specimens; phylogenetic analysis; soil; species discovery

■ INTRODUCTION

Diclinanona Diels is a genus of three species in the tribe Annoneae Endl. in the family Annonaceae Juss. (Nge & al., 2024) mainly occurring in tropical, broadleaf rain forests in the Amazon region (Erkens & al., 2014, 2023). *Diclinanona calycina* (Diels) R.E.Fr. and *D. tessmannii* Diels (the type of the genus name) have a wide distribution, occurring in Amazonian Colombia, Venezuela, Brazil and Peru (Fig. 1). *Diclinanona matogrossensis* Maas has a much narrower distribution and is only known from the Brazilian state of Mato Grosso (Fig. 1). All species occur in non-inundated, terra firme forest with *D. calycina* having one collection from campinarana forest, on clayey to white sandy soil, *D. tessmannii* rarely occurring in periodically inundated (tahuampa) forest, mostly on white sandy or sometimes clayey soil, and *D. matogrossensis* with one collection from creek forest (Erkens & al., 2014).

The study of Erkens & al. (2014) also included a taxonomic revision (in the Electronic Supplement) with a description of the three species. However, for many years a collection made during the Tratado de Cooperación Amazónica (TCA) expedition of 1992 to Venezuelan Amazonia by *Basil Stergios & al.* (*15538*) was in a folder in the former Utrecht Herbarium (U; Erkens & Baas, 2008) as "unidentified Annonaceae". This specimen was collected in the flooded swamp forests of the blackwater Pasimoní River (B. Stergios, pers. comm.), a tributary of the Casiquiare River. Van Setten & Koek-Noorman (1992) analysed a similar specimen in the context of their work on the fruits and seeds of Annonaceae. With pencil Van Setten wrote on the cover of the herbarium specimen that the seeds looked like the ones of several other genera, one of which was *Diclinanona*. However, over the years when studying the specimens we noticed that the leaves (texture, venation, etc.) were very different from the other three species of that genus (Erkens & al., 2014). Unfortunately, flowers were lacking and it was unclear whether this taxon should be described as a new species or a new genus.

The morphological affinities of *Diclinanona* to other Annonaceae have been a source of discussion (Fries, 1959; Walker, 1971; Van Heusden, 1992; Van Setten & Koek-Noorman, 1992; Erkens & al., 2014). Based on morphology, it was suggested to be affiliated with several other Neotropical genera. The raceme- or panicle-like inflorescence structures, for instance, resemble those in *Unonopsis* R.E.Fr. (Malmeoideae Chatrou & al.) and *Xylopia* L. (Annonoideae Raf.). Unisexual and bisexual flowers (androdioecism), as in *Diclinanona*, can also be found in *Klarobelia* Chatrou and

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other genera in tribe Malmeeae Chatrou & R.M.K.Saunders (Chatrou, 1998; Lopes & al., 2018). For suggested affinities to non-Neotropical genera we refer to Van Heusden (1992). For an in-depth discussion on past changes in classification of *Diclinanona* we refer to Erkens & al. (2014).

To pinpoint the phylogenetic position of *Diclinanona*, Erkens & al. (2014) undertook an analysis using plastid markers. The genus was reconstructed as part of subtribe Annoninae Hutch. emend. Couvreur with *Annona* L., *Asimina* Adans., *Disepalum* Hook.f. and *Goniothalamus* (Blume) Hook.f. & Thomson. Subtribe Anonidiinae Couvreur (with genera *Neostenanthera* Exell and *Anonidium* Engl. & Diels) was recovered as sister lineage to Annoninae, together making up tribe Annoneae Endl. This was in line with early results of Richardson & al. (2004). Couvreur & al. (2019) corroborated this result based on phylogenomic data, although not all genera of the tribe were sampled. In the latest, complete genus-level phylogenomic tree of Annonaceae (Nge & al., 2024), *Diclinanona* was again placed in Annoninae (with slightly altered relationships between genera) and subtribe Anonidiinae was once more the earliest-branching lineage in Annoneae. Since the placement of *Diclinanona* as a whole has stayed nearly constant over the past decade, the discussion on its phylogenetic position in Erkens & al. (2014) is still valid.

Finally, the species of *Diclinanona* are not well known in terms of their biology. In fact, they show six out of seven shortfalls as described by Hortal & al. (2015) (Wallacean, Prestonian, Darwinian, Raunkiæran, Hutchinsonian, Eltonian) stemming from the low number of specimens collected per

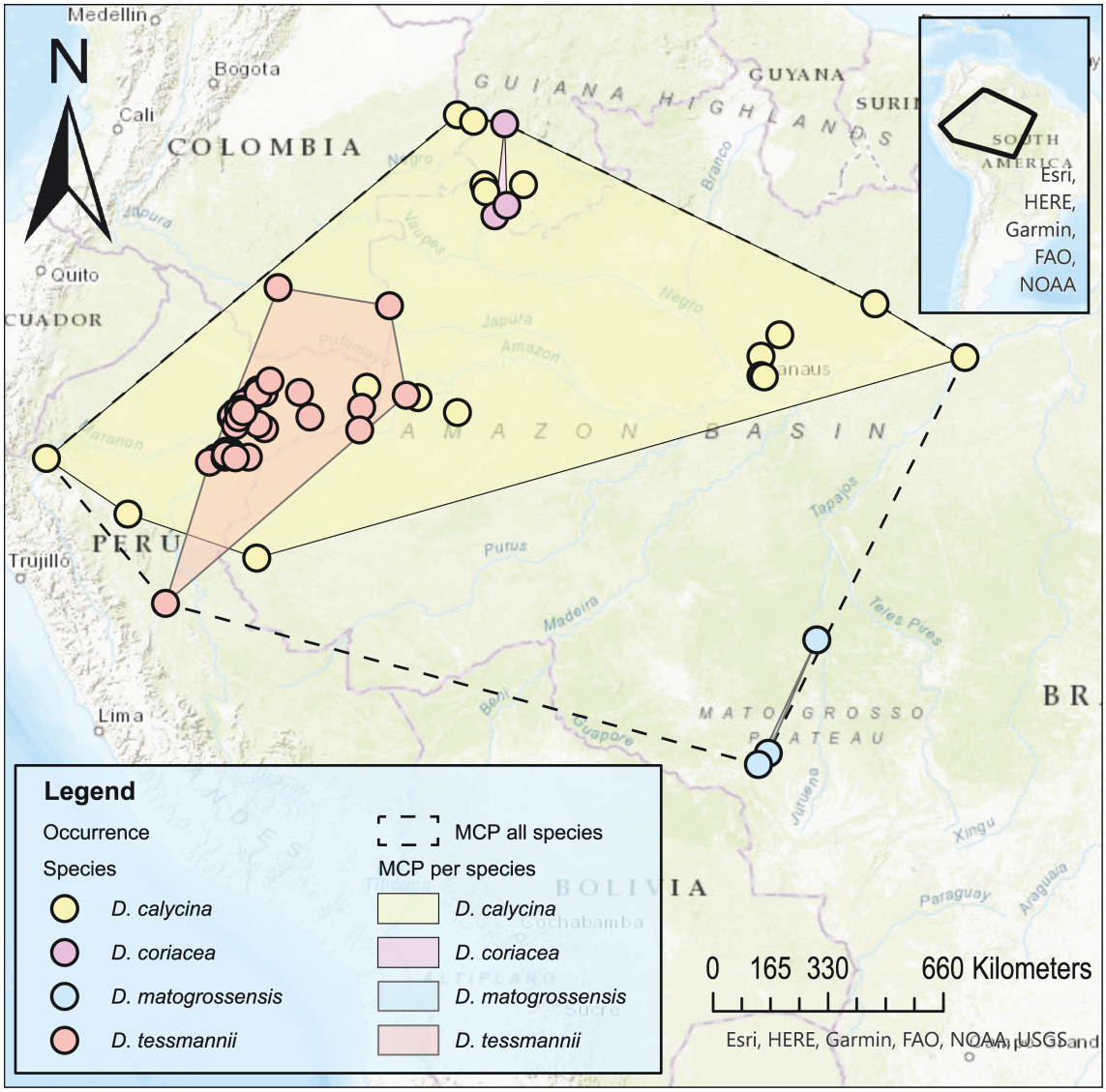

Fig. 1. Distributional and range map of the four species of *Diclinanona*. Individual dots indicate the location of sampled trees. For each species the minimum convex polygon (MCP) is shown as an indication for the potential distributional range of the species (*D. calycina*: 1,634,116 km^2, *D. coriacea*: 4073 km^2, *D. matogrossensis*: 2274 km^2, and *D. tessmannii*: 261,739 km^2). The dashed line indicates the MCP for all four *Diclinanona* species together (area of 2,867,003 km^2). Inset shows the location of the MCP in South America.

species (120 for *D. tessmannii*, c. 60 for *D. calycina*, 5 for *D. matogrossensis*, and only 3 for the newly described taxon). To overcome some of these shortfalls and inform, for example, hypotheses on the abiotic tolerances of the species (Hutchinsonian shortfall), collaborative efforts can be employed (e.g., The Brazil Flora Group, 2022), sampling increased (e.g., Cardoso & al., 2011), and/or linear transformation techniques used. The latter can, for instance, provide insights into the environmental similarity and dissimilarity between species based on macro-environmental variables (such as soil, temperature, precipitation etc. characteristics).

In this study, we present a molecular phylogenomic analysis of the "unidentified Annonaceae" to determine its phylogenetic position. We conclude that the taxon is a yet undescribed species of *Diclinanona* and present a key to the four species of the genus. We also employ linear transformation techniques (principal component analysis [PCA], linear discriminant analysis [LDA]) to show that macro-environmental variables (precipitation, temperature, soil) explain the split between species. With the description of this species nearly 25 years after its first collection, the time lag between the oldest collection and this description is well above the median and average time for new species described from Venezuela (Luján & al., 2024).

■ MATERIALS AND METHODS

Phylogenomic analyses. — To assess the phylogenetic placement of the new taxon, we included 25 accessions: for the first time all three *Diclinanona* species and the new taxon, along with representatives of all other genera of Annoneae as well as three outgroups (*Desmos* Lour., *Monodora* Dunal., *Xylopia*) from other tribes of Annonoideae (Nge & al., 2024). Specimen voucher details can be found in Appendix 1.

We utilised a high-throughput sequencing approach with a custom Annonaceae baiting kit targeted towards the family to recover up to 469 nuclear loci (Couvreur & al., 2019). DNA extraction (Soulé & al., 2023) and sequencing processing protocols (Soulé & al., 2024) follow those from our previous studies on Annonaceae (Couvreur & al., 2019; Brée & al., 2020). In brief, raw sequences were demultiplexed, trimmed for quality and sorted into paired reads per sample. The HybPiper pipeline v.1.2 (Johnson & al., 2016) processed paired reads and retrieved cleaned alignments. Prior to alignment, supercontig outputs were extracted from the HybPiper pipeline as well as excluded loci flagged as potential paralogs. All flagged paralogous loci were conservatively excluded from downstream analyses (Shee & al., 2020; Kuhnhäuser & al., 2021), as paralogous loci from recent duplication events may not be detected from manual filtering. Sequences with poor coverage across targeted loci were filtered out (following Shee & al., 2020) and noise was reduced by excluding underrepresented, incomplete, and unevenly distributed sequences. Per sample, the overall coverage score was determined by combining these three metrics. Sequences with an overall score < 0.5 were excluded from subsequent alignment (available from: https://doi.org/10.6084/m9.figshare.32144290) and phylogenetic analyses. The paired fastq sequences for individuals included in this study are available in Genbank SRA under Bioproject numbers PRJNA1265870 (https://www.ncbi.nlm.nih.gov/bioproject/1265870), PRJNA541395 (https://www.ncbi.nlm.nih.gov/bioproject/541395), PRJNA508895 (https://www.ncbi.nlm.nih.gov/bioproject/508895).

Phylogenetic analyses were conducted using both concatenated and multi-species coalescent (MSC) approaches. In the concatenated approach, all loci were concatenated into a single data matrix, and analysed using a maximum likelihood (ML) phylogenetic analysis with RAxML v.8.2.9 (Stamatakis, 2014). The GTR + GAMMA substitution model (Abadi & al., 2019) without the proportion of invariant sites to avoid over-parameterisation was selected (Yang, 2006). For coalescent phylogenetic analyses weighted ASTRAL v.1 was used (wASTRAL; Zhang & Mirarab, 2022), shown to improve species-tree support by reduction of noise from low support and long terminal branches. The used hybrid function command in wASTRAL accounts for node support and branch lengths (astral-hybrid.exe -x 100 -n 10 -o tree -i genetrees 2>LOG_hyb_file). The input gene trees for wASTRAL were constructed individually with RAxML v.8.2.9 using the GTR + GAMMA substitution model (Abadi & al., 2019). Nodes with very low bootstrap support (<10) were collapsed for all gene trees using Newick utilities v.1.6 (Junier & Zdobnov, 2010) to further improve the accuracy of MSC inference in wASTRAL (Zhang & al., 2017). The raw sequence filtering, HybPiper pipeline steps, and RAxML analyses were completed on a local high-computing cluster in Montpellier, France.

To visualise putative differences between the outcomes of the two phylogenetic approaches, a co-phylogenetic plot was made using the co-phylo object class in the Phytools package (v.2.4.4), using R v.4.4.2 (R Core Team, 2023).

Linear transformation analyses. — Species occurrences were gathered from the specimens cited below. Based on these coordinates, environmental data was sourced from CHELSA v.2.1 (Bioclimatic variables; Karger & al., 2017) and soil grids (soil variables; Poggio & al., 2021; Turek & al., 2023) available from ISRIC - WDC Soils (2023). As for two of the four species of *Diclinanona* not enough occurrences are known, species distribution modelling was not feasible (Rivers & al., 2011; Verspagen & Erkens, 2023). Therefore, we performed two linear transformation techniques (PCA, LDA) to investigate environmental similarity and dissimilarity between species. PCA was first done with 19 bioclimatic and 14 soil variables (Poggio & al., 2021; Turek & al., 2023), then with a subset of temperature (bio1, mean annual temperature; bio4, temperature seasonality), precipitation (bio13, precipitation in the wettest month; bio14, precipitation in the driest month) and four soil variables (cation exchange capacity, nitrogen content as well as sand and clay proportions of the fine earth fraction), and finally only with all soil variables. These analyses were performed in R v.4.4.2 (R Core Team, 2023).

Taxonomic study and Red List assessment. — In this study, specimens from MO, PORT, U, US, VEN and WIS were consulted. Based on the georeferenced occurrences of these specimens and those from Erkens & al. (2014) the distribution map was created with ArcGIS PRO v.3.4.2 (ESRI, Redlands, California, U.S.A.) using the World Topographic Map (ESRI, 2025) as a base layer. Minimum convex polygons (MCPs) were drawn using the Minimum Bounding Geometry geoprocessing tool. Surface areas of the MCPs were calculated using the Calculate Geometry tool.

The IUCN Red List threat assessment was done using the IUCN Red List Categories and Criteria (IUCN, 2012), using the Red List Guidelines (IUCN Standards and Petitions Committee, 2024). The extent of occurrence (EOO) and area of occupancy (AOO) were calculated using the sRedList platform v.1.4 (Cazalis & al., 2024) based on the georeferenced coordinates of the specimens. The map of protected areas was taken from UNEP-WCMC & IUCN (2025), and the spatial data on habitat threats from Global Forest Watch (Curtis & al., 2018; Hansen & al., 2013) and the subsets 1.1 and 1.10 from the SPECTRE dataset (Branco & al., 2025).

■ RESULTS

Phylogenomic analyses. — For the phylogenomic analyses, 415 loci were included in the final dataset across the 25 samples, with 54 loci removed: 50 loci were flagged as paralogous and another 4 loci had poor coverage and recovery across samples.

The coalescent approach is in complete agreement with the concatenated approach. They both show that the focal taxon forms a maximally supported monophyletic clade with *Diclinanona matogrossensis*, *D. calycina* and *D. tessmannii* (Fig. 2). *D. coriacea* sp. nov. is sister to the other three species. *Diclinanona* is sister to *Annona*, and this clade is sister to *Disepalum* and *Asimina* (Fig. 2). The *Diclinanona* clade is subtended by a long branch, but the branch lengths within the clade are rather short.

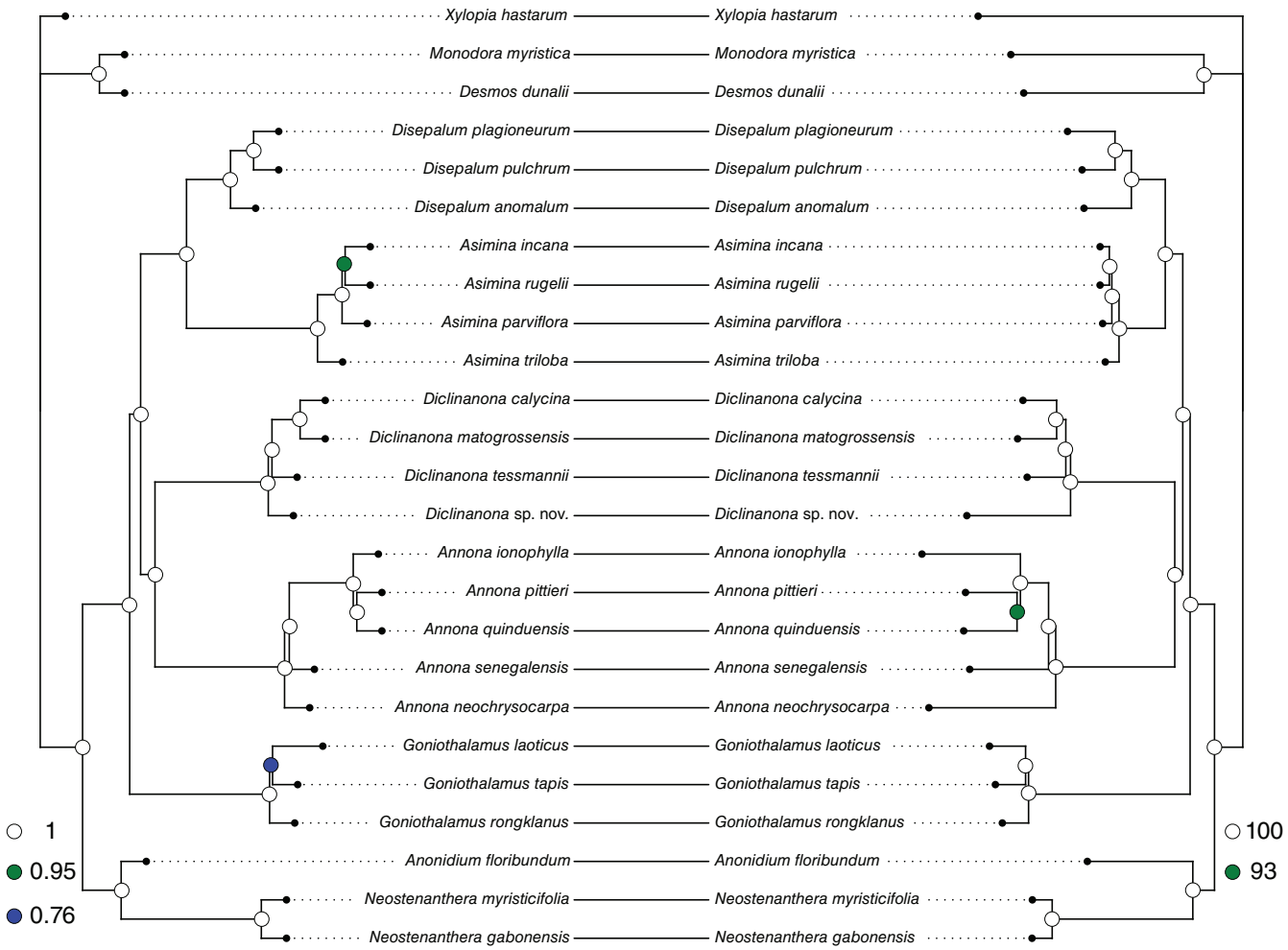

Fig. 2. Co-phylogenetic plot for the two hypotheses of relationships within tribe Annoneae (Annonaceae) estimated with coalescent (wASTRAL, left) and concatenated (RAxML, right) approaches. Pies at the nodes show support values: local posterior probability (LPP) values are included for the wASTRAL topology; bootstrap values are indicated for the RAxML tree.

Linear transformation analyses. — The PCA with all bioclimatic and soil variables included shows 34.4% explained variance across the first axis (PC1) and 21.8% across the second axis (PC2; 56.2% explained variation in total; Fig. 3A). The most important variable for PC1 was bio12 mean annual precipitation and for PC2 bio16 precipitation in wettest quarter. Both along the first axis (annual precipitation and temperature variables) and second axis (soil nutrients and physical properties as well as climate seasonality variables) *Diclinanona tessmannii*, *D. matogrossensis* and *D. coriacea* are separated, from each other, while *D. calycina* overlaps with *D. tessmannii* and *D. coriacea* but not with *D. matogrossensis*. PCA with a subset of temperature, precipitation, and soil variables shows 34.5% and 21.6% across PC1 and PC2 (Fig. 3B; 56.1% explained variation in total) and the same separation as described for all. PCA with only soil variables

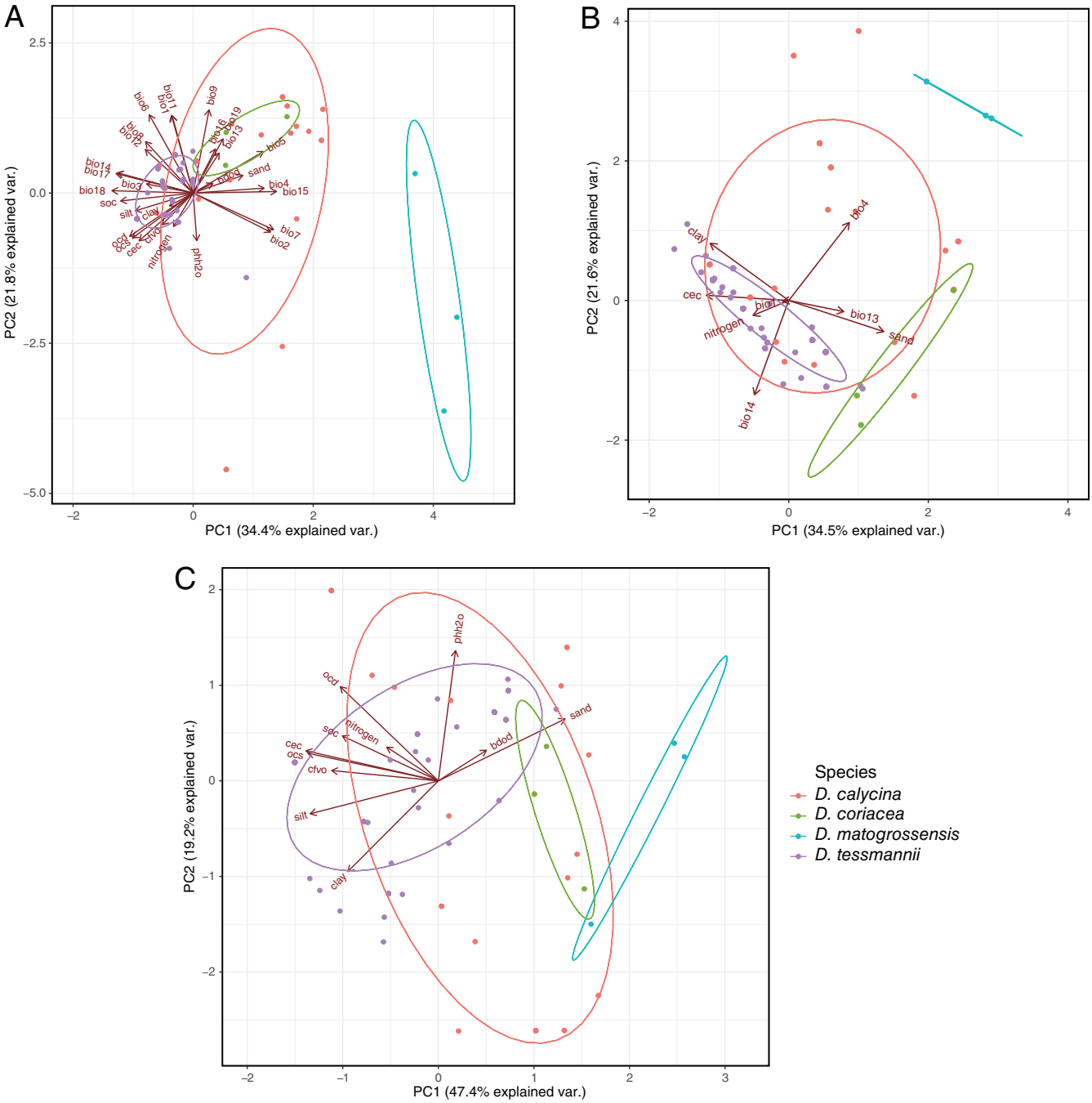

Fig 3. Principal component analysis for four species of *Diclinanona* based on (**A**) 19 bioclimatic and 14 soil variables; (**B**) a subset of temperature (bio1, mean annual temperature; bio4, temperature seasonality), precipitation (bio13, precipitation in the wettest month; bio14, precipitation in the driest month) and four soil variables (cation exchange capacity, nitrogen content as well as sand and clay proportions of the fine earth fraction); and (**C**) all 14 soil variables. Bioclimatic variables from CHELSA v.2.1 (Karger & al., 2017) and soil variables from ISRIC (2023).

(Fig. 3C) shows a higher 47.4% and 19.2% for first and second axis respectively (66.6% explained variation in total). PC1 (soil nutrients and coarse fraction of physical soil structure) strongly separates *D. tessmannii*, *D. matogrossensis* and *D. coriacea* from each other, while *D. calycina* partially overlaps with all three. PC2 (fine physical soil structure: clay proportion and soil pH) does not have a clear impact on the separation of species.

The LDA (Figs. 4A,B) with the reduced set of variables shows that LD1 (88.2%) classifies *Diclinanona tessmannii*, *D. calycina*, and *D. coriacea* separate from *D. matogrossensis*. This classification is strongly driven by precipitation seasonality (bio14, precipitation in the driest month) and soil physical properties (clay proportion in fine earth fraction). *Diclinanona tessmannii* has a very tight distribution (Fig. 4A), indicating low within-group variability. LD2

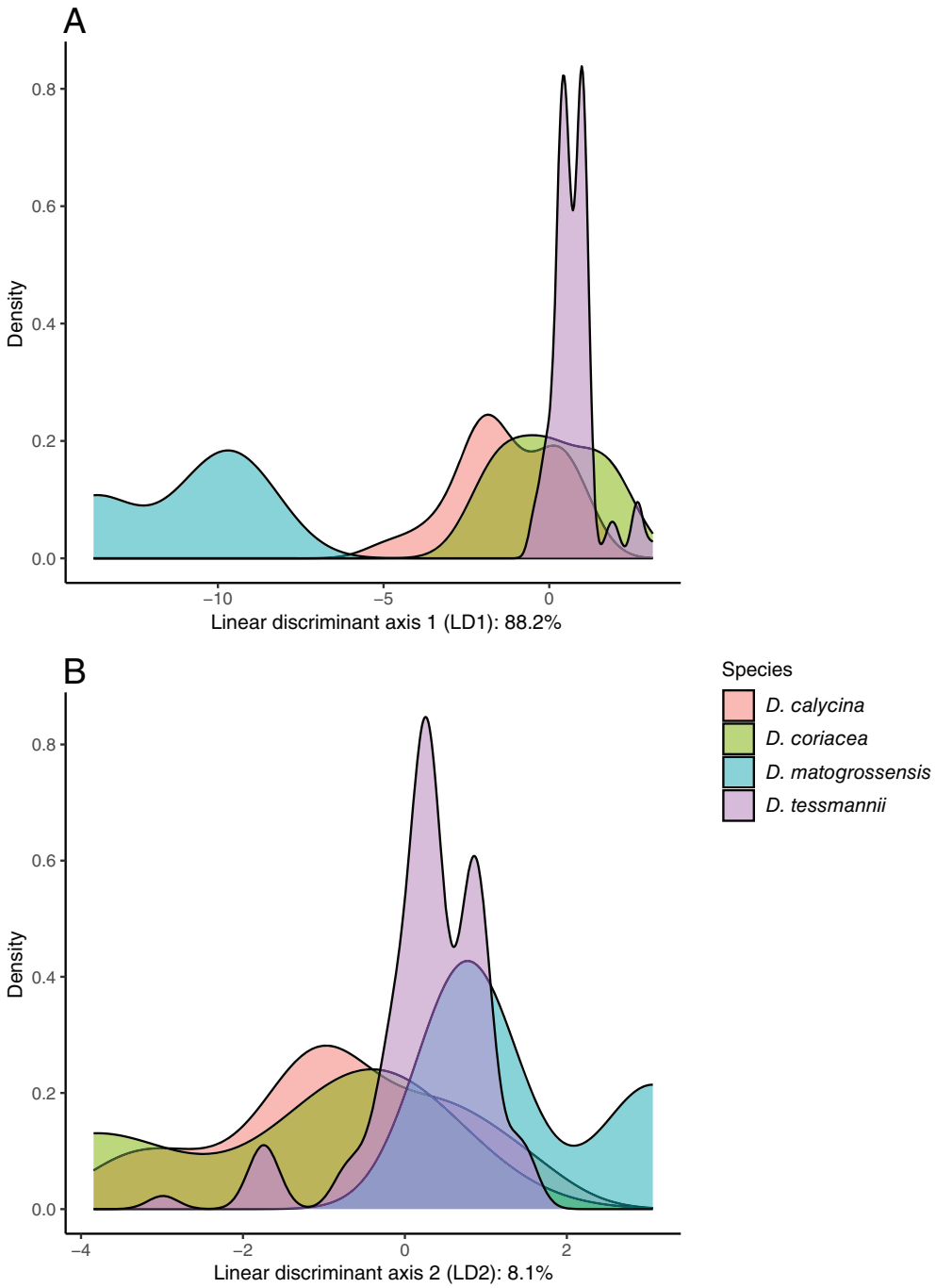

Fig. 4. Linear discriminant analysis for four species of *Diclinanona* based on a subset of temperature (bio1, mean annual temperature; bio4, temperature seasonality), precipitation (bio13, precipitation in the wettest month; bio14, precipitation in the driest month) and four soil variables (cation exchange capacity, nitrogen content as well as sand and clay proportions of the fine earth fraction). Bioclimatic variables from CHELSA v.2.1 (Karger & al., 2017) and soil variables from ISRIC (2023). **A**, First discriminant axis (LD1); **B**, Second discriminant axis (LD2).

(8.1%) separates *D. matogrossensis, D. tessmannii* and somewhat *D. calycina* from *D. coriacea*. This corresponds to soil physical properties (sand and clay proportion in fine earth fraction) along with soil nitrogen content.

Together PCA and LDA suggest that precipitation, temperature and physical soil properties (sand, silt & clay proportion) are the most important factors differentiating the distributions of the species.

Taxonomic study. — The taxonomic work concluded that the taxon under study matches the three recognized species of *Diclinanona* in its gross morphology and the molecular phylogenetic analysis definitively confirmed the phylogenetic affiliation of this species to the already described species of *Diclinanona*. Therefore, it is described as new to science here. As a result, the generic circumscription was updated and presented below accompanied by a key to the four species of *Diclinanona*. The IUCN threat assessment yields a status of Endangered.

Basil Stergios (pers. comm.) indicated that according to his field book there were nine specimens of *B. Stergios & al. 15538*, and that these were destined for distribution to seven institutions: MO, NY, PORT, TFAV, U, VEN, and WIS. However, he could only find confirmation of a shipment to MO (B. Stergios, pers. comm.). We studied specimens from MO, PORT, U, VEN and WIS but could not trace the specimens in NY and TVAF. However, we did locate specimens in US.

■ DISCUSSION

Phylogenetic placement. — This study builds on previously published phylogenetic and phylogenomic work on *Diclinanona* (Erkens & al., 2014; Couvreur & al., 2019; Nge & al., 2024). As before, *Diclinanona* is placed in subtribe Annoninae. It is sister to *Annona*, and together these two genera are sister to a clade consisting of *Disepalum* and *Asimina*. *Goniothalamus* is sister to these four genera. For a more elaborate discussion on this phylogenetic placement of *Diclinanona*, we refer to Erkens & al. (2014).

The new species described here is placed sister to the three accepted species of *Diclinanona*. Because of the long branch subtending the *Diclinanona* clade and the relatively short branch lengths within the clade we favour the description of a new species instead of a new genus, even though morphologically the new species is quite different from the other three species of *Diclinanona*. In terms of the seed type, the transversely striate to smooth seed surface resembles *D. tessmannii* and *D. matogrossensis* most (Fig. 5). In *D. coriacea*, *D. tessmannii* and *D. matogrossensis* the seeds are covered with a powdery, brownish, scurfy layer which is absent in *D. calycina*. In a phylogenetic context, this might mean that the smooth seed type with a scurfy layer is plesiomorphic for *Diclinanona* (Fig. 2). For more discussion on the morphology of the genus, we again refer to Erkens & al. (2014).

Ecology. — In the case of *Diclinanona* the linear transformation analyses show that macro-environmental variables (precipitation, temperature, soil) explain the split between species, in line with a regional-scale analysis showing the importance of cumulative water-deficit and temperature seasonality (Ter Steege & al., 2023). Especially the soil variable "soil organic carbon" here strongly separates *D. tessmannii*, *D. matogrossensis* and *D. coriacea* (Fig. 3C), although the differentiation from *D. calycina* is less strong. Some studies indeed found an interaction between forest biomass and, amongst other factors, soil organic carbon (e.g., Laurance & al., 1999), although other studies did not (Baraloto & al., 2011). It is known that soil biota can strongly influence the temporal and spatial availability of nutrients such as carbon (Bardgett & Van der Putten, 2014). However, although at the regional level soil parameters might influence tree species-richness (Ter Steege & al., 2006, 2023), this relationship is not always found at the local level (Clinebell & al., 1995). Nevertheless, the here identified factors underline the importance that soils might play in species differentiation, especially in the Amazon region (e.g., Fine & al., 2004, 2014, 2013; Tuomisto, 2006; Bacon & al., 2021). The coriaceous leaves of this species lend further support for the idea that adaptation to a specific soil type is at play. Whitesand soils are characterised by high acidity, extreme nutrient-scarcity and low organic-matter content (Adeney & al., 2016) and are characteristically inhabited by species with sclerophyllous leaves (Medina & al., 1990). Adaptation to different soils has been hypothesised to play a role in other Annonaceae as well (Erkens & al., 2007), although definite support for this idea is lacking so far. Further research is needed to substantiate the importance of soil properties (including microbes and symbionts) in this case.

Phylogeny, diversification and spatial distribution. — Interestingly, no phylogenomic conflict was noted in *Diclinanona* between concatenated and coalescent topologies in contrast to other clades in Annonaceae and other plant groups (Nge & al., 2024; Jin & al., 2025; Lin & al., 2025; Xie & al., 2025). The reason for this is unknown.

Since *Diclinanona coriacea* is the sister lineage to the other three species of *Diclinanona* (Fig. 2) and it has a non-overlapping distribution with *D. tessmannii* and *D. matogrossensis* (Fig. 2), it might be that the ancestors of these species split from each other by allopatric speciation, perhaps by adaptation to different soils or differences in precipitation (Figs. 3, 4). *Diclinanona calycina* currently has a widespread distribution. It might also have originated allopatrically and then increased its range. It can be hypothesised based on this wide distribution and overlap with the other three species in the PCA and LDA (Figs. 3, 4) that *D. calycina* today has a wider environmental tolerance. Although this scenario is highly speculative at this moment, the four species of *Diclinanona* seem to present an interesting and practical case for studying the causes for speciation and ecological differentiation in the Amazon region given the morphological variation in the clade and its geographic

distribution with some species ranges overlapping while others being distinctly separated.

■ TAXONOMY

Diclinanona Diels in Notizbl. Bot. Gart. Berlin-Dahlem 10: 174. 1927 – Type: *Diclinanona tessmannii* Diels.

Description. – Tree or shrub; young twigs covered with appressed, simple hairs, becoming glabrous with age. *Leaves* distichous, simple, entire, long-petiolate, lamina medium-sized, elliptic to obovate or narrowly so, leaf index varying from 1.8 to 3.8, chartaceous, rarely coriaceous, not verruculose, base acute to slightly attenuate, apex acuminate, rarely rounded or emarginate to acute, upper side sparsely covered with simple, appressed or erect hairs to glabrous, lower side sparsely covered with appressed hairs, or densely covered with erect hairs, venation brochidodromous, primary vein flat to impressed above, secondary veins distinct, 7–18 on either side of primary vein, impressed above to slightly raised, tertiary venation reticulate to percurrent, impressed above, rarely flat to raised. *Inflorescences* in axils of leaves or on leafless branchlets, 1–10-flowered, raceme- or panicle-like with the axis ending in a terminal flower, comparatively lax in *D. calycina*, (often) more or less umbellately clustered in *D. tessmannii*, and reduced to 1–3 flowers in

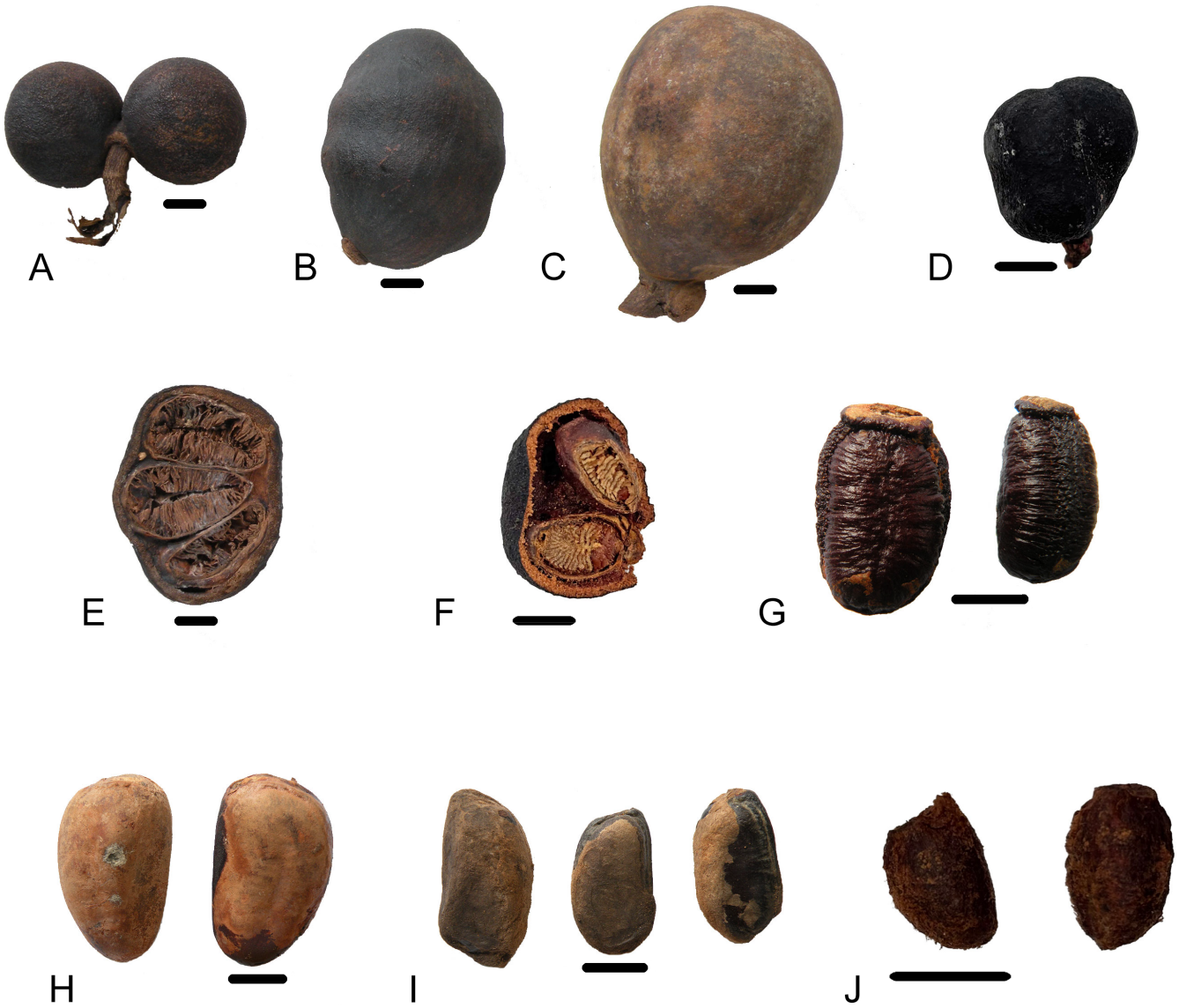

Fig. 5. Fruits and seeds of *Diclinanona*. **A**, Fruits/monocarps of *D. calycina* (*C.A. Cid Ferreira & al. 7925*, U); **B**, Fruit/monocarp of *D. tessmannii* (*D.C. Daly & al. 5083*, U); **C**, Fruit/monocarp of *D. matogrossensis* (*B. Maguire & al. 56530*, U); **D**, Fruit/monocarp of *D. coriacea* (*B. Stergios & al. 15538*, U); **E**, Monocarp of *D. tessmannii* in longitudinal section (*J. Aronson & P.E. Berry 674*, U); **F**, Monocarp of *D. coriacea* in longitudinal section (*B. Stergios & al. 15538*, U); **G**, Seeds of *D. calycina* (*P.E. Berry 2194*, U); **H**, Seeds of *D. tessmannii* (*J. Aronson 684*, U); **I**, Seeds of *D. matogrossensis* (*B. Maguire & al. 56530*, U); **J**, Seeds of *D. coriacea* (*B. Stergios & al. 15538*, U). — Scale bars (A–J) = 10 mm. Figure updated from Erkens & al. (2014).

D. matogrossensis, infra-axillary in *D. coriacea*; pedicels 3–40 mm long; articulated at the base, bract 1 below the articulation, small, <10 mm long, present at flowering time or soon falling off, or (possibly) lacking, rarely foliaceous. Indument of flower parts composed of simple hairs. Flower buds: ovoid to rhombic or narrowly so. Flowers actinomorphic, unisexual or bisexual, perianth consisting of one whorl of 3 sepals and two whorls of 3 petals; sepals valvate, 3, free or basally connate, much smaller than the petals; petals 6, green, cream to white, valvate, free, linear to narrowly ovate, 8–30 mm long, equal or distinctly unequal, inner base of inner petals concave and with 2 marginal glands; stamens numerous (but in bisexual flowers few), 1–4 mm long, apex discoid or elongate, glabrous or papillate; carpels free, few, 2–2.5 mm long, ovary 1-locular with 3–20, lateral, 1-seriate ovules, style absent, stigma spheroid. Fruit apocarpous, composed of 1–5, free monocarps; monocarps ellipsoid to globose, fleshy, mostly brown to black, 15–90 mm diam., mostly glabrous, apex rounded, wall 2–10 mm thick; monocarps sessile. Seeds (1–)3–20 per monocarp, lateral, ellipsoid, 10–50 mm long, covered with a brownish, scurfy layer, smooth or transversely striate, raphe with an indistinct to distinct rib, hilum present, not arillate, ruminations in 2–4 equal parts.

Distribution. – Four species, occurring in Colombia (Amazonas), Venezuela (Amazonas), Brazil (Acre, Amazonas, Mato Grosso, Pará), and Peru (Amazonas, Huánuco, Loreto, San Martín).

Fig. 6. Isotype of *Diclinanona coriacea* Erkens, Couvreur & Maas (*B. Stergios & al. 15538*; MO barcode MO-1947863 [No. 04945206]). Inset shows close up of one of the residual stamens present on the collection. Bar = 1 mm.

Habit and ecology. – In rain forest, savannas, or riverine white-sand swamp forest. At elevations of 0–1600 m.

Notes. – The unisexual flowers have given *Diclinanona* its generic name (roughly meaning the Annona-type plant with two-gendered flowers). This feature is rarely seen in Annonaceae (for a review of this trait, see Saunders, 2010) but evolved several times independently (Saunders, 2010; Lopes & al., 2018). When Diels (1927) described the genus, he only found staminate flowers.

Diclinanona can be distinguished from other genera in Annonaceae by a combination of the following characters: the absence of orbicules (Huysmans & al., 2010), the presence of oil cells in the rays of the wood (Koek-Noorman & Westra, 2012), the pedicel that only has one bract (not two as in many Annonaceae; Fries, 1959), and the tetragonal pollen tetrads (Walker, 1971).

Key to the species of *Diclinanona*

1. Leaves coriaceous, apex rounded, sometimes emarginate or acute ..... ***D. coriacea***
1. Leaves chartaceous, apex acuminate 2
2. Lower side of leaves densely to rather densely covered with erect hairs; monocarps ca. 20-seeded ..... ***D. matogrossensis***
2. Lower side of leaves rather densely to sparsely covered with appressed hairs; monocarps 3–10-seeded 3
3. Monocarps 20–40 mm long; upper side of leaves shiny with densely hairy primary vein and flat to slightly impressed secondary veins; inner petals slightly longer than outer petals, 2–5 mm wide; seeds 15–20 mm long ..... ***D. calycina***
3. Monocarps 60–90 mm long; upper side of leaves dull with glabrous primary vein and strongly impressed secondary veins; petals of inner and outer whorls equal, 1–2 mm wide; seeds 20–50 mm long ..... ***D. tessmannii***

Diclinanona coriacea Erkens, Couvreur & Maas, **sp. nov.** – Holotype: VENEZUELA. Amazonas, Dep. Río Negro, Brazo Casiquiare, 3 Feb 1992, *B. Stergios & al. 15538* (VEN No. 292271!; isotypes: MO barcode MO-1947863! [No. 04945206], U barcodes U 0073488!, U 0073489!, U 0073490!, US barcode 00890109!, WIS [unnumberd/not barcoded]!).

The isotype in MO is illustrated in Fig. 6.

Diagnosis. – *Diclinanona coriacea* clearly differs from the other three species of the genus by its coriaceous and obovate to obovate-elliptic leaves. It is a member of this genus because of its sessile, few (1–3) monocarps that are several-seeded. This is the only genus in the Amazon region with this combination of characteristics.

Description. – *Tree* or *shrub* 2.5–6 m tall; young twigs sparsely covered with appressed hairs to glabrous. *Leaves*: petioles 2–10 by 1–2 mm; lamina obovate to obovate-elliptic, 6–11 by 3–6 cm (leaf index 1.8–2.2), coriaceous, greyish above, brown below, glabrous above, sparsely covered with appressed hairs to glabrous below, base acute to slightly attenuate, apex rounded, sometimes emarginate or acute, primary vein flat to slightly impressed above, secondary veins 7–10 on either side of primary vein, slightly raised above, tertiary venation flat to raised on both sides, reticulate. *Flowers* in 1–2-flowered inflorescences, infra-axillary; fruiting pedicels 6–10 by 1–2 mm, sparsely covered with appressed hairs, bracts not seen; flower buds not seen; sepals free, ovate-triangular, ca. 3 by 2 mm, outer side sparsely covered with appressed hairs; petals not seen; stamens 3–4 mm long, apex of connective broadly ovoid, glabrous. *Monocarps* 1–3, salmon, brownish-red, orange, or yellow *in vivo*, black *in sicco*, globose to broadly ellipsoid, 15–28 by 15–22 mm, glabrous, stipes absent, endocarp fleshy, wall ca. 2 mm thick. *Seeds* (1–)3 per monocarp, lateral, ellipsoid,10–14 × 5–10 mm, transversely striate to smooth, raphe distinct.

Distribution. – Venezuela (Amazonas).

Preliminary conservation status. – Endangered (EN) under criteria B1ab(iii) + 2ab(iii). This species is only known from three localities, solely from the Venezuelan Amazon. This results in an estimated EOO of 4073 km^2 and AOO of 12 km^2, based on herbarium data. It is however, not expected that the true EOO and AOO exceed 5000 km^2 and 500 km^2, respectively. The species was found in close vicinity to protected areas, but its habitat is subject to ongoing decline due to commodity-driven deforestation, shifting agriculture, (gold) mining, and increased fire frequency. These threats are projected to cause continuing decline in the extent and quality of habitat. Therefore, this species is preliminarily placed in the Endangered category of the IUCN Red List.

Habitat and ecology. – In savannas or riverine white-sand swamp forest. At elevations of ca. 100 m. Flowering and fruiting: February and March.

Etymology. – The specific epithet refers to the thick (coriaceous) leaf blade.

Additional specimens examined. – VENEZUELA. Amazonas: Dep. Río Negro, base of Cerro Cucuy, 2 Mar 1944, *J.T. Baldwin 3186* (US 1878772); Dep. Atabapo, NE of Cerro Cucurito, ribera SE del Caño Yagua, 120 m, 18 Feb 1979. 03° 36′N 066°34′W, *O. Huber 3183* (U 0011902; VEN No. 213640).

Notes. – Further possible locations for isotypes are NY, PORT, and TFAV (B. Stergios, pers. comm.) but these specimens could not be located so far.

Monocarps taste good (*Huber 3183*). Even though the material was fruiting, we still found some loose stamens in the Stergios specimen. The date of the collection was apparently during the early fruiting period, and the presence of residual stamens indicated they clung to the specimen shortly after flowering had passed (B. Stergios, pers. comm.). Without flowering material, it cannot be determined whether this species is bisexual, or bisexual and male as in *Diclinanona tessmannii* and *D. calycina*. *D. coriacea* also seems to share the evenly spaced, straight secondary veins that only join near the leaf margins with the other species. However, since this characteristic is variable in the material

studied by the authors, it is not included in the diagnosis of the species.

■ AUTHOR CONTRIBUTIONS

RHJE and PJMM did the taxonomic work and wrote the species description, TLPC obtained funding for the phylogenomic work, TLPC and FJN executed the phylogenetic analysis, SJRS executed the PCA and LDA, RHJE edited the figures, RRHGL did the IUCN Red List assessment, RHJE wrote the first draft and all authors reviewed and edited the manuscript.

■ CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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Appendix 1. Taxa used in phylogenetic analysis with sequence run number, unique (TC-S) identification number, country of origin, year of collection, collector and number, and barcode of the herbarium specimen when applicable. Newly generated sequences for this study are marked with an asterisk (*). The paired fastq sequences included in this study are available in Genbank SRA under Bioproject numbers PRJNA1265870 (https://www.ncbi.nlm.nih.gov/bioproject/1265870), PRJNA541395 (https://www.ncbi.nlm.nih.gov/bioproject/541395), PRJNA508895 (https://www.ncbi.nlm.nih.gov/bioproject/508895).

Annona ionophylla Triana & Planch., RUN108_I10_T66, TC-S6427, Colombia, 1852, *Triana, J., 4723-11* (COL000001304); ***Annona neochrysocarpa*** H.Rainer, RUN89_I1_T39, TC-S1783, Peru, 2003, *Pirie, M.D., 95* (U.1081529); ***Annona pittieri*** Donn.Sm., RUN102_I10_T96, TC-S4394, Costa Rica, 1993, *Thomsen, K., 424* (WU020286); ***Annona quinduensis*** Kunth, RUN107_I1_T35, TC-S6412, Colombia, 1985, *Alvarez, W.D., 937* (COL000214654); ***Annona senegalensis*** Pers., RUN102_I7_T48, TC-S3624, Madagascar, 1971, *Debray, M.M., 1593-D* (P01981963); ***Anonidium floribundum*** Pellegr., RUN62_I12_T93, TC-S0595, Gabon, 2015, *Couvreur, T.L.P., 895* (WAG.1575672); ***Asimina incana*** (W.Bartram) Exell, RUN89_I4_T77, TC-S3097, United States of America, 2021, *Mercier, K.D., 111* (n.a.); ***Asimina parviflora*** (Michx.) Dunal, RUN100b_I6_T72, TC-S3105, United States of America, 2021, *Mercier, K.D., 51* (n.a.); ***Asimina rugelii*** B.L.Rob., RUN105_I8_T69, TC-S5104, United States of America, 2022, *Goodrich, K., s.n*. (n.a.); ***Asimina triloba*** (L.) Dunal., RUN100b_I6_T74, TC-S3108, United States of America, 2021, *Mercier, K.D., 154* (n.a.); ***Desmos dunalii*** (Wall. ex Hook.f. & Thomson) Saff., RUN89_I7_T37, TC-S2046, Singapore, 2020, *Niissalo, M., SING2020-207* (n.a.); ***Diclinanona calycina*** (Diels) R.E.Fr., RUN62_I10_T20, TC-S1089, Peru, 2003, *Pirie, M.D., 140* (U.1068570); ***Diclinanona matogrossensis*** Maas, RUN104_I9_T23, TC-S4173, Brazil, 1985, *Thomas, W.W., 4808* (U.1068588); ***Diclinanona coriacea**** Erkens, Couvreur & Maas, RUN102_I11_T52, TC-S4494, Venezuela, 1992, *Stergios, B.G., 15538* (U 0073488); ***Diclinanona tessmannii*** Diels, RUN88_I9_T57, TC-S1726, Peru, 1994, *Maas, P.J.M., 8198* (U.1068534); ***Disepalum anomalum*** Hook.f., RUN106_I1_T19, TC-S5444, Malaysia, 1957, *Yakup, F.R., 7723* (L.2068903); ***Disepalum plagioneurum*** (Diels) D.M.Johnson, RUN101AN_I1_T42, TC-S2136, Vietnam, 1997, *Averyanov, L.V., VH4548* (MO5157206); ***Disepalum pulchrum*** (King) J.Sinclair, RUN104_I10_T73, TC-S4790, Malaysia, 1975, *Balgooy, V., 2645* (n.a.); ***Goniothalamus laoticus*** (Finet & Gagnep.) Bân, RUN101AN_I3_T24, TC-S2658, Thailand, 2002, *Kessler, P.J.A., 3203* (L.1765528); ***Goniothalamus rongklanus*** R.M.K.Saunders & Chalermglin, RUN107_I1_T16, TC-S6237, Thailand, 2004, *Saunders, R.M.K., apr-43* (L.3724509); ***Goniothalamus tapis*** Miq., RUN101AN_I1_T24, TC-S2068, Singapore, 2020, *Thomas, D.C., 3401* (n.a.); ***Monodora myristica*** (Gaertn.) Dunal, RUN79_I2_T51, TC-S1067, Ghana, n. a., *Hawthorne, W.D., 93* (n.a.); ***Neostenanthera gabonensis*** (Engl. & Diels) Exell, RUN62_I12_T84, TC-S0321, Gabon, 2013, *Couvreur, T.L.P., 605* (MPU1374927); ***Neostenanthera myristicifolia*** (Oliv.) Exell, RUN62_I12_T89, TC-S0559, Gabon, 2015, *Couvreur, T.L.P., 841* (WAG.1576103); ***Xylopia hastarum*** M.L.Green, RUN107_I6_T56, TC-S6787, Jamaica, 1965, *Webster, G.L., 13676* (U.1074589).